Human disturbance on high Andean forests in Colombia: Spatio-temporal dynamics and vegetation analysis of forests fragments around Bogotá, and potential effects of climate change on treeline species distribution

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Declaration of independent work

I hereby declare that the present work was carried out independently and without unauthorized third-party help. I did not use any sources, figures and resources other than those specified. I marked all passages and sentences in my work that were taken from other sources clearly as such and named the exact source in the references.

1st reviewer: Prof. Dr. Thomas Borsch

2nd reviewer: Prof. Dr. Britta Tietjen

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"Soy parte de quienes alzan la voz para parar la destrucción de los ríos, bosques y páramos. De aquellos que sueñan en que un día los seres humanos vamos a cambiar el modelo económico de muerte, para darnos paso a construir un modelo que garantice vida."

— Francia Márquez

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Summary

This research presents a multi-scalar work on the effects of human disturbance on high Andean forests in Colombia. It focuses on the analysis of vegetation composition and structure and on the dynamics of forest cover change and connectivity through time in selected localities around Bogotá. Additionally, a distribution model exercise is carried out to further the understanding of the environmental constraints driving the present distribution of a distinctive Andean treeline species and to examine its response to climate change in the future.

High Andean forests are a unique and highly biodiverse ecosystem, located at high elevations in one of the world's biodiversity hotspots, the Tropical Andes. Unfortunately, these forests are extremely fragmented and particularly vulnerable to climate change. Despite the fact that they provide essential ecosystem services to neighboring high Andean cities, such as the capital of Colombia, Bogotá, overall, high Andean forests have been poorly studied. Their fragility and their great value in terms of environmental services, together with their outstanding diversity, make them ecosystems with high priority for conservation. Nevertheless, especially around Bogotá, the vegetation studies carried out often have been rather circumscribed, rarely incorporating more complex parameters such as landscape fragmentation and anthropic disturbance metrics nor assessing functional and phylogenetic diversity attributes and ecosystem services. Also, there is a lack of studies that consider multiple vegetation strata at once and that address long-term changes in the extent and structure of high Andean forests, pairing plot-based work with forest cover change analysis. Lastly, few efforts have been made so far to model the response to climate change of high Andean forests and their species. Investigating these aspects could provide meaningful insights into species' responses to anthropic influences and community assembly mechanisms, broadening our understanding of high Andean forests and strengthening strategies to conserve them.

The aim of the present study is to explore the relationship between human disturbance and the condition of high Andean forest in the surroundings of Bogotá, the growing capital city of Colombia. Therefore, three parallel approaches were developed and implemented. On one hand, permanent plots establishment and plot-based fieldwork was carried out in several localities in the surroundings of Bogotá. Here, tree

layer and understory vegetation were assessed and analyzed in terms of their taxonomic, functional and phylogenetic diversity, but also as to their structure and above-ground biomass production. A broad array of environmental factors and anthropic disturbance-related indicators was compiled and subsequently used to characterize the tree layer and understory plant communities using a cluster analysis in combination with ordination techniques (Non-metric Multidimensional Scaling and partial Redundancy Analysis). Finally, environmental and disturbance predictors were related to tree and understory diversity metrics and above-ground biomass by means of Generalized Linear Models (GLMs). As a result, a noticeable effect of anthropic related predictors on both tree and understory layer community composition and also a direct negative effect on tree layer diversity and above-ground biomass production have been documented.

On the other hand, a thorough analysis of aerial pictures from the studied localities of the first study has been conducted, covering the period between the 1940s to early 2000s, in order to deepen the understanding of the history of forest fragmentation in the area. The images were classified into three land cover classes (Forest, Grasslands and Bare ground), utilizing texture analysis and object-based image segmentation. Then, the extent of forested areas was assessed through time. Additionally, forest connectivity metrics were calculated by performing a Morphological Spatial Pattern Analysis (MSPA) and correlated with the forest cover dynamics over the same period. For the period 1940-2000, in all except one of the studied localities a general restoration of forest cover and connectivity was determined. The highlighted forest cover and connectivity trends were related to the individual history of each locality in terms of population displacement and urban expansion.

Lastly, to further expand the geographical and temporal coverage of this study, species distribution models were performed for *Weinmannia fagaroides* (Cunoniaceae)*,* a tree species that was found to be distinctive of the higher elevation forest fragments that were studied in this project. This species is found throughout the Central and Northern Andes, and is a typical component of high elevation treelines, ecotonal zones that are believed to be highly vulnerable to climate change impacts. The main aim was to understand which are the focal drivers of the current distribution of *W. fagaroides*, and to hypothesize its response to climate change in the future. At the same time, a comparison of the efficacy of environmental predictors pertaining to three different climate datasets (Chelsa 1.2, Worldclim 1.4 and Worldclim 2) and of

three different modelling algorithms (GLMs, Random Forests - RF, MaxEnt) was carried out for predicting the current distribution of *W. fagaroides*. The current species distribution was found to be driven mostly by one temperature, one precipitation and one soil-related variables. In regards to the performance of the three different climate datasets no significant difference was found, although Chelsa 1.2 retrieved slightly higher model evaluation scores. As to the algorithms, RF and MaxEnt retrieved the highest model evaluation scores. Moreover, the modeled distribution of *W. fagaroides* was predicted to decrease by 38% and to shift towards higher elevations in the period 2060-2080 for a high CO_2 emission scenario. Considering that at present only around 22% of the modeled species distribution is situated in protected areas, an adaptation of currently implemented conservation efforts is strongly recommended to protect this and other fragile high Andean treeline species.

Overall, this study contributes to the characterization of forest fragments in the vicinity of Bogotá and is an important addition for a better understanding of the effects of anthropic disturbances on high Andean forests and their species. Also, several methodological approaches are provided that may serve as a basis to better understand the situation of other species and ecosystems in similar regions.

Zusammenfassung

Die vorliegende Arbeit ist eine multiskalare Studie über die Auswirkungen anthropogener Störung auf hochandine Wälder in Kolumbien. Ihr Schwerpunkt liegt auf der Analyse der Vegetationszusammensetzung und -struktur sowie auf der Dynamik der Waldbedeckungs-veränderung und -konnektivität in ausgewählten Orten im Umland von Bogotá. Darüber hinaus werden die Ergebnisse einer Verbreitungsmodellierung vorgestellt, die durchgeführt wurde, um zu zeigen, welche Umweltfaktoren die derzeitige Verbreitung einer im andinen Raum für Baumgrenzen typischen Baumart beeinflussen, und um die Folgen durch den Klimawandel für diese Art zu untersuchen.

Hochandine Wälder sind einzigartige Ökosysteme mit einer immensen biologischen Vielfalt, die in hohen Lagen der tropischen Anden vorkommen, einem der Biodiversitäts-Hotspots des Planeten. Leider sind diese Wälder extrem fragmentiert und besonders anfällig für Veränderungen durch den Klimawandel. Obwohl hochandine Wälder für umliegende Städte, wie der kolumbianischen Hauptstadt Bogotá, eine große Anzahl von ökosystemischen Dienstleistungen zur Verfügung stellen, wurden sie bisher nur unzureichend untersucht. Ihre Fragilität und ihre große Bedeutung hinsichtlich ökosystemischer Dienstleistungen sowie ihre herausragende Vielfalt machen sie zu Ökosystemen mit hoher Priorität für den Naturschutz. Insbesondere in der Umgebung von Bogotá wurden Vegetationsstudien jedoch bisher nur sehr punktuell durchgeführt und berücksichtigten weder komplexere Parameter wie Landschaftsfragmentierung und anthropische Störungsmetriken, noch bezogen sie funktionelle und phylogenetische Diversitätsattribute und Ökosystemleistungen mit ein. Es fehlten auch Studien, die mehrere Vegetationsstrata gleichzeitig berücksichtigten, sich mit langfristigen Veränderungen der Fragmentgröße und Vegetationsstruktur von hochandinen Wäldern befassten und welche Plot-basierte Feldaufnahmen mit Analysen zur Veränderung der Waldbedeckung kombinierten. Letztendlich wurden bisher kaum Anstrengungen unternommen, um die Reaktion der hochandinen Wälder und ihrer Pflanzenarten auf den Klimawandel zu modellieren. Die Untersuchung dieser Aspekte lieferte jedoch wichtige Einblicke in die Reaktionen der hier vorkommenden Pflanzenarten auf anthropische Einflüsse und in Mechanismen der Bildung hier ansässiger Pflanzengemeinschaften, was insgesamt zu einem

tieferen Verständnis der hochandinen Wälder führen und Strategien zu deren Erhaltung stärken würde.

Ziel der vorliegenden Studie ist es, den Zusammenhang zwischen menschlicher Störung und dem Zustand des hochandinen Waldes in der Umgebung von Bogotá, der wachsenden Hauptstadt Kolumbiens, zu untersuchen. Daher wurden drei parallele Forschungsansätze entwickelt und durchgeführt. Einerseits wurden in mehreren Lokalitäten in der Umgebung von Bogotá permanente Plots etabliert und Plot-basierte Vegetationsaufnahmen durchgeführt. Auf diese Weise wurden Baum- und Krautschichtvegetation hinsichtlich ihrer taxonomischen, funktionellen und phylogenetischen Vielfalt, aber auch hinsichtlich ihrer Struktur und oberirdischen Biomasseproduktion bewertet und analysiert. Dazu wurde hier eine große Anzahl von Umweltfaktoren und Indikatoren für anthropische Störungen zusammengestellt und anschließend verwendet, um die Baum- und Krautschichtgemeinschaften mithilfe einer Clusteranalyse in Kombination mit Ordinationstechniken (Non-metric Multidimensional Scaling und partial Redundancy Analysis) zu charakterisieren. Schließlich wurden Umwelt- und Störungsprädiktoren mithilfe von Generalisierten Linearen Modellen (GLMs) mit Baum- und Krautschicht-Diversitätsmetriken und ihrer oberirdischen Biomasseproduktion in Beziehung gesetzt. Als Ergebnis wurde ein starker Effekt anthropischer Prädiktoren auf die Zusammensetzung der Baum- und Krautschichtgemeinschaften sowie ein direkter negativer Effekt auf die Diversität der Baumschicht und die oberirdische Biomasseproduktion nachgewiesen.

Des Weiteren wurde eine gründliche Analyse von Luftbildern zu den im Zuge der ersten Studie untersuchten Lokalitäten durchgeführt, welche den Zeitraum zwischen den 1940er und den frühen 2000er Jahren abdeckte, um Einblick in die Geschichte der Waldfragmentierung in der Region zu gewähren. Die Luftbilder wurden unter Verwendung von Texturanalyse und objektbasierter Bildsegmentierung in drei Landbedeckungsklassen (Wald, Grasland und unbedeckter Boden) eingeteilt. Auf dieser Basis wurde dann die Veränderung der Waldflächengröße über die Zeit ermittelt. Hierzu wurden Waldkonnektivitätsmetriken berechnet, indem die Ergebnisse einer morphologisch-räumlichen Musteranalyse (MSPA) mit der Dynamik der Waldbedeckung desselben Zeitraums korreliert wurden. Für den Zeitraum 1940-2000 wurde mit einer Ausnahme in allen Lokalitäten eine allgemeine Regeneration der Waldbedeckung und der Konnektivität festgestellt. Die ermittelten Trends der Waldbedeckung und Konnektivität konnten mit der individuellen Geschichte der

untersuchten Lokalitäten hinsichtlich Bevölkerungsverlagerung und Stadterweiterung in Bezug gesetzt werden.

Um die geografische und zeitliche Abdeckung dieser Studie weiter auszubauen, wurden Verbreitungsmodellierungen für die Baumart *Weinmannia fagaroides* (Cunoniaceae) durchgeführt, welche typischerweise in den höher gelegenen Waldfragmenten auftrittt, die in diesem Projekt untersucht wurden. Diese Art kommt in den Zentral- und Nordanden vor und ist ein typischer Bestandteil der Baumgrenzen in Hochgebirgen, welche ökotonalen Zonen darstellen, von denen angenommen wird, dass sie sehr anfällig hinsichtlich der Auswirkungen des Klimawandels sind. Das Hauptziel war es, zu verstehen, welches die Haupttreiber der gegenwärtigen Verbreitung von *W. fagaroides* sind, und welche Auswirkungen durch den Klimawandel auf diese Art in der Zukunft zu erwarten sind. Gleichzeitig wurde ein Vergleich der Effizient einer Reihe von Umweltprädiktoren in Bezug auf drei verschiedene Klimadatensätze (Chelsa 1.2, Worldclim 1.4 und 2) und drei verschiedene Modellierungsalgorithmen (GLMs, Random Forests - RF, MaxEnt) zur Modellierung der aktuellen Verbreitung von *W. fagaroides* durchgeführt. Es wurde festgestellt, dass die aktuelle Artverbreitung hauptsächlich von Temperatur, Niederschlag und bodenbezogenen Variablen abhängt. In Bezug auf den Leistungsvergleich der drei unterschiedlichen Klimadatensätze wurde kein signifikanter Unterschied festgestellt, obwohl Chelsa 1.2 geringfügig höhere Modellbewertungsergebnisse erzielte als die anderen beiden verfügbaren Datensätze. In Bezug auf den Vergleich der Algorithmen haben RF und MaxEnt die höchsten Modellbewertungsergebnisse erzielt. Darüber hinaus ergab die Modellierung, dass sich das Verbreitungsgebiet von *W. fagaroides* im Zeitraum 2060-2080 für ein Szenario mit hohem CO_2-Ausstoß um 38 % verkleinern und sich in höhere Lagen verschieben wird. Angesichts der Tatsache, dass sich nur etwa 22 % des aus der Modellierung resultierenden Verbreitungsareals in Schutzgebieten befindet, wird dringend empfohlen, die derzeit durchgeführten Bemühungen zum Erhalt dieser Art daran zu orientieren, um diese und andere fragile Arten, die in den Hochanden die Baumgrenze bilden, zu schützen.

Insgesamt trägt diese Studie zur Charakterisierung von Waldfragmenten in der Umgebung von Bogotá bei und ist eine wichtige Ergänzung für ein besseres Verständnis der Auswirkungen anthropisch bedingter Störungen auf hochandine Wälder und ihrer Pflanzenarten. Darüber hinaus werden verschiedene methodische

Ansätze bereitgestellt, die als Grundlage dienen können, um die Situation anderer Arten und Ökosysteme in ähnlichen Regionen besser zu verstehen.

Resumen

Esta investigación presenta un trabajo multiescala sobre los efectos del disturbio humano en los bosques altoandinos de Colombia, incluyendo el análisis de la composición y estructura de la vegetación, y de la cobertura y conectividad del bosque a través del tiempo en varias localidades alrededor de Bogotá. Además, se realizó un ejercicio de modelado de la distribución potencial para ampliar el entendimiento de los factores ambientales que condicionan la distribución actual de una especie característica de las franjas superiores del bosque en los Andes, para predecir su respuesta al cambio climático.

Los bosques altoandinos son un ecosistema único y sumamente biodiverso, que se localiza en uno de los hotspots de la biodiversidad a nivel mundial: los Andes Tropicales. Desafortunadamente, estos bosques están extremadamente fragmentados y son particularmente vulnerables al cambio climático. También, a pesar del hecho que proveen servicios ecosistémicos fundamentales a las ciudades andinas cercanas, entre las cuales destaca la capital de Colombia, Bogotá, estos bosques son poco conocidos en general. Su fragilidad y su gran valor en términos de servicios ambientales, junto a su sobresaliente diversidad, los hace uno de los objetivos prioritarios para la conservación. Sin embargo, los estudios sobre la vegetación realizados en estos ecosistemas y especialmente alrededor de Bogotá, son a menudo muy puntuales y raramente incorporan parámetros más complejos como por ejemplo la fragmentación del paisaje o índices de disturbio antrópico, ni evalúan la diversidad filogenética y los servicios ecosistémicos. Además, hay muy pocos estudios que consideren los diferentes estratos de la vegetación a la vez y que investiguen cambios a larga escala temporal en la cobertura y estructura de los bosques altoandinos, complementando el trabajo de análisis de cambios de cobertura con estudios en parcelas. Finalmente, pocos estudios han tratado de modelar la respuesta al cambio climático de los bosques y las especies altoandinas. Profundizar en estos aspectos podría generar información esencial sobre la respuesta de las especies a la presión antrópica y sobre los mecanismos de formación de las comunidades vegetales, elevando el entendimiento de los bosques altoandinos y fortaleciendo las estrategias de conservación.

El objetivo del presente trabajo es explorar las relaciones entre el disturbio humano y el estado de los bosques altoandinos cerca de Bogotá, la ciudad capital de

Colombia con una población creciente. Para esto se adoptaron tres metodologías en paralelo. Por un lado se implementó el establecimiento de parcelas de vegetación permanentes en varias localidades alrededor de Bogotá. En dichas parcelas, se muestreó la vegetación de los estratos arbóreo y herbáceo, se analizó en términos de diversidad taxonómica, funcional y filogenética, y también en términos de estructura y biomasa aérea. Se midieron o calcularon también varios factores ambientales y relacionados con el disturbio humano, que luego, mediante técnicas multivariadas (Non-Metric Multidimensional Scaling and Partial Redundancy Analysis), se utilizaron para caracterizar las comunidades arbóreas y herbáceas obtenidas a través de un análisis de conglomerados. Finalmente, las variables ambientales y de disturbio se relacionaron con la diversidad y la biomasa aérea mediante el uso de Modelos Lineares Generalizados (GLM). Se registró un notable efecto de las variables relacionadas con el disturbio humano sobre la composición del estrato arbóreo y herbáceo, y también un efecto negativo sobre la diversidad del estrato arbóreo y la biomasa aérea.

Paralelamente, para profundizar en el conocimiento de la historia de los fragmentos de bosque en el área de estudio, se realizó el análisis de las imágenes aéreas tomadas desde 1940 hasta la primera década del siglo XXI (2000-2010), de las localidades de las parcelas permanentes. Se clasificó la cobertura de las imágenes en tres categorías (Bosque, Pastizal y Terreno desnudo), utilizando un análisis de la textura y ‘segmentación de imagen basada en objetos’. Después se calcularon las dinámicas en el área de bosque a través del tiempo. Además, se obtuvieron unas métricas de conectividad del bosque a través de un Análisis Morfológico de Patrones Espaciales (Morphological Spatial Pattern Analysis), que se correlacionaron con las dinámicas de cobertura de bosque a través del tiempo. En general se encontró una recuperación de la cobertura forestal y de la conectividad para el periodo 1940-2000 en todas las localidades estudiadas excepto una. Las tendencias encontradas se relacionan con la historia individual de las localidades y los patrones de migraciones y desplazamientos de la población humana.

Por último, para fortalecer el alcance geográfico y temporal de este trabajo, se realizaron unos modelos de distribución para *Weinmannia fagaroides* (Cunoniaceae), una especie de árbol que resultó ser importante en las parcelas de mayor altitud de este proyecto. Esta especie se encuentra distribuida en los Andes centrales y septentrionales, y a menudo está presente en los límites superiores del bosque, esas zonas eco tonales que se hipotetiza pueden ser muy vulnerables al cambio climático. Se buscó identificar cuales los factores principales que determinan la distribución actual de *W. fagaroides*, y formular una hipótesis sobre su respuesta futura al cambio climático. Además, se comparó la eficacia de tres diferentes bases de datos climáticos (Chelsa 1.2, Worldclim 1.4 and Worldclim 2) y de tres algoritmos de modelado (Generalized Linear Models, Random Forests y MaxEnt) al predecir la distribución actual de *W. fagaroides*. Se encontró que la distribución actual de la especie es determinada sobretodo por una variable relacionada con la temperatura, una con la precipitación y una relacionada con las propiedades del suelo. Además, no se detectó ninguna diferencia significativa entre el desempeño de los tres conjuntos de datos climáticos, aunque las predicciones generadas con Chelsa 1.2 tuvieron puntajes de evaluación del modelo ligeramente mas altos que los de Worldclim. En cuanto a los algoritmos, Random Forest y MaxEnt fueron los que obtuvieron los puntajes de evaluación mas altos. Adicionalmente, se predijo que la distribución modelada de *W. fagaroides* se reduciría en un 38% y se desplazaría a altitudes mayores para el periodo 2060-2080, en un escenario de altas emisiones de CO_2. Considerando que actualmente solo cerca del 22% de la distribución esta bajo alguna figura de protección, se recomienda la implementación de medidas de conservación para esta y otras especies de los bordes superiores de los bosques Andinos.

En general, este trabajo representa una contribución a la caracterización de los fragmentos de bosque alrededor de Bogotá, y una adicción significativa al conocimiento de los efectos del disturbio humano sobre los bosques y las especies altoandinas. Además, este proyecto proporciona varias bases metodológicas que pueden aplicarse para poner a prueba los resultados obtenidos aquí, en otras áreas geográficas o ecosistemas similares.

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Chapter 1. General introduction

1.1. Geographical context

1.1.1. Brief introduction to the geography and biodiversity of Colombia

Colombia is a country of Northwestern South America that has been identified as "mega-diverse" due to its outstanding biodiversity, considerable species richness and high levels of endemism (Hernández-Camacho et al., 1992; Chaves & Arango, 1998). The country's high spatial and environmental variability in relation to its medium size promotes the coexistence of a variety of ecosystems, ranging from desert and tropical savannas to very humid rainforests and tropical snow-covered mountains (Etter et al., 2006a). Accordingly, Colombia has been identified as the most biodiverse country in in regard to its terrestrial area (Gonzalez-Salazar et al., 2017), hosting about 10% of the world's biodiversity (IAvH, 1998; Clerici et al., 2019a). The country harbours more than 8,000 species of vertebrates, of which 520 are mammals and 1,999 birds; almost 18,000 species of invertebrates, of which 11,764 of insects; and around 1,800 species of fungi (Sistema de Información sobre Biodiversidad de Colombia, 2021). Moreover, the Catalogue of Colombian Plants and Lichens Species lists around 28,000 species of plants, of which 3,179 are species of orchids and 1,054 of bromeliads, and around 1,530 species of lichens (Bernal, Gradstein, & Celis, 2015).

Colombian complex topography is marked by the Andean mountains (Fig. 1) that cross the country from North to South, spanning 11 degrees of latitude and around 300,000 km^2 (Kattan et al., 2004). The Colombian Andes consist of three mountain ranges – Western, Central and Eastern Cordilleras – separated by the interandean valleys of the rivers Magdalena and Cauca (Kattan et al., 2004). The Western Cordillera has an avarage elevation of 2,000 m, while the Central and Eastern Cordilleras reach average elevation values above 3,000 m and up until 5,000 m with their highest peaks (Gregory-Wodzicki, 2000). These three Cordilleras do not share the same geological history nor orogenic events with the other Colombian mountain systems (Bürgl, 1961; Irving, 1975). Among the latter, the massif of the Sierra Nevada de Santa Marta, that is found at the northernmost end of the Andes, surrounded by the Caribbean plains, reaches elevations as high as 5,775 m (Tschanz et al., 1974). Two other important mountainous formations that include rocky outcrops forming part of the Guyana Shield, the Serranias of the Macarena and the Lindosa, are located respectively in the administrative departments of Meta and Guaviare (Duvier, 2019). Additionally, in the Western part of the country, close to Panamá, two other massifs are found: the Serranía of Darién and *El Cerro Pirre* (Andrade, 2011). The three Colombian Cordilleras converge only once in the southwest of the country, in the "*Macizo Colombiano*" that is the continuation of the main axis of the Ecuadorian Andes (Kattan et al., 2004).

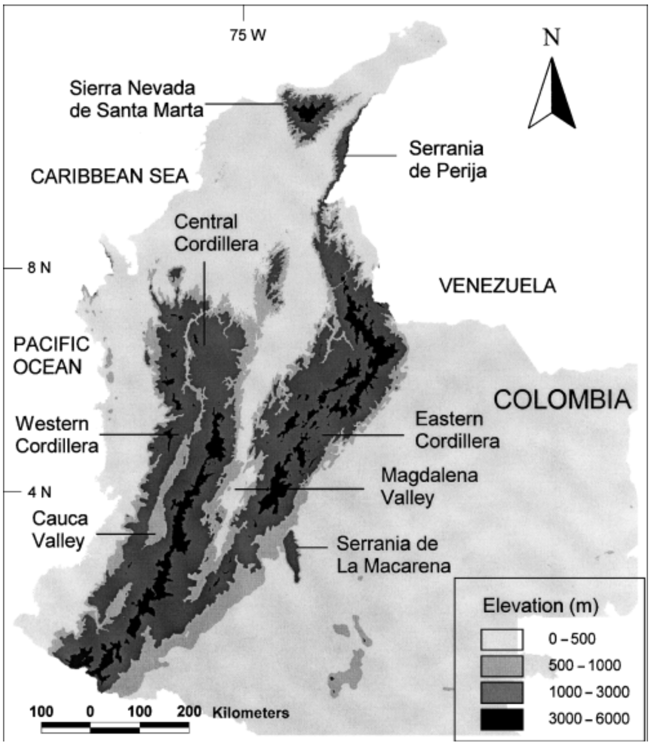

Figure 1: The Colombian Andes (Kattan et al., 2004)

In relation to its physical and biological complexity, the country has been traditionally divided into five major biogeographic regions, each one showing dissimilar biophysical and land use characteristics: Andes, Caribbean, Pacific or *Chocò*, the Orinoco plains or *Llanos orientales*, and the Colombian Amazon (Etter et al., 2006a). The Andes region rises at the crossroads between two continents, where the uplift of the Andean mountain ranges played a key role in the diversification of the tropical South American biota (Kattan et al., 2004) leading to an explosive radiation of plant families of Gondwanan origin (Gentry, 1982). The Caribbean plains harbour a variety of ecosystems including humid forests, dry forests, savannas, wetlands and deserts, and span from the northern reaches of the Andes to the Caribbean Sea, including the center of endemism Sierra Nevada de Santa Marta massif. This region hosts around 51% of what is left of Colombian tropical dry forests, and particularly, the forest fragments in best conservation status (Pizano & García, 2014). The Pacific region is also mostly flat and characterized by an extremely humid climate. This includes the western coastal areas and the lowland area of the Magdalena river valley (WWF, 2016). The region is highly biodiverse and covered by dense rainforest, rivers, swamps, and mangroves and was separated from the Amazon by the uplift of the Andes beginning around 25 million years ago (Gregory-Wodzicki, 2000). The other two regions are found in the East and Southern part of the country. The Orinoco plains are a riverine and mostly flat area that encompasses more than a quarter of Colombia's extension, dominated by tropical savannah formation (Rippstein, 2001). Lastly, the Colombian Amazon plains are covered by tropical moist forests and still host some of the largest intact patches of forest (Potapov et al., 2017). Moreover, this region stands out as one of the most biodiverse places in the world for vertebrate species and vascular plants (Jenkins et al., 2013; Lessmann et al., 2019). In the Orinoco plains and the Amazon very few mountain massifs are found and if present these are reaching only relatively low elevations, as the Serranía de La Macarena and Chiribiquete (Andrade, 2011).

1.1.2. Conservation issues

Despite Colombia's immense biological heritage, the country has a centuries-long history of severe habitat loss and fragmentation (Kappelle & Brown, 2001; Etter et al. 2006a, 2006b; Sánchez-Cuervo & Aide, 2013). Colombian biodiversity is still highly threatened today, especially by deforestation (Armenteras et al. 2003) even inside protected areas (Clerici et al., 2020) (Fig. 2). The magnitude of the observed land cover change is impressive, with about 2,4 million hectares of forest loss reported between 1967 and 2012 (IGAC, 2015). Furthermore, overall human impact escalated between 1970 and 2015 in Colombia (Correa Ayram et al., 2020) and increasing trends and alarming figures have been widely reported in recent years (*e.g.* a net forest loss of 178,597 hectares for the year 2016) (Minambiente, 2017; SIAC, 2017, Clerici et al., 2019b).

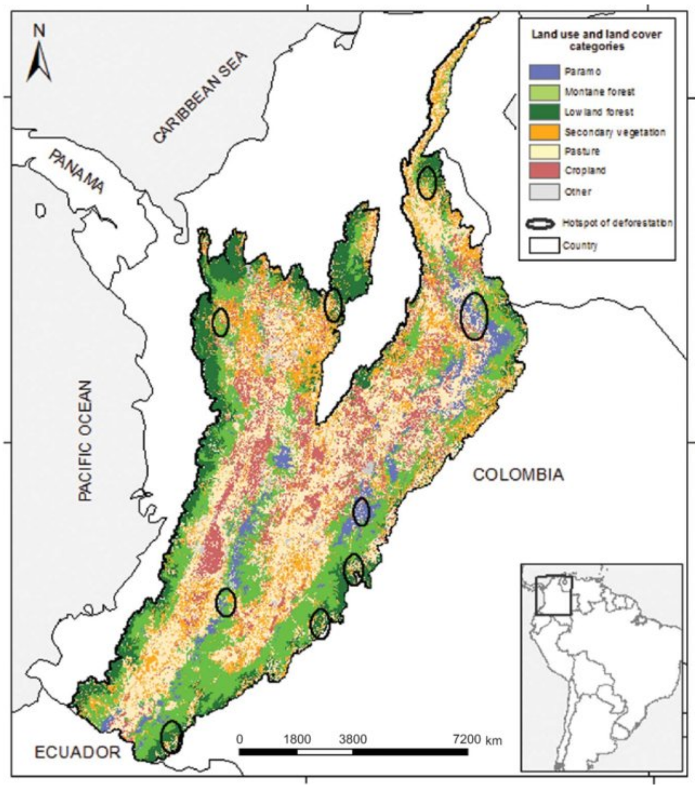

Figure 2: Example of deforestation hotspots in Colombia: land cover map of the Colombian Andes (year 2000) with identifyied hotspots of deforestation (between 1985 and 2000), from Rodríguez Eraso et al., 2013.

In addition, climate change is predicted to cause strong perturbations of natural ecosystems and thus ecosystem service provision, especially in the tropical Andes (Grimm et al., 2013; Clerici et al., 2019b). These predictions are even more worrying when considering the interaction of climate change with the cumulative effects of land use change and anthropic disturbance on one hand, and instable politics, badly planned environmental policies, inadequate environmental goals (Eufemia et al., 2019) and armed conflicts (Clerici et al., 2019a; Clerici et al., 2020) on the other. As an example, it has been estimated that one century of armed conflicts has led to 1 million hectares of forest loss in Colombia (Baptiste et al., 2017). In fact, most of the areas that have been historically affected by the Colombian armed conflict coincide with fragile natural forest ecosystems (Morales, 2017) and the forest found in these regions are left in vulnerable condition (Sánchez-Cuervo & Aide, 2013; Boron et al., 2016).

1.2. Andean forests of Colombia

Given the high diversity of climatological, meteorological, geological and geomorphological features, as well as the steep and extended environmental gradient, the Andean region of Colombia exhibits a complex mosaic of ecosystems which includes a wide array of vegetation types distributed along a marked altitudinal zonation (Fig. 3 and 4): (I) Sub-Andean forest (*bosque subandino*; ca. 1,000-2,300 meters above sea level (masl); (II) Andean forest (*bosque andino*; ca. 2,000-2,600 masl); (III) High Andean forest (*bosque altoandino*; ca. 2,600-3,600 masl); (IV) a shrubby intermediating zone of dryer enclaves (*matorrales;* ca. 3,200-3,500 masl); and (V) the emblematic tundra-like mountain grass lands called "*páramo*" (ca. 3,200-4,700 masl), which are further categorized into *subpáramo* (ca. 3,200-3,700 masl), *páramo* (ca. 3,500-4,200 masl) and *superpáramo* (ca. 4,000-4,700 masl) (Cortés-Duque et al., 2013). These ecosystems are however not exclusive of Colombia as they are present, with regional variations, throughout the tropical Andean region, defined as the mountainous area spanning north from Bolivia and above about 800-1,000 masl (Young et al., 2011).

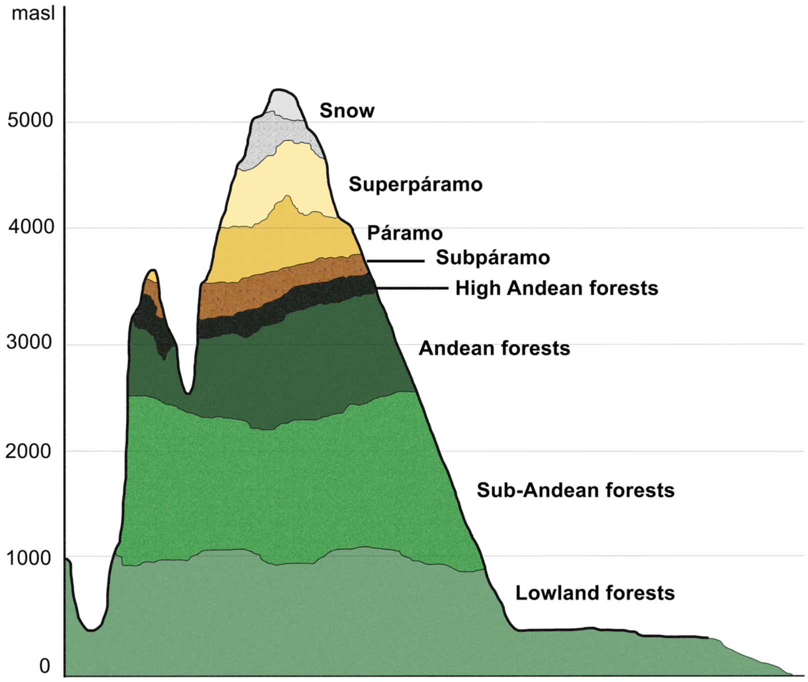

Figure 3: Altitudinal zonation of Andean vegetation (adapted from Cortés-Duque et al., 2013).

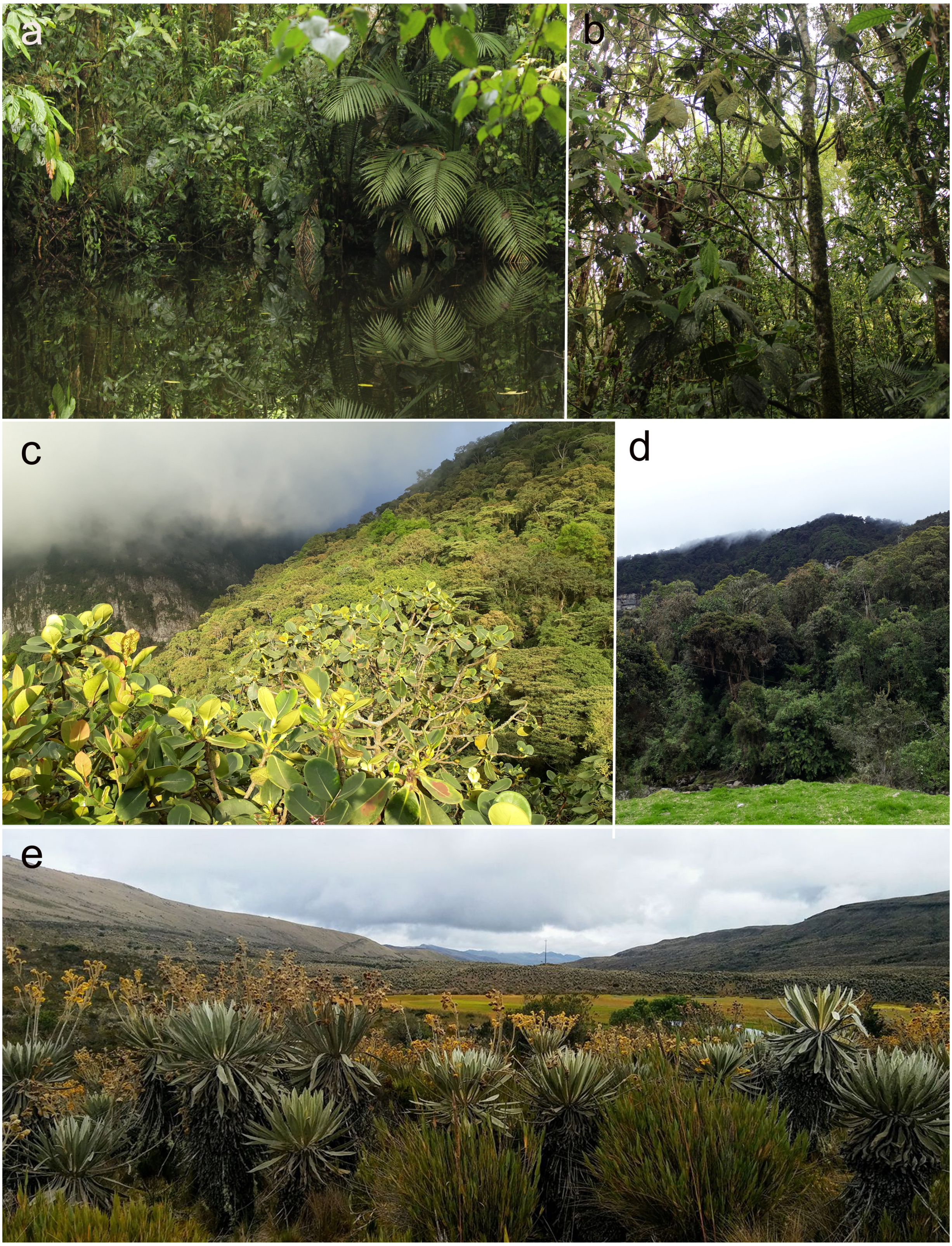

Figure 4: Example of Andean ecosystems of Colombia: a) and b) Sub-Andean forests in the *Santuario de Fauna y Flora Otun Quimbaya* (Pereira, Risaralda department), around 1,900 masl; c) Andean forests of the *Parque Natural Chicaque* (San Antonio del Tequendama, Cundinamarca department), ca. 2,200 masl; d) high Andean forests near Nazareth, in the locality of Sumpaz (Bogotá), ca. 2,900 mals; e) view of the *páramos* near the *Laguna de los Tunjos*, Sumapaz (Bogotá), about 3,800 masl. Images a and b copyright © Francisco Fajardo and c-e © M. Calbi.

Andean forests *sensu latu* (*i.e.* Sub-Andean, Andean and high Andean) are extremely fragmented (Armenteras et al., 2003; Etter et al., 2006a; Young et al., 2011), and as it is typically postulated for mountain ecosystems, they are also particularly vulnerable to climate change impacts (Anderson et al., 2011). Nonetheless, in the Colombian Andes, these unique and extremely biodiverse forests harbour more than 10,000 species of plants, 1,200 species of birds, 400 species of frogs, and 270 species of rodents and bats (Rangel, 1997a, 1997b). It has been suggested that this outstanding species richness is a result of the availability of new ecological niches and complex topography brought about by the Andean orogeny (Simpson, 1983), and of the rapid diversification rates that characterize many of the tropical Andean emblematic clades (Hughes & Eastwood, 2006; Madriñán et al*.,* 2013; Givnish et al*.,* 2014).

1.2.1. High Andean forests of Colombia

In Colombia, high Andean forests or *bosques altoandinos* (Fig. 4d and 5a) can be found mainly in the humid and relatively cold part of the three Andean Cordilleras, generally between 2,600 and 3,600 masl (Cuatrecasas 1958; Van der Hammen 1974), although the altitudinal limits vary according to different microclimates (Cortés-Duque et al., 2013). These forests are characterized by the presence of different stand structures including young even-aged shrub-like patches dominated by early successional species, to more mature patches with a diverse species composition (Chazdon, 2014; Rodriguez et al., 2021). In general, tree height is lower than 15-25 m and in terms of plant communities, the *Bosque Altoandino* remnants found in Colombia are most commonly populated by species belonging to the genera *Weinmannia* (Cunoniaceae) (Fig. 5b and 5c), *Myrsine* (Myrsinaceae), *Myrcianthes* (Myrtaceae) (Fig. 5d), *Clusia* (Clusiaceae), *Diphlostephium* (Asteraceae), *Ageratina* (Asteraceae) (Fig. 5e), *Viburnum* (Adoxaceae), *Miconia* (Melastomataceae) (Fig. 5f), *Oreopanax* (Araliaceae), *Ilex* (Aquifoliaceae), *Gaiadendron* (Loranthaceae) and *Drimys* (Winteraceae) (Van der Hammen, 1998; Cortés-Sánchez et al., 2011; Restrepo-Abadía, 2016; Hurtado-Martilletti et al., 2020). More mature forest growth is characterized by the abundance of species belonging to the Lauraceae and Rosaceae families (*i.e. Prunus* sp.), or the genera *Weinmannia*, *Xeroxylon* (Arecaceae) and *Meliosma* (Sabiaceae) (Hurtado-Martilletti et al., 2020; Calbi and Fajardo-Gutierrez, personal observation). Oppositely, in secondary growth, high shrub species belonging to the genera *Cavendishia* (Ericaceae), *Miconia*, *Tibouchina* (Melastomataceae), *Escallonia* (Escalloniaceae) and *Clethra* (Clethraceae) are usually the most abundant, and when canopy gaps occur they are often rapidly occupied by bamboos *Chusquea* sp. (Poaceae) (Fig. 6b) (Cortés-Sánchez, 2003; Cortés-Sánchez, 2008; Hurtado-Martilletti et al., 2020).

High Andean forests display a dense understory with abundant epiphytic plants, lichens, and moss cover on trees as well as on the forest floor, forming thick layers (Bader, 1999). The lower forest stratum is characterized by the presence and great diversity of orchids, bromeliads, aroids, ericads, peperomiads, ferns, bryophytes, lichens, and other epiphytic groups (Fig. 6) (Bader, 1999; Gradstein, 2008). These abundant epiphytic taxa play a disproportionate role in influencing the terrestrial hydrological and nutrient cycles in these environments (Veneklaas et al., 1990; Lai et al., 2020), and their biomass is estimated to be as high as 44 tonnes per hectare in Colombian montane forests (Hofstede, 1993). In particular, the diversity and abundance of epiphytes is one of the distinguishing characters between mature high Andean forests and secondary growth (Hartshorn, 1980; Gradstein, 2008).

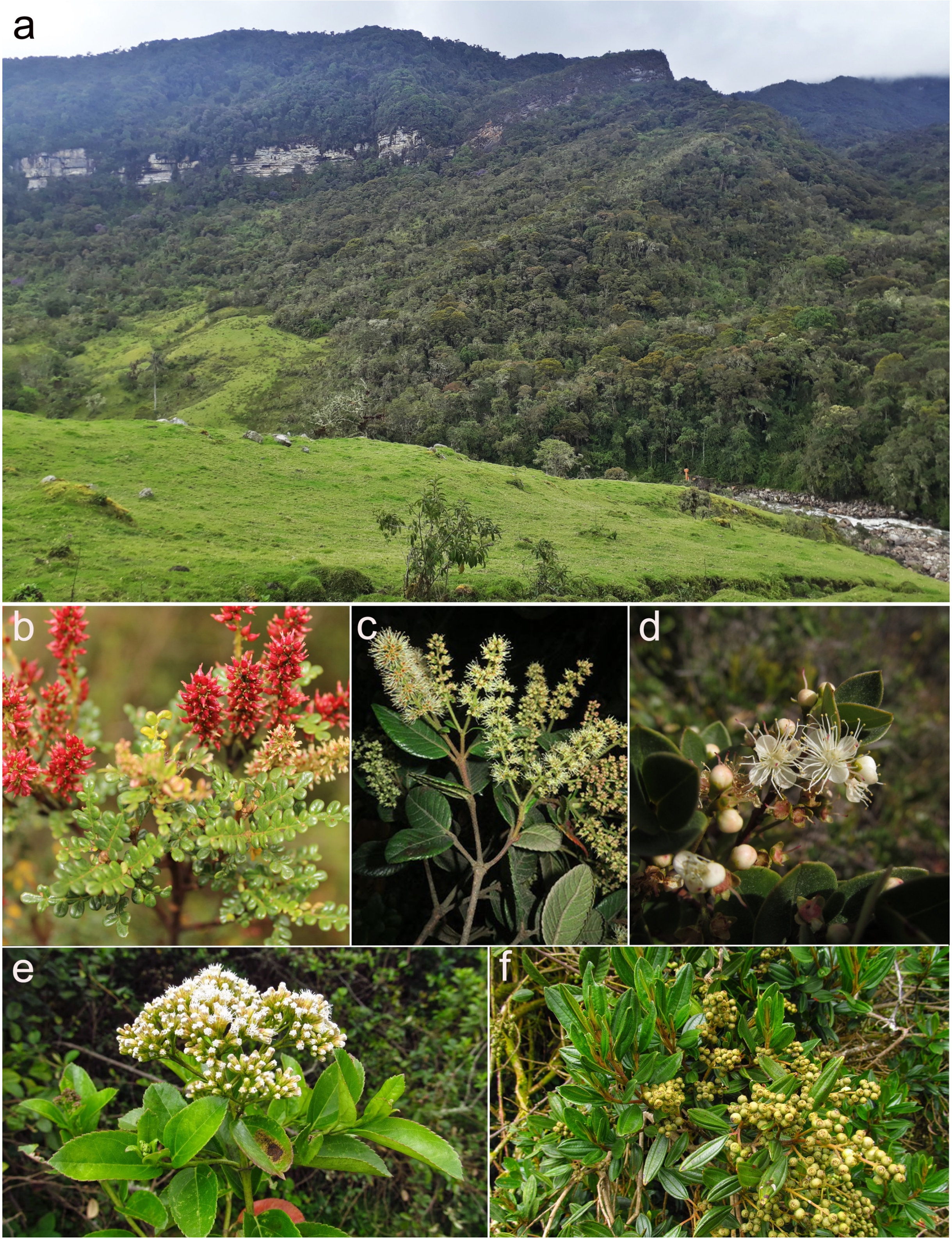

Figure 5: Examples of high Andean forests tree and shrub species commonly found in the vicinity of Bogotá a) high Andean forests near Nazareth, Sumapaz (Bogotá); b) *Weinmannia fagaroides;* c) *Weinmannia rollottii*; d) *Myrcianthes leucoxyla*; e) *Ageratina tinifolia;* f) *Miconia* sp. Images *a* copyright © *M. Calbi* and *b-f* © *F. Fajardo.*

Figure 6: Example of species that can be found in the understory of high Andean forests near Bogotá: a) *Epidendrum cylindraceum*; b) *Chusquea scandens*; c) *Peperomia hartwegiana*; d) *Passiflora tripartita*; e) *Yoshimuriella peltigera*; f) *Elaphoglossum antioquianum*; g) *Asplenium radicans*; h) *Pleurothallis lilijae*; i) the forest ground covered by undecomposed leaves, terrestrial orchids and liverworts of the family Plagiochilaceae. Images copyright a-e © *F. Fajardo* and *f-i* © *M. Calbi.*

Bosques altoandinos are also considered one of the least known ecosystems in the tropics, (Gentry, 1995; Stadtmüller, 1987; Kessler, 2000; Ataroff 2003; Bubb et al., 2004; Garavito et al., 2012). Accordingly, the quantity of studies focused on *bosque altoandinos* is scarce and generally carried out at a national scale (Young & León, 1999; Grubb et al., 1963; La Torre et al., 2007), while very little has been done at regional to local scale (Kappelle and Brown, 2001; Cuesta et al., 2009; Herzog et al., 2011; Jørgensen et al., 2011; Restrepo-Abadía, 2016).

The fragility and the great strategical value of high Andean forests in terms of environmental services, together with the Colombian Andean region´s outstanding diversity make it one of the priorities for conservation (Mittermeier et al., 1999; Myers et al., 2000). However, the *bosques altoandinos* are one of the most fragmented vegetation types in Colombia (Armenteras et al., 2003), and it has been estimated that only 20%–40% of the original forest cover remains today (Mendoza & Etter, 2002; Rubiano et al., 2017; Cortés-Sánchez, 2018).

1.2.2. Current threats and ecosystem services provision to the city of Bogotá

The city of Bogotá is located at around 2,650 masl on the *Cundiboyacense* highland plateau in the Eastern Colombian Andean Cordillera. It is surrounded by hills on its eastern and southern sides and enclosed to the west and north by the Bogotá River (Andrade et al., 2013). The *Distrito Capital* of Bogotá was one of the fastest growing regions in the urbanization and industrialization process Colombia experienced during the late 20th century. With today more than 8 million inhabitants, Bogotá represents a “mega-city” with an enormous population growth since the 1970s which led to an increased demand of services, resources and goods (Etter et al., 2006b). Furthermore, roughly 50 years of political instability and armed conflicts have had major impacts on the country and on the development of its capital city, contributing to increasing pressure on ecological systems and biodiversity (Fjeldså et al., 2005). Consequently, within the tropical Andes the area of Bogotá, the capital of Colombia, represents one of the best areas to study the impact of human-induced alterations on *bosques altoandinos*.

Bogotá, and thus millions of people, rely heavily on the provision of fresh water, food and many other ecosystem goods and services, as well as culturally relevant practices and traditions, from the surrounding high mountain ecosystems (Buytaert et al., 2006; Escobedo et al., 2015). The *pàramos* wetlands and high Andean forests are key actors in water purification and supply.

Nonetheless, these ecosystems are under increasing pressure from a combination of land use intensification and land use change, over-exploitation, mismanagement (*e.g.*

large-scale farming and husbandry, mining, fracking), and climate change, resulting in ecosystem degradation and fragmentation, often visible through soil compaction, low fertility, and/or erosion (Armenteras et al., 2003). Moreover, high-Andean forests remnants in the vicinity of Bogotá are mostly unprotected from rural management activities (Armenteras et al. 2003), which involve a wide range of local disturbances including selective logging, intentional fires, and cattle grazing (Etter & Villa, 2000; Armenteras et al., 2003; Etter et al., 2006a), together with an increasing number of invasive species (Fig. 7). These combined disturbances dramatically affect local biodiversity and soil condition, therefore hydrological regulation (Etter et al., 2000). Consequently, the capability of high Andean forests to provide ecosystem services suffers a strong reduction, with serious negative impacts on the system of water storage and water quality for the Bogotá metropolis (Borrelli et al., 2015).

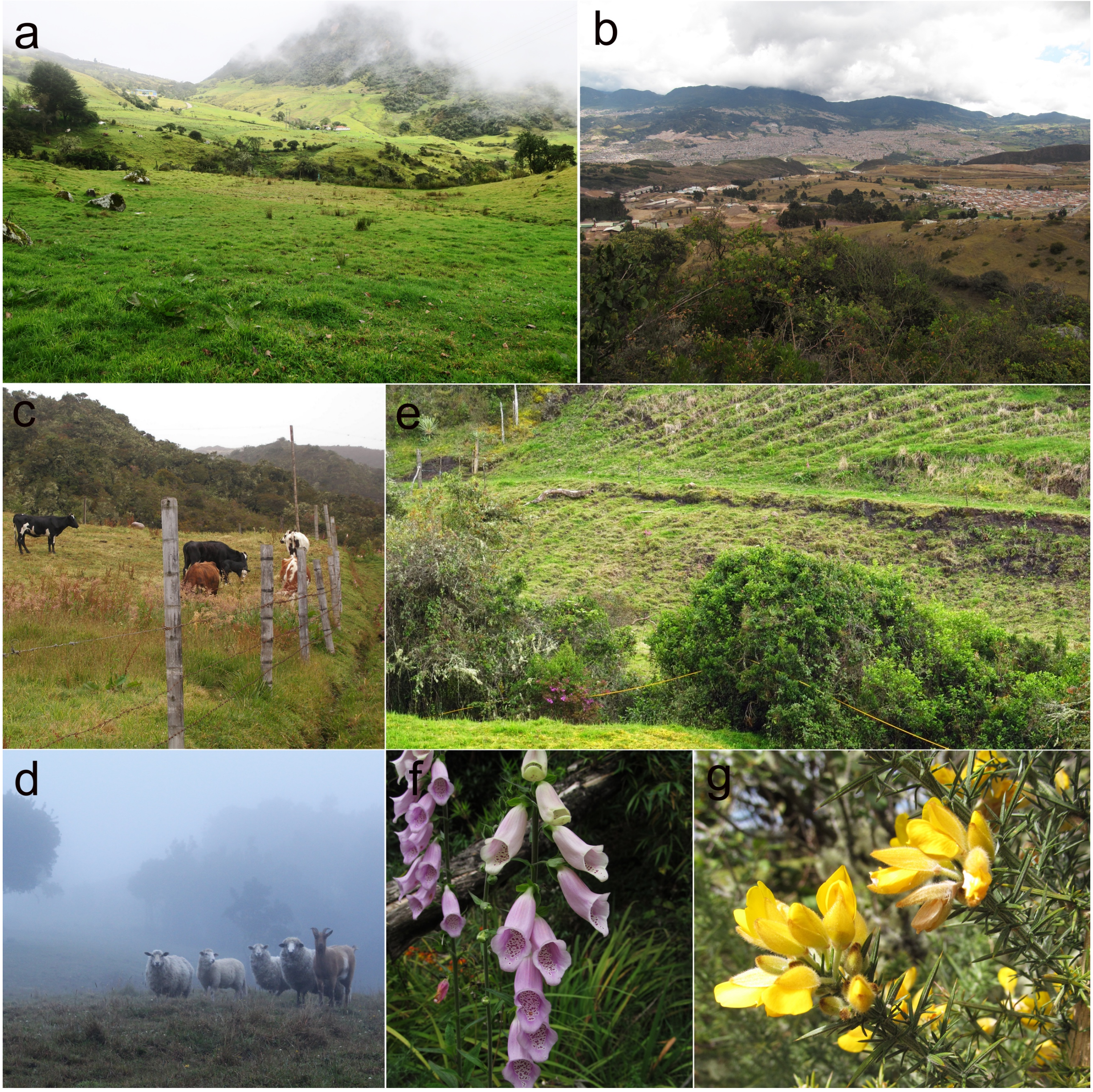

Figure 7: Appereance of forest fragments around Bogotá and human disturbance related factors: a) forest cover fragmentation in Nazareth, Sumapaz; b) urban expansion in the northern part of the *Sabana de Bogotá*; c) and d) cattle and sheep farming in the localities of Pasquilla and Sumapaz; d) evidence of soil erosion in heavily farmed fields in Nazareth, Sumapaz; f) and g) invasive species *Digitalis purpurea* and *Ulex europaeus*, commonly found in rural localities near Bogotá. Images copyright a-c and f-g © *F. Fajardo* and e-d © *M. Calbi*

1.3. Review of vegetation studies on high Andean forests in the area of Bogotá

1.3.1. Plot-based vegetation studies

The characterization of high Andean plant communities in the area surrounding Bogotá has its historical origins in the contributions of Caldas and von Humboldt (Van der Hammen & Rangel, 1997). Over the years, several phytosociological studies based on the Zúrich-Montpelier methodology (Braun-Blanquet, 1932) have been performed in Colombia's capital district beginning with Cuatrecasas (1934, 1958) who first defined a classification system for the local plant communities. This classification, with posterior contributions from Cleef and Rangel, has then been widely applied by many members of the local scientific community to identify high Andean vegetation units and the associated species richness and diversity (Van der Hammen & González, 1960; Forero, 1965; Lozano & Schnetter, 1976; Cleef, 1979; Cleef, 1981; Cleef & Hooghiemstra, 1984; Sánchez & Rangel, 1990; Rangel, 1991; Van der Hammen, 1998; Cortés-Sánchez et al., 1999; Franco & Betancur, 2000; Cortés-Sánchez, 2008; Van der Hammen, 2008; Cantillo Higuera & Gracia, 2013; Avella et al., 2014).

Further plot-based characterizations of the local flora and its relevant features (*e.g.* corology as in Fajardo-Gutierrez, 2013) that were not based on the phytosociological approach were carried out by public organizations, namely the Jardín Botánico de Bogotá (JBB) and the Universidad Distrital of Bogotá (Jardín Botánico de Bogotá – Universidad Distrital, 2001; 2002; Cortés-Sánchez, 2003; 2006; 2007; Chisacá, 2005, Arellano, 2009; García & Mayorga, 2009; Hernández, 2010; Trujillo 2010; 2011; 2012a; 2012b). Studies focusing on ecological features were also carried out to evaluate the structure of the arboreal and shrubby vegetation (Vargas, 1986; Cortés-Sánchez, 2003), the associated above-ground biomass (Cardozo & Schnetter 1975). These studies were conducted to assess the floristic, ecological and physiognomic characterization of changes in species assemblages (Cortés-Sánchez, 2011) and the biological activity patterns in different plant associations (Schnetter & Cardozo 1976). Moreover, further investigations focusing on plant-soil-microorganisms and plants-artropofauna interactions, regeneration and developmental strategies of *páramo* and *bosque altoandino* plant species can be found in Gómez (2005).

Among the few efforts to include biological interactions in the study of high Andean vegetation around Bogotá, Romero et al. (2004) evaluated the importance of plant-fungi relationship in adaptation and colonization processes in high Andean plant communities.

In the context of multidisciplinary studies, there are two outstanding and comprehensive pieces of work focusing on the surrounding of Bogotá, worth mentioned. One is the work of Van der Hammen et al. (2008), which includes a collection of studies aiming to characterize the vegetation of the *páramos* and *bosques altoandinos* of the "Sumapaz Transect". Within this collection of studies, the topics range from classical floristic inventories, species richness and turnover patterns of plants and lichens species, to the evaluation of the relationship between structural diversity and environmental factors. The other is the work of Mora-Osejo & Sturm (1994), which incorporates a wide range of ecological studies carried out in mountain areas immediately neighbouring the city of Bogotá.

Additionally, a considerable amount of plot-based studies focusing on specific aspects of restoration ecology is available. These include the characterization of *bosques altoandinos* regeneration stadia (Rojas, 2017), the planning of restoration strategies for differently impacted bosque altoandino fragments (Vargas et al., 2007), or the assessment of plant functional groups and their role during secondary succession (Castellanos-Castro & Bonilla; 2011). Moreover, several studies targeting invasive species ecology were performed in the surroundings of Bogotá, especially on the European invasive *Ulex europaeus* (*e.g.* Beltrán & Barrera-Cataño, 2014; Ocampo-Zuleta & Solorza-Bejarano, 2017) or invasive grasses of the Poaceae family (Giraldo-Cañas; 2010).

Among the efforts aiming to characterize high Andean ecosystem condition and regeneration potential in the area, the work by Acuña (2013), Arias-Escobar & Barrera-Cataño (2007), and Agudelo Valencia (2010), the latter two specifically centering on forest regeneration after mining disturbance, represent notable contributions. Moreover, the recent work of Hurtado-Martilletti et al. (2021) stands out as the authors performed a comprehensive assessment of the floristic composition and regeneration potential in secondary and mature forest fragments in the north of Bogotá, highlighting the lack of strong floristic homogenization processes. Lastly, the ecological connectivity, regeneration and conservation status of *bosques altoandinos* near Bogotá were also assessed by Isaacs et al. (2012), as well as the relationship between forest fragmentation, tree species above-ground biomass and functional diversity (Rodríguez-Alarcón et al., 2018).

1.3.2. Studies on forest cover change

Forest cover extent and its changes through the course of the last few decades have been extensively studied in Colombian high Andean forests (Etter & Villa, 2000; Armenteras et al., 2003; Sánchez-Cuervo et al., 2012; Rodríguez Eraso et al., 2013), and also specifically in the surrounding area of Bogotá (Mendoza & Etter, 2002; Anselm et al., 2018). Nevertheless, forest cover extent is not a *per se* indicator of habitat quality, as also the nature of the forest cover (*i.e.* forest plantation with commercial species *vs* natural regeneration stadia), or the heritage of past land-use history and present land management may still convey habitat degradation (Aide, 2004), leaving lands vulnerable to erosion, loss of soil nutrients or organic matter (Vanwalleghem et al., 2017) or to the establishment of invasive species (Aide, 2004; Waldner, 2008). For this reason, there is a growing number of studies that integrate forest cover change with environmental and anthropic constraints (Rubiano et al., 2017; Clerici et al., 2020), or relate forest cover attributes with ecosystem services as carbon storage (Borrelli et al., 2015; Clerici et al., 2016; Clerici et al., 2019a).

1.3.3. Studies on the status and distribution modelling of characteristic species

Not many studies focusing on the ecology of single high Andean species native to the surroundings of Bogotá are available. One example is the evaluation of the current status of *bosques altoandinos'* emblematic species *Weinmannia tomentosa* ("*Encenillo*"), paired with the outlining of adequate conservation strategies (Pulido, 2011). Furthermore, Rangel and Arellano (2010) evaluated the extent of remaining *Polylepis* forests, while Moreno and collaborators (2011) defined the conservation status of the endangered arborescent fern *Dicksonia sellowiana*, modelling its spatial distribution. Moreover, a detailed study by León and colleagues (2011) modelled the distribution and investigated extant population attributes and propagation strategies of the endangered tree *Centronia mutisii* (Melastomataceae). Furthermore, Ordóñez-Blanco and Rosselli (2017) explored the relationship between phenology and climate for four common high Andean orchid species, while Gíl Amaya (2012), evaluated the current status of the entire family Orchidaceae within the Cundinamarca department. More recently, Valencia et al. (2020) assessed the climate vulnerability of the *Espeletia* complex, Fajardo-Gutiérrez et al. (2018) modelled the distribution of all the species of *Polylepis* found in Colombia, and Caballero-Villalobos et al. (subm.), modelled the distribution of the treeline forming *Polylepis quadrijuga*, projecting it to future climatic conditions.

1.3.4. Summary of the status of studies on bosques altoandinos in the area of Bogotá

In summary, the available studies focusing on Bogotá's high Andean forests classically revolve around biodiversity inventories of the canopy or the shrub layers, with almost all of the studies overlooking lower vegetation strata *i.e.* the forest floor, understory or epiphytic layers. More recently, vegetation inventories started to be paired with the assessment of ecosystem services, or the ecological characterization of secondary forest fragments and successional regeneration pathways, seldomly incorporating the analysis of remote sensing data. In addition, a large part of the studies on high Andean forests around Bogotá are published as thesis work or 'end of contract reports' from different institutions, falling into the category of 'grey literature' and thus not easily available to the general public.

Furthermore, the amount of studies on high Andean forests is still somehow scarce if compared to the number of studies on local *páramo* ecosystems. Very little has been done at a regional scale, with most of the works inside the capital district being quite circumscribed, spanning one or two administrative localities at most. The large majority of studies take place around the Sumapaz-Cruz Verde complex or in some already well-studied localities such as Chisacá, Usme, Pasquilla and Monserrate, or in the northern part of the *Sabana de Bogotá.*

In addition, there are very few studies that aim to long-lasting monitoring purposes, for instance establishing permanent plots, or that address long-term changes in the extension and structure of high Andean forests by analysing longer time series of remotely sensed data (*i.e.* longer than the mere satellite data coverage). This would allow the gathering of detailed information on landscape history and patterns of landscape change through several decades. In this context, the chance of pairing plot-based work with forest cover change analysis (*e.g.* Clerici et al., 2016) could provide meaningful insights into the drivers of local plant communities composition and the underlying assembly mechanisms (Poos et al. 2009, Swenson 2014, Bovendrop et al., 2018).

Besides the overall limited temporal and geographical extent, several knowledge gaps concerning the study of high Andean forests in the Capital District can be identified, especially regarding the study of biological interactions and multi-trophic associations, but also concerning ecosystem condition characterization or the assessment of anthropogenic impact. Specifically, the review of the available literature on high Andean forest around Bogotá underpins the need for the incorporation of more complex parameters such as landscape history and fragmentation and anthropic disturbance metrics and their relation to the taxonomic but also functional and phylogenetic diversity and ecosystem services. Accordingly, a wider implementation of permanent plots in the area could be highly beneficial, as well as the development and application of alternative categorization and monitoring methodologies (*e.g.* Ramírez-Morán et al, 2016) that could provide cost-efficient tools for the effective characterizations of high Andean forests in terms of disturbance.

Lastly, while some distribution modelling exercises have been carried out for high Andean species in the area surrounding Bogotá, the efforts to model the potential future distribution of treeline species in Colombia are very scarce. Thus, transcending the regional scale to model the future response to climate change of indigenous treeline species could contribute to knowledge on the environmental constraints driving the current distribution of high Andean forest species and the potential future trajectories of high Andean ecotones in general. Overall, a multi-scalar and comprehensive approach in the study of high Andean forests could serve as a basis to estimate the present and future range and extent of the ecosystem services provided by high-Andean communities (Diaz & Cabido, 2001; Petchey et al. 2007; Bovendrop et al, 2018), placing these into the context of drivers of anthropogenic disturbance.

1.4. Outline of the doctoral project

This doctoral project is embedded in the Colombian-German research program “Integrated Biodiversity Management in exemplar regions of Colombia” and contributes to work package 2 “Land use and vegetation cover” of the BMBF-funded project “Kooperation mit dem Botanischen Garten Bogotá und der Universidad del Norte Barranquilla” (ColBioDiv, BMBF, FK 01DN17006). The main aim of ColBioDiv is to implement multi-disciplinary biodiversity research to further the development of sustainable biodiversity management as an integral part of sustainable research in the two model regions of Bogotá and Barranquilla. The project is built on the collaboration between researchers from several institutions, including the Botanic Garden and Botanical Museum of Berlin (BGBM), the Institute of Geographical Sciences and the Institute for Latin American Studies of the FU Berlin, as well as the Botanical Garden José Celestino Mutis in Bogotá (JBB), the Universidad del Norte in Barranquilla and the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Colombia).

The PhD project presented here contributes to the understanding of tropical Andean ecosystems in Colombia by analysing the current status of *bosque altoandinos* in the surrounding area of Bogotá. Specifically, this project aims to cover some of the identified knowledge gaps on the ecology and disturbance history of *bosques altoandinos* in the study area. The ecosystems on which this dissertation specifically focuses on are exposed to high anthropic pressure, not only from the expanding city and its growing human impact, namely the change or intensification of land-use, but also due to the consequences of local climate change (Armenteras et al., 2003). This, together with the high population density in this part of the Andes calls for urgent conservation measures (Fandiño & Ferreira, 1998). To develop conservation strategies and to guide policymakers, a better understanding of ecological processes is always the necessary foundation. Therefore, this doctoral work could supply some of the baseline knowledge necessary to build urgently needed sustainable management strategies, addressing the fragility and lack of adequate protection of high Andean forests.

The main objective of this dissertation is to acquire a better understanding of forest composition, structure and above-ground biomass in relation to human disturbance, and to perform the reconstruction of forest cover trends around Bogotá, together with the evaluation of the potential future response to climate change of a distinctive high Andean treeline species. Accordingly, we developed a permanent plot-based integrated assessment of taxonomic diversity with underlying evolutionary relationships between taxa (phylogenetic component) and signal of the ecological niches those taxa occupy (functional component), paired with an analysis of temporal trends in forest cover and forest connectivity metrics. Additionally, based on its presence and key ecological role in our high elevation study-plots, we modelled the distribution of the high Andean treeline species *Weinmannia fagaroides* and projected it to the period 2060-2080 under a high CO_2 emission scenario. Specifically, within this PhD project, we wanted to answer the following research questions: *i) What is the current state of high-Andean forests in the surrounding area of Bogotá in terms of plant species diversity, above-ground biomass, fragment age and forest cover fragmentation?; ii) What are the aspects of anthropic disturbance that have the strongest impact on vegetation composition and structure and which variables can be used as indicators of disturbance?; iii) How has forest cover and forest connectivity developed through time?; iv) How will climate change affect the distribution and the successful establishment of a representative high Andean species found in our permanent plots network?*

1.5. Structure of the document and content

This document follows a cumulative format and therefore contains five chapters. Chapter 1 provides the general introduction. Chapters 2 to 4 correspond to three research manuscripts and are structured as journal articles, thus, they contain their own summary, introduction, material and methods, results, discussion, conclusions, figures, tables, reference list and appendices. Chapter 2 corresponds to the paper entitled "Seeing the wood despite the trees: exploring the impact of human disturbance on plant diversity, community structure, and standing biomass in fragmented high Andean forests" published in the journal Ecology and Evolution. Chapter 3 corresponds to the paper entitled "Reconstructing Long Term High Andean Forest Dynamics Using Historical Aerial Imagery: A Case Study in Colombia" published in the journal Forests. Chapter 4 corresponds to a manuscript entitled: "Modelling the potential present and future distribution of a Tropical Andean treeline species using three different climate datasets". Chapter 5 presents the general conclusions. The references list of Chapters 1 and 5, as well as the Supplementary material for Chapters 2, 3 and 4 are provided at the end of this document.

Chapter 2 presents the work on the simultaneous analysis of the role of multiple factors in shaping disturbed high Andean plant communities. The obtained results enable to [1] categorize tree and understory layer communities in the study area; [2] identify the main environmental and anthropic-related drivers of the composition of tree and understory layer communities; [3] assess the impact of environmental and anthropic-related drivers on taxonomic, functional and phylogenetic diversity, and on above-ground biomass production as well as the impact of tree layer attributes on understory layer diversity metrics.

Chapter 3 presents the reconstruction of the forest cover dynamics in selected localities in the surroundings of Bogotá for the period 1940-2000. The result allows to [1] track the trends of forest cover extent through several decades in 9 administrative localities, including the forest fragments studied in Chapter 2; [2] simultaneously track forest connectivity and the evolution through time of forest configuration (*i.e.* edge *vs.* core zones *etc.*); [3] correlate forest cover with forest connectivity and to the individual history of each locality.

Chapter 4 presents the modelling of the present and future distribution of the Andean treeline species *Weinmannia fagaroides*. The resulting models enable to [1] compare the effectiveness of three different climate datasets (Chelsa, worldclim 1.4 and 2) and three modelling algorithms (glms, random forest and maxent) in predicting the current distribution of *W. fagaroides*; [2] evaluate the current extent and identify the main environmental drivers of *W. fagaroides distribution*; [3] compare the present and future distribution of the species, highlighting climatically stable areas for potential conservation projects; [4] assess the representativeness in protected areas of the modelled present and future distribution.

Chapter 5 presents the main conclusion of each chapter, answering the formulated research questions and evaluating the contribution to the knowledge of disturbed high Andean forests in the surrounding areas of Bogotá.

“Education, if it means anything, should not take people away from the land, but instill in them even more respect for it, because educated people are in a position to understand what is being lost. The future of the planet concerns all of us, and all of us should do what we can to protect it.”

— Wangari Maathai

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ORIGINAL RESEARCH

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Seeing the wood despite the trees: Exploring human disturbance impact on plant diversity, community structure, and standing biomass in fragmented high Andean forests

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Abstract

High Andean forests harbor a remarkably high biodiversity and play a key role in providing vital ecosystem services for neighboring cities and settlements. However, they are among the most fragmented and threatened ecosystems in the neotropics. To preserve their unique biodiversity, a deeper understanding of the effects of anthropogenic perturbations on them is urgently needed. Here, we characterized the plant communities of high Andean forest remnants in the hinterland of Bogotá in 32 0.04 ha plots. We assessed the woody vegetation and sampled the understory and epiphytic cover. We gathered data on compositional and structural parameters and compiled a broad array of variables related to anthropogenic disturbance, ranging from local to landscape-wide metrics. We also assessed phylogenetic diversity and functional diversity. We employed nonmetric multidimensional scaling (NMDS) to select meaningful variables in a first step of the analysis. Then, we performed partial redundancy analysis (pRDA) and generalized linear models (GLMs) in order to test how selected environmental and anthropogenic variables are affecting the composition, diversity, and aboveground biomass of these forests. Identified woody vegetation and understory layer communities were characterized by differences in elevation, temperature, and relative humidity, but were also related to different levels of human influence. We found that the increase of human-related disturbance resulted in less phylogenetic diversity and in the phylogenetic clustering of the woody vegetation and in lower aboveground biomass (AGB) values. As to the understory, disturbance was associated with a higher diversity, jointly with a higher phylogenetic dispersion. The most relevant disturbance predictors identified here were as follows: edge effect, proximity of cattle, minimum fragment age, and median patch size. Interestingly, AGB was efficiently predicted by the proportion of late successional species. We therefore recommend the use of AGB and abundance of late successional species as indicators of human disturbance on high Andean forests.

KEYWORDS
aboveground biomass, biodiversity, *bosque altoandino*, Colombia, cryptic forest degradation, understory

1 | INTRODUCTION

High Andean tropical montane forests (herein *bosques altoandinos*) can be found between ca. 2,700 and 3,300 m in the Northern Andes, extending from Venezuela to Ecuador, with considerable levels of species diversity and endemism (Gentry & Ortiz, 1993; Girardin et al., 2014; Killeen et al., 2007; Still et al., 1999; Young, 1992). These forests provide vital ecosystem services to the neighboring cities and settlements, such as the regulation of water fluxes (Armenteras et al., 2003; Chaves & Arango, 1998; Linares & Ríos, 2004; Rangel, 2000) or carbon capture and storage (Brown & Kappelle, 2001; Torres et al., 2012).

Bosques altoandinos have been subjected to extensive anthropogenic transformation across their natural range. In Colombia, large portions of the forest cover were cleared during the past four centuries and turned into agricultural or residential areas, in order to satisfy the growing demand for resources of an increasing human population (Brown & Kappelle, 2001; Cavelier et al., 2001; Etter et al., 2008; Heath & Binswanger, 1996; Sánchez-Cuervo et al., 2012; Wassenaar et al., 2007). Such a reduction of forest cover can not only lead to loss of biodiversity but also to a lower structural integrity and resilience of the remaining fragments (Mori et al., 2013). Changes in species composition also go along with shifts in functional diversity and biological interactions (Bovendorp et al., 2019; Diaz & Cabido, 2001; Flynn et al., 2011; Petchey & Gaston, 2002, 2007; Poos et al., 2009; Swenson, 2014). Eventually, this affects ecosystem services (González et al., 2011; Menon et al., 2007; Rangel, 2000; Torres et al., 2012).

In the recent past, forest cover has increasingly been monitored using remote sensing techniques. For the Colombian high Andean forests, this has shown modest signs of recovery in some areas (Calbi et al., 2020; Etter, 2002; Rubiano et al., 2017; Sánchez-Cuervo et al., 2012; but see Anselm et al., 2018). However, remote sensing cannot detect cryptic forms of forest degradation, such as selective logging or understory grazing. Even plot-based surveys focusing on trees may not reveal such alterations. Yet, cryptic forest degradation has significant impact on soil erosion, successional dynamics, and regeneration, since understory and epiphytic plants are major drivers of ecosystem functioning (Nilsson & Wardle, 2005). Understanding the effects of anthropogenic disturbance on all major forest components, that is, tree, shrub, understory, and epiphyte layers, is therefore essential to elaborate and implement effective strategies for the sustainable management of these forest ecosystems (Battles et al., 2001; Fahey & Puettmann, 2007; Halpern & Spies, 1995; Roberts & Gilliam, 1995). In addition, multiple predictor and response variables should be analyzed simultaneously to properly address disturbance effects within this complex environment.

One of the best areas to study the impact of human-induced alterations on *bosques altoandinos* in the northern Andes is the area of Bogotá, the capital of Colombia, which is situated at approximately 2,600 m altitude. With a population of around 9 million inhabitants, Bogotá is by far the largest city in the Andean high montane forest belt, putting tremendous pressure on the surrounding ecosystems. Remnants of high Andean forests near Bogotá are mostly affected by rural activities, which include logging, fires, and agriculture, typically resulting in soil compaction, low fertility, and/or erosion (Armenteras et al., 2003; Linares & Ríos, 2004; Posada & Norden, unpublished results). *Bosques altoandinos* in the surroundings of Bogotá have mostly been studied using phytosociological analysis of plot inventory data (Avella et al., 2014; Cantillo Higuera & Gracia, 2013; Cleef, 1981; Cortés, 2008; Sturm & Rangel, 1985; Van der Hammen, 2008). Beyond such floristically oriented approaches, few studies have addressed the effects of disturbance on these forest ecosystems. Some preliminary research works on forest succession and regeneration were carried out as thesis works (Acuña, 2013; Restrepo Abadia, 2016). In a recent study, Rodríguez-Alarcón et al. (2018) found a negative effect of forest fragmentation on functional diversity and aboveground biomass, a first indication that more complex parameters such as functional diversity are indeed related to ecosystem services such as carbon storage. However, studies that simultaneously consider multiple disturbance predictors and different plant communities response variables were so far lacking.

According to the available literature, the most relevant disturbance factors, which variation proved to be significantly related to differences in forest species composition or diversity metrics, are as follows: age of forest fragment (Köster et al., 2009; Laurance et al., 2006), proximity to houses or roads and people and livestock density (Ribeiro et al., 2015, 2016), edge effect, and proximity to pastures (Parra Sánchez et al., 2016; Werner & Gradstein, 2009), as well as forest cover fragmentation metrics (Fahrig, 2003; Hertzog et al., 2019; Laurance et al., 2006). Nonetheless, it has not yet been tested whether these factors would be still relevant when a larger number of variables are considered simultaneously. For this reason, we conducted a comprehensive integrated assessment of the potential effects of multiple environmental and disturbance variables on the taxonomic, phylogenetic, and functional diversity of the two main forest layers (tree layer and understory) and on epiphytes cover.

We therefore hypothesized that anthropogenic disturbance as a whole, understood as a composite variable sensu Paine et al. (1998), affects the composition, and aboveground biomass of *bosques altoandinos*, with impacts on community diversity metrics, that is, taxonomic, phylogenetic, and functional diversity. We also hypothesized that our comprehensive analysis would identify significant predictor and response variables other than those found in previous studies. We specifically set out to answer three questions: (a) Which environmental and disturbance variables best explain species diversity and composition of tree and understory layers? (b) What are the effects of *facilitators* (parameters that increase the likeliness of disturbance) and *causes* (direct sources) of disturbance on species diversity, phylogenetic structure, functional diversity, and aboveground biomass? (c) Which vegetation variables are best indicators of disturbance?

2 | METHODS

2.1 | Study area

The study area encompasses ca. 4,600 km^2 within the *Cundiboyacense* high plain in the *Cordillera Oriental* of Colombia, spanning peri-urban and rural areas of the department of Cundinamarca and the administrative region of the city of Bogotá (Bogotá D.C. or Distrito Capital). The capital region is the most densely populated area of the country, with nearly 9 million inhabitants and approximately 4,500 people per km^2 (DANE, 2019). The climate is characterized by isothermality with an annual mean temperature of around 14°C and mean annual precipitation between 600 and 1,300 mm. There are two rainy seasons: from April to June and from September to November, with a drier and warmer season from January to March (Anselm et al., 2020; IDEAM, 2007, 2015). The topography is marked by an extended plain, situated at around 2,600 m, which hosts most of the urban and agricultural area, and steep elevation gradients including mountains of up to 4,100 m altitude. Dominant soils in the study area were classified as Andisols (IGAC, 1985; Etter, 2002; Sturm & Rangel, 1985).

Rural areas in the region are highly influenced by the adjacent city of Bogotá and contiguous suburbs. Hence, sparse remnants of original vegetation are intermixed with secondary forests (Cortés, 2008; Rubiano et al., 2017). These remnants are largely dominated, by trees and shrubs in genera such as *Weinmannia*, *Miconia*, *Clusia*, *Hesperomeles*, *Clethra*, *Myrcianthes*, *Myrsine*, *Gaultheria* and *Escallonia*, various genera of Lauraceae, and *Cedrela montana*. Hygrophytic communities with prevalence of *Drimys granadensis* or *Hedyosmum* or higher elevation heliophyte associations of *Gynoxys*, *Diplostephium*, and *Vallea stipularis* also form part of these ecosystems (Rangel, 2000; Sturm & Rangel, 1985; Van der Hammen, 1998). The forest patches are embedded in a landscape mosaic with cattle pastures and small-scale cultivation of potatoes (*Solanum tuberosum*), green beans (*Pisum sativum*), and *cubios* (*Tropaeolum tuberosum*). The size of remaining forest fragments is generally small, and their regeneration is threatened by further fragmentation, invasive species, erosion (Linares & Ríos, 2004), and urbanization (Rubiano et al., 2017).

2.2 | Plot setup

Due to the usually small size of forest fragments, we used a plot size of 20 × 20 m (0.04 ha) as established in the framework of the *Rastrojos* project (Acuña, 2013; Hurtado-Martilletti et al., 2020; Muñoz-Camacho et al., 2017). We complemented the data from the tree layer assessments of 20 plots obtained from the *Rastrojos* project with data from 12 plots set up and assessed during this study. In addition to the tree layer data, we also assessed the understory layer, and epiphyte cover in the totaling 32 plots, which are located in six administrative regions of Bogotá D.C. and Cundinamarca (Figure 1; Appendix A1). We aimed for a widely scattered position of plots in order to represent the landscape (e.g., including differently inclined slopes). Our sampling design was influenced by the distribution of available and accessible fragments. Plot locations belonged to privately owned protected areas and farms, for which we obtained the required permits of entry from the corresponding owners.

2.3 | Macro-environmental variables

For each plot, macro-environmental variables were compiled from different sources in QGIS 2.18.12 "Las Palmas" (QGIS Development Team, 2018). Altitude, slope, and aspect (northness and eastness) were derived from an Aster Digital elevation model of the study area; for this, ASTGTM2_N04W075, ASTGTM2_N05W075, ASTGTM2_N05W074, and ASTGTM2_N04W074 data products were retrieved from the NASA Land Processes Distributed Active Archive Center (LP DAAC; https://lpdaac.usgs.gov/tools/data-pool, NASA/METI/AIST/Japan Spacesystems & U.S./Japan ASTER Science Team, 2009). Mean annual precipitation and mean and maximum temperature data for the period 1981–2010 were obtained from the IDEAM meteorological station closest to each plot (http://www.pronosticosyalertas.gov.co/mapas-graficos-tiempo-clima/indicadores-climatologicos). Mean population density was extracted in two buffers (radius 1 km and 5 km) around the plots from the worldpop database for South America at 1 ha resolution (https://www.worldpop.org, Sorichetta et al., 2015). A complete list of all macro-environmental variables can be found in the Appendix A2.

2.4 | Tree and shrub layer assessment

Following the protocol of Hurtado-Martilletti et al. (2020), for every woody plant with basal diameter > 5 cm (measured at 5 cm from the ground—DAH: Diameter at "ankle" height), we recorded its DAH, DBH and visually estimated tree height, a method that proved to be quite precise for lower canopies such as the ones studied here (Silva et al., 2012). Plant material was collected and identified with the available literature (Gentry & Vasquez, 1993; Trelease & Yuncker, 1950; or webpages: https://plantasdecolombia.com), by comparison with herbarium specimens, digitized specimens available online (JBB: http://herbario.jbb.gov.co; COL: http://www.biovirtual.unal.edu.co/en/collections/search/plants), or with additional help from local experts. Specimens were deposited in the herbarium of the Jardín Botánico de Bogotá José Celestino Mutis (JBB); high-resolution

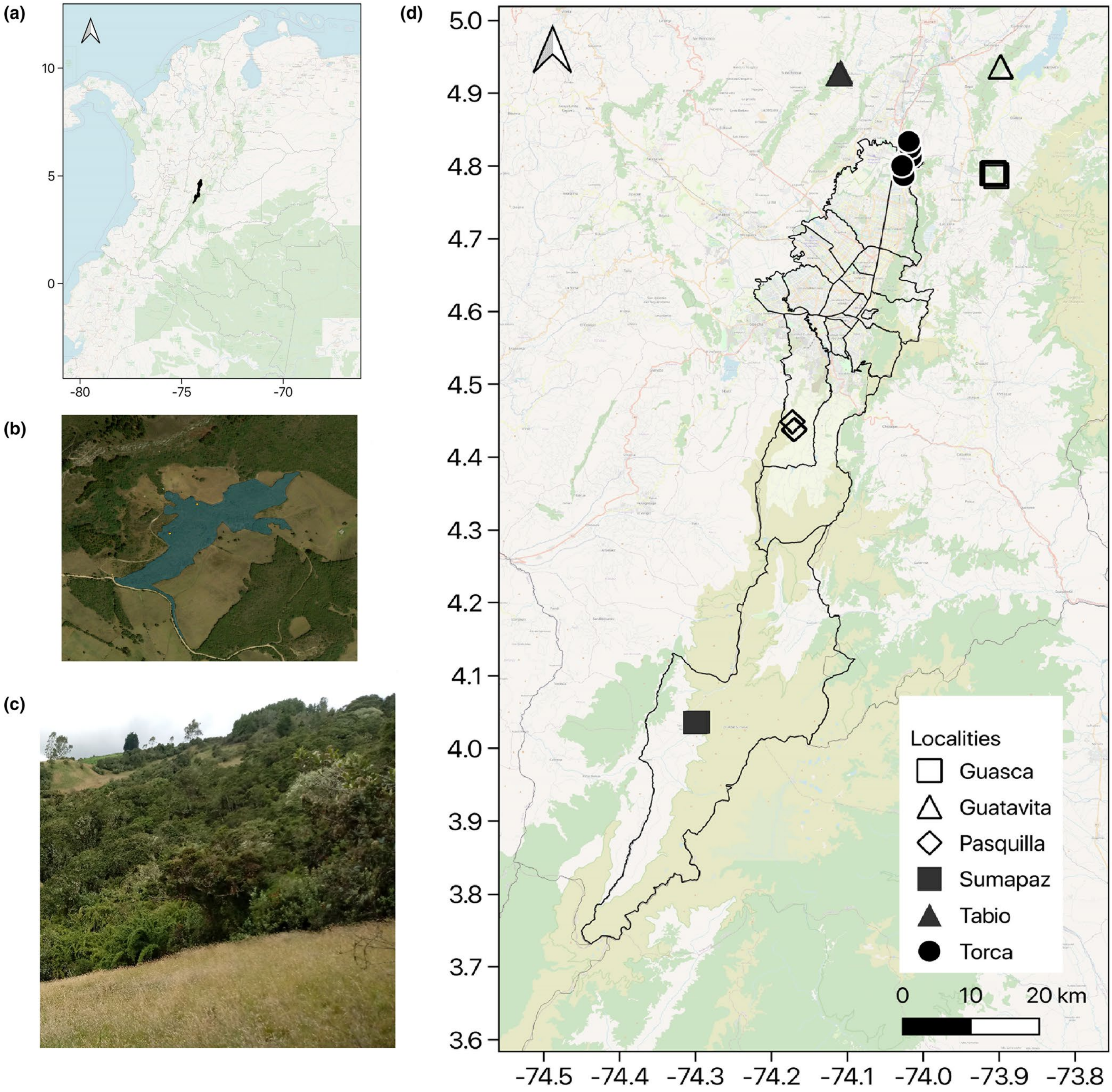

FIGURE 1 Study area and plot locations. (a) Colombia with Bogotá Capital Department in black; (b) manually vectorized forest fragment in Guatavita; (c) Typical aspect of forest fragment in the study area: (d) Bogotá Capital Department and plot locations. Base map modified from Bing and OSM

digital specimen images can be provided upon request; and a plot-resolved list of vouchers can be found in the Appendix A3.

2.5 | Understory assessment

In each 20 × 20 m plot, eight 1 × 1 m quadrants (with marked 10 cm subgrids) were placed randomly. All vascular plants, including tree seedlings, were recorded, and mean height and total cover (the sum of all individuals cover) were measured for every species in each quadrant. When available, fertile material was collected and deposited in the JBB. Additionally, cover of bare soil, leaf litter, bryophytes, lichens, and coarse woody debris was visually estimated for every quadrant.

2.6 | Epiphyte cover

In each plot, we sampled 40 randomly selected trees to estimate the epiphyte cover. Categorical cover classes (ranging from 0 to 3) were assigned to each of five major epiphyte groups (bryophytes, lichens, ferns, bromeliads, and orchids), separately for trunk and canopy branches.

2.7 | Functional traits and functional diversity

Three leaf functional traits (specific leaf area: SLA; leaf thickness: LT; and leaf dry matter content: LDMC) were measured for each tree species following the protocols provided by Pérez-Harguindeguy et al., (2013). Five leaves were collected from each of up to three different individuals per species and stored in wet paper for at least 12 hr, then weighted (petiole included). LT was measured with a digital micrometer, and a digital scan of the fresh leaves was taken with a Hewlett-Packard F4280 scanner. Leaf area was calculated with ImageJ 1.8.0 (Schneider et al., 2012). Leaves were oven-dried at 60°C until constant weight and weighted; SLA was then calculated as one-sided area of a fresh leaf divided by its dry mass, expressed in cm^2/g. LDMC was calculated as the dry mass (mg) divided by its fully hydrated fresh mass (g), and expressed in mg/g. Additionally, wood density (WD) was obtained from Rodríguez-Alarcón et al. (2018) and the global wood density database (Chave et al., 2009) for all tree species or, depending on availability, at genus or family level estimates, using the R package *biomass* (Réjou-Méchain et al., 2018) in R Studio (R Core Team, 2018). The traits used to estimate functional diversity were SLA, LDMC, LT, WD, maximum recorded height in the plots, and life form (tree or shrub). The final trait database was completed with data from the *Rastrojos* project including data from published reports (Muñoz-Camacho et al., 2017) and Posada (unpublished results).

To reduce skewness, traits were $\log_{10}$-transformed and computation of functional divergence, functional dispersion, functional richness, functional evenness, and Rao's quadratic entropy (FDiv, FDis, FRic, FEve and Rao's Q) was performed as indicated in Villéger et al. (2008), using the R package *FD* (Laliberté & Legendre, 2010; Laliberté et al., 2014). We specified "corr + lingoes, m = 3" to reduce dimensionality. Functional diversity (FD) index (Petchey & Gaston, 2002) was calculated as the total branch length of a functional dendrogram generated on a distance matrix of traits with the R function hclust, using the PD function in the R package *picante* (Kembel et al., 2010). We decided to compute functional diversity according to the framework proposed by Mason et al. (2005) and Villéger et al. (2008). The calculated indices provide independent information about the position and relative abundances of species in a multidimensional functional space, allowing for a more detailed examination of the mechanisms linking biodiversity to ecosystem function (Villéger et al., 2008).

2.8 | Landscape metrics

A Landsat 8 raster was downloaded from the US Geological Survey and processed in QGIS with the *SCP* plugin (Congedo, 2016) to obtain a land cover map. Landscape metrics refer to the size, shape, configuration, number, and position of land-use patches within a landscape and were obtained for the *forest* class within a 1,000 m diameter buffer zone around the plots with the *LecoS* plugin (Jung, 2013).

Additionally, fragments of forests were manually vectorized and the area was calculated on a prepared Bing aerial map obtained through the *Openlayers* plugin (see Figure 1 for an example). Distance to closest roads was calculated with the *NNJoin* plugin on a shapefile downloaded from the DANE Web site (2018). Also, the type of closest road (main, secondary, or track) was noted. Distances to closest houses or tracks were manually measured on the map. Presence or absence of cattle or active cultivated fields in different buffers (0 m, 50 m, 100 m, or 500 m radius) was surveyed in the field. A complete list of all landscape metrics can be found in the Appendix A2.

Minimum age of the forest cover of each plot was estimated through the visual analysis of 43 aerial pictures of the plot locations acquired from the IGAC (Instituto Geográfico Agustín Codazzi, Bogotá; a detailed list of images can be found in the Appendix A4). The pictures ranged from the year 1940 to 2000 at roughly 10-year intervals. We searched for available pictures from our plot locations and visually located the plots on the nongeoreferenced images. For each plot, we estimated the minimum age based on the oldest documented continuous occurrence of closed forest. A further analysis of forest cover change during the last seven decades around the study plots, carried out on the same set of aerial pictures, is presented in Calbi et al. (2020).

2.9 | Community composition and structural variables

Based on the available literature (Cleef, 1981; Cortés, 2008; Cuatrecasas, 1958; Sturm & Rangel, 1985; Van der Hammen, 1998), tree layer species were classified either as late successional slow-growing, early successional fast-growing, exotic, or "other" (see Appendix A3 for details). Additionally, understory exotic species cover was calculated. The number of species and the relative proportion of individuals (in case of trees) or the percent cover (in case of the understory) of exotic species were used as indicators of disturbance versus conservation. Variance of tree DBH and height was also computed across all trees within each plot, together with the overall number of tree individuals, stems, stems per tree, and the percentage of large trees (DBH > 30 cm). Mean understory height and cover was calculated, as well as mean epiphytes cover.

The Gini coefficient, a measure of inequality within a distribution widely used in forestry (Bourdier et al., 2016; Latham et al., 1998; Lexerød & Eid, 2006), was calculated in each plot for stem basal areas with the gini function in the R package *reldist* (Handcock, 2016).

2.10 | Taxonomic and phylogenetic diversity

Alpha-diversity indices (Shannon's diversity, Simpson's and Pielou's evenness) were computed for each plot with the R package *vegan* (Oksanen et al., 2013). Phylogenetic community structure was assessed on the basis of a published angiosperm supertree (Phylomatic tree R20120829, available at https://github.

com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new). First, a regional pool tree was generated with the Phylomatic webtool (Webb & Donoghue, 2005), and then, branch lengths were assigned with the *bladj* algorithm in the software Phylocom 4.2 (Webb et al., 2008), using the *wikstrom.ages* file (Wikström et al., 2001). Phylogenetic diversity (PD), mean pairwise distance (MPD), mean nearest taxon distance (MNTD), and their standardized counterparts (sesPD, sesMPD, and sesMNTD) were calculated for both trees and understory in the R package *picante* (Kembel et al., 2010). Moreover, abundance-weighted MPD and MNTD were calculated to account for differences in species abundance (Webb et al., 2011). Four species of the Lycopodiaceae had to be removed from the understory regional pool since the family was not included in the used supertree.

The standardized PD metrics express the difference between observed and average value in units of standard deviation (*SD*). Positive values indicate phylogenetic overdispersion (co-occurring species are more distantly related than expected by chance) and negative values phylogenetic clustering (co-occurring species are more closely related than expected by chance).

2.11 | Aboveground biomass

Aboveground tree biomass was calculated with the R package *biomass*. Field measurements of DBH contained less than 5% missing data, so imputation of missing values was performed with the R package *mice* (van Buuren & Groothuis-Oudshoorn, 2011). To balance the missing data in height measurements, a regional diameter–height model was built in *biomass*. Error propagation was carried out using the AGBmonteCarlo function. Wood density error (errWD) was obtained with the getWoodDensity function as prior values on the uncertainty on wood density values, obtained using the mean sd at the species, genus, and family levels of taxa having at least 10 wood density values in the Global Wood Density database (Réjou-Méchain et al., 2017). Height error (errH) was calculated as the RSE resulting from the local height–diameter models, as in Réjou-Méchain et al. (2017), and diameter measurements propagation error (Dpropag) was set to "*chave2004*," which assigns a standard important error on 5 percent of the measures, and a smaller error on 95 percent of the trees (Réjou-Méchain et al., 2018).

Mean stand aboveground biomass (AGB) and 95% credibility interval following the error propagation were calculated with the following equation (Chave et al., 2014):

$$\mathrm{AGB} = 0.0673 * \left(\mathrm{WD} * H * D^2\right)^{0.976}$$

where AGB = aboveground biomass [kg], WD = wood density [g/cm^3], H = height [m], and D = DBH [cm]. Mean AGB per tree was calculated by dividing the total AGB value of each plot by the number of tree individuals.

2.12 | Data analysis

2.12.1 | Drivers of species composition of tree layer and understory

Presence and abundance of all tree, shrub, and liana species were compiled for each plot. Relative abundance was calculated for tree and understory layer mean cover.

Environmental and disturbance-related variables as well as calculated diversity and biomass metrics were assigned to one of five categories relative to disturbance: *geo-environmental* = predicting, *causes* = predicting, *facilitators* (parameters that increase the likeliness of disturbance) = predicting, *level* (calculated complex parameters of disturbance outcomes) = response, *indicators* (parameters that indicate directly the degree of disturbance) = response (Appendix A2). For instance, signs of grazing or logging were considered a potential *cause* of disturbance, whereas the nearest distance to a road was considered a potential *facilitator*. Diversity indices and biomass estimation were included in the *level* category.

To filter for dominant variables, we first ordinated the plots based on relative species abundances using nonmetric multidimensional scaling (NMDS) in *vegan*, using the mds function with Bray–Curtis distances, and specifying three as maximum number of axes. Subsequently, we fitted all variables using the envfit function and examined variable ordination scores, in order to identify the variables most strongly correlated with community composition and to assess redundancy. Both predictor and response variables were included in the same analyses, and NMDS was performed separately for tree and understory layer. Second, using Sørensen distances and flexible beta (set to −0.25) as group linkage method (McCune & Mefford, 2015), cluster analysis and subsequently indicator species analysis for each cluster were carried out in PCORD 7 (McCune & Mefford, 2015), in order to further classify community types and their characteristic elements.

Following this preliminary analysis, we determined a subset of variables that correlated with the main axes above a given threshold ($R_{sq} > 0.35$; Table 1) and performed either Kruskal–Wallis or parametric ANOVA, depending on the determined conditional distribution, using the clusters as independent variables and the filtered subsets of variables as response variables.

To verify the presence of spatial autocorrelation in our predictors and responses, we calculated a geographical distance matrix between study plots and performed Moran's I test for all calculated variables. We detected spatial autocorrelation for 24 predictors, but none in our response variables (i.e., diversity metrics).

Finally, partial redundancy analysis (pRDA) was performed in *vegan*, separately for tree and understory layer. To take into account spatial autocorrelation, we fitted a pRDA specifying “locality” as condition, to be able to rule out locality effect on the ordination. The “condition” argument thereby defines partial terms that are fitted before other constraints and can be used to remove the effects

TABLE 1 Variables (only predictors retained) correlating with axes above $R_{Sq} > 0.35$ for trees and understory NMDS

	Variable	R_{sq}	*p*
Trees	elev	0.84	0.001
	rel_hum	0.81	0.001
	like_adjacencies	0.72	0.001
	splitting_index	0.71	0.001
	patch_cohesion_index	0.68	0.001
	logg	0.63	0.001
	greatest_patch	0.63	0.001
	largest_patch_index	0.62	0.001
	land_cover	0.61	0.001
	landscape_porportion	0.61	0.001
	overall_core	0.59	0.001
	mean_T	0.54	0.001
	landscape_shannon	0.53	0.001
	effective_meshsize	0.52	0.002
	landscape_division	0.52	0.002
	cult_100	0.49	0.001
	cattle	0.49	0.001
	landscape_simpson	0.45	0.003
	cattle_100	0.42	0.003
	age	0.41	0.004
	cattle_50m	0.39	0.006
	road_dist	0.36	0.001
Understory	elev	0.74	0.001
	fragment	0.62	0.001
	overall_core	0.58	0.001
	nn_distance	0.57	0.001
	road_dist	0.55	0.001
	edge_density	0.55	0.001
	edge_lenght	0.55	0.001
	m_DBH	0.54	0.001
	like_adjacencies	0.53	0.001
	landscape_pielou	0.53	0.001
	people_density_1km	0.49	0.001
	landscape_simpson	0.49	0.001
	mAGBT	0.48	0.001
	people_density_5km	0.45	0.001
	effective_meshsize	0.43	0.001
	landscape_division	0.43	0.001
	landscape_shannon	0.43	0.001
	n_stems	0.43	0.001
	land_cover	0.41	0.002
	landscape_porportion	0.41	0.002
	n_trees	0.40	0.001
	cult_500	0.40	0.001
	mean_H	0.39	0.001
	greatest_patch	0.38	0.003
	largest_patch_index	0.38	0.003
	mean_patch	0.38	0.001
	age	0.36	0.001
	cattle_100	0.36	0.002

of background variables, and their contribution to decomposing inertia (variance) is reported separately (Oksanen et al., 2013). Additionally, we performed Hellinger transformation of our community data as recommended by Legendre and Gallagher (2001). We further selected predictors from the set obtained with the NMDS screening, by checking for correlation ($r > 0.7$), performing Variance Inflation Factor (VIF) analysis (setting the threshold to 10), and then using the *vegan* ordistep function which performs automatic stepwise model building for constrained ordination methods (Oksanen et al., 2013).

2.12.2 | Generalized linear models between main causes and facilitators of disturbance and main response variables

To select meaningful variables to fit our GLMs, we inspected the NMDS and pRDA graph and selected a set of uncorrelated response variables based on the direction of the arrows in the graphs. We then compiled a set of predictor variables that correlated with each selected response and checked for correlation within each set, removing one of the elements in pairs with $r > 0.7$. In parallel, we merged all predictor sets and removed highly correlated and spatially autocorrelated variables. Once a set of consensus predictors was obtained, we conducted a VIF analysis (setting the threshold to 10) and obtained a reduced set of primary and secondary predictors (Table 2). We thus reduced the pool of *geo-environmental* variables to four, that of *causes* to four, and that of *facilitators* to seven. In addition, we selected response variables for *level*, including diversity metrics and *indicators*.

For each selected response, we identified the best conditional distribution and then performed automated selection of the optimal Generalized Linear Model (GLM) with the regsubsets function in the *leaps* package (Lumley & Lumley, 2013), unifying all groups of predictor variables. We specified a maximum number of predictors of four. Predictors were scaled, and a "*log*" link was specified in the *family* argument.

Thus, our GLMs related separately number of species (trees and understory), species diversity (Shannon and Pielou's indices for trees and understory), abundance-weighted phylogenetic diversity and structure (trees sesPD, sesMPDABU, sesMNTDABU; understory sesPD, sesMPDABU, sesMNTDABU), functional diversity (FDiv, FRic, FEve, FDis), and aboveground biomass (AGBplot) as response variables with selected explanatory variables among each group of predictors (*geo-environmental causes* and *facilitators*).

Second, we performed automated selection of the optimal GLMs with AGB, understory number of species, understory Shannon's and Pielou's indices, understory phylogenetic diversity and structure, as response variables and tree diversity indices, *level* and *indicators* of disturbance as sets of secondary predictor variables.

3 | RESULTS

3.1 | Plot-based species inventory of tree and understory layers

3.1.1 | Tree layer

We recorded 9,841 tree individuals belonging to 98 taxa. From these, 89 were identified to species level, six to genus, one to family, and two lianas remained unidentified due to lack of leaves, flowers, or fruits required for identification (see the Appendix A3 for the complete list of species and collected herbarium vouchers). Identified taxa belonged to 64 genera and 41 families. The only conifer recorded in the study area was *Podocarpus oleifolia*, and the only tree fern was *Blechnum schomburgkii*.

Asteraceae (14 species), Melastomataceae, Ericaceae, Primulaceae (with 6 species each), Lauraceae, and Rosaceae (5) were found to be the most diverse families in the study area. *Miconia squamulosa* (1,194 individuals) and *Cavendishia bracteata* (1,130) were the most abundant species across the study area, followed by *Weinmannia tomentosa* (805) and *Daphnopsis caracasana* (522).

3.1.2 | Understory layer

Overall, 326 understory taxa were recorded, with 266 of them identified to species level, 59 to genus, and one to family level (Appendix A3). Identified taxa belonged to 174 genera and 82 families. Orchidaceae (41 species), Asteraceae (38), and Polypodiaceae (16) were the most diverse families, followed by Piperaceae (13), Bromeliaceae (12), Melastomataceae (11), Dryopteridaceae (10), Ericaceae (9), and Rosaceae (9). Dryopteridaceae, Orchidaceae, Poaceae, Blechnaceae, and Bromeliaceae were the most abundant families.

3.2 | Plot-based community ordination (NMDS, cluster analysis and Kruskal–Wallis test/ANOVA)

3.2.1 | Tree layer

For the 3D ordination solution, we obtained a final stress value of 0.1160879 after 206 iterations. Visual interpretation of the NMDS graph led to the identification of three main groups. The subsequent cluster analysis revealed three additional groups, which showed deep divergence in the dendrogram (nodes at less than 50% remaining information), totaling six groups/clusters, which were used for the indicator species analysis (see Appendix A5 for further details on the indicator species analysis results).

The NMDS graph (Appendix A6) showed numerous statistically significant axis correlations of environmental variables including elevation, relative humidity, and mean temperature, while the

TABLE 2 Retained predictors for GLMs building

Predictors		Responses	
Geo-environmental		***Tree layer diversity***	
north	northness	TSR	tree species richness
slope	slope	TPielou	tree Pielou's evenness
mean_prec	mean annual precipitation	Tshann	tree Shannon's diversity
mean_T	mean annual temperature	TsesPD	tree standardized phylogenetic diversity
Causes		TsesMPDABU	abundance-weighted trees standardized mean pairwise distance
cult_50m	cultivated fields in 50 m buffer	TsesMNTDABU	abundance-weighted trees standardized mean nearest taxon distance
cattle	presence of cattle	FDis	Functional Dispersion
logg	logging signs	Feve	Functional Evenness
protected	pretected status	FDiv	Functional Divergence
Facilitators		FRic	Functional Richness
path_dist	distance from closest path	AGBplot	plot above-ground biomass
house_dist	distance from closest house	***Understory diversity***	
track_dist	distance to closest track	HSR	understory species richness
edge	the plot is located at the edge of the fragment	Hpielou	understory Pielou's evenness
age	minimum age of the plot	Hshann	understory Shannon's diversity index
cattle_100	presence of cattle in 100 m buffer	HsesPD	understory standardized phylogenetic diversity
median_patch	median forest patch size in 1 km buffer	HsesMPDABU	abundance-weighted understory standardized mean pairwise distances
Indicators		HsesMNTDABU	abundance-weighted understory standardized mean nearest taxon distances
n_inv_sp_T	number of invasive species of trees		
n_FST_sp_T	number of fast-growing species of trees		
n_FST_ind_T	number of fast-growing species of trees individuals		
%_n_CON_sp_T	% of species of trees associated with conserved forests		
Level			
n_large_trees	number of trees with DBH $>$ 30 cm		
n_stems	number of stems		
n_trees	number of trees		
n_sp > 10DBH	number of species with DBH $>$ 10 cm		
Tree layer diversity			
FDiv	Functional divergence		
FRic	Functional richness		
FDis	Functional dispersion		
FEve	Functional evenness		
Tshann	Trees Shannon diversity index		
TsesMPD	Trees standardized mean pair distance		
TsesMPDABU	Abundance-weighted trees standardized mean pairwise distance		
TMNTDABU	Abundance-weighted trees standardized mean nearest taxon distance		
AGBplot	plot aboveground biomass		

Note: Predictor categories refer to the groups of predictor variables categorized in (Appendix A2).

Kruskal–Wallis test and parametric ANOVA showed that floristic differences among all groups were related to elevation (chi-sq = 25.94, $p = .0009$), mean temperature (chi-sq = 20.99, $p = .0008$), relative humidity (chi-sq = 25.71, $p = .0001$), presence of logging (chi-sq = 17.57, $p = .0035$), presence of cattle (chi-sq = 21.05, $p = .0008$), presence of cattle in a 50 m buffer (chi-sq = 15.90, $p = .0071$), presence of cultivated fields in a 100 m buffer (chi-sq = 23.94, $p = .0002$), Shannon's landscape diversity ($F = 5.58$, $p = .0013$), like adjacencies (chi-sq = 18.37, $p = .0025$), distance to roads (chi-sq = 19.45, $p = .0016$), and minimum age of the fragment (chi-sq = 11.95, $p = .0355$).

The resulting NMDS graphs highlighted some interesting patterns. The NMDS graph of axis 1 versus 2 depicted the variables linked to aboveground biomass (AGB), percentage of late successional species, DBH, height and minimum age on the right hand side, opposite to the variables linked to the number of fast-growing species of trees, mean exotic species cover in the understory, or to the number of trees and the number of stems in the plots (inverse correlation). In the same plot, the AGB showed high positive correlation with distances to roads, lichen cover in the canopy and mosses cover on the soil and inverse correlation with functional diversity, and Gini coefficient. Moreover, trees abundance-weighted mean nearest taxon distance (TMNTDABU) lied opposite to the indicators of fragmentation. A complete table of NMDS variable correlation filtered through species abundance can be found in Appendix A7.

3.2.2 | Understory layer

For the 3D ordination solution, we obtained a final stress value of 0.1514607 after 20 iterations. Visual grouping within the NMDS graph was not feasible (Appendix A8). The cluster analysis identified five main groups/clusters selecting nodes at less than 20% remaining information. Indicator species analysis did not clearly separate the plot localities from each other (Appendix A5).

Kruskal–Wallis test and parametric ANOVA showed that floristic differences among all groups were related to elevation (chi-sq = 24.06, $p = .0001$), distance to roads (chi-sq = 14.23, $p = .0066$), edge density ($F = 4.93$, $p = .004$), presence of cultivated fields in a 100 m buffer (chi-sq = 23.93, $p = .0002$), mean tree AGB (chi-sq = 13.69, $p = .01774$), Shannon's landscape diversity ($F = 3.04$, $p = .0343$), people density in a 5 km buffer (chi-sq = 15.88, $p = .0032$), and presence of cultivated fields in a 500 m buffer (chi-sq = 8.35, $p = .0797$).

In the understory, elevation again was the most correlated environmental variable with species abundances (see Appendix A7 for details on variables correlation with NMDS axis). In the NDMS graph of axis 1 versus 2, the indicators of fragmentation, together with the presence of cattle and cultivated fields in the vicinity, were located opposite to the indicators of continuous forest cover and most of trees diversity metrics. AGB correlated directly with number of late successional species and distance to paths and tracks, and inversely with the number of fast-growing species of trees and exotic understory species. Most of understory diversity metrics pointed toward the lower part of the graphs, together with fragmentation indicators and exotic species cover in the understory, number of trees, stems, and fast-growing species of trees. Understory phylogenetic mean pairwise distances were correlated with AGB.

3.3 | pRDA

3.3.1 | Tree layer

From the set of 25 variables with $R_{sq} > 0.35$ (Table 1), after testing for redundancy, we limited our analysis to a subset of 10 variables: elevation, presence of logging, Shannon's landscape diversity, mean temperature, presence of cattle, presence of cultivated fields in a 100 m buffer, minimum fragment age, distance to roads, and presence of cattle in a 50 m buffer. The ordistep function selected seven of these: elevation, presence of logging, Shannon's landscape diversity, mean temperature, presence of cattle, minimum fragment age, and distance to roads.

The pRDA had an R_{sq} of 0.23 and adjusted R_{sq} of 0.17. The proportional conditional explained variance was 0.45, while the constrained explained variance was 0.24. The unconstrained explained variance was 0.31. Presence of cattle and lower distances to roads were associated with tree layer group 1 which was also positively correlated with Shannon's landscape diversity and negatively with elevation. Group 4 was defined by lower values of Shannon's landscape diversity and was positively correlated with minimum fragment age. Group 5 had some degree of negative correlation with minimum fragment age. Group 6 had an inverse correlation with elevation and minimum fragment age, and was associated with signs of logging, higher Shannon's landscape diversity, and absence of cattle. Groups 2 and 3 were not characterized by any particular association with the ordination variables (Figure 2).

3.3.2 | Understory layer

From the set of 38 variables with $R_{sq} > 0.35$ (Table 1), after the assessment of redundancy, we limited our analysis to a subset of 10: elevation, number of trees, edge density, Shannon's landscape diversity, mean tree aboveground biomass (mAGBT), presence of cultivated fields in a 500 m buffer, minimum fragment age, distance to roads, people density in a 5 km buffer, and fragment size. The ordistep function selected seven of these: elevation, edge density, Shannon's landscape diversity, mAGBT, presence of cultivated fields in a 500 m buffer, distance to roads, and people density in a 5 km buffer.

The pRDA had an R_{sq} of 0.26 and adjusted R_{sq} of 0.11. The proportional conditional explained variance was 0.29, while the constrained explained variance was 0.26. The unconstrained was 0.45.

The results of the pRDA indicated that group 1 was characterized by higher values of Shannon's landscape diversity, lower values for distance from roads, lower elevation, and lower edge density. In

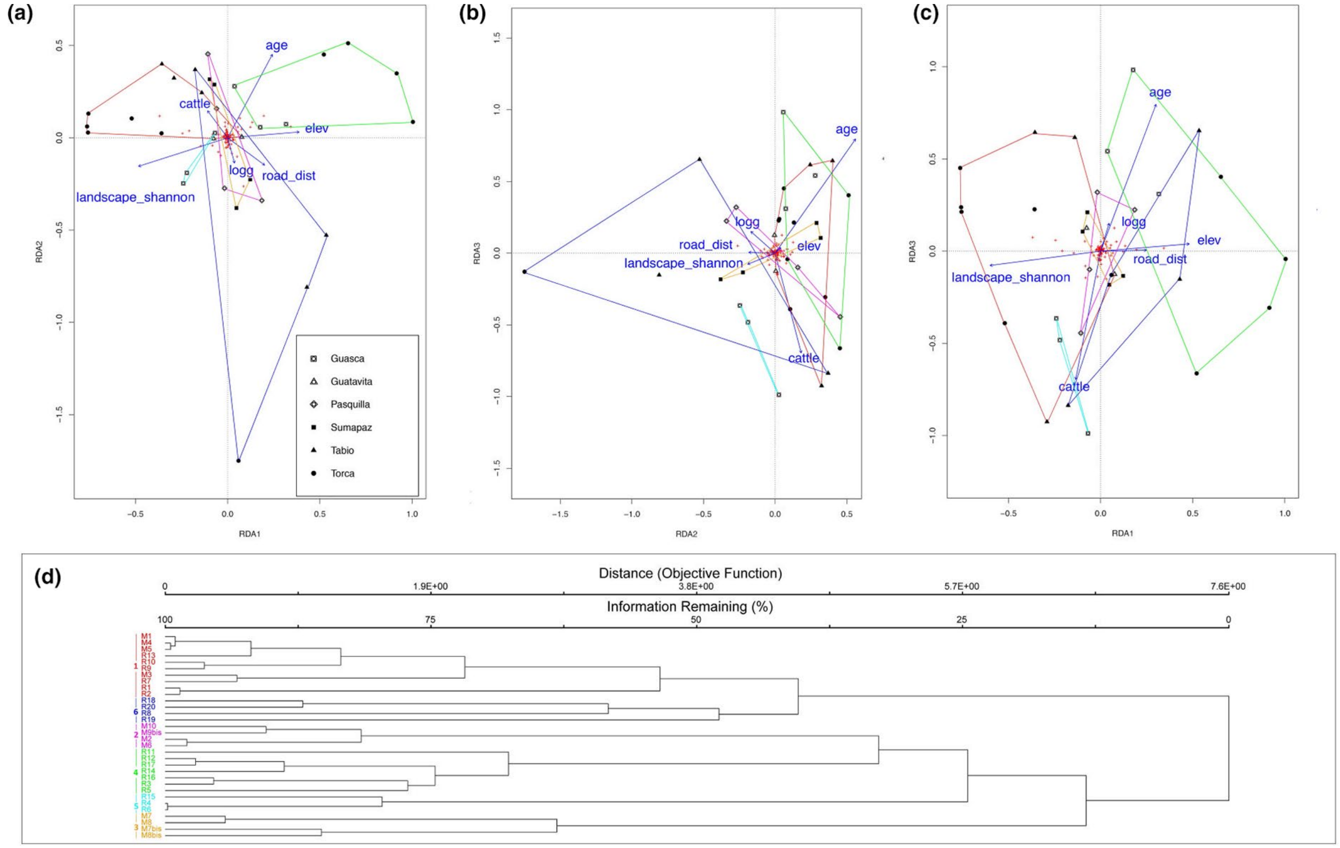

FIGURE 2 pRDA and Cluster analysis convex hulls of the tree layer. RDA graphs with convex hull volumes of tree layer groups for axis 1–2 (a), 2–3 (b), and 1–3 (c). (d) cluster dendrogram of plots species communities. Group 1 had *Myrcianthes leucoxyla*, *Viburnum triphyllum*, and *Miconia elaeoides* as statistically significant indicator species and comprised plots from Torca, Tabio, and Guatavita. Group 2 was characterized by *Monticalia pulchella*, *Macleania rupestris*, and *Ilex kunthiana*, and comprised plots exclusively from Pasquilla. Group 3 had *Gaultheria anastomosans*, *Ageratina glyptophlebia*, *Buquetia glutinosa*, *Ageratina boyacensis*, *Berberis glauca*, and *Vaccinium floribundum* as statistically significant indicator species, and comprised exclusively plots form Sumapaz. Group 4 was characterized by *Myrsine coriacea* and *Clusia multiflora* and included plots from Torca and Guasca. Group 5 included *Cavendishia bracteata*, *Diplostephium rosmarinifolium*, *Gaiadendron punctatum*, and *Ulex europaeus*, and comprised only plots from Guasca. Group 6 had *Varronia cylindrostachia* and *Myrsine guianensis* and included plots from Tabio and from Torca. For detailed IVI values and relative *p*-values refer to the Appendix A5

contrast with that, group 2 was linked with higher values for distance from roads, higher elevation, lower Shannon's landscape diversity, absence of cultivated fields in a 500 m buffer, and lower population density. Group 3 had lower values of mean tree biomass and higher values of population density. Group 5 was associated with lower values of mean tree biomass. Group 4 was not characterized by any particular association with the ordination variables (Figure 3).

3.4 | Generalized linear models

A total of 15 primary predictors, 17 secondary predictors, and 17 responses were retained for GLM building (Table 2). Significant variables in GLMs with either a good fit (McFadden $R_{sq} > 0.2$) or a high Nagelkerke value (variance explained > 0.50) are reported below (Tables 3, 4 and 5). A complete table of all fitted GLMs is provided in Table S1. None of the variables associated with epiphytes cover was retained through the variable selection process and analysis.

Tree layer Shannon's diversity decreased with slope. Understory Shannon's diversity increased with distance to tracks, mean precipitation, and tree layer functional richness (FRic), but decreased with minimum age and functional dispersion (FDis). Understory abundance-weighted phylogenetic mean pairwise distances (HsesMPDABU) increased with functional divergence (FDiv) and tree layer abundance-weighted phylogenetic mean pairwise distances (TsesMPDABU) and decreased with FRic. Aboveground biomass (AGB) increased with increasing minimum age of the plot and presence of cattle within the plot, and decreased with slope and proximity of cultivated fields. AGB also increased with the number of trees and large trees and with the proportion of late successional species of tree.

3.4.1 | Other general trends (from models without a good fit)

Among environmental predictors, slope had a negative effect on FDis, FRic, HsesMPDABU, tree layer species richness (TSR), tree layer Pielou's

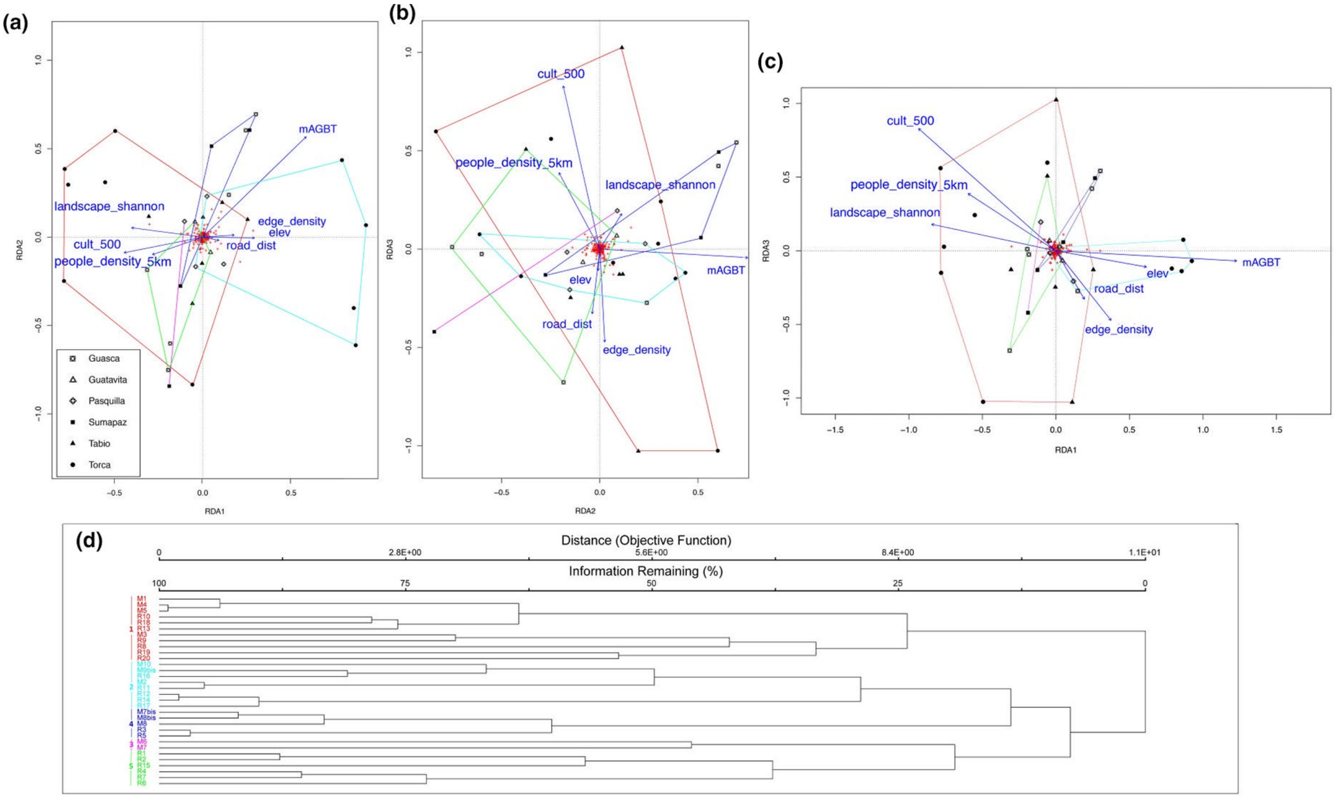

FIGURE 3 pRDA and Cluster analysis convex hulls of the understory. RDA graphs with convex hull volumes of understory groups for axis 1–2 (a), 2–3 (b), and 1–3 (c). (d) cluster dendrogram of plots species communities. The first group had *Oreopanax incisus* and *Passiflora bogotensis* as indicator species (Appendix A5) and included plots from Torca and Tabio. The second group had *Elaphoglossum lingua* as indicator species, including plots form Pasquilla, Guasca, and Torca. The third group had *Monnina aestuans*, *Peperomia rotundata*, and *Nertera granadensis* among higher valued indicator species. It included only two plots, one from Sumapaz and one from Pasquilla. The fourth group had *Greigia stenolepis* and *Rubus acanthophyllos* among indicator species and comprised plots from Sumapaz and Guasca. The last group had *Ageratina asclepiadea* as indicator species and comprised plots from Guatavita, Guasca, and Tabio. For detailed IVI values and relative *p*-values refer to the Appendix A5

evenness (Tpielou), tree layer abundance-weighted mean phylogenetic nearest neighbor distance (TsesMNTDABU). Mean temperature had a negative effect on understory phylogenetic diversity (HsesPD) and Tpielou. Northness had a positive effect on TSR. Among the *causes* predictors, logging had negative effect on functional evenness (FEve) and TSR, and a positive effect on understory layer Pielou's evenness (Hpielou). The presence of cultivated fields in the immediate surrounding of plots (50 m) had a negative effect on HSR and TsesMNTDABU and a positive effect on understory abundance-weighted mean phylogenetic nearest neighbor distance (HsesMNTDABU). Protection status had a negative effect on HsesMNTDABU and tree layer phylogenetic diversity (TsesPD). As to the *facilitators*, the edge effect was linked with higher values of FDis and HsesMPDABU, and lower values of HsesMNTDABU, HsesPD, FDiv, and FRic. Increasing distance from houses had a negative effect on TSR, while increasing distance from tracks had negative effect on HsesPD. The presence of cattle in a 100 m buffer was linked to higher values of HsesMNTDABU, and lower values of tree layer abundance-weighted mean phylogenetic pairwise distance (TsesMPDABU) and TsesMNTDABU. Median patch size had negative effect on HSR. Increasing minimum fragment age had a negative effect on HPielou. Coming to the secondary predictors, the number of species with DBH > 10 cm and the number of trees had positive effect on HsesMNTDABU. The number of fast-growing trees species individuals had a positive effect on HsesMNTDABU and HsesPD. The number of stems had a positive effect on Hpielou. FDiv had a positive effect on HSR. FRic had negative effect on HsesMNTDABU and positive on HsesPD. FDis had a negative effect on HsesPD. Finally, TsesMPDABU had positive effect on HsesPD and TsesMPD had positive effect on Hpielou.

4 | DISCUSSION

Pressure of urbanization on natural environments and its consequences has been the subject of numerous studies. However, high Andean forests (*bosques altoandinos*) have rarely been investigated in this context. Our study is the first to analyze the role of multiple factors in shaping environmental impact on these forests through urbanization and associated factors in the metropolitan area of Bogotá. However, we are aware of the limitations of this research, which is of rather explorative character and based on data from an area of in total 1.28 ha only. Our sampling design reflects the hurdles

TABLE 3 GLMs of predictors versus responses, showing only GLMs with a good fit

			Coefficients				Pseudo R^2	
Response	Best model	Variable	Estimate	*SE*	*t* value	*p* value (>|t|)	McFadden	Nagelkerke
Tshann	Tshann ~ slope+mean_T + house_dist+cult_50m	(Intercept)	0.70361	0.02540	27.699	**<2e−16**	**0.752990**	**0.814632**
		slope	−0.08664	0.02698	−3.211	**.0034**		
		mean_T	−0.02686	0.02873	−0.935	.3580		
		house_dist	−0.04705	0.02583	−1.822	.0796		
		cult_50m	−0.04004	0.02870	−1.395	.1744		
Hshann	Hshann ~ track_dist+mean_prec + age+house_dist	(Intercept)	0.89579	0.02215	40.441	**<2e−16**	**0.669964**	**0.759986**
		track_dist	0.06937	0.02916	2.379	**.024680**		
		mean_prec	0.08776	0.02867	3.061	**.004944**		
		age	−0.10445	0.02380	−4.389	**.000157**		
		house_dist	−0.03438	0.02257	−1.523	.139413		
AGB	AGBplot ~ slope+age + cattle+cult_50m	(Intercept)	1.7145	0.07224	23.734	**<2e−16**	0.150415	**0.525516**
		slope	−0.17248	0.07773	−2.219	.035092		
		age	0.31665	0.07803	4.058	**.000379**		
		cattle	0.23182	0.09783	2.370	**.025207**		
		cult_50m	−0.23070	0.09631	−2.395	**.023807**		

Note: Predictor categories refer to the groups of predictor variables categorized in the Appendix A2.

TABLE 4 GLMs of secondary predictors versus responses, showing only GLMs with a good fit

			Coefficients				Pseudo R^2	
Response	Best model	Variable	Estimate	*SE*	*t* value	*p* value (>|t|)	McFadden	Nagelkerke
Hshann	Hshann ~ FDis+FRic + n_stems+n_inv_sp_T	(Intercept)	0.89802	0.02507	35.825	**<2e−16**	**0.370602**	0.474078
		FDis	−0.07597	0.03485	−2.180	**.0382**		
		FRic	0.07827	0.03082	2.540	**.0172**		
		n_stems	0.03100	0.02455	1.262	.2176		
		n_inv_sp_T	−0.04740	0.02916	−1.626	.1156		
HsesMPDABU	HsesMPDABU ~ FDiv+FRic + n_sp.10DBH + TsesMPDABU	(Intercept)	0.82655	0.07123	11.605	**5.32e−12**	**0.261149**	**0.581732**
		FDiv	0.24527	0.08248	2.974	**.00613**		
		FRic	−0.26250	0.08501	−3.088	**.00463**		
		n_sp.10DBH	0.12922	0.07900	1.636	.11351		
		TsesMPDABU	0.15706	0.05962	2.634	**.01380**		
AGB	AGBplot ~ TsesMPD+n_large_trees + n_trees+%n_CON_sp_T	(Intercept)	1.7140	0.07467	22.955	**<2e−16**	0.151863	**0.528924**
		TsesMPD	−0.06882	0.11824	−0.582	.56535		
		n_large_trees	0.36350	0.11200	3.246	**.00312**		
		n_trees	0.22454	0.10409	2.157	**.04005**		
		%n_CON_sp_T	0.29929	0.11420	2.621	**.01423**		

Note: Predictor categories refer to the groups of predictor variables categorized in the Appendix A2.

TABLE 5 GLMs variables relationships: + indicates a positive relationship and − indicates a negative relationship. Higlighted cells represent GLMs with a good fit

	TSR	Tshann	Tpielou	TsesPD	TsesMPDABU	TsesMNTDABU	HSR	Hshann	Hpielou	HsesPD	HsesMNTDABU	HsesMPDABU	FDis	FDiv	FEve	FRic	AGB
mean_T			−							−							−
mean_prec								+									
north	+																
slope	−	−	−			−						−	−			−	−
logg	−								+						−		
cattle																	+
cult_50m						−	−				+						−
protected				−							−						
edge										−	−	+	+	−		−	
house_dist	−																
cattle_100					−	−					+						
median_patch							−										
age								−	−								+
track_dist								+		−							
n.sp_10DBH											+						
n_trees											+						+
n_large_trees																	+
%n_CON_sp_T																	+
n_FST_ind_T										+	+						
n_stems									+								
FDiv							+					+					
FRic								+		+	−	−					
FDis								−		−							
TsesMPDABU										+		+					
TsesMPD									+								

of working in a mixed urban–rural matrix, mostly privately owned. Also, having a limited number of plots, we decided to put a stronger emphasis on the variables filtering, to drastically reduce the number of tested hypotheses. Nevertheless, the studied forest fragments belong to several of the localities harboring the highest forest cover within the Capital District and we find the types of high Andean forests covered here to be representative for the hinterland of Bogotá.

Using the composition of natural vegetation as a benchmark, our study plots were dominated by Melastomataceae, Ericaceae, and Asteraceae in the tree layer, which is in accordance with previous work (Cuatrecasas, 1934, 1958; Franco et al., 2010; Torres & Marina, 2016). Bromeliaceae and Orchidaceae were the most diverse families in the understory, coinciding with reports by Cuatrecasas (1934, 1958) and Rangel et al. (2008). Notably, with the exception of Rangel et al. (2008), no recent inventories of the understory were undertaken in the target area prior to this study. The fact that many epiphytic species were found terrestrial in the understory may be due to certain favorable environmental conditions, such as low incidence of light, high humidity, and lower influence of wind than in the canopy (Krömer et al., 2007).

Overall tree species richness of the total area assessed (98) was similar to the 90 taxa reported by Rodríguez-Alarcón et al. (2018) for an ecologically similar study area near Bogotá. Van der Hammen (1998) reported 50–60 species for 500 m^2 plots of high Andean forest in the watershed of the Rio Bogotá, 20–30 of which belonged to trees and shrubs. Our own tree species count ranged between 10 and 24, with an average of 16, per 400 m^2 plot, and Shannon's tree diversity varied between 1.05 and 2.6. Overall, these figures also compare well to those reported for high Andean forest ecosystems (2,300–2,900 m) in Southern Ecuador by Cabrera et al. (2019), who used a higher DBH threshold (10 cm) and obtained about 21 tree species and an average value of 2.44 for Shannon's diversity.

Thus far, only few published studies exist for the target area that aimed at characterizing the various communities of *bosques altoandinos* in terms of species composition. Using a phytosociological approach, Cortés et al. (1999) and Cortés (2008) described the *Myrcianthes leucoxyla-Miconia squamulosa* community for the internal slopes of the Rio Bogotá watershed, characterized by scarce humidity and low precipitation, with high abundance of *Oreopanax incisus* and conspicuous lianas in the understory. This community corresponds to our tree clusters 1 and 6 and understory clusters 1 and 5. The pRDA further revealed a lower elevation, higher Shannon's landscape diversity, lower minimum fragment age, presence of logging and lower distance to roads as characteristic for this community, supporting the notion that it represents secondary forest, probably developing on patches of abandoned agricultural areas on the slopes surrounding cultivated and farmed plains (Cortés, 2008). Understory cluster 5 was generally found at medium elevations, on small high plains, with a drier climate (Cortés, 2008; Cortés et al., 1999), and in forest patches with generally low values of aboveground biomass.

The *Drimys granadensis-Weinmannia tomentosa* community is a second *bosque altoandino* subtype (Vargas & Zuluaga, 1980), corresponding to our tree clusters 2 and 4. Cluster 2 is similar to the *Criotoniopsis bogotana-Weinmannia tomentosa* forest subtypes described for elevations between 3,100 and 3,300 m (Cortés, 2008), whereas cluster 4 is found at the slopes and peaks of the watershed of the Río Bogotá between 2,700 and 3,200 m (Cortés, 2008). According to Cortés (2008) and Luteyn (2002), the presence of *Macleania rupestris* in the lower canopy of these communities points toward recent human intervention. This association is known to prefer humid, cold climates and steep grounds; according to our field observations, it is also associated with high lichen and moss cover in the canopy, which prosper in such a relatively high humidity (Batke et al., 2015; Munzi et al., 2014; Wolf, 1993). As shown in the pRDA ordination, it is also linked to low Shannon's landscape diversity, and higher minimum fragment age, probably representing secondary forest fragments approaching the structure of natural forest communities.

Our tree clusters 3 and 5 did not correspond to previously described communities. Cluster 3 was restricted to *bosques altoandinos* near Sumapaz, the largest known paramo on Earth. Characteristic elements of this cluster are families of high elevations such as Asteraceae and Ericaceae (Bach et al., 2007; Cuatrecasas, 1958; Sturm & Rangel, 1985), also typically found in areas subjected to fires or selective logging (Cuatrecasas, 1958). The latter notion is supported by the observed presence of both cattle and cultivated fields in the immediate surrounding, by a high Shannon's landscape diversity, and by the presence of logging, indicating recent and ongoing intervention in the area. Nonetheless, full-grown individuals of *Weinmannia fagaroides* and *Polylepis quadrijuga* were found in two of the plots of this cluster, together with some young individuals of *Podocarpus oleifolia* and *Berberis glauca* abundant in the lower canopy, and a dense cover of mosses and ferns, which suggests that some small "islands" of mature forest elements were able to persist within the disturbed, secondary forest matrix. Understory cluster 3 did not fit any previously described communities either, but the indicator species of this cluster are known to be either dispersed by birds, for example, *Monnina aestuans* (Romero, 2002) and *Nertera granadensis* (Vargas-Ríos, 1997), or by small mammals or birds, for example, in the case of the sticky fruits of *Peperomia* (Frenzke et al., 2016). Possibly, this cluster represents a successional understory community mainly dispersed by animals, which prosper in previously disturbed areas, as suggested by the high people density within 5 km radius and relatively low mean tree biomass. Tree cluster 5 was found in the Guasca region only and exhibits features of a disturbed, gap-filled forest (azonal *páramo*) including the presence of invasive *Ulex europaeus*, which is confirmed by the pRDA correlation with lower minimum fragment age values. Another common species, *Cavendishia bracteata*, has been associated with secondary growth (Cortés, 2008). This cluster had rather low like adjacencies values and average Shannon's landscape diversity and distances to roads, which point to a somehow continued disturbance regime in the past. Indeed, this area, up to the 1990s, used to be an open-pit limestone mine (Pèrez Sanz de Santamaría, 2013).

Notably, tree and understory communities found in the same plots did not always correspond to the same community's type, which suggests that different types of intervention act differentially on the tree and understory layers. For instance, cattle grazing, erosion, and expansion of edge species will affect the understory at a different pace than the tree layer (Halpern & Lutz, 2013; Millspaugh & Thompson, 2011; Thrippleton et al., 2016).

Our findings support the notion that *bosques altoandinos* in the vicinity of Bogotá are floristically and structurally not homogeneous, resulting in overall high species diversity, especially in the understory, with each of the study sites and plots contributing a portion to this diversity (i.e., high beta diversity). The observed differences in species composition between the study sites, and the high proportion of pRDA-explained variance that was linked to the “locality” condition, may be determined by topographic variation, which promotes changes in structure, composition, and dynamics of the vegetation, even at small scales in high Andean ecosystems (Homeier et al., 2010; López & Duque, 2010). Our results are similar to a recent study that found substantial differences in species composition between municipalities in the region (Hurtado-Martilletti et al., 2020), pointing toward the importance of landscape and habitat heterogeneity as a relevant criterion when assessing the impact of urbanization, since each locality may contribute unique elements of diversity not present at other localities, even within close distances. Following up on our first research question, taken aside the effects of local homogenization processes, our data show that plant communities in *bosques altoandinos* are mainly driven by a limited suite of geo-environmental and disturbance factors, namely: elevation, mean temperature and relative humidity on one hand, and by the presence of cultivated fields and cattle in the immediate sourroundings of the plots, population density, Shannon's landscape diversity, and forest edge density on the other.

The compositionally based clustering of tree and understory communities was largely correlated with both geo-environmental and disturbance variables, namely, elevation, people density, Shannon's landscape diversity and distance to roads. Mean temperature, relative humidity, logging, and minimum plot age were important factors driving tree species composition, but not the composition of understory species. For the latter, additional variables associated with edge effects, such as the proximity to cultivated fields, edge density, and distance from main roads were relevant. Additionally, mean tree aboveground biomass was a determinant factor in shaping the understory community. These results support the notion of a higher sensitivity of the understory to fragmentation and habitat heterogeneity (Forman & Alexander, 1998; Tyser & Worley, 1992).

Our results show effects of both geo-environmental parameters and disturbance-related variables as predictors of both community structure and diversity. Among the geo-environmental parameters, the negative effects of the increase in slope on tree and understory diversity and aboveground biomass were evident. Slope is related to soil erosion, water drainage, and other unfavorable growth conditions which may act as environmental filters, reducing the number of taxa that can cope with them effectively and may also limit aboveground productivity. Higher mean temperatures were linked to lower tree Pielou's evenness and Understory phylogenetic diversity. This fact could be linked to the higher density of human activities at milder temperatures/lower parts of our study area, which are associated with highly disturbed forest communities, mostly dominated by species as *Miconia squamulosa* or *Cavendishia bracteata*, and host poorer understory communities. Higher precipitation values were linked to higher understory Shannon's diversity, possibly due to increased soil nutrients and moisture and thus by the absence of an environmental filter related to water availability.

With regard to human disturbance predictors, many of the previously identified relevant variables in literature were also selected through our multi-step analysis, such as minimum age of the forest fragment, distance to houses, edge effect, and presence or proximity of cattle and cultivated fields. People density, on the other hand, showed to be too spatially autocorrelated to be used in our GLMs. Also, among all calculated forest fragmentation metrics, the only one which was selected was (median) forest patch size, already reported to be relevant for plant diversity as an indirect measure of habitat loss in the review of Fahrig (2003). As to the selected responses, tree layer diversity metrics were not particularly sensitive, retrieving only one GLM with a good fit. The correlation between higher distance from houses and forest protection status with lower tree species richness and low phylogenetic diversity was not immediately intuitive, but could be a sign of the deliberate introduction of useful tree species in the vicinity of rural houses, to be harvested for wood or other uses, or of the lack of edge-related tree species in the interior of protected forest fragments. However, the presence of cattle and cultivated fields in the immediate proximity of plots leading to tree phylogenetic clustering, but on the other hand to understory phylogenetic dispersion, illustrates the disrupting, multi-layer impact of landscape-level patchiness and human activities.

Disturbed forests tend to exhibit functional and phylogenetical clustering due to the elimination of entire lineages sensible to disturbance, an effect known as environmental filtering (Chun & Lee, 2018; Gerhold et al., 2015; Kusuma et al., 2018; Mouchet et al., 2010; Ribeiro et al., 2016). Phylogenetic dispersion is expected to be higher in undisturbed, more mature forests than in early successional forests, due to competitive exclusion (Ding et al., 2012; Letcher, 2009; Norden et al., 2012; Purschke et al., 2013). In our study, local, chronic disturbances, such as proximity to farming activities or the presence of cattle in the immediate surroundings, had indeed a negative effect on tree phylogenetic diversity and resulted in phylogenetic clustering, supporting findings by Ribeiro et al. (2015, 2016). Likely, the floristic drift associated with this type of disturbance results in the co-occurrence of more closely related taxa by decreasing effects of competitive exclusion. On the other hand, the observed increase of phylogenetic dispersion in the understory in close proximity of cattle or cultivated fields may be the result of opportunistic pioneer or exotic species, which introduce different lineages from those associated with more mature forest fragments (Hill & Curran, 2001; Kupfer et al., 2004).

Identified understory diversity metrics with the highest sensitivity to human disturbance were Shannon's diversity and phylogenetic clustering. As suggested by Forman and Alexander (1998) and Tyser and Worley (1992), the number and diversity of understory species were positively related to disturbance-related variables. Proximity to human activities such as farming and the more recent establishment of forest patches (lower minimum age) fosters generalists or fast-growing, nutrient-, and light-demanding species (Marcantonio et al., 2013). However, at the same time the edge effect promotes less phylogenetic diversity of the understory vegetation, which is in accordance with Ribeiro et al. (2016). This could be explained, in our case, by the fact that ferns and other early diverging taxa diversity tends to diminish toward the edge of a forest fragment to leave place to generalists and agricultural weeds, which can cope better with the site conditions. Larger median forest fragments size also resulted in less understory species, suggesting that recruitment of edge-related species increment the number of species in smaller forest patches.

The observation that increasing tree functional divergence, and tree phylogenetic dispersion were linked to higher understory phylogenetic dispersion, may indicate that higher trait diversity in the upper stratum allows for more species to colonize the understory. This is partially supported through similar findings by Ampoorter et al. (2014) and Evy et al. (2016), who reported that a multi-tree species mixture may induce a higher number of understory species, for instance, by modifying environmental conditions relevant to herbaceous plants and seedlings (Vockenhuber et al., 2011). At the same time, functional richness and functional dispersion showed contrasting effects on understory metrics, underlining the multifaceted effect of the multidimensional functional diversity indices. Moreover, the number of trees, large trees, fast-growing tree individuals, and stems were related to higher understory phylogenetic diversity and dispersion, and to understory Pielou's evenness, confirming that intrastand heterogeneity allows for different understory taxa to thrive due to differences in nutrients, light and water availability (Huebner et al., 1995).

Averaging 149 Mg/ha, the obtained values for aboveground biomass are within the figures reported from other high Andean forest fragments, ranging between 130 and 165 Mg/ha and in some cases up to 640 Mg/ha (Álvarez-Dávila et al., 2017; Girardin et al., 2014; Rodríguez-Alarcón et al., 2018). The relatively low mean values obtained here are probably explained by the inclusion of areas characterized by early regeneration stages in several plots. However, our results are higher than those of Moser et al. (2011), who reported 112 Mg/ha for forest plots within a similar elevation range. In regard to our models, AGB seemed to decrease at higher values of slope, which in our study area may relate to eroded soils and drier conditions, supporting a trend that has been reported for relatively moist forests in the Americas (Keith et al., 2009; Stegen et al., 2011), which is perhaps related to the lower soil water content available to sustain photosynthesis (Parton et al., 2012; Stegen et al., 2011), but that can also be a secondary effect of the different rate of agricultural exploitation or forest clearing history between lower and drier and higher and wetter soils in the study area in recent times (Etter et al., 2008; Etter & van Wyngaarden, 2000). Notably, low AGB was linked to the proximity of cultivated fields, suggesting a clear correlation between intervention causing patchy landscapes and lower biomass accumulation. However, the presence of cattle within the plot was linked to higher AGB values. This may be particular to our study area, in which we observed forest fragments with large trees but a much depauperate understory, located in proximity to farms. This is alarming as grazing may interfere with tree species recruitment and stamping may lead to higher soil erosion which in turn will reduce productivity over time in these last standing carbon stock fragments (Nepstad et al., 2002).

The positive correlation that AGB exhibits with the minimum fragment age, and number of trees and large trees, summed to a positive correlation with the percentage of late successional tree species, suggests that AGB is positively influenced by the abundance of slow-growing species that stock large amount of carbon (Aldana et al., 2017; Álvarez-Dávila et al., 2017). This finding relates to the question of biomass storage in forest plantations or tree monocultures. Conversely, the increment of environmental stressors in highly fragmented landscapes can increase the mortality of large trees (D'Angelo et al., 2004; Laurance et al., 2000). This promotes the uncontrolled growth of fast-growing species with lower wood density, which reduces AGB (Berenguer et al., 2014; Chaplin-Kramer et al., 2015; Laurance & Bierregaard, 1997; de Paula et al., 2011).

In conclusion, the increase of disturbance resulted overall in a negative effect on tree phylogenetic diversity and dispersion. Notably, disturbance affected aboveground biomass negatively. As to the understory, disturbance was associated with more diversity and more phylogenetic dispersion. The *causes* and the *facilitators* category variables were quite efficient in predicting diversity or AGB, among which edge effect, proximity of cattle and cultivated fields, and minimum fragment age appear to be the most important ones.

The plurality of diversity metrics can be difficult to interpret in the light of human disturbance. However, AGB proved to be sensitive to human disturbance and was closely related with the proportion of late successional species. Such indicators could serve as immediate proxies of human disturbance, rather than diversity measures themselves, which have also been shown to react ambiguously to the effects of fragmentation (Fahrig, 2003).

5 | CONCLUSIONS

In summary, our study on taxonomic, phylogenetic, functional diversity and ABG of high Andean forest underscores the complexity and singularity of interactions between disturbance drivers and plant communities. The main goal of our approach was to test and quantify the alteration of high Andean forest composition, structure, and functioning through human disturbance, testing the effectiveness of known relevant drivers and indicators when a large number of variables are considered simultaneously. We contributed to the characterization of high Andean patterns of tree and understory diversity and local and regional human disturbance, which is usually considered to have a negative effect on native biodiversity and carbon storage. In our case, this fact was confirmed by lower tree layer diversity and a lower ABG in relation to increasing human disturbance, but was however not always apparent through the score of all the diversity metrics that we employed. Decline of AGB and disappearance of the forest ecosystem's late successional species is a warning signal that should impulse protection efforts and restoration measures. Yet, it is also true that the study area has now undergone anthropic disturbance over centuries, with continuous agropastoral activities and subsequent land cover change. In the context of the recovery of forest cover and ecosystem services, then our findings could be interpreted as a positive sign of resilience at a regional scale. Relatively small isolated fragments of high Andean forests can still host high plant diversity and serve as stepping stones or temporary refuges for the local fauna within the rural modified matrix. In this sense, efforts to implement forest connectivity and corridors and to guarantee land-use continuity even in partially forested areas are priorities that should be taken into account by local decision-makers. Successful conservation strategies require a sound understanding of community and ecosystem dynamics, and we hope that with the predictors and indicators of disturbance that we pointed out, it will be possible to improve the management strategies for the passive or active restoration and protection of the remaining forest fragments in the study area.

Our results contribute to urgently needed but yet missing baseline knowledge on main drivers of disturbance and its effects on the biodiversity in the study area. However, we strongly recommend that future studies should expand further the established plot network and that more investigations test our results on similar ecosystems to further disentangle the relationship between natural and human-induced causes of diversity loss and their underlying mechanisms. As shown here, a first approximation can be achieved through an exploratory approach like the one that we employed.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

Mariasole Calbi: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); writing–original draft (lead); writing–review and editing (lead). **Francisco Fajardo-Gutiérrez:** Data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); writing–original draft (supporting); writing–review and editing (supporting). **Juan Manuel Posada:** Conceptualization (equal); data curation (equal); investigation (supporting); methodology (lead); project administration (equal); resources (equal); visualization (equal); writing–original draft (supporting); writing–review and editing (supporting). **Robert Lücking:** Conceptualization (equal); data curation (supporting); formal analysis (equal); investigation (equal); methodology (lead); supervision (equal); writing–original draft (equal); writing–review and editing (equal). **Grischa Brokamp:** Funding acquisition (equal); methodology (supporting); project administration (lead); resources (equal); supervision (equal); writing–original draft (equal); writing–review and editing (supporting). **Thomas Borsch:** Conceptualization (supporting); funding acquisition (lead); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (lead); writing–original draft (equal); writing–review and editing (supporting).

DATA AVAILABILITY STATEMENT

The tree layer and understory sampling datasets and the complete table of variables have been submitted to the Dryad digital repository (https://doi.org/10.5061/dryad.z612jm6b5).

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REFERENCES

Acuña, C. A. (2013). *Potencial de regeneración de rastrojos y bosques secundarios en la sabana de Bogotá*. Master's degree Thesis. Pontificia Universidad Javeriana.

Aldana, A. M., Villanueva, B., Cano, Á., Correa, D. F., Umaña, M. N., Casas, L. F., Cárdenas, S., Henao-Diaz, L. F., & Stevenson, P. R. (2017). Drivers of biomass stocks in Northwestern South American forests: Contributing new information on the Neotropics. *Forest Ecology and Management*, *389*, 86–95. https://doi.org/10.1016/j.foreco.2016.12.023

Álvarez-Dávila, E., Cayuela, L., González-Caro, S., Aldana, A. M., Stevenson, P. R., Phillips, O., Cogollo, Á., Peñuela, M. C., von Hildebrand, P., Jiménez, E., Melo, O., Londoño-Vega, A. C., Mendoza, I., Velásquez, O., Fernández, F., Serna, M., Velázquez-Rua, C., Benítez, D., & Rey-Benayas, J. M. (2017). Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. *PLoS One*, *12*(3), e0171072. https://doi.org/10.1371/journal.pone.0171072

Ampoorter, E., Baeten, L., Koricheva, J., Vanhellemont, M., & Verheyen, K. (2014). Do diverse overstoreys induce diverse understoreys? Lessons learnt from an experimental–observational platform in Finland. *Forest Ecology and Management*, *318*, 206–215. https://doi.org/10.1016/j.foreco.2014.01.030

Anselm, N., Brokamp, G., & Schütt, B. (2018). Assessment of land cover change in peri-urban high andean environments South of Bogotá, Colombia. *Land*, *7*(2), 75. https://doi.org/10.3390/land7020075

Anselm, N., Rojas, O., Brokamp, G., & Schütt, B. (2020). Spatiotemporal variability of precipitation and its statistical relations to ENSO in the high Andean Rio Bogotá watershed, Colombia. *Earth Interactions*, *24*(3), 1–17. https://doi.org/10.1175/EI-D-19-0019.1

Armenteras, D., Gast, F., & Villareal, H. (2003). Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation*, *113*(2), 245–256. https://doi.org/10.1016/S0006-3207(02)00359-2

Avella, A., Torres, S., Gómez, W., & Pardo, M. (2014). Los páramos y bosques altoandinos del pantano de Monquentiva o pantano de Martos (Guatavita, Cundinamarca, Colombia): Caracterización ecológica y estado de conservación. *Biota Colombiana*, *15*(1), 3–39.

Bach, K., Kessler, M., & Gradstein, S. (2007). A simulation approach to determine statistical significance of species turnover peaks in a species-rich tropical cloud forest. *Diversity and Distributions*, *13*(6), 863–870. https://doi.org/10.1111/j.1472-4642.2007.00357.x

Batke, S. P., Murphy, B. R., Hill, N., & Kelly, D. L. (2015). Can air humidity and temperature regimes within cloud forest canopies be predicted from bryophyte and lichen cover? *Ecological Indicators*, *56*, 1–5. https://doi.org/10.1016/j.ecolind.2015.03.022

Battles, J. J., Shlisky, A. J., Barrett, R. H., Heald, R. C., & Allen-Diaz, B. H. (2001). The effects of forest management on plant species diversity in a Sierran conifer forest. *Forest Ecology and Management*, *146*(1–3), 211–222. https://doi.org/10.1016/S0378-1127(00)00463-1

Berenguer, E., Ferreira, J., Gardner, T. A., Aragão, L. E. O. C., De Camargo, P. B., Cerri, C. E., Durigan, M., Oliveira, R. C. D., Vieira, I. C. G., & Barlow, J. (2014). A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, *20*(12), 3713–3726. https://doi.org/10.1111/gcb.12627

Bourdier, T., Cordonnier, T., Kunstler, G., Piedallu, C., Lagarrigues, G., & Courbaud, B. (2016). Tree size inequality reduces forest productivity: An analysis combining inventory data for ten European species and a light competition model. *PLoS One*, *11*(3), e0151852. https://doi.org/10.1371/journal.pone.0151852

Bovendorp, R. S., Brum, F. T., McCleery, R. A., Baiser, B., Loyola, R., Cianciaruso, M. V., & Galetti, M. (2019). Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. *Ecography*, *42*(1), 23–35. https://doi.org/10.1111/ecog.03504

Brown, A. D., & Kappelle, M. (2001). *Introducción a los bosques nublados del neotrópico: Una síntesis regional* (pp. 25–40). Bosques Nublados del Neotrópico Editorial INBio.

Buuren S. V., Groothuis-Oudshoorn K. (2011). mice: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software*, *45*(3), 1–67. http://dx.doi.org/10.18637/jss.v045.i03

Cabrera, O., Benítez, Á., Cumbicus, N., Naranjo, C., Ramón, P., Tinitana, F., & Escudero, A. (2019). Geomorphology and altitude effects on the diversity and structure of the vanishing montane forest of southern ecuador. *Diversity*, *11*(3), 32. https://doi.org/10.3390/d11030032

Calbi, M., Clerici, N., Borsch, T., & Brokamp, G. (2020). Reconstructing long term high Andean forest dynamics using historical aerial imagery: A case study in Colombia. *Forests*, *11*(8), 788. https://doi.org/10.3390/f11080788

Cantillo Higuera, E. E., & Gracia, C. M. (2013). Diversidad y caracterización florística de la vegetación natural en tres sitios de los cerros orientales de Bogotá D. C. *Colombia Forestal*, *16*(2), 228.

Cavelier, J., Lizcaino, D., & Pulido, M. (2001). *Bosques nublados del neotrópico: Colombia*. (p. 700). Bosques nublados del neotrópico Instituto Nacional de Biodiversidad Santo Domingo de Heredia.

Chaplin-Kramer, R., Sharp, R. P., Mandle, L., Sim, S., Johnson, J., Butnar, I., Milà i Canals, L., Eichelberger, B. A., Ramler, I., Mueller, C., McLachlan, N., Yousefi, A., King, H., & Kareiva, P. M. (2015). Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. *Proceedings of the National Academy of Sciences*, *112*(24), 7402–7407. https://doi.org/10.1073/pnas.1406485112

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., … Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), 3177–3190. https://doi.org/10.1111/gcb.12629

Chaves, M. E., & Arango, N. (1998). *Informe nacional sobre el estado de la biodiversidad: Diversidad biológica: Instituto de Investigación de Recursos Biológicos*. Alexander von Humboldt.

Chun, J.-H., & Lee, C.-B. (2018). Partitioning the regional and local drivers of phylogenetic and functional diversity along temperate elevational gradients on an East Asian peninsula. *Scientific Reports*, *8*(1), 2853. https://doi.org/10.1038/s41598-018-21266-4

Cleef, A. M. (1981). The vegetation of the páramos of the Colombian Cordillera Oriental. *Mededelingen Van Het Botanisch Museum En Herbarium Van De Rijksuniversiteit Te Utrecht*, *481*(1), 1–320.

Congedo, L. (2016). Semi-automatic classification plugin documentation. *Release*. *4*(0.1), 29.

Cortés, S. (2008). La vegetación boscosa y arbustiva de la cuenca alta del río Bogotá/Forest and shrub vegetation of the upper basin of the Bogotá river. T. van der Hammen O. Rangel-Churio & A. Cleef (Eds.), *La cordillera Oriental colombiana, transecto Sumapaz. Estudios de Ecosistemas Tropandinos*, *7*, (915–960). Berlin-Stuttgart: J. Cramer.

Cortés, S., Van der Hammen, T., & Rangel, O. (1999). Comunidades vegetales y patrones de degradación y sucesión en la vegatación de los cerros occidentales de Chia Cundinamarca-Colombia. *Revista De La Academia Colombiana Deficiencias*, *23*(89), 529–554.

Cuatrecasas, J. (1934). *Observaciones geobotánicas en Colombia*. Junta para Ampliación de Estudios e Investigaciones Científicas.

Cuatrecasas, J. (1958). Aspectos de la vegetación natural de Colombia. *Revista De La Academia Colombiana De Ciencias Exactas, Físicas Y Naturales.*, *10*(40), 221–268.

DANE Departamento Administrativo Nacional de Estadística (DANE), (2018). Retrieved from http://www.dane.gov.co/?descarga-marco-geoestadistico-nacional

DANE Departamento Administrativo Nacional de Estadística (DANE) (2019). Retrieved from https://geoportal.dane.gov.co/?estimaciones-proyecciones

D'Angelo, S. A., Andrade, A. C., Laurance, S. G., Laurance, W. F., & Mesquita, R. C. (2004). Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology*, *20*(2), 243–246.

de Paula, M. D., Costa, C. P. A., & Tabarelli, M. (2011). Carbon storage in a fragmented landscape of Atlantic forest: The role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*, *4*(3), 349–358. https://doi.org/10.1177/194008291100400310

Diaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646–655.

Ding, Y., Zang, R., Letcher, S. G., Liu, S., & He, F. (2012). Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos*, *121*(8), 1263–1270. https://doi.org/10.1111/j.1600-0706.2011.19992.x

Etter, A., McAlpine, C., & Possingham, H. (2008). Historical patterns and drivers of landscape change in Colombia since 1500: A regionalized spatial approach. *Annals of the Association of American Geographers*, *98*(1), 2–23. https://doi.org/10.1080/00045600701733911

Etter, A., & van Wyngaarden, W. (2000). Patterns of landscape transformation in Colombia, with emphasis in the Andean region. *AMBIO: A Journal of the Human Environment*, *29*(7), 432–440. https://doi.org/10.1579/0044-7447-29.7.432

Evy, A., Federico, S., Harald, A., Lander, B., Sigrid, B., Elisa, C., Andrea, C., Mariangela, F., Kalliopi, R., Nurlaila, S. N., Margot, V., & Kris, V. (2016). Driving mechanisms of overstorey–understorey diversity relationships in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, *19*, 21–29. https://doi.org/10.1016/j.ppees.2016.02.001

Fahey, R. T., & Puettmann, K. J. (2007). Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *Journal of Ecology*, *95*(5), 1098–1109. https://doi.org/10.1111/j.1365-2745.2007.01283.x

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Flynn, D. F., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, *92*(8), 1573–1581. https://doi.org/10.1890/10-1245.1

Forman, R. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*(1), 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Franco, M., Betancur, J., & Franco, P. (2010). Diversidad florística y estructura de remanentes de bosque andino en la zona de amortiguación del Parque Nacional Natural los Nevados, Cordillera Central Colombiana. *Caldasia*, *32*(1), 39–63.

Frenzke, L., Lederer, A., Malanin, M., Eichhorn, K.-J., Neinhuis, C., & Voigt, D. (2016). Plant pressure sensitive adhesives: Similar chemical properties in distantly related plant lineages. *Planta*, *244*(1), 145–154. https://doi.org/10.1007/s00425-016-2496-4

Gentry, A., & Ortiz, R. (1993). *Patrones de composición florística en la Amazonía peruana* (pp. 155–166). vegetación húmeda tropical en el llano subandino.

Gentry, A. H., & Vasquez, R. (1993). *A field guide to the families and genera of woody plants of northwest South America (Colombia, Ecuador, Peru): with supplementary notes on herbaceous taxa*.

Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, *29*(5), 600–614. https://doi.org/10.1111/1365-2435.12425

Girardin, C. A. J., Espejob, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., Marthews, T. R., Aragao, L. E. O. C., Farfán-Rios, W., García-Cabrera, K., Halladay, K., Fisher, J. B., Galiano-Cabrera, D. F., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora, L., -Revilla, N. S., Silman, M. R., Meir, P., & Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222

González, W., Llambí, L. D., Smith, J. K., & Gámez, L. E. (2011). Dinámica sucesional del componente arbóreo en la zona de transición bosque-Páramo en Los Andes Tropicales. *Ecotrópicos*, *24*(1), 60–79.

Halpern, C. B., & Lutz, J. A. (2013). Canopy closure exerts weak controls on understory dynamics: A 30-year study of overstory–understory interactions. *Ecological Monographs*, *83*(2), 221–237. https://doi.org/10.1890/12-1696.1

Halpern, C. B., & Spies, T. A. (1995). Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications.*, *5*(4), 913–934. https://doi.org/10.2307/2269343

Handcock, M. S. (2016). *Relative Distribution Methods*. Version 1.6–6. R package.

Heath, J., & Binswanger, H. (1996). Natural resource degradation effects of poverty and population growth are largely policy-induced: The case of Colombia. *Environment and Development Economics*, *1*(1), 65–84. https://doi.org/10.1017/S1355770X00000383

Hertzog, L. R., Boonyaritichaikij, R., Dekeukeleire, D., de Groote, S. R. E., van Schrojenstein Lantman, I. M., Sercu, B. K., Smith, H. K., de la Peña, E., Vandegehuchte, M. L., Bonte, D., Martel, A., Verheyen, K., Lens, L., & Baeten, L. (2019). Forest fragmentation modulates effects of tree species richness and composition on ecosystem multifunctionality. *Ecology*, *100*(4), e02653.

Hill, J., & Curran, P. (2001). Species composition in fragmented forests: Conservation implications of changing forest area. *Applied Geography*, *21*(2), 157–174. https://doi.org/10.1016/S0143-6228(01)00002-9

Homeier, J., Breckle, S. W., Günter, S., Rollenbeck, R. T., & Leuschner, C. (2010). Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica*, *42*(2), 140–148. https://doi.org/10.1111/j.1744-7429.2009.00547.x

Huebner, C. D., Randolph, J. C., & Parker, G. R. (1995). Environmental factors affecting understory diversity in second-growth deciduous forests. *American Midland Naturalist*, *134*, 155–165. https://doi.org/10.2307/2426492

Hurtado-M A. B., Echeverry-Galvis M. Á., Salgado-Negret B., Muñoz J. C., Posada J. M., Norden N. (2020). Little trace of floristic homogenization in peri-urban Andean secondary forests despite high anthropogenic transformation. *Journal of Ecology*. http://dx.doi.org/10.1111/1365-2745.13570

IDEAM (2007). *Estudio de la Caracterización Climática de Bogotá y Cuenca Alta del Río Tunjuelo*.

IDEAM (2015). *Atlas Climatológico de Colombia – Interactivo – año 2015*.

IGAC (1985). *Estudio General de Suelos de los Sectores Sur y Suroeste del Departamento de Cundinamarca* (Vol. 1). IGAC. 978-958-8067-73-5.

Jung, M. (2013). *LecoS-A QGIS plugin for automated landscape ecology analysis*. PeerJ PrePrints. Report No.: 2167–9843.

Keith, H., Mackey, B. G., & Lindenmayer, D. B. (2009). Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, *106*(28), 11635–11640. https://doi.org/10.1073/pnas.0901970106

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Killeen, T. J., Douglas, M., Consiglio, T., Jørgensen, P. M., & Mejia, J. (2007). Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography*, *34*(8), 1357–1373. https://doi.org/10.1111/j.1365-2699.2006.01682.x

Köster, N., Friedrich, K., Nieder, J., & Barthlott, W. (2009). Conservation of epiphyte diversity in an Andean landscape transformed by human land use. *Conservation Biology*, *23*(4), 911–919. https://doi.org/10.1111/j.1523-1739.2008.01164.x

Krömer, T., Kessler, M., & Gradstein, S. R. (2007). Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: The importance of the understory. *Plant Ecology*, *189*(2), 261–278. https://doi.org/10.1007/s11258-006-9182-8

Kupfer, J. A., Webbeking, A. L., & Franklin, S. B. (2004). Forest fragmentation affects early successional patterns on shifting cultivation fields near Indian Church, Belize. *Agriculture, Ecosystems & Environment*, *103*(3), 509–518. https://doi.org/10.1016/j.agee.2003.11.011

Kusuma, Y. W. C., Rembold, K., Tjitrosoedirdjo, S. S., & Kreft, H. (2018). Tropical rainforest conversion and land use intensification reduce understorey plant phylogenetic diversity. *Journal of Applied Ecology*, *55*(5), 2216–2226. https://doi.org/10.1111/1365-2664.13201

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). *Package 'FD'. Measuring functional diversity from multiple traits, and other tools for functional ecology*.

Latham, P. A., Zuuring, H. R., & Coble, D. W. (1998). A method for quantifying vertical forest structure. *Forest Ecology and Management*, *104*(1–3), 157–170. https://doi.org/10.1016/S0378-1127(97)00254-5

Laurance, W. F., & Bierregaard, R. O. (1997). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*. University of Chicago Press.

Laurance, W. F., Delamônica, P., Laurance, S. G., Vasconcelos, H. L., & Lovejoy, T. E. (2000). Conservation: Rainforest fragmentation kills big trees. *Nature*, *404*(6780), 836. https://doi.org/10.1038/35009032

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., Lovejoy, T. E., Condit, R., Chave, J., Harms, K. E., & D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences*, *103*(50), 19010–19014. https://doi.org/10.1073/pnas.0609048103

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Letcher, S. G. (2009). Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1678), 97–104. https://doi.org/10.1098/rspb.2009.0865

Lexerød, N. L., & Eid, T. (2006). An evaluation of different diameter diversity indices based on criteria related to forest management planning. *Forest Ecology and Management*, *222*(1–3), 17–28. https://doi.org/10.1016/j.foreco.2005.10.046

Linares, P. V., & Ríos, O. V. (2004). Dinámica de la dispersión de plantas ornitócoras, reclutamiento y conectividad en fragmentos de bosque altoandino secundario (Reserva Natural Protectora, Cogua Cundinamarca). *Acta Biológica Colombiana*, *9*(2), 121–122.

López, W., & Duque, Á. (2010). Patrones de diversidad alfa en tres fragmentos de bosques montanos en la región norte de los Andes. *Colombia. Revista De Biología Tropical*, *58*(1), 483–498.

Lumley, T., & Lumley, M. T. (2013). *Package 'leaps'. Regression Subset Selection*. Thomas Lumley Based on Fortran Code by Alan Miller. 2013. Retrieved from http://CRAN.R-project.org/package=leaps (accessed on 5 September 2020).

Luteyn, J. L. (2002). Diversity, adaptation, and endemism in neotropical Ericaceae: Biogeographical patterns in the Vaccinieae. *The Botanical Review*, *68*(1), 55–87.10.1663/0006-8101(2002)068[0055:DAAEIN]2.0.CO;2

Marcantonio, M., Rocchini, D., Geri, F., Bacaro, G., & Amici, V. (2013). Biodiversity, roads, & landscape fragmentation: Two Mediterranean cases. *Applied Geography*, *42*, 63–72.

Mason, N. W., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

McCune, B., & Mefford, M. J. (2015). *PC-ORD Version 7.287. Multivariate Analysis of Ecological Data*. MjM Software.

Mendoza S., J. E., & Etter R., A. (2002). Multitemporal analysis (1940–1996) of land cover changes in the southwestern Bogotá highplain (Colombia). *Landscape and Urban Planning*, *59*(3), 147–158. https://doi.org/10.1016/S0169-2046(02)00012-9

Menon, S., Denman, K. L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M., Dickinson, R. E., Hauglustaine, D., Heinze, C., Holland, E., & Jacob, D. (2007). *Couplings between changes in the climate system and biogeochemistry*. Lawrence Berkeley National Lab. (LBNL).

Millspaugh, J., & Thompson, F. R. (Eds.) (2011). *Models for planning wildlife conservation in large landscapes*. Academic Press.

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, *88*(2), 349–364. https://doi.org/10.1111/brv.12004

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., & Iost, S. (2011). Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the belowground compartment. *Global Change Biology*, *17*, 2211–2226.

Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Muñoz-Camacho, J. C., Hurtado, A. B., & Norden, N. (2017). *Composición florística de tres fragmentos de bosque altoandino en los alrededores de la sabana de Bogotá: Parcelas permanentes del Proyecto Rastrojos*.

Munzi, S., Correia, O., Silva, P., Lopes, N., Freitas, C., Branquinho, C., & Pinho, P. (2014). Lichens as ecological indicators in urban areas: Beyond the effects of pollutants. *Journal of Applied Ecology*, *51*(6), 1750–1757. https://doi.org/10.1111/1365-2664.12304

NASA/METI/AIST/Japan Spacesystems, and U.S./Japan ASTER Science Team (2009). ASTER Global Digital Elevation Model [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/10.5067/ASTER/ASTGTM.002

Nepstad, D. C., Moutinho, P., Dias-Filho, M. B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., & Guerreiros, J. B. (2002). The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research: Atmospheres*, *107*(D20), LBA-53, https://doi.org/10.1029/2001JD000360

Nilsson, M.-C., & Wardle, D. A. (2005). Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, *3*(8), 421–428.10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2

Norden, N., Letcher, S. G., Boukili, V., Swenson, N. G., & Chazdon, R. (2012). Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. *Ecology*, *93*(sp8), S70–S82. https://doi.org/10.1890/10-2179.1

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2013). *Community ecology package*. R package version, 2–0.

Paine, R. T., Tegner, M. J., & Johnson, E. A. (1998). Compounded perturbations yield ecological surprises. *Ecosystems*, *1*(6), 535–545. https://doi.org/10.1007/s100219900049

Parra Sánchez, E., Armenteras, D., & Retana, J. (2016). Edge influence on diversity of orchids in Andean cloud forests. *Forests*, *7*(3), 63. https://doi.org/10.3390/f7030063

Parton, W., Morgan, J., Smith, D., Del Grosso, S., Prihodko, L., LeCain, D., Kelly, R., & Lutz, S. (2012). Impact of precipitation dynamics on net ecosystem productivity. *Global Change Biology*, *18*(3), 915–927. https://doi.org/10.1111/j.1365-2486.2011.02611.x

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2013). New handbook for stand-ardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234. https://doi.org/10.1071/BT12225

Pèrez Sanz de Santamaría, J. A. (2013). *Aplicación del cuadro de mando integral para la selección de proyectos en reservas forestales-caso de la Reserva Biológica del Encenillo, Guasca, Cundinamarca*, (9–10). Universidad de los Andes. https://repositorio.uniandes.edu.co/handle/1992/25448

Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, *5*(3), 402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x

Petchey, O. L., & Gaston, K. J. (2007). Dendrograms and measuring functional diversity. *Oikos*, *116*(8), 1422–1426. https://doi.org/10.1111/j.0030-1299.2007.15894.x

Poos, M. S., Walker, S. C., & Jackson, D. A. (2009). Functional-diversity indices can be driven by methodological choices and species richness. *Ecology*, *90*(2), 341–347. https://doi.org/10.1890/08-1638.1

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M., & Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology*, *101*(4), 857–866. https://doi.org/10.1111/1365-2745.12098

QGIS Development Team (2018). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. Retrieved from http://qgis.osgeo.org

R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rangel, O. (2000). *Colombia diversidad biótica III: La región de vida paramuna*. Universidad Nacional de Colombia, Facultad de Ciencia, Instituto de Ciencias Naturales.

Rangel, O., Rivera, O., & Cleef, A. M. (2008). Flora vascular del macizo de Sumapaz. *Estudios De Ecosistemas Tropandinos: La Cordillera Oriental Colombiana-Transecto Sumapaz*, *7*, 204–210.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., & Hérault, B. (2017). biomass: An r package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution*, *8*(9), 1163–1167.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., & Herault, B. (2018). *BIOMASS: Estimating aboveground biomass and its uncertainty in tropical forests*. R Package Version.

Restrepo Abadia, J. F. (2016). *Caracterización vegetal del bosque altoandino en diferentes estados sucesionales de la reserva biológica Encenillo, Guasca-Cundinamarca*. Master's degree thesis. Pontificia Universidad Javeriana: Facultad De Estudios Ambientales Y Rurales.

Ribeiro, E. M., Arroyo-Rodríguez, V., Santos, B. A., Tabarelli, M., & Leal, I. R. (2015). Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. *Journal of Applied Ecology*, *52*(3), 611–620. https://doi.org/10.1111/1365-2664.12420

Ribeiro, E. M., Santos, B. A., Arroyo-Rodríguez, V., Tabarelli, M., Souza, G., & Leal, I. R. (2016). Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology*, *97*(6), 1583–1592. https://doi.org/10.1890/15-1122.1

Roberts, M. R., & Gilliam, F. S. (1995). Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. *Ecological Applications*, *5*(4), 969–977. https://doi.org/10.2307/2269348

Rodríguez-Alarcón, S., Rodríguez-Eraso, N., Pineda-Rincón, I., & López-Camacho, R. (2018). Effects of fragmentation on functional diversity associated with aboveground biomass in a high Andean forest in Colombia. *Landscape Ecology*, *33*(11), 1851–1864. https://doi.org/10.1007/s10980-018-0719-8

Romero, M. P. S. (2002). Fenología reproductiva y dispersión de semillas del arbusto altoandino Monnina salicifolia R&P (Polygalaceae) en el embalse San Rafael La Calera-Cundinamarca. *Acta Biológica Colombiana*, *7*(2), 64–65.

Rubiano, K., Clerici, N., Norden, N., & Etter, A. (2017). Secondary forest and shrubland dynamics in a highly transformed landscape in the Northern Andes of Colombia (1985–2015). *Forests*, *8*(6), 216. https://doi.org/10.3390/f8060216

Sánchez-Cuervo, A. M., Aide, T. M., Clark, M. L., & Etter, A. (2012). Land cover change in Colombia: Surprising forest recovery trends between 2001 and 2010. *PLoS One*, *7*(8), e43943. https://doi.org/10.1371/journal.pone.0043943

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671. https://doi.org/10.1038/nmeth.2089

Silva, G. F. D., Curto, R. D. A., Soares, C. P. B., & Piassi, L. D. C. (2012). Avaliação de métodos de medição de altura em florestas naturais. *Revista Árvore*, *36*(2), 341–348.

Sorichetta A., Hornby G. M., Stevens F. R., Gaughan A. E., Linard C., Tatem A. J. (2015). High-resolution gridded population datasets for Latin America and the Caribbean in 2010, 2015, and 2020. *Scientific Data*, *2*(1). http://dx.doi.org/10.1038/sdata.2015.45

Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jørgensen, P. M., Weiser, M. D., Monteagudo Mendoza, A., & Núñez Vargas, P. (2011). Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, *20*(5), 744–754. https://doi.org/10.1111/j.1466-8238.2010.00645.x

Still, C. J., Foster, P. N., & Schneider, S. H. (1999). Simulating the effects of climate change on tropical montane cloud forests. *Nature*, *398*(6728), 608. https://doi.org/10.1038/19293

Sturm, H., & Rangel, C. O. (1985). *Ecología de los páramos andinos: una visión preliminar integrada*.

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R*. Springer.

Thrippleton, T., Bugmann, H., Kramer-Priewasser, K., & Snell, R. S. (2016). Herbaceous understorey: An overlooked player in forest landscape dynamics? *Ecosystems*, *19*(7), 1240–1254.

Torres, A. M., & Marina. (2016). Floristic characterization of a high andean forest in the Purace national natural park, Cauca, Colombia. *Boletín Científico Centro De Museos Museo De Historia Natural*, *20*(2), 33–42.

Torres, A. M., Peña, E. J., Zúñiga, O., & Peña, J. (2012). Evaluación del impacto de actividades antrópicas en el almacenamiento de carbono en biomasa vegetal en ecosistemas de alta montaña de Colombia. *Boletín Científico Museo De Historia Natural*, *16*(1), 132–142.

Trelease, W., & Yuncker, T. G. (1950). *The Piperaceae of Northern South America*. University of Illinois Press.

Tyser, R. W., & Worley, C. A. (1992). Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). *Conservation Biology*, *6*(2), 253–262. https://doi.org/10.1046/j.1523-1739.1992.620253.x

Van der Hammen, T. (1998). *Plan ambiental de la cuenca alta del río Bogotá: Análisis y orientaciones para el ordenamiento territorial*. Corporación Autónoma Regional de Cundinamarca Bogotá.

Van der Hammen, T. (2008). *La Cordillera Oriental Colombiana: Transecto Sumapaz*.

Vargas, O., & Zuluaga, S. (1980). *Contribución al estudio fitoecológico de la región de Monserrate*. Trabajo de grado, Departamento de Biología, Universidad Nacional de Colombia (inédito).

Vargas-Ríos, O. (1997). Un modelo de sucesión-regeneración de los páramos después de quemas. *Caldasia*, 331–345.

Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Vockenhuber, E. A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., & Tscharntke, T. (2011). Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(2), 111–119. https://doi.org/10.1016/j.ppees.2011.02.004

Wassenaar, T., Gerber, P., Verburg, P., Rosales, M., Ibrahim, M., & Steinfeld, H. (2007). Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. *Global Environmental Change*, *17*(1), 86–104. https://doi.org/10.1016/j.gloenvcha.2006.03.007

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*(18), 2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2011). *Phylocom: Software for the analysis of phylogenetic community structure and character evolution (with phylomatic and ecoevolve)*. User's manual.

Webb, C. O., & Donoghue, M. J. (2005). Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes*, *5*(1), 181–183. https://doi.org/10.1111/j.1471-8286.2004.00829.x

Werner, F. A., & Gradstein, S. R. (2009). Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. *Journal of Vegetation Science*, *20*(1), 59–68. https://doi.org/10.1111/j.1654-1103.2009.05286.x

Wikström, N., Savolainen, V., & Chase, M. W. (2001). Evolution of the angiosperms: Calibrating the family tree. *Proceedings of the Royal Society of London Series B. Biological Sciences*, *268*(1482), 2211–2220.

Wolf, J. H. (1993). Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden*, *80*, 928–960. https://doi.org/10.2307/2399938

Young, K. (1992). Biogeography of the montane forest zone of the eastern slopes of Peru. *Memorandum Del Museo Historia Natural Javier Prado*, *21*, 119–140.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX A1

Plots localities and coordinates

Plot	Locality	Sector	Latitude	Longitude	Elevation
M1	Torca	La Francia	4°47′12.1″	–74°1′34.2″	2,664 m
M2	Pasquilla	Finca Porras	4°26′16.6″	–74°10′09.4″	3,216 m
M3	Torca	La Francia	4°47′11.5″	–74°01′32.8″	2,692 m
M4	Torca	Colegio Nuevo Horizonte	4°48′01.6″	–74°01′42.5″	2,639 m
M5	Torca	Colegio Nuevo Horizonte	4°48′1″	–74°1′41.1″	2,668 m
M6	Pasquilla	Finca Porras	4°26′14.4″	–74°10′14.7″	3,278 m
M7	Sumapaz	Predio Hernan	4°2′10.5″	–74°17′47.6″	3,402 m
M7bis	Sumapaz	Predio Alexandra	4°2′7.7″	–74°18′1.2″	3,395 m
M8	Sumapaz	Predio Hernan	4°2′9.2″	–74°17′51″	3,390 m
M8bis	Sumapaz	Predio Alexandra	4°2′8.0″	–74°18′2.1″	3,387 m
M9bis	Pasquilla	Finca Alveiro	4°26′53.3″	–74°10′21.2″	3,313 m
M10	Pasquilla	Finca Alveiro	4°26′55.9″	–74°10′19.7″	3,307 m
R1	Guatavita	predio Juan	4°56′9.716″	–73°53′54.237″	3,035 m
R2	Guatavita	predio Juan	4°56′12.618″	–73°53′51.825″	3,028 m
R3	Guasca	Encenillo	4°47′20.3172″	–73°54′31.8132″	3,140 m
R4	Guasca	Encenillo	4°47′28.667″	–73°54′25.886″	3,085 m
R5	Guasca	Encenillo	4°47′24.124″	–73°54′31.332″	3,106 m
R6	Guasca	Encenillo	4°47′26.609″	–73°54′25.904″	3,095 m
R7	Tabio	Predio suizo	4°55′40.858″	–74°6′29.194″	2,696 m
R8	Tabio	Predio suizo	4°55′47.149″	–74°6′31.021″	2,707 m
R9	Tabio	Predio suizo	4°55′33.961″	–74°6′47.225″	2,821 m
R10	Tabio	Predio suizo	4°55′31.683″	–74°6′31.579″	2,685 m
R11	Torca	Conjunto floresta	4°48′48.674″	–74°0′58.527″	2,945 m
R12	Torca	Conjunto floresta	4°48′47.937″	–74°0′56.997″	2,965 m
R13	Torca	Conjunto floresta	4°48′31.216″	–74°1′19.178″	2,708 m
R14	Torca	Conjunto floresta	4°48′45.912″	–74°0′58.852″	2,847 m
R15	Guasca	Predio Rosita	4°47′16.5″	–73°54″15.4″	3,056 m
R16	Guasca	Predio Rosita	4°47′05.2″	–73°54′13.8″	3,101 m
R17	Torca	Conjunto portal de Fusca	4°49′30.41″	–74°01′02.49″	3,080 m
R18	Torca	Conjunto portal de Fusca	4°50′00.37″	–74°01′08.96″	2,789 m
R19	Tabio	Predio suizo	4°55′31.79″	–74°06′44.42″	2,736 m
R20	Tabio	Predio suizo	4°55′35.03″	–74°06′40.15″	2,737 m

APPENDIX A2

Variables used for the preliminary analysis (NMDS)

Variable acronym	Variable full name	PRED/RESP	Type	Unit	Source
east	eastness = sin(aspect)	PRED	ENV		DEM
elev	elevation	PRED	ENV	m	DEM
mean_prec	mean annual precipitation (1981–2010)	PRED	ENV	mm	IDEAM
mean_T	mean annual temperature (1981–2010)	PRED	ENV	C	IDEAM
north	northness = cos(aspect)	PRED	ENV		DEM
rel_hum	relative humidity (1981–2010)	PRED	ENV	%	IDEAM
sol_rad	solar radiation (1981–2010)	PRED	ENV	kW/m^2	IDEAM
cattle	cattle inside the plot	PRED	CAU	0/1	Field survey
cattle_50m; cattle_100, cattle_500	cattle in 50, 100 or 500 m from the plot	PRED	CAU	0/1	Field survey
tour	tourism inside the plot	PRED	CAU	0/1	Field survey
logg	logging sings inside the plot	PRED	CAU	0/1	Field survey
other	conservation activities inside the plot	PRED	CAU	0/1	Field survey
protected	protection status	PRED	CAU	0/1	Field survey
age	Minimum age of plot	PRED	FAC	years	Aerial pictures: IGAC
cult_50m; cult_100; cult_500	cultivated fields in 50, 100 and 500 m	PRED	FAC	0/1	Field survey
edge	if the plot was located in the edge = 1, or interior = 0 of fragment	PRED	FAC	0/1	Edge until 50 m
edge_density	Edge density in 1 km buffer	PRED	FAC	m/ha	LC LANDSAT 8 Raster
edge_lenght	Edge length in 1 km buffer	PRED	FAC	km	LC LANDSAT 8 Raster
effective_meshsize	Effective Meshsize in 1 km buffer	PRED	FAC	ha	LC LANDSAT 8 Raster
fractal_dimesion_index	Fractal Dimension Index in 1 km buffer and 500 m	PRED	FAC		LC LANDSAT 8 Raster
fragment	Fragment size	PRED	FAC	km^2	Bing maps
greatest_patch	Greatest patch area in 1 km buffer and 500 m	PRED	FAC	Ha	LC LANDSAT 8 Raster
land_cover	Land Cover in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
landscape_division	Landscape division in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
landscape_pielou	Pielou's landscape equitability in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
landscape_porportion	Landscape Proportion in 1 km buffer	PRED	FAC	%	LC LANDSAT 8 Raster
landscape_shannon	Shannon,s landscape diversity in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
landscape_simpson	Simpson's landscape diversity in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
largest_patch_index	Largest Patch Index in 1 km buffer	PRED	FAC	%	LC LANDSAT 8 Raster
like_adjacencies	Like adjacencies in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
m_patchshape_ratio	Mean patch shape ratio in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
mean_patch	Mean patch area in 1 km buffer	PRED	FAC	ha	LC LANDSAT 8 Raster
median_patch	Median patch area in 1 km buffer	PRED	FAC	ha	LC LANDSAT 8 Raster
n_patches	Number of Patches in 1 km buffer and 500 m	PRED	FAC	n	LC LANDSAT 8 Raster
nn_distance	Euclidean Nearest-Neighbor Distance in 1 km buffer	PRED	FAC	m	LC LANDSAT 8 Raster
overall_core	Overall Core area in 1 km buffer	PRED	FAC	m	LC LANDSAT 8 Raster
patch_cohesion_index	Patch cohesion index in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster

(Continues)

APPENDIX A2 (Continued)

Variable acronym	Variable full name	PRED/RESP	Type	Unit	Source
patch_density	Patch density in 1 km buffer	PRED	FAC		LC LANDSAT 8 Raster
path_dist	distance from path	PRED	FAC	m	BING map
people_density_1km; people_density_5km	population density in 1 km buffer and 5 km around the plots	PRED	FAC	n/ha	WordPop
road_dist	distance to main roads or not main roads	PRED	FAC	m	DANE
slope	slope in percent	PRED	FAC	%	DEM
smallest_patch	Smallest patch area in 1 km buffer	PRED	FAC	ha	LC LANDSAT 8 Raster
splitting_index	Splitting Index in 1 km buffer and 500 m	PRED	FAC		LC LANDSAT 8 Raster
track_dist	distance from track	PRED	FAC	m	BING map
m_cov_inv_U	mean cover of understory exotic/invasive species	RESP	IND	%	Field survey
m_cov_nat_U	mean cover of native species	RESP	IND	%	Field survey
n.10DBH; n.20DBH	number of individuals of trees with DBH > than 10 or 20 cm	RESP	IND	n	Field survey
n_CON_sp_T; n_CON_ind_T	number of late successional tree species and individuals	RESP	IND	n	Field survey
n_FST_sp_T; n_FST_ind_T	number of fast-growing tree species and individuals	RESP	IND	n	Field survey
n_inv_sp_T; n_inv_sp_U	number of exotic/invasive tree and understory species	RESP	IND	n	Field survey
n_large_trees	number of large trees (DBH > 30 cm)	RESP	IND	n	Field survey
n_sp.10DBH; n_sp.20DBH	number of species of trees with DBH > than 10 or 20 cm	RESP	IND	n	Field survey
n_stems	number of stems	RESP	IND	n	Field survey
n_trees	number of trees (individuals)	RESP	IND	n	Field survey
stems_tree	mean number of stems per each tree individual	RESP	IND	n	Field survey
%n_CON_sp_T; %n_CON_ind_T	%of total late successional tree species and individuals	RESP	IND	%	Field survey
AGBplot	total aboveground biomass per plot	RESP	LEV	ton	Field survey
DBH_var	DBH variance	RESP	LEV	cm	Field survey
FD	Functional Diversity	RESP	LEV		Field survey
FDis	Functional Dispersion	RESP	LEV		Field survey
FDiv	Functional Evenness	RESP	LEV		Field survey
FEve	Functional Divergence	RESP	LEV		Field survey
FRic	Functional Richness	RESP	LEV		Field survey
Giniun; Giniwe	Gini unweighted and weighted coefficient for basal areas of single trees	RESP	LEV		Field survey
H_var	canopy height variance	RESP	LEV	m	Field survey
m_DBH	mean DBH	RESP	LEV	cm	Field survey
m_H_understory	mean understorey height	RESP	LEV	%	Field survey
mAGBT	mean AGB per tree	RESP	LEV	kg	Field survey
max_H	maximum tree height	RESP	LEV	m	Field survey
mbrioT; mbrioC	mean briophytes cover in trunk and canopy	RESP	LEV	0–3	Field survey
mbroT; mbroC	mean bromeliads cover in trunk and canopy	RESP	LEV	0–3	Field survey
mcobT; mcobC	mean epiphyte cover trunk and canopy	RESP	LEV	0–3	Field survey
morqT; morqC	mean orchids cover in trunk and canopy	RESP	LEV	0–3	Field survey

(Continues)

APPENDIX A2 (Continued)

Variable acronym	Variable full name	PRED/RESP	Type	Unit	Source
mliqT; mliqC	mean lichens cover in trunk and canopy	RESP	LEV	0–3	Field survey
mhelT; mhelC	mean ferns cover in trunk and canopy	RESP	LEV	0–3	Field survey
mCWD	mean coarse woody debris cover	RESP	LEV	%	Field survey
mean_H	mean canopy height	RESP	LEV	m	Field survey
mmoss	mean moss cover	RESP	LEV	%	Field survey
msoil	mean soil cover	RESP	LEV	%	Field survey
mundstr	mean understorey cover	RESP	LEV	%	Field survey
TMNTD; HMNTD	Trees and understory mean nearest taxon distance	RESP	LEV		Field survey
TMNTD-ABU; HMNTD-ABU	Trees and understory mean nearest taxon distance (abundance weighted)	RESP	LEV		Field survey
TMPD; HMPD	Trees and understory mean pairwise distances	RESP	LEV		Field survey
TMPD-ABU; HMPD-ABU	Trees and understory mean pairwise distances (abundance weigthed)	RESP	LEV		Field survey
TPD; HPD	Trees and understory Phylogentic diversity index	RESP	LEV		Field survey
TPIELOU; HPIELOU	Tree and understory Pielou's evenness	RESP	LEV	n	Field survey
TsesMNTD; HsesMNTD	Trees and understory standardized mean nearest taxon distance	RESP	LEV		Field survey
TsesMNTD-ABU; HsesMNTD_ABU	Trees and understory standardized mean nearest taxon distance (abundance weighted)	RESP	LEV		Field survey
TsesMPD; HsesMPD	Trees and understory standardized mean pairwise distances	RESP	LEV		Field survey
TsesMPD-ABU; HsesMPD-ABU	Trees and understory standardized mean pairwise distances (abundance weighted)	RESP	LEV		Field survey
TsesPD; HsesPD	Trees and understory standardized phylogentic diversity index	RESP	LEV		Field survey
Tshann; Hshann	Trees and understory Shannon's diversity index	RESP	LEV		Field survey
Tsimp; Hsimp	Trees and understory Simpson's diversity index	RESP	LEV		Field survey
TSR; HSR	Tree and understory species count	RESP	LEV	n	Field survey
RaoQ	Rao's Q functional diversity	RESP	LEV		Fieldsurvey
%_5;%_all	percent of the 5 more abundant and all tree species found in the understory	RESP	LEV	%	Field survey

Abbreviations: CAU, causes of disturbance; ENV, geo-environmental; FAC, facilitators of disturbance; IND, indicators of disturbance; LEV, level of disturbance; PRED, predictor; RESP, response.

APPENDIX A3

List of taxa of the tree and understory layer and list of plot-resolved collected vouchers

TREES

Accepted name	Accepted author	Accepted family
Abatia parviflora	Ruiz & Pav.	Salicaceae
Ageratina asclepiadea^{b}	(L.f.) R.M.King & H.Rob.	Asteraceae
Ageratina boyacensis	R.M.King & H.Rob.	Asteraceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Ageratina fastigiata	(Kunth) R.M.King & H.Rob.	Asteraceae
Ageratina glyptophlebia	(B.L.Rob.) R.M.King & H.Rob.	Asteraceae
Ageratina tinifolia	(Kunth) R.M.King & H.Rob.	Asteraceae
Aiouea dubia	(Kunth) Mez	Lauraceae
Aiouea sp		Lauraceae
Alnus acuminata[b]	Kunth	Betulaceae
Baccharis macrantha	Kunth	Asteraceae
Baccharis prunifolia	Kunth	Asteraceae
Barnadesia spinosa	L.f.	Asteraceae
Bejaria resinosa	Mutis ex L.f.	Ericaceae
Berberis glauca	Kunth	Berberidaceae
Blechnum schomburgkii	(Klotzsch) C. Chr.	Blechnaceae
Bocconia frutescens	L.	Papaveraceae
Bucquetia glutinosa	(L. f.) DC.	Melastomataceae
Carica sp[a]		Caricaceae
Cavendishia bracteata	(Ruiz & Pav. ex J.St.Hil.) Hoerold	Ericaceae
Cavendishia nitida	(Kunth) A.C.Sm.	Ericaceae
Cedrela montana	Moritz ex Turcz.	Meliaceae
Cestrum buxifolium	Kunth	Solanaceae
Cestrum sp		Solanaceae
Citharexylum sulcatum	Moldenke	Verbenaceae
Clethra fagifolia	Kunth	Clethraceae
Clethra fimbriata	Kunth	Clethraceae
Clethra lanata	M.Martens & Galeotti	Clethraceae
Clusia multiflora	Kunth	Clusiaceae
Critoniopsis bogotana[b]	(Cuatrec.) H.Rob.	Asteraceae
Croton bogotanus	Cuatrec.	Euphorbiaceae
Cybianthus iteoides	(Benth.) G.Agostini	Primulaceae
Daphnopsis caracasana	Meisn.	Thymelaeaceae
Diplostephium ochraceum	(Kunth) Nees	Asteraceae
Diplostephium rosmarinifolium	(Benth.) Wedd.	Asteraceae
Drimys granadensis	L.f.	Winteraceae
Duranta mutisii	L.f.	Verbenaceae
Escallonia myrtilloides	L.f.	Escalloniaceae
Escallonia paniculata	(Ruiz & Pav.) Schult.	Escalloniaceae
Frangula goudotiana	(Triana & Planch.) Grubov	Rhamnaceae
Frangula sphaerosperma	(Sw.) Kartesz & Gandhi	Rhamnaceae
Gaiadendron punctatum	(Ruiz & Pav.) G.Don	Loranthaceae
Gaultheria anastomosans	(Mutis ex L.f.) Kunth	Ericaceae
Hediosmum sp		Chloranthaceae
Hesperomeles ferruginea	(Pers.) Benth.	Rosaceae
Hesperomeles goudotiana	(Decne.) Killip	Rosaceae
Hesperomeles obtusifolia	(Pers.) Lindl.	Rosaceae
Ilex kunthiana	Triana	Aquifoliaceae
Ilex sp		Aquifoliaceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Lippia hirsuta	L.f.	Verbenaceae
Macleania rupestris[b]	(Kunth) A.C.Sm.	Ericaceae
Macrocarpaea glabra	(L. f.) Gilg	Gentianaceae
Maytenus laxiflora	Triana & Planch.	Celastraceae
MELASTOMATACEAE sp		Melastomataceae
Miconia elaeoides	Naudin	Melastomataceae
Miconia ligustrina	(Sm.) Triana	Melastomataceae
Miconia squamulosa	Triana	Melastomataceae
Myrcianthes leucoxyla[b]	(Ortega) McVaugh	Myrtaceae
Myrcianthes rhopaloides	(Kunth) McVaugh	Myrtaceae
Morella parvifolia	(Benth.) Parra-Os.	Myricaceae
Morella pubescens	(Humb. & Bonpl. ex Willd.) Wilbur	Myricaceae
Myrsine coriacea	(Sw.) R.Br. ex Roem. & Schult.	Primulaceae
Myrsine dependens	(Ruiz & Pav.) Spreng.	Primulaceae
Myrsine guianensis	(Aubl.) Kuntze	Primulaceae
Myrsine latifolia	(Ruiz & Pav.) Spreng.	Primulaceae
Myrsine pellucida	(Ruiz & Pav.) Spreng.	Primulaceae
Ocotea caesariata	van der Werff	Lauraceae
Ocotea heterochroma	Mez & Sodiro	Lauraceae
Oreopanax bogotensis	Cuatrec.	Araliaceae
Oreopanax incisus[b]	(Willd. ex Schult.) Decne. & Planch.	Araliaceae
Palicourea angustifolia	Kunth	Rubiaceae
Palicourea demissa	Standl.	Rubiaceae
Palicourea lineariflora	Wernham	Rubiaceae
Pentacalia sp		Asteraceae
Monticalia pulchella[b]	(Kunth) C.Jeffrey	Asteraceae
Persea ruizii	J.F.Macbr.	Lauraceae
Phyllanthus salviifolius	Kunth	Phyllanthaceae
Piper bogotense	C.DC.	Piperaceae
Podocarpus oleifolius	D.Don	Podocarpaceae
Polylepis quadrijuga	Bitter	Rosaceae
Prunus buxifolia	Koehne	Rosaceae
Psychotria boqueronensis	Wernham	Rubiaceae
Sessea corymbiflora	Goudot ex Rich. Taylor & R. Phillips	Solanaceae
Solanum cornifolium	Dunal	Solanaceae
Symplocos theiformis	(L. f.) Oken	Symplocaceae
Tibouchina grossa	(L. f.) Cogn.	Melastomataceae
Ulex europaeus[a]	L.	Fabaceae
Vaccinium floribundum	Kunth	Ericaceae
Valeriana clematitis	Kunth	Caprifoliaceae
Vallea stipularis	L.f.	Elaeocarpaceae
Cordia cylindrostachya	(Ruiz & Pav.) Roem. & Schult.	Boraginaceae
Verbesina arborea[b]	Kunth	Asteraceae
Viburnum tinoides	L.f.	Adoxaceae
Viburnum triphyllum	Benth.	Adoxaceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Weinmannia fagaroides	Kunth	Cunoniaceae
Weinmannia tomentosa	L.f.	Cunoniaceae
Xylosma spiculifera	(Tul.) Triana & Planch.	Salicaceae

Late successional.[a] Exotic. [b] Fast-growing.

UNDERSTORY

Accepted name	Accepted author	Accepted family
Acaena cylindristachya	Ruiz & Pav.	Rosaceae
Achyrocline satureioides	(Lam.) DC.	Asteraceae
Adiantum andicola	Liebm.	Pteridaceae
Ageratina asclepiadea	(L.f.) R.M.King & H.Rob.	Asteraceae
Ageratina boyacensis	R.M.King & H.Rob.	Asteraceae
Ageratina glyptophlebia	(B.L.Rob.) R.M.King & H.Rob.	Asteraceae
Ageratina gracilis	(Kunth) R.M.King & H.Rob.	Asteraceae
Ageratina tinifolia	(Kunth) R.M.King & H.Rob.	Asteraceae
Agrostis perennans	(Walter) Tuck.	Poaceae
Alansmia sp		Grammitidaceae
Alnus acuminata	Kunth	Betulaceae
Alonsoa meridionalis	(L.f.) Kuntze	Scrophulariaceae
Anchietea frangulifolia	(Kunth) Melch.	Violaceae
Anthoxanthum odoratum[a]	L.	Poaceae
Anthurium caramantae	Engl.	Araceae
Arracacia sp		Apiaceae
Arrhenatherum elatius[a]	(L.) P.Beauv. ex J.Presl & C.Presl.	Poaceae
Asplenium cladolepton	Fée	Aspleniaceae
Asplenium monanthes	L.	Aspleniaceae
Asplenium praemorsum	Sw.	Aspleniaceae
Asplenium radicans	L.	Aspleniaceae
Asplundianthus densus	(Benth.) R.M.King & H.Rob.	Asteraceae
ASTERACEAE sp		Asteraceae
Athyrium filix-femina	(L.) Roth	Woodsiaceae
Baccharis bogotensis	Kunth	Asteraceae
Baccharis latifolia	(Ruiz & Pav.) Pers.	Asteraceae
Baccharis lehmannii	Klatt	Asteraceae
Baccharis macrantha	Kunth	Asteraceae
Barnadesia spinosa	L.f.	Asteraceae
Bejaria resinosa	Mutis ex L. f.	Ericaceae
Berberis glauca	Kunth	Berberidaceae
Berberis goudotii	Triana & Planch.	Berberidaceae
Bidens rubifolia	Kunth	Asteraceae
Blechnum cordatum	(Desv.) Hieron.	Blechnaceae
Blechnum loxense	(Kunth) Hook. ex Salomon	Blechnaceae
Blechnum occidentale	L.	Blechnaceae
Blechnum schomburgkii	(Klotzsch) C. Chr.	Blechnaceae
Boehmeria cylindrica	(L.) Sw.	Urticaceae
Boehmeria sp		Urticaceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Bomarea multiflora	(L. f.) Mirb.	Alstroemeriaceae
Bomarea sp		Alstroemeriaceae
Botrychium virginianum	(L.) Sw.	Ophioglossaceae
Bucquetia glutinosa	(L. f.) DC.	Melastomataceae
Calamagrostis effusa	(Kunth) Steud.	Poaceae
Calceolaria microbefaria	Kraenzl.	Calceolariaceae
Campyloneurum angustifolium	(Sw.) Fée	Polypodiaceae
Campyloneurum latum	T. Moore	Polypodiaceae
Capsella bursa-pastoris	(L.) Medik.	Brassicaceae
Cardamine ovata	Benth.	Brassicaceae
Carex pichinchensis	Kunth	Cyperaceae
Carex sp		Cyperaceae
Castilleja fissifolia	L.f.	Orobanchaceae
Cavendishia bracteata	(Ruiz & Pav. ex J.St.Hil.) Hoerold	Ericaceae
Cedrela montana	Moritz ex Turcz.	Meliaceae
Cestrum buxifolium	Kunth	Solanaceae
Chaetolepis lindeniana	(Naudin) Triana	Melastomataceae
Chromolaena bullata	(Klatt) R.M.King & H.Rob.	Asteraceae
Chromolaena leivensis	(Hieron.) R.M.King & H.Rob.	Asteraceae
Chromolaena perglabra	(B.L.Rob.) R.M.King & H.Rob.	Asteraceae
Chromolaena scabra	(L.f.) R.M.King & H.Rob.	Asteraceae
Chromolaena sp1		Asteraceae
Chromolaena sp2		Asteraceae
Chusquea scandens	Kunth	Poaceae
Citharexylum sulcatum	Moldenke	Verbenaceae
Clematis dioica	L.	Ranunculaceae
Clematis haenkeana	C.Presl	Ranunculaceae
Clethra fimbriata	Kunth	Clethraceae
Clusia multiflora	Kunth	Clusiaceae
Erigeron canadensis[a]	L.	Asteraceae
Cortaderia nitida	(Kunth) Pilg.	Poaceae
Cranichis ciliata	Kunth	Orchidaceae
Cranichis sp		Orchidaceae
Critoniopsis bogotana	(Cuatrec.) H.Rob.	Asteraceae
Croton bogotanus	Cuatrec.	Euphorbiaceae
Cuphea hyssopifolia[a]	Kunth	Lythraceae
Cyperus sp		Cyperaceae
Cystopteris fragilis	(L.) Bernh.	Cystopteridaceae
Daphnopsis caracasana	Meisn.	Thymelaeaceae
Digitalis purpurea[a]	L.	Plantaginaceae
Lycopodium thyoides	Humb. & Bonpl. ex Willd.	Lycopodiaceae
Diplostephium floribundum	(Benth.) Wedd.	Asteraceae
Diplostephium ochraceum	(Kunth) Nees	Asteraceae
Diplostephium rosmarinifolium	(Benth.) Wedd.	Asteraceae
Diplostephium rosmarinifolium	(Benth.) Wedd.	Asteraceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Drimys granadensis	L.f.	Winteraceae
Dryopteris sp		Dryopteridaceae
Duranta mutisii	L.f.	Verbenaceae
Elaphoglossum cuspidatum	(Willd.) T. Moore	Dryopteridaceae
Elaphoglossum engelii	(H. Karst.) Christ	Dryopteridaceae
Elaphoglossum gayanum	(Fée) T. Moore	Dryopteridaceae
Elaphoglossum latifolium	(Sw.) J. Sm.	Dryopteridaceae
Elaphoglossum lindenii	(Bory ex Fée) T. Moore	Dryopteridaceae
Elaphoglossum lingua	(C. Presl) Brack.	Dryopteridaceae
Elaphoglossum minutum	(Pohl ex Fée) T. Moore	Dryopteridaceae
Elaphoglossum sp		Dryopteridaceae
Elleanthus aurantiacus	(Lindl.) Rchb.f.	Orchidaceae
Elleanthus maculatus	(Lindl.) Rchb.f.	Orchidaceae
Elleanthus purpureus	(Rchb.f.) Rchb.f.	Orchidaceae
Elleanthus sp		Orchidaceae
Epidendrum caesaris	Hágsater & E.Santiago	Orchidaceae
Epidendrum cylindraceum	Lindl.	Orchidaceae
Epidendrum excisum	Lindl.	Orchidaceae
Epidendrum moritzii	Rchb.f.	Orchidaceae
Epidendrum scutella	Lindl.	Orchidaceae
Epidendrum sisgaense	Hágsater	Orchidaceae
Epidendrum sp1		Orchidaceae
Epidendrum sp2		Orchidaceae
Epidendrum sp3		Orchidaceae
Epidendrum sp4		Orchidaceae
Equisetum bogotense	Kunth	Equisetaceae
Eriosorus flexuosus	(Kunth) Copel.	Pteridaceae
Escallonia myrtilloides	L.f.	Escalloniaceae
Espeletiopsis corymbosa	(Humb. & Bonpl.) Cuatrec.	Asteraceae
Faramea sp		Rubiaceae
Fernandezia crystallina	(Lindl.) M.W.Chase	Orchidaceae
Fernandezia sanguinea	(Lindl.) Garay & Dunst.	Orchidaceae
Fragaria vesca[a]	L.	Rosaceae
Frangula goudotiana	(Triana & Planch.) Grubov	Rhamnaceae
Frangula sp		Rhamnaceae
Frangula sphaerosperma	(Sw.) Kartesz & Gandhi	Rhamnaceae
Fuchsia boliviana[a]	Carrière	Onagraceae
Fuchsia magellanica[a]	Lam.	Onagraceae
Fuchsia paniculata[a]	Lindl.	Onagraceae
Gaiadendron punctatum	(Ruiz & Pav.) G.Don	Loranthaceae
Galianthe bogotensis	(Kunth) E.L.Cabral & Bacigalupo	Rubiaceae
Galium ascendens	Willd. ex Spreng.	Rubiaceae
Galium hypocarpium	(L.) Endl. ex Griseb.	Rubiaceae
Gnaphalium americanum	Mill.	Asteraceae
Gaultheria anastomosans	(Mutis ex L.f.) Kunth	Ericaceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Gaultheria erecta	Vent.	Ericaceae
Geissanthus andinus	Mez	Primulaceae
Geranium holosericeum	Willd. ex Spreng.	Geraniaceae
Greigia stenolepis	L.B.Sm.	Bromeliaceae
Habenaria sp		Orchidaceae
Hedyosmum racemosum	(Ruiz & Pav.) G.Don	Chloranthaceae
Heppiella ulmifolia	(Kunth) Hanst.	Gesneriaceae
Hesperomeles goudotiana	(Decne.) Killip	Rosaceae
Hesperomeles obtusifolia	(Pers.) Lindl.	Rosaceae
Hieracium avilae	Kunth	Asteraceae
Huperzia hippuridea	(Christ) Holub	Lycopodiaceae
Hydrocotyle bonplandii	A.Rich.	Araliaceae
Hydrocotyle gunnerifolia	Wedd.	Araliaceae
Hydrocotyle tenerrima	Rose ex Mathias	Araliaceae
Hymenophyllum myriocarpum	Hook.	Hymenophyllaceae
Hypericum juniperinum	Kunth	Hypericaceae
Hypochaeris radicata[a]	L.	Asteraceae
Ilex kunthiana	Triana	Aquifoliaceae
Ilex sp		Aquifoliaceae
Jungia ferruginea	L.f.	Asteraceae
Lantana camara	L.	Verbenaceae
Lantana rugosa	Thunb.	Verbenaceae
Lepanthes gargantua	Rchb.f.	Orchidaceae
Lepidaploa canescens	(Kunth) Cass.	Asteraceae
Luzula gigantea	Desv.	Juncaceae
Lycopodium clavatum	L.	Lycopodiaceae
Lycopodium jussiaei	Desv. ex Poir.	Lycopodiaceae
Macleania rupestris	(Kunth) A.C.Sm.	Ericaceae
Macrocarpaea glabra	(L. f.) Gilg	Gentianaceae
Malaxis crispifolia	(Rchb.f.) Kuntze	Orchidaceae
Malaxis sp		Orchidaceae
Matelea mutisiana	Morillo	Apocynaceae
Maxillariella graminifolia	(Kunth) M.A.Blanco & Carnevali	Orchidaceae
Maxillaria sp		Orchidaceae
Ctenopteris flabelliformis	(Poir.) J. Sm.	Polypodiaceae
Melpomene moniliformis	(Lag. ex Sw.) A.R. Sm. & R.C. Moran	Polypodiaceae
Miconia elaeoides	Naudin	Melastomataceae
Miconia latifolia	(D. Don) Naudin	Melastomataceae
Miconia ligustrina	(Sm.) Triana	Melastomataceae
Miconia micropetala	Cogn.	Melastomataceae
Miconia squamulosa	Triana	Melastomataceae
Miconia theizans	(Bonpl.) Cogn.	Melastomataceae
Monnina aestuans	(L.f.) DC.	Polygalaceae
Monnina fastigiata	(Bonpl.) DC.	Polygalaceae
Monochaetum bonplandii	(Humb. & Bonpl.) Naudin	Melastomataceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Monochaetum myrtoideum	Naudin	Melastomataceae
Morella parvifolia	(Benth.) Parra-Os.	Myricaceae
Munnozia senecionidis	Benth.	Asteraceae
Myrcianthes leucoxyla	(Ortega) McVaugh	Myrtaceae
Myrsine coriacea	(Sw.) R.Br. ex Roem. & Schult.	Primulaceae
Myrsine dependens	(Ruiz & Pav.) Spreng.	Primulaceae
Myrsine guianensis	(Aubl.) Kuntze	Primulaceae
Myrsine sp		Primulaceae
Nertera granadensis	(Mutis ex L.f.) Druce	Rubiaceae
Niphogeton		Apiaceae
Ocotea heterochroma	Mez & Sodiro	Lauraceae
Ocotea longifolia	Kunth	Lauraceae
Oligactis sessiliflora	(Kunth) H.Rob. & Brettell	Asteraceae
Oreopanax bogotensis	Cuatrec.	Araliaceae
Oreopanax incisus	(Willd. ex Schult.) Decne. & Planch.	Araliaceae
Oreopanax mutisianus	(Kunth) Decne. & Planch.	Araliaceae
Orthrosanthus chimboracensis	(Kunth) Baker	Iridaceae
Oxalis acetosella[a]	L.	Oxalidaceae
Oxalis corniculata[a]	L.	Oxalidaceae
Oxalis medicaginea	Kunth	Oxalidaceae
Oxalis spiralis	Ruiz & Pav. ex G.Don	Oxalidaceae
Oxalis tuberosa	Molina	Oxalidaceae
Palicourea angustifolia	Kunth	Rubiaceae
Palicourea lineariflora	Wernham	Rubiaceae
Panicum sp		Poaceae
Paspalum bonplandianum	Flüggé	Poaceae
Passiflora adulterina	L. f.	Passifloraceae
Passiflora bogotensis	Benth.	Passifloraceae
Passiflora capsularis	L.	Passifloraceae
Passiflora sp		Passifloraceae
Passiflora tripartita	(Juss.) Poir.	Passifloraceae
Pecluma divaricata	(E. Fourn.) Mickel & Beitel	Polypodiaceae
Pecluma paradiseae	(Langsd. & Fisch.) M.G. Price	Polypodiaceae
Pecluma sp		Polypodiaceae
Pentacalia nitida	(Kunth) Cuatrec.	Asteraceae
Monticalia pulchella	(Kunth) C.Jeffrey	Asteraceae
Peperomia alibacophylla	Trel. & Yunck.	Piperaceae
Peperomia dendrophila	Schltdl.	Piperaceae
Peperomia arthurii	Trel. & Yunck.	Piperaceae
Peperomia emarginulata	C.DC.	Piperaceae
Peperomia galioides	Kunth	Piperaceae
Peperomia glabella	(Sw.) A.Dietr.	Piperaceae
Peperomia hartwegiana	Miq.	Piperaceae
Peperomia microphylla	Kunth	Piperaceae
Peperomia rotundata	Kunth	Piperaceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Peperomia suratana	Trel. & Yunck.	Piperaceae
Pernettya sp		Ericaceae
Gaultheria myrsinoides	Kunth	Ericaceae
Persea ruizii	J.F.Macbr.	Lauraceae
Phenax rugosus	(Poir.) Wedd.	Urticaceae
Phyllanthus salviifolius	Kunth	Phyllanthaceae
Physalis peruviana[a]	L.	Solanaceae
Pilea alsinifolia	Wedd.	Urticaceae
Pilea goudotiana	Wedd.	Urticaceae
Pilea lindeniana	Wedd.	Urticaceae
Pilea sp		Urticaceae
Piper artanthe	C.DC.	Piperaceae
Piper bogotense	C.DC.	Piperaceae
Piper marginatum	Jacq.	Piperaceae
Plagiogyria pectinata	(Liebm.) Lellinger	Plagiogyriaceae
Pleopeltis macrocarpa	(Bory ex Willd.) Kaulf.	Polypodiaceae
Pleopeltis sp 1		Polypodiaceae
Pleopeltis sp 2		Polypodiaceae
Pleopeltis sp 3		Polypodiaceae
Pleurothallis lindenii	Lindl.	Orchidaceae
Pleurothallis linguifera	Lindl.	Orchidaceae
Podocarpus oleifolius	D.Don	Podocarpaceae
Polystichum lehmannii	Hieron.	Dryopteridaceae
Ponthieva similis	C.Schweinf.	Orchidaceae
Prunus sp		Rosaceae
Psychotria boqueronensis	Wernham	Rubiaceae
Pteridium aquilinum	(L.) Kuhn	Dennstaedtiaceae
Pteris muricata	Hook.	Pteridaceae
Rhynchospora macrochaeta	Steud. ex Boeckeler	Cyperaceae
Rhynchospora nervosa	(Vahl) Boeckeler	Cyperaceae
Rhynchospora sp		Cyperaceae
Rubus floribundus	Kunth	Rosaceae
Rubus wardii	Merr.	Rosaceae
Rubus sp		Rosaceae
Rubus ulmifolius	Schott	Rosaceae
Salvia sp		Lamiaceae
Sauvagesia erecta	L.	Ochnaceae
Serpocaulon eleutherophlebium	(Fée) A.R. Sm.	Polypodiaceae
Serpocaulon lasiopus	(Klotzsch) A.R. Sm.	Polypodiaceae
Serpocaulon levigatum	(Cav.) A.R. Sm.	Polypodiaceae
Serpocaulon sp		Polypodiaceae
Serpocaulon sessilifolium	(Desv.) A.R. Sm.	Polypodiaceae
Setaria italica[a]	(L.) P.Beauv.	Poaceae
Siphocampylus brevicalyx	E.Wimm.	Campanulaceae
Smallanthus pyramidalis	(Triana) H.Rob.	Asteraceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Smilax cuspidata	Duhamel	Smilacaceae
Smilax sp 1		Smilacaceae
Smilax sp 2		Smilacaceae
Smilax tomentosa	Kunth	Smilacaceae
Solanum caripense	Dunal	Solanaceae
Solanum cornifolium	Dunal	Solanaceae
Solanum pseudocapsicum	L.	Solanaceae
Solanum sp 1		Solanaceae
Solanum sp 2		Solanaceae
Sphyrospermum buxifolium	Poepp. & Endl.	Ericaceae
Stachys arvensis[a]	(L.) L.	Lamiaceae
Stelis argentata	Lindl.	Orchidaceae
Stelis galeata	(Lindl.) Pridgeon & M.W.Chase	Orchidaceae
Stelis pulchella	Kunth	Orchidaceae
Stelis pusilla	Kunth	Orchidaceae
Stelis sp 1		Orchidaceae
Stelis sp 2		Orchidaceae
Stelis sp 3		Orchidaceae
Stelis sp 4		Orchidaceae
Stelis sp 5		Orchidaceae
Stelis sp 6		Orchidaceae
Stelis sp 7		Orchidaceae
Stelis sp 8		Orchidaceae
Stelis sp 9		Orchidaceae
Stenorrhynchos speciosum	(Jacq.) Rich.	Orchidaceae
Styrax sp		Styracaceae
Symplocos lucida	(Thunb.) Siebold & Zucc.	Symplocaceae
Thelypteris rudis	(Kunze) Proctor	Thelypteridaceae
Tibouchina grossa	(L. f.) Cogn.	Melastomataceae
Tigridia pavonia[a]	(L.f.) DC.	Iridaceae
Tillandsia biflora	Ruiz & Pav.	Bromeliaceae
Tillandsia complanata	Benth.	Bromeliaceae
Tillandsia elongata	Kunth	Bromeliaceae
Tillandsia sp 1		Bromeliaceae
Tillandsia sp 2		Bromeliaceae
Tillandsia sp 3		Bromeliaceae
Tillandsia sp 4		Bromeliaceae
Tillandsia sp 5		Bromeliaceae
Tillandsia sp 6		Bromeliaceae
Tillandsia sp 7		Bromeliaceae
Tillandsia sp 8		Bromeliaceae
Tradescantia sp 1[a]		Commelinaceae
Tradescantia sp 2[a]		Commelinaceae
Ulex europaeus[a]	L.	Fabaceae
Uncinia hamata	(Sw.) Urb.	Cyperaceae

(Continues)

APPENDIX A3 (Continued)

Accepted name	Accepted author	Accepted family
Vaccinium floribundum	Kunth	Ericaceae
Valeriana clematitis	Kunth	Caprifoliaceae
Vallea stipularis	L.f.	Elaeocarpaceae
Cordia cylindrostachya	(Ruiz & Pav.) Roem. & Schult.	Boraginaceae
Villanova oppositifolia	Lag.	Asteraceae
Viburnum tinoides	L.f.	Adoxaceae
Viburnum triphyllum	Benth.	Adoxaceae
Weinmannia fagaroides	Kunth	Cunoniaceae
Weinmannia tomentosa	L.f.	Cunoniaceae
Xylosma spiculifera	(Tul.) Triana & Planch.	Salicaceae

[a] Exotic or mainly cultivated.

LIST OF PLOT-RESOLVED COLLECTED VOUCHERS

Collection number (MSC)	Locality	Plot	Species
1	Torca, La Francia	M1	*Ocotea heterocroma*
2	Torca, La Francia	M1	*Daphnopsis caracasana*
3	Torca, La Francia	M1	*Oligactis volubilis*
4	Torca, La Francia	M1	*Oligactis volubilis*
5	Torca, La Francia	M1	*Viburnum tinoides*
6	Torca, La Francia	M1	*Daphnopsis caracasana*
7	Torca, La Francia	M1	*Palicourea (angustifolia)*
8	Torca, La Francia	M1	*Oreopanax incisus*
9	Torca, La Francia	M1	*Daphnopsis caracasana*
10	Torca, La Francia	M1	*Bejaria aestuans*
11	Torca, La Francia	M1	*Piper arthanthe*
12	Torca, La Francia	M1	*Daphnopsis caracasana*
13	Torca, La Francia	M1	*Miconia squamulosa*
14	Torca, La Francia	M1	*Viburnum tryphyllum*
15	Torca, La Francia	M1	*Macleania rupestris*
16	Torca, La Francia	M1	*Daphnopsis caracasana*
17	Torca, La Francia	M1	*Myrcianthes leucoxyla*
18	Torca, La Francia	M1	*Vallea stipularis*
19	Torca, La Francia	M1	*Bejaria resinosa*
20	Torca, La Francia	M1	*Myrsine coriacea*
21	Torca, La Francia	M1	*Cytarexylum sulcatum*
22	Torca, La Francia	M1	*Macleania rupestris*
23	Torca, La Francia	M1	*Smilax tomentosa*
24	Torca, La Francia	M1	*Bejaria aestuans*
25	Torca, La Francia	M1	*Ilex kunthiana*
26	Torca, La Francia	M1	*Bidens pilosa*
27	Torca, La Francia	M1	*Bejaria resinosa*
28	Torca, La Francia	M1	*Oreopanax incisus*
29	Torca, La Francia	M1	*Daphnopsis caracasana*
30	Torca, La Francia	M1	*Daphnopsis caracasana*
31	Torca, La Francia	M1	*Myrcianthes leucoxyla*

(Continues)

APPENDIX A3 (Continued)

Collection number (MSC)	Locality	Plot	Species
32	Torca, La Francia	M1	*Daphnopsis caracasana*
33	Torca, La Francia	M1	*Daphnopsis caracasana*
34	Torca, La Francia	M1	*Xylosma spiculifera*
35	Torca, La Francia	M1	*Psycothrya boqueronensis*
36	Torca, La Francia	M1	*Miconia squamulosa*
37	Torca, La Francia	M1	*Psycothrya boqueronensis*
38	Torca, La Francia	M1	*Xylosma spiculifera*
39	Torca, La Francia	M1	*Myrsine coriacea*
40	Torca, La Francia	M1	*Daphnopsis caracasana*
41	Torca, La Francia	M1	*Daphnopsis caracasana*
42	Torca, La Francia	M2	*Alnus accuminata*
43	Torca, La Francia	M2	*Cavendishia bracteata*
44	Torca, La Francia	M2	*Vallea stipularis*
45	Torca, La Francia	M2	*Cavendishia bracteata*
46	Torca, La Francia	M2	*Cavendishia nitida*
47	Torca, La Francia	M2	*Vallea stipularis*
48	Torca, La Francia	M2	*Hesperomeles goudotiana*
49	Torca, La Francia	M2	*Diplostephium rosmarinifolius*
50	Torca, La Francia	M2	*Viburnum tryphyllum*
51	Torca, La Francia	M2	*Miconia squamulosa*
52	Torca, La Francia	M2	*Viburnum tinoides*
53	Torca, La Francia	M2	*Viburnum tinoides*
54	Torca, La Francia	M2	*Bejaria aestuans*
55	Torca, La Francia	M2	*Clusia multiflora*
56	Torca, La Francia	M2	*Viburnum tryphyllum*
57	Torca, La Francia	M2	*Daphnopsis caracasana*
58	Torca, La Francia	M2	*Daphnopsis caracasana*
59	Torca, La Francia	M2	*Daphnopsis caracasana*
60	Torca, La Francia	M2	*Xylosma spiculifera*
61	Torca, La Francia	M2	*Daphnopsis caracasana*
62	Torca, La Francia	M2	*Cavendishia bracteata*
63	Torca, La Francia	M2	*Myrcianthes leucoxyla*
64	Torca, La Francia	M2	*Gaiadendron punctatum*
65	Torca, La Francia	M2	*Oreopanax incisus*
66	Torca, La Francia	M2	*Oreopanax incisus*
67	Torca, La Francia	M1	*Xylosma spiculifera*
68	Torca, La Francia	M2	*Bejaria resinosa*
69	Torca, La Francia	M2	*Miconia squamulosa*
70	Torca, La Francia	M2	*Hesperomeles goudotiana*
71	Torca, La Francia	M2	*Myrsine pellucida*
72	Torca, La Francia	M2	*Viburnum tinoides*
73	Torca, La Francia	M2	*Myrsine guianensis*
74	Torca, La Francia	M2	*Aiouea dubia*
75	Torca, La Francia		*Alnus accuminata*
76	Torca, La Francia	M3	*Cavendishia bracteata*

(Continues)

APPENDIX A3 (Continued)

Collection number (MSC)	Locality	Plot	Species
77	Torca, La Francia	M3	*Gaiadendron punctatum*
78	Torca, Colegio	M4	*Gaiadendron punctatum*
79	Torca, Colegio	M4	*Peperomia rotundata*
80	Torca, Colegio	M4	*Frangula sphaerosperma*
81	Torca, Colegio	M4	*Cavendishia nitida*
82	Torca, Colegio	M4	*Palicourea angustifolia*
86	San Juan de Sumapaz, don Hernan	M8	*Hesperomeles ferruginea*
87	Torca colegio	M5	*Aiouea dubia*
88	Torca colegio	M5	*Phyllantus salvifolius*
89	Pasquilla los Encenillales	M2-M6	*Gaiadendron punctatum*
90	Pasquilla los Encenillales	M2-M6	*Bejaria resinosa*
91	Pasquilla los Encenillales	M2-M6	*Myrsine dependens*
92	Pasquilla los Encenillales	M2-M6	*Myconia ligustrina*
93	Pasquilla los Encenillales	M2-M6	*Diplostephium rosmarinifolius*
94	Pasquilla los Encenillales	M2-M6	*Vallea stipularis*
95	Pasquilla los Encenillales	M2-M6	*Cavendishia bracteata*
96	Pasquilla los Encenillales	M2-M6	*Hesperomeles goudotiana*
97	Pasquilla los Encenillales	M2-M6	*Bucquetia glutinosa*
98	Pasquilla los Encenillales	M2-M6	*Viburnum tryphyllum*
99	Pasquilla los Encenillales	M2-M6	*Ageratina glyptophlebia*
100	Torca la francia	M1	*Peperomia glabella*
101	Torca la francia	M1	*Pleopeltis macrocarpa*
102	Torca la francia	M1	*Pleopeltis murora*
103	Torca la francia	M1	*Pleurothallis linguifera*
104	Pasquilla los Encenillales	M2	*Ponthieva similis*
105	Torca colegio	M4	*Chromolaena perglabra*
106	Torca colegio	M4	*Peperomia suratana*
107	Torca colegio	M4	*Epidendrum* sp.
108	Torca colegio	M4	*Serpocaulon eleutherophlebium*
109	Pasquilla los Encenillales	M2-M6	*Hymenophyllum myriocarpum*
110	Pasquilla los Encenillales	M2-M6	*Melpomene flabelliformis*
111	Pasquilla los Encenillales	M2-M6	*Pecluma paradisiaca*
112	Pasquilla los Encenillales	M2-M6	*Elaphpglossum gayanum*
113	Pasquilla los Encenillales	M2-M6	*Hydrocotile tenerrima*
114	Pasquilla los Encenillales	M2-M6	*Lycopodium clavatum*
115	Pasquilla los Encenillales	M2-M6	*Bidens triplinervia*
116	Pasquilla los Encenillales	M2-M6	*Passiflora adulterina*
117	Pasquilla los Encenillales	M2-M6	*Malaxis crispifolia*
118	Torca colegio	M5	*Pilea parietaria*
119	Torca colegio	M5	*Thelypteris* sp.
120	Torca colegio	M5	*Pilea* sp.
121	Torca colegio	M5	*Gaultheria* sp.
122	Sumapaz san Juan	M7-M7bis	*Ageratina glyptophlebia*
123	Sumapaz san Juan	M7-M7bis	*Miconia eleanoides*

(Continues)

APPENDIX A3 (Continued)

Collection number (MSC)	Locality	Plot	Species
124	Sumapaz san Juan	M7-M7bis	*Hesperomeles goudotiana*
125	Sumapaz san Juan	M7-M7bis	*Hesperomeles ferruginea*
126	Sumapaz san Juan	M7-M7bis	*Ilex* sp.
127	Sumapaz san Juan	M7-M7bis	*Persea ferruginea*
128	Sumapaz san Juan	M7-M7bis	*Vaccinium floribundum*
129	Sumapaz san Juan	M7-M7bis	*Ageratina glyptophlebia*
130	Sumapaz san Juan	M7-M7bis	*Ilex kunthiana*
131	Torca- conjunto floresta	R11-R12-R14	*Serpocaulon sessilifolium*
132	Torca- conjunto floresta	R11-R12-R14	*Epidendrum excisum*
133	Torca- conjunto floresta	R11-R12-R14	*Elleanthus purpureus*
134	Torca- conjunto floresta	R11-R12-R14	*Stelis cassidis*
135	Torca- conjunto floresta	R11-R12-R14	*Epidendrum brachyorodochilum*
136	Torca- conjunto floresta	R11-R12-R14	*Pleurothallis* sp.
137	Torca- conjunto floresta	R11-R12-R14	*Stelis* sp.
138	Torca- conjunto floresta	R11-R12-R14	*Frangula sphaerosperma*
139	Torca- conjunto floresta	R11-R12-R14	*Ocotea longifolia*
140	Tabio	R8-R7	*Cardamine ovata*
141	Tabio	R8-R7	*Valeriana clematis*
142	Tabio	R8-R7	*Rhyncospora nervosa*
143	Tabio	R8-R7	*Zeugites* sp.
144	Tabio	R8-R7	*Asplenium praemorsum*
145	Tabio	R8-R7	*Oxalis acetosella*
146	Tabio	R8-R7	*Tradescantia* sp.
147	Tabio	R8-R7	*Lantana* sp.
148	Tabio	R8-R7	*Palicourea linearifolia*
149	Tabio	R8-R7	*Piper bogotense*
150	Tabio	R8-R7	*Daphnopsis caracasana*
151	Tabio	R8-R7	*Peperomia angularis*
152	Tabio	R8-R7	*Cuphea hyssopifolia*
153	Tabio	R8-R7	*Peperomia galioides*
154	Tabio	R8-R7	*Asteraceae* sp.
155	Tabio	R8-R7	*Galianthe bogotensis*
156	Tabio	R8-R7	*Anthoxanthum odoratum*
157	Tabio	R8-R7	*Setaria italica*
158	Tabio	R8-R7	*Serpocaulon laevigatum*
159	Tabio	R8-R7	*Uncinia hamata*
160	Sumapaz san Juan	M8-M8bis	*Ageratina tinifolia*
161	Sumapaz san Juan	M8-M8bis	*Baccharis macrantha*
162	Sumapaz san Juan	M8-M8bis	*Rhyncospora macrochaeta*
163	Sumapaz san Juan	M8-M8bis	*Miconia resima*
164	Sumapaz san Juan	M8-M8bis	*Carex pichinchensis*
165	Sumapaz san Juan	M8-M8bis	*Rubus acantophilus*
166	Sumapaz san Juan	M8-M8bis	*Bucquetia glutinosa*
167	Sumapaz san Juan	M8-M8bis	*Escallonia myrtillioides*

(Continues)

APPENDIX A3 (Continued)

Collection number (MSC)	Locality	Plot	Species
168	Sumapaz san Juan	M8-M8bis	*Hymenophyllum myriocarpum*
169	Sumapaz san Juan	M8-M8bis	*Podocarpus oleifolia*
170	Sumapaz san Juan	M8-M8bis	*Ilex* sp.
171	Sumapaz san Juan	M8-M8bis	*Miconia eleanoides*
172	Sumapaz san Juan	M8-M8bis	*Calceolaria microbefaria*
173	Torca- conjunto floresta	R13	*Conyza canadensis*
174	Torca- conjunto floresta	R13	*Arrenatherum elatius*
175	Torca- conjunto floresta	R13	*Peperomia accuminata*
176	Torca- conjunto floresta	R13	*Fuchsia boliviana*
177	Torca- conjunto floresta	R13	*Serpocaulon laevigatum*
178	Torca- conjunto floresta	R13	*Criotonopsis bogotana*
179	Torca- conjunto floresta	R13	*Miconia resima*
180	Torca- conjunto floresta	R13	*Fragaria vesca*
182	Torca- conjunto floresta	R13	*Gamochaete americana*
183	Tabio	R9-R10	*Pleopeltis macrocarpa*
184	Tabio	R9-R10	*Pleopeltis murora*
185	Tabio	R9-R10	*Peperomia cf spatulata*
186	Tabio	R9-R10	*Botrichium virginianum*
187	Tabio	R9-R10	*Peperomia* sp.
188	Tabio	R9-R10	*Asplenium sp.*
189	Tabio	R9-R10	*Oxalis cf macrocarpa*
190	Tabio	R9-R10	*Stelis* sp.
191	Tabio	R9-R10	*Miconia squamulosa*
192	Tabio	R9-R10	*Cestrum buxifolium*
193	Tabio	R9-R10	*Alonsoa meridionalis*
194	Tabio	R9-R10	*Pilea lindeniana*
195	Tabio	R9-R10	*Epidendrum scutella*
196	Tabio	R9-R10	*Phyllantus salvifolius*
197	Tabio	R9-R10	*Galium* sp.
198	Tabio	R9-R10	*Palicourea linearifolia*
199	Tabio	R9-R10	*Uncinia hamata*
200	Tabio	R9-R10	*Xylosma spiculifera*
201	Tabio	R9-R10	*Clematis*
202	Tabio	R9-R10	*Peperomia suratana*
203	Tabio	R9-R10	*Rhyncospora macrochaeta*
204	Tabio	R9-R10	*Cardamine ovata*
205	Tabio	R9-R10	*Ponthieva similis*
206	Tabio	R9-R10	*Ageratina* sp.
207	Encenillo	R3-R5	*Stelis* sp.
208	Encenillo	R3-R5	*Lepanthes gargantua*
209	Encenillo	R3-R5	*Nertera granadensis*
210	Encenillo	R3-R5	*Pleurothallis lindenii*
211	Encenillo	R3-R5	*Huperzia* sp.
212	Encenillo	R3-R5	*Stelis* sp.
213	Encenillo	R3-R5	*Sphyrospermum buxifolium*

(Continues)

APPENDIX A3 (Continued)

Collection number (MSC)	Locality	Plot	Species
214	Encenillo	R3-R5	*Peperomia arthurii*
215	Pasquilla Finca Alveiro	M9bis-M10	*Smallanthus pyramidalis*
216	Pasquilla Finca Alveiro	M9bis-M10	*Elleanthus aurantiacus*
217	Pasquilla Finca Alveiro	M9bis-M10	*Rhyncospora* sp.
218	Pasquilla Finca Alveiro	M9bis-M10	*Peperomia microphylla*
219	Pasquilla Finca Alveiro	M9bis-M10	*Gaultheria anastomosans*
220	Pasquilla Finca Alveiro	M9bis-M10	*Epidendrum caesaris*
221	Pasquilla Finca Alveiro	M9bis-M10	*Elaphoglossum lindenii*
222	Pasquilla Finca Alveiro	M9bis-M10	*Apiaceae* sp.
223	Pasquilla Finca Alveiro	M9bis-M10	*Serpocaulon lasiopus*
224	Pasquilla Finca Alveiro	M9bis-M10	*Melastomataceae*
225	Pasquilla Finca Alveiro	M9bis-M10	*Digitalis purpurea*
226	Pasquilla Finca Alveiro	M9bis-M10	*Oxalis cf spiralis*
227	Pasquilla Finca Alveiro	M9bis-M10	*Berberis rigidifolia*
228	Pasquilla Finca Alveiro	M9bis-M10	*Bidens* sp.
229	Pasquilla Finca Alveiro	M9bis-M10	*Elaphoglossum gayanum*
230	Pasquilla Finca Alveiro	M9bis-M10	*Baccharis bogotensis*
231	Pasquilla Finca Alveiro	M9bis-M10	*Ageratina asclepiadea*
232	Pasquilla Finca Alveiro	M9bis-M10	*Weinmannia tomentosa*
233	Pasquilla Finca Alveiro	M9bis-M10	*Hypochaeris radicata*
234	Pasquilla Finca Alveiro	M9bis-M10	*Peperomia* sp.
235	Pasquilla Finca Alveiro	M9bis-M10	*Cytarexylum sulcatum*
236	Pasquilla Finca Alveiro	M9bis-M10	*Morella parvifolia*
237	Pasquilla Finca Alveiro	M9bis-M10	*Vallea stipularis*
238	Pasquilla Finca Alveiro	M9bis-M10	*Bidens* sp.
239	Pasquilla Finca Alveiro	M9bis-M10	*Galium* sp.
240	Pasquilla Finca Alveiro	M9bis-M10	*Hypericum juniperinum*
241	Pasquilla Finca Alveiro	M9bis-M10	*Vaccinium floribundum*
242	Torca-Portal de Fusca	R17-R18	*Campyloneuron latum*
243	Torca-Portal de Fusca	R17-R18	*Athyrium flix-femina*
244	Torca-Portal de Fusca	R17-R18	*Clethra fimbriata*
245	Torca-Portal de Fusca	R17-R18	*Hieracium avilae*
246	Torca-Portal de Fusca	R17-R18	*Cranichis ciliata*
247	Torca-Portal de Fusca	R17-R18	*Nyphogeton* sp.
248	Torca-Portal de Fusca	R17-R18	*Jungia ferruginea*
249	Torca-Portal de Fusca	R17-R18	*Frangula goudotiana*
250	Torca-Portal de Fusca	R17-R18	*Pilea sp foglie serrate*
251	Torca-Portal de Fusca	R17-R18	*Syphocampilus columnae*
252	Torca-Portal de Fusca	R17-R18	*Pilea lindeniana*
253	Torca-Portal de Fusca	R17-R18	*Uncinia hamata*
254	Torca-Portal de Fusca	R17-R18	*Asplenium monantes*
255	Torca-Portal de Fusca	R17-R18	*Peperomia suratana*
256	Torca-Portal de Fusca	R17-R18	*Carex* sp.
257	Torca-Portal de Fusca	R17-R18	*Eriosorus flexuosus*
258	Torca-Portal de Fusca	R17-R18	*Asplenium cladolepton*

(Continues)

APPENDIX A3 (Continued)

Collection number (MSC)	Locality	Plot	Species
265	Encenillo	R15-R16	*Fernandezia sanguinea*
266	Encenillo	R15-R16	*Macrocarpaea glabra*
267	Encenillo	R15-R16	*Frangula goudotiana*
268	Encenillo	R15-R16	*Stelis* sp.
269	Encenillo	R15-R16	*Diphasiastrum thyoides*
270	Encenillo	R15-R16	*Ponthieva villosa*
271	Encenillo	R15-R16	*Stelis* sp.
272	Encenillo	R15-R16	*Stelis* sp.
273	Tabio	R20	*Maxillaria graminifolia*
274	Tabio	R19	*Phenax rugosus*
275	Tabio	R19	*Pleurothallis* sp.
277	Tabio	R19	*Pecluma divaricata*
278	Tabio	R19	*Pleopeltis murora*
279	Tabio	R19	*Cystopteris fragilis*
280	Tabio	R19	*Adiantum andicola*
281	Tabio	R19	*Asplenium radicans*

APPENDIX A4

List of retrievable aerial pictures

Quadrant	Year	Folder number	Flight number	Picture number	Corresponding plot
K-11	1962	s-222336A	c-1063	1800	Torca
K-11	1940	s-501	a-136	157;156	Torca
K-11	1940	s-777	c-16	387;385;383;381	Torca
K-11	1962	22214B	c-1058	1165;1164	Torca
K-11	1978	s-4542	r-750	153;152;151	Torca
K-11	1986	digitalized	c-2265	9	Torca
K-11	1993	digitalized	c-2523	217	Torca
K-11	2000	digitalized	r-1212	129	Torca
K-11	2004	digitalized	c-2717	259	Torca
K-10	1940	s-913	c-71	704;703	Tabio
K-10	1957	s-239	m-127	1863	Tabio
K-10	1961	s-22340	c-1082	2478	Tabio
K-10	1993	s-36949	c-2521	82	Tabio
K-10	1998	s-37851	c-2636	225	Tabio
K-10	2007	s-40778	c-2800	83	Tabio
L-10	1948	s-2159	c-502	281	Sumapaz
L-10	1951	s-2715	c-606	290	Sumapaz
L-10	1961	s-2282	R-487	46	Sumapaz
L-10	1963	s-1136	M-1266	26084	Sumapaz
L-10	1987	s-34455	c-2323	220	Sumapaz
L-10	1996	s-37521B	c-2584	120	Sumapaz
L-10	1941	s-668	a-232	72;70	Pasquilla
L-10	1961	s-895	m-1142	18941;18940	Pasquilla
L-10	1977	s-29014	?	81:86	Pasquilla

(Continues)

APPENDIX A4 (Continued)

Quadrant	Year	Folder number	Flight number	Picture number	Corresponding plot
L-10	1981	s-30657	c-1985	94	Pasquilla
L-10	1993	s-36950	c-2521	129	Pasquilla
L-10	2007	s-40802	c-2803	170	Pasquilla
K-11	1940	s-530	a-148	152	Guatavita
K-11	1958	s-21249	c-859	531	Guatavita
K-11	1962	s-222236B	c-1063	1812	Guatavita
K-11	1997	digitalized	c-2611	12	Guatavita
K-11	2007	digitalized	c-2799	63	Guatavita
K-11	?	digitalized	c-2471	54	Guatavita
K-11	?	digitalized	c-2673	667	Guatavita
K-11	1940	s-501	a-136	164	Guasca
K-11	1955	s-148	m-46	4475	Guasca
K-11	1958	s-21265	c-860	174	Guasca
K-11	1963	s-22194A	c-1055	425	Guasca
K-11	1978	s-29190	c-1808	13	Guasca
K-11	1985	digitalized	c-2183	39	Guasca
K-11	1993	digitalized	c-2523	144	Guasca
K-11	2007	digitalized	c-2799	56	Guasca
K-11	2010	digitalized	22803002012010	500	Guasca

APPENDIX A5

Indicator species analysis values (IVI) for tree and understory layer

TREES

Species	Cluster	Value (IV)	Mean	*SD*	p^*
Miconia elaeoides	1	92	22.8	8.87	.0002
Myrcianthes leucoxyla	1	63.4	26.7	11.24	.0122
Viburnum triphyllum	1	52	26.2	8.07	.0062
Vallea stipularis	1	32.8	25.8	7.42	.1664
Psychotria boqueronensis	1	30	18.7	10.34	.144
Aiouea dubia	1	20	18.7	9.16	.4105
Duranta mutisii	1	20	19.1	9.58	.5653
Frangula sphaerosperma	1	20	18.6	8.89	.2769
Lippia hirsuta	1	20	18.7	8.82	.4151
Maytenus laxiflora	1	20	19.2	10	.4747
Symplocos theiformis	1	18.5	20	10.47	.3391
Abatia parviflora	1	10	18.7	7.84	1
Barnadesia spinosa	1	10	18.7	7.84	1
Carica sp	1	10	18.7	7.84	1
Melastomataceae NA	1	10	18.7	7.84	1
Myrsine pellucida	1	10	18.9	8	1
Ocotea heterocroma	1	10	18.8	7.9	1
Pentacalia NA	1	10	18.7	8	1
Phyllanthus salviifolius	1	10	18.8	7.9	1

(Continues)

APPENDIX A5 (Continued)

Species	Cluster	Value (IV)	Mean	*SD*	p^*
Sessea corymbosa	1	10	18.8	7.98	1
Monticalia pulchella	2	80.1	23.3	11.3	.0002
Macleania rupestris	2	76.6	27.8	10.25	.0002
Ilex kunthiana	2	65.9	29.5	9.65	.001
Myrcianthes ropaloides	2	50	18.6	9.01	.045
Ageratina asclepiadea	2	45.1	25	13.52	.0792
Viburnum tinoides	2	34.8	19.5	10.85	.1012
Diplostephium ochraceum	2	30.8	18	10.22	.1236
Tibouchina grossa	2	25	18.8	7.93	.4757
Gaultheria anastomosans	3	100	19.3	10.97	.0004
Ageratina glyptophlebia	3	90.9	24.9	12.84	.0006
Bucquetia glutinosa	3	77.2	24.4	12.2	.0028
Ageratina boyacensis	3	75	20	10.42	.0032
Berberis glauca	3	75	20	11.34	.0038
Vaccinium floribundum	3	75	18.2	10.33	.0038
Myrsine dependens	3	67.5	23.3	11.28	.0056
Ageratina tinifolia	3	50	19.6	10.34	.0462
Blechnum schomburgkii	3	50	20.7	10.27	.0468
Hesperomeles ferruginea	3	50	19.3	9.97	.0462
Ilex sp1	3	50	18.9	9.17	.0468
Persea ferruginea	3	50	20.1	10.38	.0468
Polylepis quadrijuga	3	50	20.8	10.26	.0468
Weinmannia fagaroides	3	49.5	20.6	10.28	.046
Hesperomeles goudotiana	3	46	28.2	10.38	.0672
Miconia ligustrina	3	44.9	22.7	12.58	.076
Clethra fagifolia	3	25	18.7	7.88	.4699
Escallonia myrtilloides	3	25	18.8	7.92	.4701
Hesperomeles obtusifolia	3	25	18.9	7.98	.4753
Podocarpus oleifolia	3	25	18.8	7.92	.4701
Cestrum buxifolium	3	20.3	19.2	10.02	.4803
Myrsine coriacea	4	71.2	23.8	8.76	.0002
Clusia multiflora	4	67.7	21.9	11.04	.0038
Drimys granadensis	4	61.2	22.8	11.49	.0076
Weinmannia tomentosa	4	45.8	25.4	8.02	.0214
Hediosmum sp	4	42.9	20.3	11.21	.0846
Bejaria resinosa	4	41.7	23.6	9.28	.0532
Cavendishia nitida	4	31.5	22.2	11.12	.1824
Macrocarpaea glabra	4	28.6	19	9.56	.123
Ocotea calophylla	4	28.6	18.8	8.78	.0838
Palicourea demissa	4	28.6	18.5	8.84	.085
Myrsine latifolia	4	27.5	22.7	11.48	.2296
Frangula goudotiana	4	24.6	20.5	9.86	.2454

(Continues)

APPENDIX A5 (Continued)

Species	Cluster	Value (IV)	Mean	*SD*	*p**
Critoniopsis bogotana	4	16.5	20.2	10.33	.5909
Clethra lanata	4	14.3	18.7	7.99	.6699
Cybianthus iteoides	4	14.3	18.8	7.94	.6927
Aiouea sp1	4	11.4	19.4	10.29	.7518
Cavendishia bracteata	5	80.5	29	10.32	.0004
Diplostephium rosmarinifolius	5	78.5	29.7	13.98	.0054
Gaiadendron punctatum	5	75.2	22.1	10.95	.0018
Ulex europaeus	5	66.7	19.7	10.14	.0064
Alnus acuminata	5	54	19.1	10.64	.0148
Clethra fimbriata	5	43.9	20.9	11.39	.0528
Oreopanax bogotensis	5	36.4	20.9	11.38	.1054
Ageratina fastigiata	5	33.3	18.8	7.99	.096
Baccharis prunifolia	5	33.3	18.8	7.99	.096
Varronia cylindrostachya	6	73.1	20.9	11.42	.002
Myrsine guianensis	6	60	32.5	13.06	.0498
Oreopanax incisus	6	51.8	24.4	9.37	.0186
Daphnopsis caracasana	6	47	22.2	10.07	.023
Miconia squamulosa	6	46	28.8	11.19	.085
Piper bogotense	6	45.2	22.7	12.22	.0546
Xylosma spiculifera	6	40.1	23	10.16	.0666
Palicourea lineariflora	6	36.8	23.7	11.49	.1302
Baccharis macrantha	6	25	18.6	7.91	.4609
Bocconia frutescens	6	25	18.7	7.88	.4653
Cestrum sp	6	25	18.7	7.88	.4653
Solanum cornipholium	6	25	18.7	7.92	.4663
Valeriana clematitis	6	25	18.6	7.91	.4609
Verbesina arborea	6	22.8	19.3	10.18	.3721
Prunus buxifolia	6	22.6	19.2	10.09	.3765
Citharexylum sulcatum	6	21.1	22	11.9	.3553
Cedrela montana	6	19.8	19.5	10.43	.3109
Escallonia paniculata	6	18.9	18.6	8.9	.4337
Myrica parvifolia	6	18	21.6	11.77	.4799
Palicourea angustifolia	6	16	21.8	11.46	.6393
Croton bogotanus	6	13.5	19.1	10.31	.7337
Myrica pubescens	6	13	19.5	10.8	.7037

UNDERSTORY

Species	Group	Value (IV)	Mean	*SD*	*p**
Oreopanax incisus	1	78	25.1	11.18	.0002
Passiflora bogotensis	1	66.2	24.2	11.73	.0118
Serpocaulon levigatum	1	59.7	24.3	13.14	.0304
Piper bogotense	1	54.5	20.9	11.46	.0212
Oligactis sessiliflora	1	54.2	26.8	14.52	.033
Blechnum occidentale	1	53.8	22	11.93	.0336

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	*SD*	p^{*}
Smilax tomentosa	1	50.5	31.4	14.34	.0798
Cedrela montana	1	44	24.4	14.07	.1132
Miconia squamulosa	1	41.7	28.8	12.23	.1228
Frangula sphaerosperma	1	39.8	28.8	12.86	.1474
Uncinia hamata	1	39.4	26.2	13.1	.1168
Peperomia suratana	1	39.2	27.4	11.95	.1384
Xylosma spiculifera	1	37.3	21.7	11.9	.0738
Maxillaria graminifolia	1	36.4	22.4	13.36	.1552
Pleurothallis linguifera	1	36.4	19.3	11.93	.0886
Anthoxanthum odoratum	1	34.9	25.2	12.98	.1844
Smilax sp1	1	33.3	26.1	11.97	.2146
Daphnopsis caracasana	1	29.5	25.6	13.12	.2757
Barnadesia spinosa	1	28.9	20.9	12.45	.1968
Palicourea angustifolia	1	28.8	25	11.16	.2621
Palicourea lineariflora	1	28.4	20	11.31	.1848
Critoniopsis bogotana	1	27.3	19	12.4	.2354
Pilea lindeniana	1	27.3	19.6	12.43	.1992
Valeriana clematitis	1	25.1	31.5	10.51	.6753
Stelis sp1	1	23.4	22.4	11.79	.3619
Frangula sp1	1	19.3	22.1	12.16	.4903
Ageratina gracilis	1	18.2	17.9	11.18	.4121
Boehmeria cylindrica	1	18.2	17.1	11.63	.3429
Botrychium virginianum	1	18.2	17.2	11.99	.3413
Chromolaena perglabra	1	18.2	17.9	10.91	.4119
Chromolaena scabra	1	18.2	17.4	11.23	.3811
Chromolaena sp1	1	18.2	16.8	11.37	.3353
Clematis dioica	1	18.2	17.1	11.63	.3359
Clematis haenkeana	1	18.2	17	11.49	.3415
Conyza canadensis	1	18.2	17	11.2	.3287
Maxillaria sp1	1	18.2	17.8	11.17	.4121
Pecluma divaricata	1	18.2	17	11.76	.3359
Peperomia emarginulata	1	18.2	17	11.6	.3333
Pilea alsinifolia	1	18.2	17.6	10.9	.4031
Solanum cornifolium	1	18.2	17.8	11.04	.4117
Stelis pulchella	1	18.2	17.1	11.69	.3465
Tillandsia complanata	1	18.2	17	11.74	.3465
Chromolaena bullata	1	14.9	20	12.39	.5255
Varronia cylindrostachya	1	14.9	19.6	12.31	.5537
Bomarea sp1	1	14.6	25.3	12.66	.841
Capsella bursapastoris	1	14.6	19.6	12.22	.5441
Miconia theizans	1	14.3	19.5	12.12	.5299
Pleopeltis macrocarpa	1	13.6	20.7	12.09	.6725

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	SD	p^*
Epidendrum moritzii	1	12.3	17.9	11.19	.5925
Citharexylum sulcatum	1	9.6	17.9	11.79	.6985
Adiantum andicola	1	9.1	15.7	9.87	1
Alansmia sp1	1	9.1	15.7	9.75	1
Alonsoa meridionalis	1	9.1	15.8	9.95	1
Anchietea frangulifolia	1	9.1	15.9	10.04	1
Anthurium caramantae	1	9.1	15.7	9.75	1
Arrhenatherum elatius	1	9.1	15.6	9.53	1
Asplenium cladolepton	1	9.1	15.5	9.69	1
Asplenium praemorsum	1	9.1	15.5	9.48	1
Asplundianthus densus	1	9.1	15.6	9.71	1
Baccharis latifolia	1	9.1	15.6	9.53	1
Boehmeria sp1	1	9.1	15.7	9.75	1
Campyloneurum latum	1	9.1	15.5	9.69	1
Carex sp1	1	9.1	15.5	9.69	1
Castilleja fissifolia	1	9.1	15.5	9.59	1
Chromolaena leivensis	1	9.1	15.6	9.71	1
Croton bogotanus	1	9.1	15.8	9.95	1
Cuphea hyssopifolia	1	9.1	15.5	9.48	1
Cyperus sp1	1	9.1	15.6	9.53	1
Cystopteris fragilis	1	9.1	15.7	9.87	1
Dryopteris sp1	1	9.1	15.5	9.69	1
Duranta mutisii	1	9.1	15.4	9.46	1
Epidendrum sp3	1	9.1	15.9	10.04	1
Epidendrum sp4	1	9.1	15.6	9.64	1
Fragaria vesca	1	9.1	15.6	9.53	1
Fuchsia boliviana	1	9.1	15.6	9.53	1
Fuchsia paniculata	1	9.1	15.5	9.69	1
Galianthe bogotensis	1	9.1	15.5	9.48	1
Gamochaeta americana	1	9.1	15.6	9.53	1
Heppiella ulmifolia	1	9.1	15.5	9.69	1
Lantana rugosa	1	9.1	15.5	9.48	1
Lepidaploa canescens	1	9.1	15.5	9.59	1
Malaxis crispifolia	1	9.1	15.7	9.75	1
Oxalis acetosella	1	9.1	15.5	9.48	1
Panicum sp1	1	9.1	15.5	9.48	1
Passiflora sp1	1	9.1	15.8	9.95	1
Passiflora tripartita	1	9.1	15.5	9.69	1
Peperomia glabella	1	9.1	15.6	9.71	1
Phenax rugosus	1	9.1	15.7	9.87	1
Phyllanthus salviifolius	1	9.1	15.7	9.75	1
Physalis peruviana	1	9.1	15.4	9.46	1
Pilea goudotiana	1	9.1	15.5	9.69	1
Piper marginatum	1	9.1	15.7	9.87	1
Ponthieva similis	1	9.1	15.5	9.59	1

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	*SD*	*p**
Pteris muricata	1	9.1	15.7	9.87	1
Rubus macrocarpus	1	9.1	15.7	9.75	1
Rubus sp1	1	9.1	15.6	9.53	1
Salvia sp1	1	9.1	15.8	9.95	1
Setaria italica	1	9.1	15.5	9.48	1
Solanum caripense	1	9.1	15.4	9.46	1
Solanum pseudocapsicum	1	9.1	15.7	9.87	1
Solanum sp1	1	9.1	15.5	9.69	1
Solanum sp2	1	9.1	15.7	9.87	1
Stelis sp2	1	9.1	15.5	9.59	1
Stenorrhynchos speciosum	1	9.1	15.6	9.53	1
Styrax sp1	1	9.1	15.6	9.64	1
Thelipteris sp1	1	9.1	15.7	9.75	1
Tigridia pavonia	1	9.1	15.5	9.48	1
Tillandsia sp5	1	9.1	15.5	9.48	1
Tradescantia sp1	1	9.1	15.5	9.48	1
Tradescantia sp2	1	9.1	15.8	9.95	1
Vasquezia anemonifolia	1	9.1	15.5	9.48	1
Cranichis ciliata	1	8.2	17.6	11.02	.8812
Miconia resima	1	8.2	17.8	10.93	1
Prunus sp1	1	7.9	17.5	11.11	.9398
Viburnum tinoides	1	7.7	22.2	12.39	.975
Berberis goudotii	1	6.7	16.9	11.22	.937
Achyrocline satureioides	1	6.6	17.5	11.21	1
Stelis sp3	1	6	17	11.44	1
Hypochaeris radicata	1	5.8	17	11.38	1
Asplenium radicans	1	5.7	19.1	12.02	1
Elaphoglossum lingua	2	71.5	23.8	11.05	.001
Chusquea scandens	2	45.4	24.4	12.15	.0634
Prunus buxifolia	2	37	20	12.15	.0862
Elaphoglossum cuspidatum	2	36	24.7	12.78	.1622
Frangula goudotiana	2	34.8	24.2	13.27	.1654
Galium hypocarpium	2	30.6	28.2	12.45	.3527
Tillandsia sp1	2	27.3	22	12.54	.2665
Clusia multiflora	2	25	16.8	11.13	.2272
Digitalis purpurea	2	25	17.9	11.07	.173
Diplostephium rosmarinifolium	2	25	17.1	11.48	.2316
Elleanthus aurantiacus	2	25	17	11.37	.207
Elleanthus purpureus	2	25	16.7	11.15	.2196
Hedyosmum racemosum	2	25	17	11.58	.2244

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	SD	p^*
Ocotea longifolia	2	25	17.2	11.48	.2078
Serpocaulon lasiopus	2	25	18	11.08	.173
Smilax floribunda	2	25	17.3	10.56	.1638
Tillandsia sp3	2	25	17.8	10.55	.1588
Ocotea heterochroma	2	23	18.7	12.21	.2875
Rhyncospora sp1	2	21.1	19.4	12.18	.3229
Ilex kunthiana	2	20.6	23.7	12.46	.4899
Hieracium avilae	2	17.7	20.7	12.56	.4343
Blechnum cordatum	2	16.8	18.3	11.71	.3985
Munnozia senecionidis	2	14.1	19.3	11.34	.6187
Acaena cylindristachya	2	12.5	15.6	9.57	.6645
Athyrium dombeyi	2	12.5	15.6	9.57	.6645
Athyrium filixfemina	2	12.5	15.6	9.83	.6439
Baccharis lehmannii	2	12.5	15.4	9.35	.6543
Bejaria resinosa	2	12.5	15.4	9.35	.6543
Calamagrostis effusa	2	12.5	15.6	9.57	.6645
Chaetolepis lindeniana	2	12.5	15.6	9.57	.6645
Elaphoglossum lindenii	2	12.5	15.6	9.79	.6505
Elleanthus sp1	2	12.5	15.4	9.35	.6543
Epidendrum caesaris	2	12.5	15.6	9.79	.6505
Epidendrum cylindraceum	2	12.5	15.6	9.57	.6561
Epidendrum excisum	2	12.5	15.5	9.67	.6523
Eriosorus flexuosus	2	12.5	15.6	9.83	.6439
Faramea sp1	2	12.5	15.6	9.83	.6439
Fernandezia crystallina	2	12.5	15.4	9.35	.6543
Fernandezia sanguinea	2	12.5	15.4	9.35	.6543
Hypericum juniperinum	2	12.5	15.6	9.57	.6645
Lycopodium jussiaei	2	12.5	15.5	9.47	.6583
Macrocarpaea glabra	2	12.5	15.4	9.35	.6543
Myrsine sp1	2	12.5	15.6	9.83	.6439
Nyphogeton sp1	2	12.5	15.6	9.79	.6505
Paspalum bonplandianum	2	12.5	15.6	9.57	.6645
Ponthieva villosa	2	12.5	15.4	9.35	.6543
Sauvagesia erecta	2	12.5	15.6	9.79	.6505
Serpocaulon sessilifolium	2	12.5	15.5	9.67	.6523
Smilax sp2	2	12.5	15.5	9.67	.6523
Stelis argentata	2	12.5	15.4	9.35	.6543
Stelis galeata	2	12.5	15.4	9.35	.6543
Stelis pusilla	2	12.5	15.4	9.35	.6543
Stelis sp4	2	12.5	15.4	9.35	.6543
Stelis sp5	2	12.5	15.4	9.35	.6543
Stelis sp6	2	12.5	15.4	9.35	.6543
Oxalis spiralis	2	11.4	17.7	11.02	.7798

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	*SD*	*p*[*]
Oxalis corniculata	2	11.2	17.2	11.32	.6857
Peperomia microphylla	2	11.1	17.9	11.26	.759
Sphyrospermum buxifolium	2	9.9	17.1	11.09	.7818
Monochaetum bonplandii	2	9.3	17.4	11.21	.7926
Jungia ferruginea	2	9.1	16.9	11.65	.7906
Tibouchina grossa	2	7.6	18.9	12.37	.9214
Monnina aestuans	3	100	17.6	11.34	.003
Peperomia rotundata	3	90.3	18.6	12.32	.0044
Vaccinium floribundum	3	87.1	23.5	13.73	.0112
Nertera granadensis	3	85.4	32	14.96	.0206
Oreopanax bogotensis	3	80.7	23	13.12	.0094
Serpocaulon eleutherophlebium	3	71.4	21.2	11.47	.0106
Ageratina boyacensis	3	50	15.7	9.76	.0638
Arracacia sp1	3	50	15.7	9.76	.0638
Bomarea multiflora	3	50	15.7	9.76	.0638
Campyloneurum angustifolium	3	50	15.7	9.76	.0638
Equisetum bogotense	3	50	15.7	9.76	.0638
Fuchsia magellanica	3	50	15.7	9.76	.0638
Geranium holosericeum	3	50	15.7	9.76	.0638
Habenaria sp1	3	50	15.7	9.76	.0638
Hydrocotyle bonplandii	3	50	15.7	9.76	.0638
Miconia elaeoides	3	50	15.7	9.76	.0638
Oxalis medicaginea	3	50	15.7	9.76	.0638
Peperomia hartwegiana	3	50	15.7	9.76	.0638
Pleopeltis rudis	3	50	15.7	9.76	.0638
Rubus choachiensis	3	50	15.7	9.76	.0638
Serpocaulon murorum	3	50	15.7	9.76	.0638
Thelipteris sp2	3	50	15.7	9.76	.0638
Asplenium monanthes	3	47.6	17.2	11.02	.028
Oreopanax mutisianus	3	46.9	17.2	11.46	.036
Hydrocotyle tenerrima	3	46.4	17.2	11.65	.0438
Tillandsia sp2	3	46.1	19.3	12.32	.0446
Epidendrum scutella	3	42.9	18.5	11.99	.0306
Melpomene moniliformis	3	38.1	18.1	11.71	.0656
Galium ascendens	3	38	18.6	12.36	.1008
Bucquetia glutinosa	3	37.8	20.8	12.71	.0884
Berberis glauca	3	36	18.3	12.18	.1064
Passiflora adulterina	3	31.9	18.2	11.81	.1366
Siphocampylus brevicalyx	3	30.3	18.4	11.67	.172
Diphasiastrum thyoides	3	29.1	19.7	11.97	.1978

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	SD	p^*
Elaphoglossum engelii	3	27.7	19.4	11.92	.208
Matelea mutisiana	3	26.8	17.2	11.49	.1672
Pentacalia pulchella	3	24.4	20.1	12.42	.2801
Pleopeltis sp1	3	24.1	17.2	11.14	.1864
Symplocos theifolia	3	24.1	18.1	11.74	.3155
Hesperomeles goudotiana	3	22.3	26.9	14.08	.5485
Clethra fimbriata	3	21.8	17.2	11.1	.204
Elaphoglossum gayanum	3	16	19.7	12.19	.4997
Orthrosanthus chimboracensis	3	15.6	18.3	11.72	.4273
Lycopodium clavatum	3	14.5	20.6	12.29	.6869
Ageratina glyptophlebia	3	13.2	21.2	12.74	.6993
Pleopeltis murora	3	9.4	21	12.74	.9032
Peperomia galioides	3	8.7	21.4	12.8	.925
Greigia stenolepis	4	99.9	21.2	11.38	.0002
Rubus acanthophyllos	4	67.7	20.8	11.93	.0128
Drimys granadensis	4	54.7	22.2	11.9	.033
Scyphostelma tenella	4	54.1	21.7	12.68	.0102
Myrsine dependens	4	47.6	19.6	11.93	.019
Elaphoglossum latifolium	4	45.8	20.9	12.56	.0334
Melpomene flabelliformis	4	41	21.2	12.44	.0656
Blechnum schomburgkii	4	40	17.1	11.47	.086
Hesperomeles obtusifolia	4	40	17.8	10.93	.0838
Huperzia hippuridea	4	39.6	19.6	12.08	.086
Luzula gigantea	4	37.6	18.9	12.07	.0896
Hymenophyllum myriocarpum	4	36.8	21.1	12.25	.0692
Persea ferruginea	4	35.9	19.9	12.33	.1052
Agrostis perennans	4	34.7	21	12.68	.151
Diplostephium ochraceum	4	30.1	19.4	11.37	.1748
Cestrum buxifolium	4	25.8	24.9	13.12	.3467
Elleanthus maculatus	4	24.6	18.3	12.1	.2525
Piper artanthe	4	21.1	24.9	12.72	.5047
Blechnum loxense	4	20	15.7	9.62	.2234
Calceolaria microbefaria	4	20	15.9	10.1	.2212
Carex pichinchensis	4	20	15.9	10.1	.2212
Diplostephium floribundum	4	20	15.4	9.48	.206
Elaphoglossum minutum	4	20	15.7	9.62	.2234
Escallonia myrtilloides	4	20	15.4	9.48	.206

(Continues)

APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	*SD*	p^*
Espeletiopsis corymbosa	4	20	15.7	9.62	.2234
Geissanthus andinus	4	20	15.4	9.48	.206
Hydrocotyle gunnerifolia	4	20	15.8	10.05	.2196
Ilex sp1	4	20	15.4	9.48	.206
Lepanthes gargantua	4	20	15.5	9.59	.2158
Miconia latifolia	4	20	15.7	9.62	.2234
Monnina fastigiata	4	20	15.7	9.62	.2234
Pecluma sp1	4	20	15.8	10.05	.2196
Pentacalia nitida	4	20	15.4	9.48	.206
Peperomia alibacophylla	4	20	15.4	9.48	.206
Pernettya gaultheria	4	20	15.4	9.48	.206
Pilea sp1	4	20	15.4	9.48	.206
Plagiogyria pectinata	4	20	15.7	9.62	.2234
Pleurothallis lindenii	4	20	15.8	10.05	.2196
Podocarpus oleifolius	4	20	15.4	9.48	.206
Scyphostelma rugosa	4	20	15.9	10.1	.2212
Smallanthus pyramidalis	4	20	15.5	9.59	.2158
Stelis sp7	4	20	15.8	10.05	.2196
Stelis sp8	4	20	15.5	9.59	.2158
Stelis sp9	4	20	15.5	9.59	.2158
Weinmannia fagaroides	4	20	15.4	9.48	.206
Epidendrum sp1	4	19.2	17.6	10.49	.2639
Epidendrum sp2	4	17.9	17.1	10.65	.4261
Rubus ulmifolius	4	17.8	17.2	11.36	.4041
Baccharis macrantha	4	17.1	17.6	11.73	.4161
Rhynchospora macrochaeta	4	16.9	21.2	11.63	.5953
Tillandsia biflora	4	15.2	16.8	11.44	.3915
Rubus floribundus	4	14.4	17.2	11.67	.4759
Oxalis tuberosa	4	12.8	17.2	11.37	.4971
Ageratina asclepiadea	5	81.6	31.1	13.06	.0018
Ulex europaeus	5	48.1	20	12.49	.022
Tillandsia sp 1	5	47.6	34.7	11.25	.1376
Vallea stipularis	5	47.1	30	11.14	.1014
Bidens rubifolia	5	46	25.6	12.5	.062
Miconia ligustrina	5	45.3	25.2	12.33	.072
Myrcianthes leucoxyla	5	42.8	22.8	12.37	.0496
Baccharis bogotensis	5	41.6	31.4	11.48	.1598
Psychotria boqueronensis	5	40.5	24.7	13.01	.1062
Monochaetum myrtoideum	5	34.9	26.3	11.44	.1796
Ageratina tinifolia	5	33.3	17.3	11.63	.1168

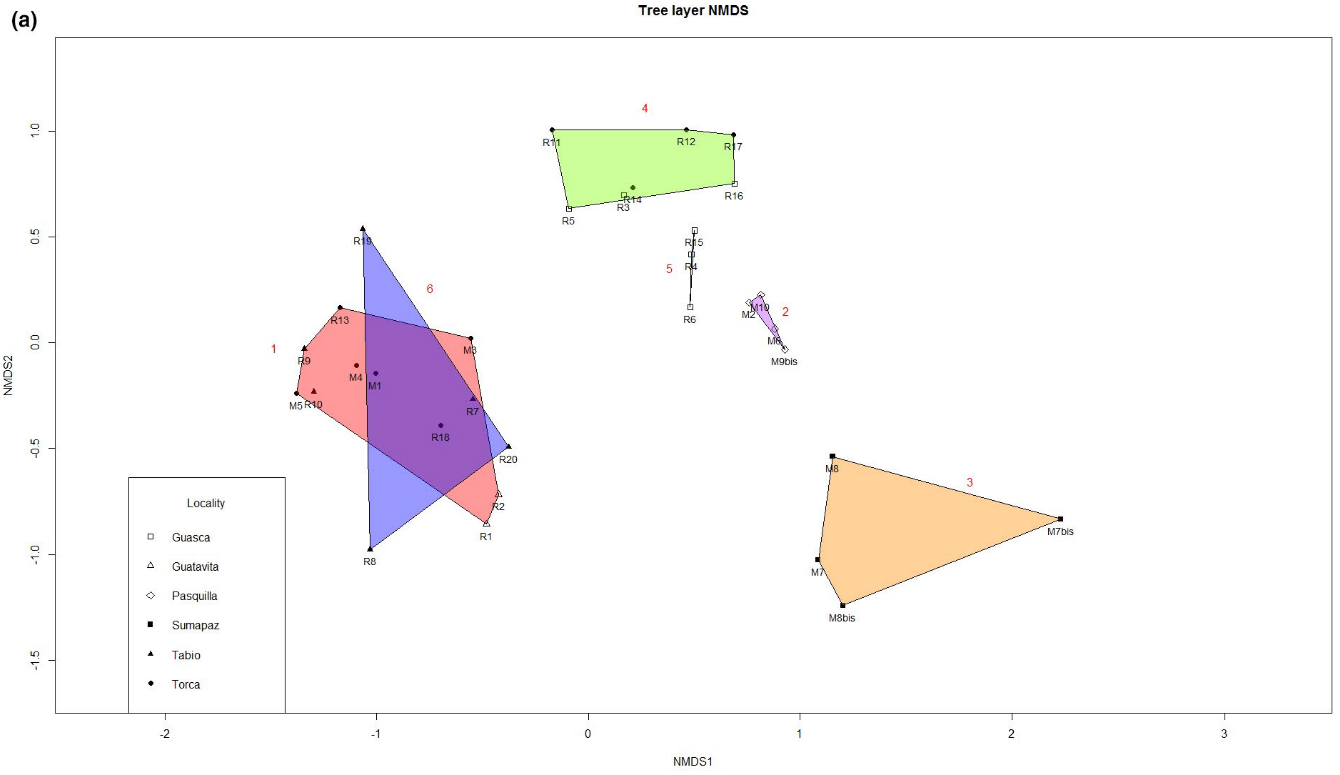
(Continues)

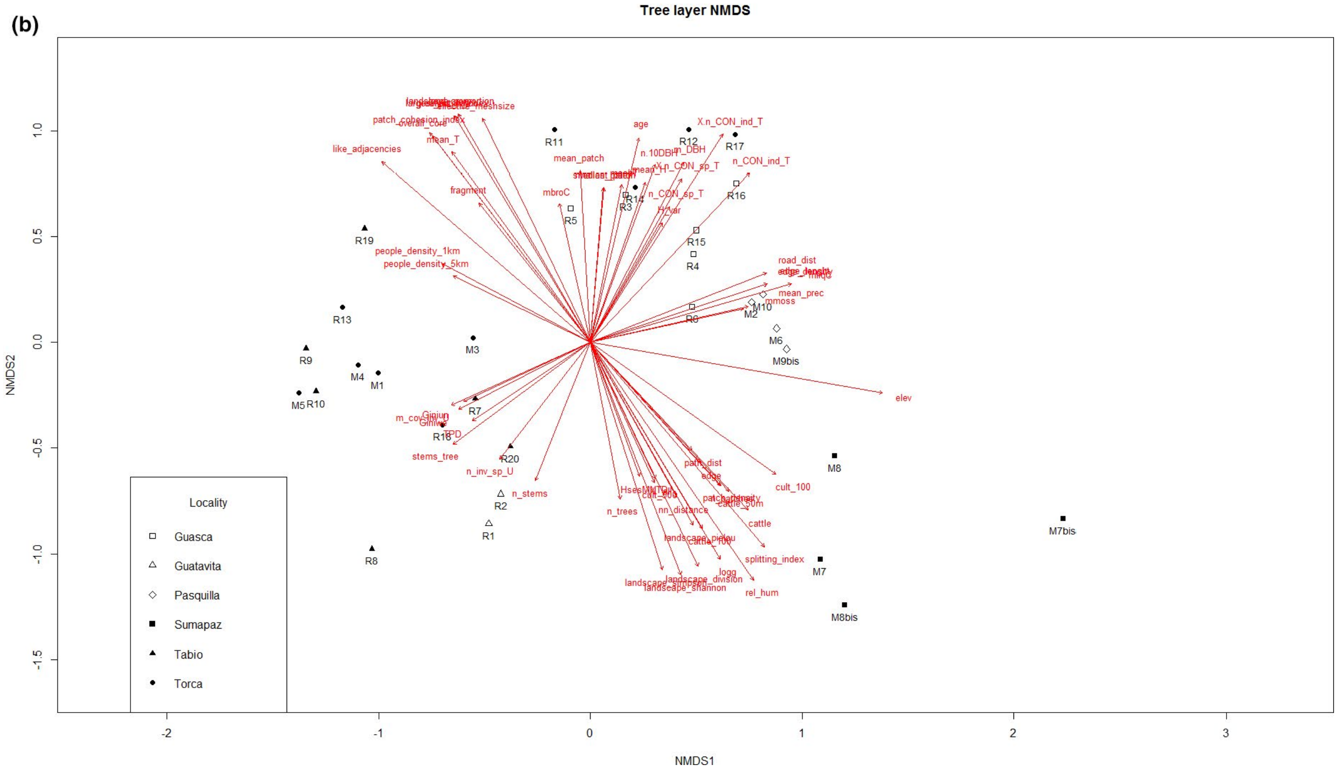
APPENDIX A5 (Continued)

Species	Group	Value (IV)	Mean	*SD*	p^*
Malaxis sp1	5	33.3	17.9	10.62	.1054
Peperomia arthurii	5	30.2	21.2	12.98	.2036
Myrsine coriacea	5	30.1	26.3	11.59	.2907
Weinmannia tomentosa	5	28.4	25.5	13.01	.3221
Cavendishia bracteata	5	28.1	19.3	12.05	.1768
Morella parvifolia	5	26.9	18.6	11.95	.23
Pteridium aquilinum	5	26.7	19.2	11.47	.2006
Gaiadendron punctatum	5	24.3	24.9	13.19	.4045
Macleania rupestris	5	23.1	27	14.39	.5399
Alnus acuminata	5	16.7	16	10.11	.4161
Asteraceae sp1	5	16.7	15.6	9.6	.4119
Cortaderia nitida	5	16.7	15.6	9.85	.4005
Diplostephium rosmarinifolius	5	16.7	15.7	9.83	.4061
Elaphoglossum sp1	5	16.7	16	10.11	.4161
Epidendrum sisgaense	5	16.7	15.5	9.44	.4015
Gaultheria erecta	5	16.7	15.6	9.85	.4005
Lantana camara	5	16.7	15.6	9.6	.4119
Passiflora capsularis	5	16.7	15.6	9.6	.4119
Peperomia angularis	5	16.7	15.6	9.6	.4119
Polystichum lehmannii	5	16.7	15.4	9.42	.3975
Stachys arvensis	5	16.7	15.6	9.6	.4119
Tillandsia sp7	5	16.7	15.6	9.6	.4119
Tillandsia sp8	5	16.7	15.6	9.6	.4119
Viburnum triphyllum	5	16	25.4	10.86	.8464
Tillandsia elongata	5	14.7	17.1	11.33	.5341
Thelypteris rudis	5	14.6	17.3	11.19	.5423
Rhynchospora nervosa	5	13.6	16.9	11.4	.5347
Gaultheria anastomosans	5	12.8	17	11.42	.5839
Cranichis sp1	5	12.5	16.6	11.45	.5659
Pernettya prostrata	5	11.8	18.8	12.09	.6569
Pecluma paradiseae	5	11.4	16.8	11.24	.6415
Cardamine ovata	5	11	18.3	11.87	.6567
Chromolaena sp2	5	10.1	16.9	11.31	.7427
Myrsine guianensis	5	7.7	16.7	11.21	.9112

APPENDIX A6

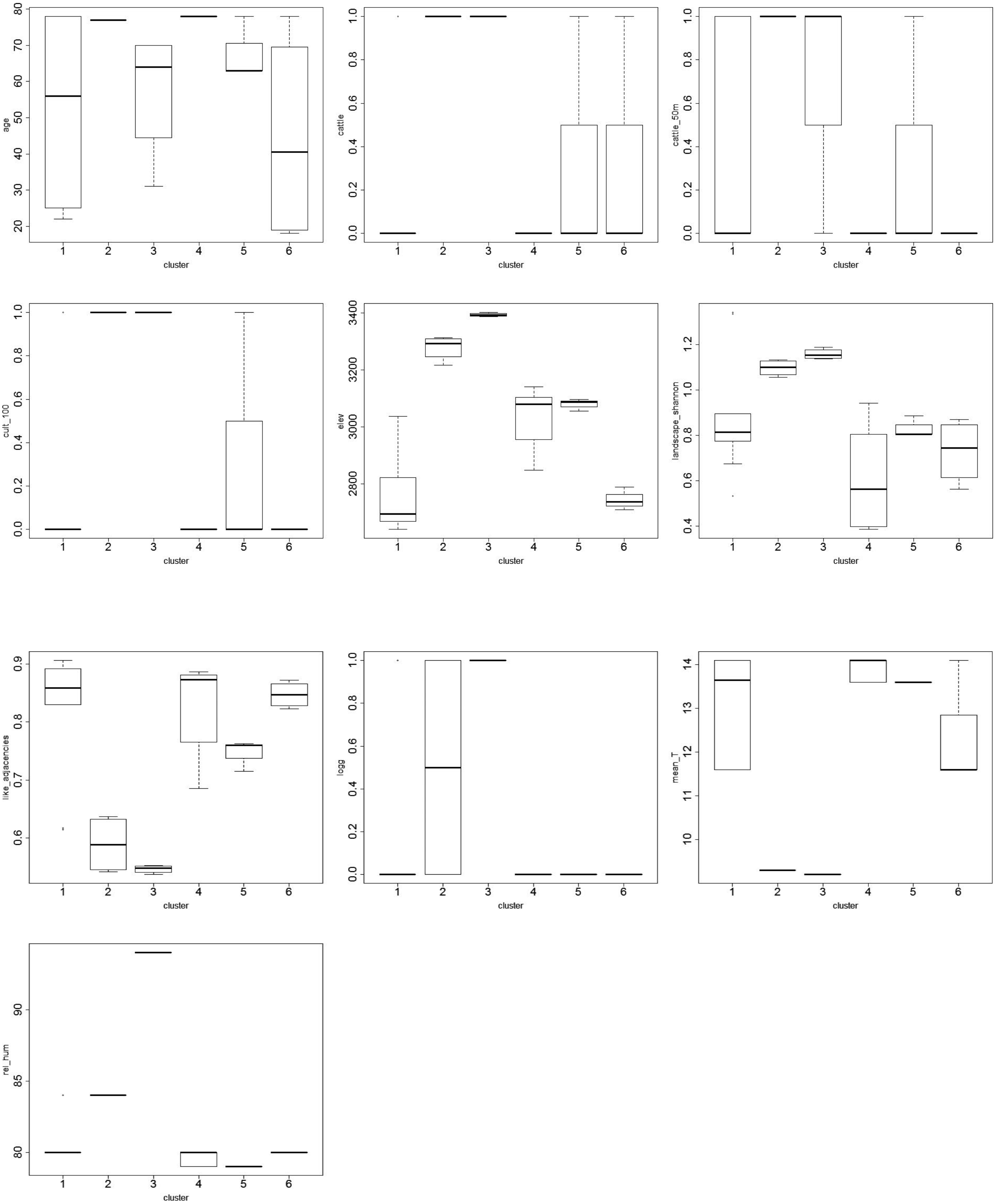
NMDS tree layer graphs and analysis of variance boxplots





NMDS graphs of the tree layer. (a) Ordination graph of plots in tree species space for axis 1–2: cluster analysis groups are outlined. (b) Ordination graph of plots in tree species space with plotted variables for axis 1–2, with only the variables with ‘p.max = 0.05’ plotted.

The variables that most correlated with the ordination axes ($R_{Sq} > 0.35$ for any of the 3 ordination axis, Table 1) and therefore with species composition and abundances are depicted clockwise. For full variable names and acronyms please refer to Appendix A2



Boxplot of analysis of variance for tree layer groups variables. Only variables that significantly differed among various tree groups (Figure 2) are shown. From right to left: age; presence of cattle inside the plot; (c) presence of cattle within 50 m from the plot; presence of cultivated fields within 100 m from the plot; elevation; Shannon's landscape diversity in 1 km buffer; Like adjacencies in 1 km buffer; logging; mean annual temperature; relative humidity.

APPENDIX A7

NMDS variables correlation with ordination axes for tree and understory layer

TREES

Variable	NMDS1	NMDS2	R_{sq}	*p*
elev	0.986936	−0.16111	0.842327	.001
rel_hum	0.557264	−0.83034	0.814799	.001
like_adjacencies	−0.77575	0.631046	0.715877	.001
splitting_index	0.647679	−0.76191	0.712051	.001
patch_cohesion_index	−0.61603	0.787721	0.681776	.001
logg	0.516505	−0.85628	0.633668	.001
greatest_patch	−0.54231	0.84018	0.62502	.001
largest_patch_index	−0.54197	0.840398	0.624739	.001
land_cover	−0.53243	0.846474	0.612971	.001
landscape_porportion	−0.53186	0.846834	0.612778	.001
overall_core	−0.64958	0.760295	0.590216	.001
mean_T	−0.5827	0.812684	0.538388	.001
landscape_shannon	0.392306	−0.91983	0.53266	.001
effective_meshsize	−0.47047	0.882414	0.519565	.002
landscape_division	0.470396	−0.88246	0.519501	.002
%n_CON_ind_T	0.598542	0.801091	0.498647	.001
cult_100	0.828407	−0.56013	0.489726	.001
cattle	0.69714	−0.71693	0.487354	.001
n_CON_ind_T	0.728414	0.685137	0.474397	.001
landscape_simpson	0.333984	−0.94258	0.450877	.003
mliqC	0.917959	0.396676	0.430102	.001
cattle_100	0.535527	−0.84452	0.421884	.003
age	0.230218	0.973139	0.407116	.004
cattle_50m	0.706548	−0.70766	0.387378	.006
road_dist	0.908312	0.418293	0.359839	.001
landscape_pielou	0.549647	−0.8354	0.353878	.004
edge_density	0.922612	0.385729	0.343423	.002
n_patches	0.715658	−0.69845	0.343347	.004
patch_density	0.716517	−0.69757	0.342699	.004
edge_lenght	0.922698	0.385524	0.341936	.002
m_DBH	0.523014	0.852324	0.316577	.004
n.10DBH	0.360665	0.932695	0.29713	.007
fragment	−0.68563	0.727951	0.263566	.016
stems_tree	−0.84893	−0.5285	0.261082	.014
edge	0.690298	−0.72352	0.256775	.025
%n_CON_sp_T	0.596982	0.802255	0.254204	.013
people_density_1km	−0.91227	0.409586	0.253024	.015
mmoss	0.908742	0.417359	0.245418	.022
mean_prec	0.925366	0.379075	0.245257	.013

(Continues)

APPENDIX A7 (Continued)

Variable	NMDS1	NMDS2	R_{sq}	*p*
mean_H	0.356376	0.934343	0.223591	.017
m_cov_inv_U	−0.95141	−0.30794	0.217533	.025
nn_distance	0.589863	−0.8075	0.216971	.031
people_density_5km	−0.92481	0.380421	0.209615	.032
n_inv_sp_U	−0.6223	−0.78278	0.20597	.027
Giniwe	−0.92763	−0.37349	0.20516	.032
mcobT	0.216899	0.976194	0.204958	.028
TPD	−0.78427	−0.62042	0.201613	.044
X._all	0.468041	−0.88371	0.200479	.041
path_dist	0.685608	−0.72797	0.195792	.048
protected	0.615398	0.788216	0.195422	.04
mean_patch	−0.06022	0.998185	0.194229	.042
Giniun	−0.92716	−0.37466	0.185068	.051
HsesMPD	0.988703	−0.14989	0.176882	.068
HsesMNTD	0.348156	−0.93744	0.171425	.065
n_CON_sp_T	0.648282	0.761401	0.17061	.067
cult_50m	0.96786	0.25149	0.16273	.074
n_stems	−0.45592	−0.89002	0.160024	.075
TsesMNTD	−0.81931	−0.57335	0.159924	.081
smallest_patch	0.118311	0.992977	0.156713	.07
median_patch	0.117137	0.993116	0.155408	.075
n_trees	0.219077	−0.97571	0.154968	.096
AGBplot	0.998705	−0.05088	0.154366	.095
cult_500	0.507842	−0.86145	0.153806	.098
mleaf	−0.85047	−0.52603	0.152094	.095
HPD	−0.228	−0.97366	0.150516	.095
TsesPD	−0.51544	−0.85693	0.148752	.102
morqT	0.372927	0.927861	0.145118	.083
mbrioT	−0.13913	0.990274	0.144544	.099
mhelC	−0.99549	0.09491	0.14296	.097
n_FST_ind_T	0.034581	−0.9994	0.141519	.125
H_var	0.642211	0.766528	0.141257	.12
FD	−0.96828	−0.24987	0.140421	.116
mCWD	0.756802	−0.65364	0.137304	.115
FRic	−0.19979	−0.97984	0.137234	.117
HMPD	0.97027	−0.24202	0.129168	.143
TsesMPD	0.417913	−0.90849	0.127914	.142
other	−0.97008	−0.2428	0.126107	.117
mliqT	0.995431	0.095486	0.124934	.171
HsesPD	0.176577	−0.98429	0.121806	.148
mbroT	0.145699	0.989329	0.121332	.176
TsesMNTDABU	−0.99881	0.048778	0.119051	.149
mbroC	−0.26677	0.96376	0.116187	.166
mhelT	−0.16551	0.986208	0.115102	.146
TSR	−0.92753	−0.37375	0.113505	.181
fractal_dimesion_index	0.501947	0.864899	0.110553	.182

(Continues)

APPENDIX A7 (Continued)

Variable	NMDS1	NMDS2	R_{sq}	*p*
m_patchshape_ratio	−0.13742	−0.99051	0.103988	.201
mAGBT	0.649443	0.760411	0.103937	.215
n_sp.10DBH	−0.80905	−0.58774	0.101004	.225
TMPD	0.336675	−0.94162	0.098842	.225
mcobC	0.265827	0.964021	0.097694	.216
sol_rad	−0.17591	0.984406	0.095741	.241
north	−0.40907	−0.9125	0.093814	.22
TPIELOU	0.314002	−0.94942	0.093106	.219
RaoQ	0.764773	−0.6443	0.092153	.264
house_dist	0.316094	0.948728	0.085966	.272
slope	−0.89386	0.448348	0.085597	.29
Hshann	0.169443	−0.98554	0.083351	.282
cattle_500	0.292148	−0.95637	0.080359	.306
n_sp.20DBH	−0.76282	0.646616	0.077075	.32
HSR	−0.34487	−0.93865	0.075683	.323
TMNTD	−0.84452	−0.53553	0.07518	.339
TMPDABU	0.162029	−0.98679	0.074487	.329
Tsimp	0.02132	−0.99977	0.074268	.306
HMNTD	0.7732	−0.63416	0.073592	.32
msoil	−0.6291	0.777325	0.071115	.372
TMNTDABU	−0.99015	−0.14002	0.06572	.38
%_5	−0.20588	−0.97858	0.06549	.365
HsesMNTDABU	−0.52315	−0.85224	0.064366	.377
n.20DBH	0.16129	0.986907	0.060851	.392
Tshann	−0.17924	−0.9838	0.060737	.393
n_FST_sp_T	−0.25137	−0.96789	0.058602	.413
mundstr	−0.55902	−0.82915	0.056845	.435
HPIELOU	0.440781	−0.89761	0.056559	.413
FEve	0.222091	0.975026	0.052515	.481
east	−0.59224	−0.80576	0.051569	.482
Hsimp	0.302214	−0.95324	0.049729	.482
FDis	0.420161	−0.90745	0.046219	.516
DBH_var	0.953164	0.302455	0.043325	.537
n_inv_sp_T	−0.17768	0.984088	0.038882	.571
HsesMPDABU	0.262408	0.964957	0.038792	.567
max_H	0.943325	0.33187	0.038476	.527
track_dist	0.613653	0.789576	0.036408	.575
FDiv	0.063578	−0.99798	0.031273	.634
TsesMPDABU	0.772151	−0.63544	0.029198	.665
morqC	−0.22709	0.973873	0.027614	.666
m_H_understory	0.719951	0.694025	0.018554	.754
HMPDABU	0.997157	0.075357	0.012729	.835
tour	0.074111	0.99725	0.011967	.849
m_cov_nat_U	−0.04515	−0.99898	0.011738	.837
HMNTDABU	−0.99539	−0.09595	0.011378	.848
mbrioC	0.532531	0.84641	0.009829	.886

(Continues)

APPENDIX A7 (Continued)

Variable	NMDS1	NMDS2	R_{sq}	p
n_large_trees	−0.57682	0.816872	0.003727	.948

UNDERSTORY

Variable	NMDS1	NMDS2	R_{sq}	p
elev	0.9541	−0.2994	0.7424	.001
%n_CON_ind_T	0.6972	0.7169	0.7030	.001
mliqC	0.8629	−0.5054	0.6210	.001
fragment	−0.4236	0.9058	0.6192	.001
n_CON_ind_T	0.7564	0.6542	0.5868	.001
overall_core	−0.5046	0.8633	0.5779	.001
nn_distance	0.2311	−0.9729	0.5678	.001
n_CON_sp_T	0.4123	0.9110	0.5652	.001
%n_CON_sp_T	0.4612	0.8873	0.5638	.001
road_dist	0.8779	−0.4788	0.5522	.001
edge_density	0.7744	−0.6327	0.5467	.001
edge_lenght	0.7760	−0.6307	0.5458	.001
m_DBH	0.5210	0.8536	0.5361	.001
like_adjacencies	−0.7263	0.6873	0.5287	.001
landscape_pielou	0.3249	−0.9457	0.5282	.001
people_density_1km	−0.6546	0.7560	0.4927	.001
landscape_simpson	0.1586	−0.9873	0.4885	.001
mAGBT	0.5001	0.8659	0.4860	.001
people_density_5km	−0.6587	0.7524	0.4508	.001
effective_meshsize	−0.3264	0.9452	0.4345	.001
landscape_division	0.3269	−0.9450	0.4341	.001
landscape_shannon	0.2587	−0.9660	0.4300	.001
n_stems	−0.3517	−0.9361	0.4254	.001
land_cover	−0.4475	0.8943	0.4112	.002
landscape_porportion	−0.4483	0.8939	0.4105	.002
n_trees	−0.0938	−0.9956	0.4001	.001
cult_500	0.2316	−0.9728	0.3953	.001
mean_H	0.6510	0.7591	0.3926	.001
n.20DBH	0.3331	0.9429	0.3919	.001
greatest_patch	−0.4765	0.8792	0.3789	.003
largest_patch_index	−0.4773	0.8787	0.3783	.003
H_var	0.7528	0.6583	0.3781	.002
mean_patch	0.1234	0.9924	0.3757	.001
age	0.5183	0.8552	0.3631	.001
cattle_100	0.4406	−0.8977	0.3629	.002
n.10DBH	0.5471	0.8371	0.3616	.002
DBH_var	0.3904	0.9206	0.3529	.001
n_patches	0.5521	−0.8338	0.3414	.002
m_patchshape_ratio	−0.2250	−0.9744	0.3411	.001
patch_density	0.5518	−0.8340	0.3409	.002
TsesMNTD	−0.6189	0.7855	0.3379	.004
fractal_dimesion_index	0.3886	0.9214	0.3230	.001
AGBplot	0.6484	0.7613	0.3213	.002

(Continues)

APPENDIX A7 (Continued)

Variable	NMDS1	NMDS2	R_{sq}	*p*
stems_tree	−0.5974	−0.8020	0.3089	.006
mbroT	0.3658	0.9307	0.3069	.005
TsesMNTDABU	−0.4415	0.8973	0.3031	.009
mbroC	0.1503	0.9886	0.3008	.007
median_patch	0.2472	0.9690	0.2962	.002
smallest_patch	0.2492	0.9685	0.2959	.003
TMNTDABU	−0.3654	0.9309	0.2951	.007
n_sp.20DBH	−0.2002	0.9798	0.2940	.003
mmoss	0.7328	−0.6804	0.2935	.011
protected	0.9616	−0.2746	0.2768	.005
mcobT	0.5901	0.8073	0.2766	.009
cattle_50m	0.6646	−0.7472	0.2739	.01
cattle	0.6734	−0.7392	0.2683	.013
HMPD	0.4505	0.8928	0.2675	.013
n_FST_ind_T	−0.0733	−0.9973	0.2597	.017
TsesPD	−0.5789	0.8154	0.2562	.015
HsesMPD	0.5830	0.8125	0.2534	.016
TMPD	0.0440	0.9990	0.2481	.02
morqT	0.7128	0.7014	0.2452	.019
TMNTD	−0.5690	0.8223	0.2441	.017
patch_cohesion_index	−0.7432	0.6691	0.2368	.017
n_large_trees	0.1904	0.9817	0.2271	.019
mleaf	−0.9005	−0.4348	0.2246	.025
mcobC	0.6767	0.7362	0.2211	.031
mliqT	0.7831	−0.6219	0.2199	.026
sol_rad	0.3578	−0.9338	0.2166	.029
tour	0.2983	−0.9545	0.2130	.037
edge	0.6123	−0.7907	0.2109	.033
splitting_index	0.8714	−0.4905	0.2087	.028
cult_100	0.8494	−0.5278	0.2079	.034
n_inv_sp_U	−0.7628	−0.6466	0.2069	.034
TsesMPD	0.0840	0.9965	0.2059	.037
mhelT	0.2106	0.9776	0.1995	.038
max_H	0.7056	0.7086	0.1992	.043
mean_prec	0.8755	−0.4832	0.1907	.053
house_dist	0.5493	−0.8356	0.1902	.055
TMPDABU	0.1551	0.9879	0.1872	.049
TsesMPDABU	0.1618	0.9868	0.1862	.046
Giniwe	−0.5636	−0.8260	0.1815	.049
n_sp.10DBH	−0.6307	0.7761	0.1762	.061
mhelC	−0.4689	0.8833	0.1745	.06
TPD	−0.6826	0.7308	0.1737	.083
cattle_500	0.0966	−0.9953	0.1703	.068
morqC	0.3163	0.9487	0.1693	.069
mean_T	−0.8561	0.5168	0.1561	.075
msoil	−0.2462	0.9692	0.1506	.102
Giniun	−0.5473	−0.8369	0.1506	.096

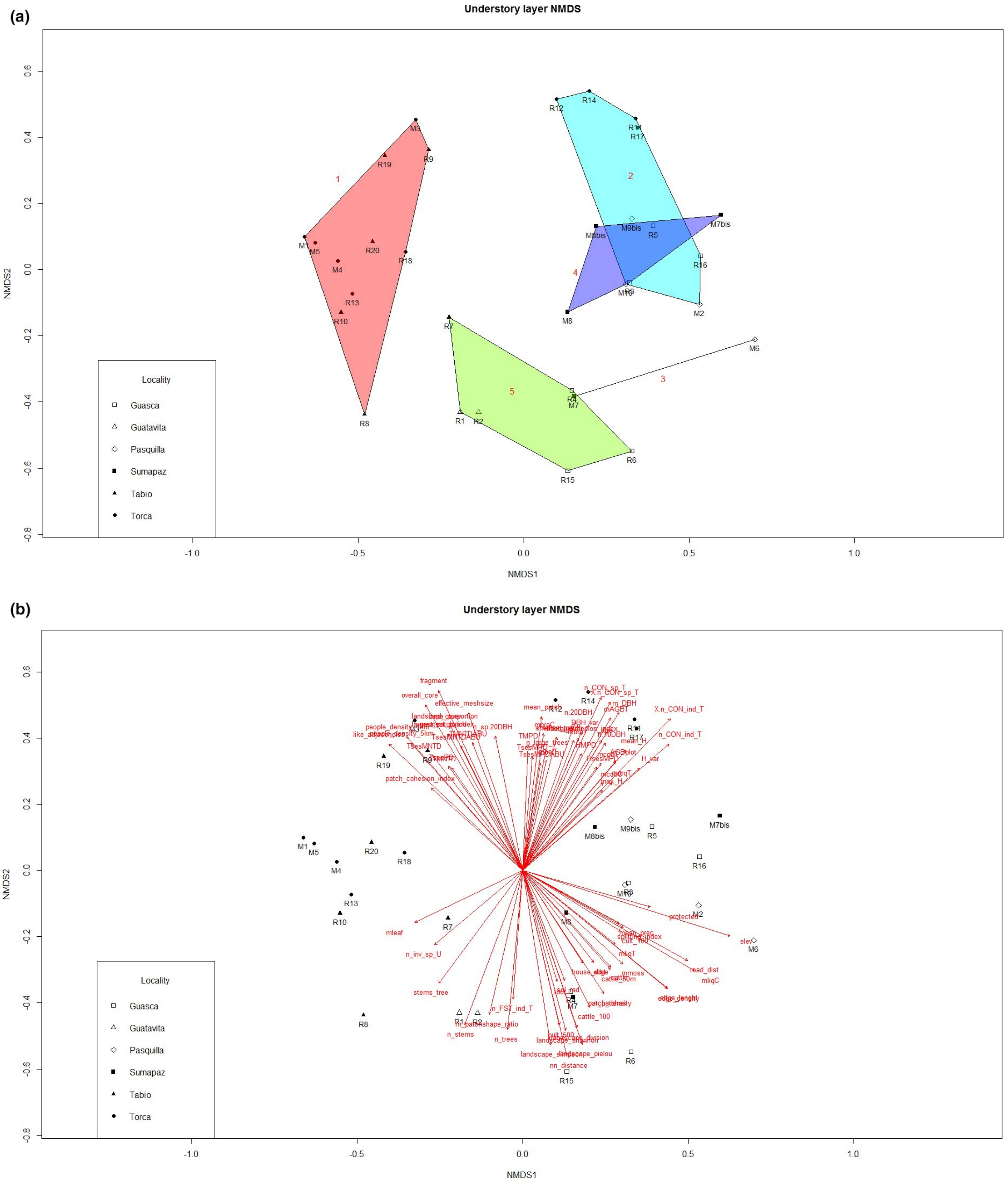
(Continues)

APPENDIX A7 (Continued)

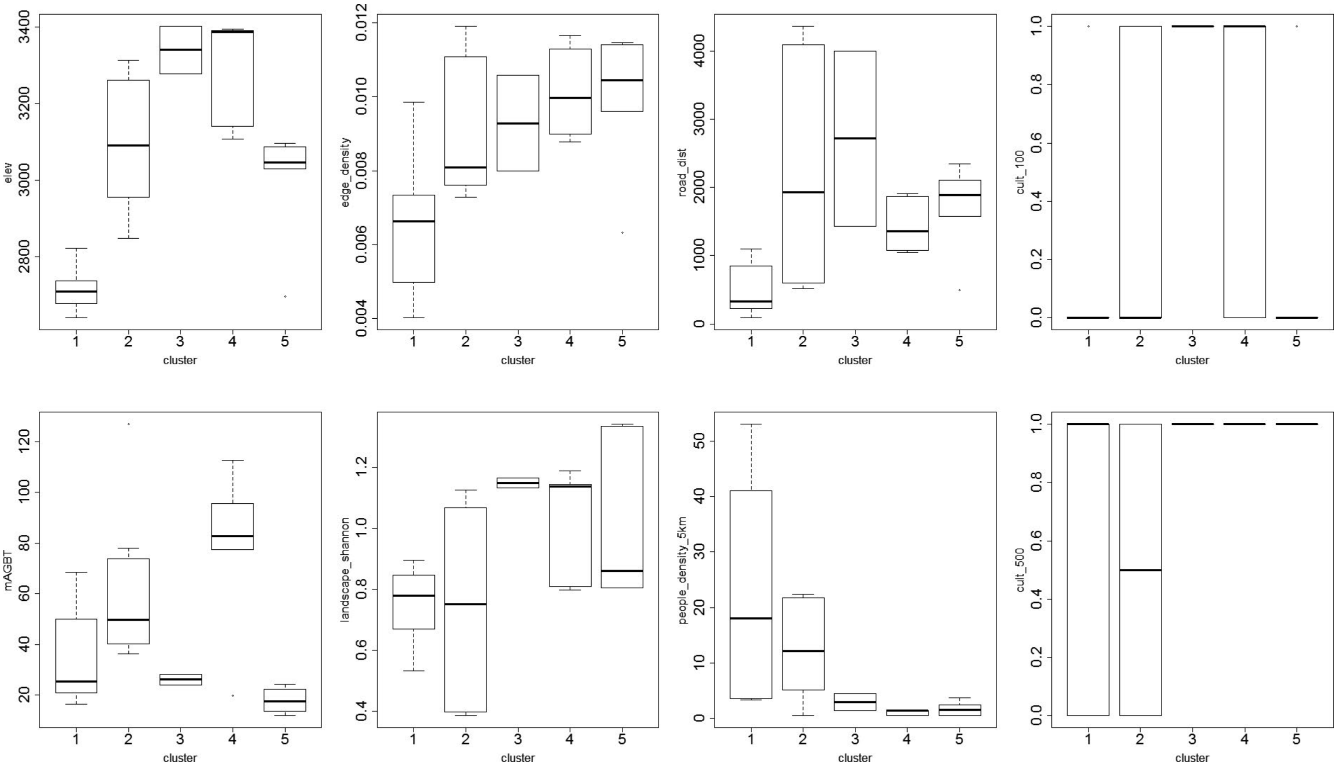
Variable	NMDS1	NMDS2	R_{sq}	*p*
other	−0.9893	0.1462	0.1492	.078
mundstr	−0.4332	0.9013	0.1469	.108
HMNTD	0.1854	−0.9827	0.1441	.117
m_cov_inv_U	−0.9990	0.0445	0.1427	.124
FDiv	−0.1388	0.9903	0.1402	.122
%_all	0.3145	−0.9492	0.1391	.124
cult_50m	0.7689	−0.6394	0.1348	.101
HsesMNTDABU	−0.8341	−0.5516	0.1219	.157
HPIELOU	0.1081	−0.9941	0.1217	.143
rel_hum	0.8988	−0.4384	0.1211	.152
logg	0.6668	−0.7452	0.1135	.157
m_cov_nat_U	−0.1436	0.9896	0.1131	.167
mCWD	0.6105	0.7920	0.1075	.171
%_5	−0.3215	−0.9469	0.1066	.196
east	−0.8527	−0.5223	0.1063	.162
HsesMNTD	−0.0559	−0.9984	0.1007	.216
HsesMPDABU	0.0924	0.9957	0.0993	.197
TPIELOU	0.4560	0.8900	0.0941	.242
n_FST_sp_T	−0.2760	−0.9611	0.0928	.267
RaoQ	0.8038	0.5949	0.0841	.288
slope	−0.9069	−0.4214	0.0770	.335
FD	−0.7789	0.6272	0.0705	.365
Tshann	0.0868	0.9962	0.0681	.372
Tsimp	0.2034	0.9791	0.0680	.385
track_dist	0.9412	0.3377	0.0674	.375
HPD	−0.8959	0.4443	0.0578	.428
HMNTDABU	−0.7611	−0.6487	0.0570	.42
Hshann	−0.1013	−0.9949	0.0562	.434
FEve	0.4481	0.8940	0.0544	.433
TSR	−0.7679	0.6406	0.0532	.46
mbrioT	0.0471	0.9989	0.0521	.44
m_H_understory	0.2972	0.9548	0.0512	.47
FDis	0.4714	0.8819	0.0497	.486
path_dist	0.7276	0.6860	0.0390	.572
Hsimp	0.0455	−0.9990	0.0381	.57
n_inv_sp_T	0.2033	−0.9791	0.0380	.575
HSR	−0.7537	0.6573	0.0378	.568
north	−0.7210	−0.6929	0.0376	.566
FRic	−0.7253	0.6885	0.0244	.722
HsesPD	−0.4330	−0.9014	0.0243	.722
mbrioC	0.7545	0.6563	0.0112	.868
HMPDABU	0.3434	0.9392	0.0067	.91

APPENDIX A8

NMDS understory layer graphs and analysis of variance boxplots



NMDS of understory. (a) ordination graph of plots in understory species space for axis 1–2: no group could be visually distinguished and cluster analysis groups are outlined (b) Ordination graph of plots in understory species space with plotted variables for axis 1–2, with only the variables with ‘p.max = 0.05’ plotted. A table offering variable correlations with the ordination axes is available in Appendix A8.



Boxplot of analysis of variance for understory groups variables. Only variables that significantly differed among various understory groups are shown: elevation; edge density in 1 km buffer; distances from roads; presence of cultivated fields within 100 m from the plot; mean tree AGB; Shannon's landscape diversity in 1 km buffer; people population density in 5 km buffer; presence of cultivated fields within 500 m from the plot.

forests

Article

Reconstructing Long Term High Andean Forest Dynamics Using Historical Aerial Imagery: A Case Study in Colombia

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Abstract: High Andean forests are biodiversity hotspots that also play key roles in the provisioning of vital ecosystem services for neighboring cities. In past centuries, the hinterland of Andean fast-growing cities often experienced a dramatic decline in forested areas, but there are reports that forest cover has been recovering recently. We analyzed aerial imagery spanning the years 1940 to 2007 from nine administrative localities in the Eastern Andean Cordillera of Colombia in order to elucidate precise patterns of forest vegetation change. To this aim, we performed image object-based classification by means of texture analysis and image segmentation. We then derived connectivity metrics to investigate whether forest cover trajectories showed an increase or decrease in fragmentation and landscape degradation. We observed a forest cover recovery in all the examined localities, except one. In general, forest recovery was accompanied by an increase in core habitat areas. The time scale of the positive trends identified partially coincides with the creation of protected areas in the region, which very likely furthered the recovery of forest patches. This study unveils the long-term dynamics of peri-urban high Andean forest cover, providing valuable information on historical vegetation changes in a highly dynamic landscape.

Keywords: aerial pictures; land cover change; habitat fragmentation; forest recovery; high Andean forests; morphological spatial pattern analysis; Bogota

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1. Introduction

Landscape change is the result of a broad variety of human activities with various effects on ecosystems, which depends on the nature and intensity of these activities [1,2]. Land cover change does not only interfere with the structure and functioning of ecosystems, but also affects the interactions with the atmosphere, ultimately contributing to local and global climate change [3,4]. In this context, habitat fragmentation modifies the availability of resources by creating artificial patch edges and by altering the degree of isolation of patches [5,6]. This, in turn, alters species distribution, abundance, and diversity [7,8], as well as carbon stocks [9], and ecosystems nutrient fluxes [10]. Particularly, landscape fragmentation poses severe threats to the native tree flora [11] and induces higher individual mortality [12] and extinction rates either at the species level [13] or at the population level [14,15]. Ultimately, the resulting biotic homogenization affects the resilience of forest remnants to current and future changes in environmental conditions [16,17].

In Latin America, one of the major drivers of forest loss and habitat fragmentation is the conversion of forests into arable lands and pastures [18,19]. The expansion of pastures into forest fragments is perceived by local inhabitants as a direct improvement of their economic situation. On the other hand, the associated biodiversity loss, and the alteration of local climate patterns and hydrological cycles [4,20] involve negative economic effects in the long term, at different geographical scales [19].

While deforestation is happening at an alarming rate in economic frontier zones [21], abandoned peri-urban farmlands and pastures are often in the process of natural recovery, which results in the establishment of shrublands or the regrowth of forest cover [22,23]. In the more recent past, i.e., the last five decades [24], the impacts of globalization (new flows of labor, capital, commodities, and ideas [25]), the intensification of agriculture and industrialization profoundly affected rural economies and led to the migration of significant parts of the rural population to urban areas. As a consequence, former agricultural areas were abandoned [24,26]. On the other hand, in many Latin American rural landscapes that remain densely inhabited, forest recovery may be driven by the drop in crop prices followed by the abandonment of agriculture [21]. Nevertheless, the landscape mosaic dynamics in coupled urban–rural systems of the Andes, such as the hinterland of Bogotá, Colombia, are very complex in space and time [27], and are still influenced by the substantial deforestation that took place during the last centuries [24].

High Andean forests represent a characteristic ecosystem in the Northern Andes, between 2600 and 3500 m [28]. They harbor a high diversity of species, high levels of endemism and are therefore recognized as a conservation priority [29]. Regrettably, these ecosystems are generally fragmented and poorly protected [30], while being essential in the provisioning of key ecosystem services to neighboring cities, including hydrologic regulation and soil conservation [31,32]. The forests in the Eastern Andean Cordillera of Colombia experienced substantial human-induced modifications throughout the last centuries, leading to a drastic reduction of their extension [30,33]. The resultant urban–rural forest mosaic has been extensively studied with regard to species composition [34–38] and more recently, regarding the regeneration stadia of forest fragments [39–41], human impact on vegetation, and the provisioning of ecosystem services [42–44].

Most cases studies on vegetation or land cover change rely on satellite imagery, which has been available since the 1970s [45,46]. In order to analyze several decades of landscape dynamics, we used aerial imagery. Although such photographs are available for the study area, they have only been scarcely employed to date (but see e.g., [33,47,48]). Aerial photographs are compatible with satellite remote sensing data, but usually come with different spatial and spectral resolution [32]. Such historical aerial imagery depicts past landscape structure and its change across decades often representing an underutilized source of information. The analysis of such multi-temporal data has been shown to play an important role in the detection of long-term landscape changes and the reconstruction of ecosystem transformations at a fine resolution [45,49]. Unveiling historical patterns of landscape connectivity is relevant to evaluate the effects of past human activities, and it is crucial for understanding the current species diversity patterns and ecosystem functioning [50]. A reconstruction of forest cover changes at a fine scale is also instrumental for correlating the observed vegetation changes with land use activities. Taken together, a detailed spatial reconstruction of the landscape dynamics can significantly contribute to planning and evaluating the potential impact of conservation measures.

Land-use and land-cover studies from the study area indicate forest fragmentation on one hand [4,31,51], but on the other hand also a recent increase in forest cover [27,47,52,53]. Although forest recovery can be taken as a positive sign, past land-use history may have resulted in severe habitat deterioration [22], leaving lands vulnerable to soil degradation [54] or invasive species [22,55]. In this context, analyses over a long period of time and at fine spatial resolution are lacking, despite their importance for the assessment of historical trends in landscape transformation and degradation. A better understanding of the main drivers of forest loss or recovery requires the precise monitoring of changes in forest cover at a small geographical scale. Recent studies on vegetation composition, structure, and the anthropogenic impact on biodiversity and biomass underpins the need for precise information on the permanency of forest fragments, as well as the clear identification of regrown forest patches with corresponding age estimates (secondary succession) and their spatial configuration through time [44].

This study aims to investigate long-term changes in the extension and structure of high Andean forests by gathering detailed information on landscape history and patterns of landscape change through several decades. Specific objectives are: (i) to assess the forest cover change in the surroundings of Bogotá by means of aerial imagery covering a range of 60 years; and (ii) to evaluate the forest cover structure as described by spatial pattern indicators in relation to forest cover trends in the region.

2. Materials and Methods

2.1. Study Area

The study area encompassed nine localities in the hinterland of Bogotá, the capital city of Colombia (Figure 1). Six of the study localities are situated in an arc north of the city in the department of Cundinamarca (Tabio, Soacha, San Francisco, El Rosal, Guasca, and Guatavita) and three are located within the capital district Bogotá D.C. (Torca, Pasquilla, and Sumapaz). These localities were selected because they match a network of permanent plots that was established as a basis for various botanical and ecological studies between 2013 and 2019 [39–41,44]. The high Andean forests close to Bogotá reach a modest height (15–25 m) and are typically dominated by trees and tall shrubs of the genera *Weinmannia*, *Miconia*, *Cavendisha*, *Myrsine*, *Myrcianthes*, *Xylosma*, and *Daphnopsis* [38,41,44,56]. Around the city, the forest remnants appear as scattered and fragmented patches. Some of these forested areas form part of a natural reserves network, created in the 1970s, and some have received their protection status only recently (as in the case of Los Encenillales in Pasquilla and El Encenillo in Guasca). The remaining forest patches are reported to be threatened by urban expansion, road construction [27,30], and by the opening of new areas to create pastures, especially in more rural localities [31,57,58]. Detailed information related to the study localities is presented in Supplementary Table S1.

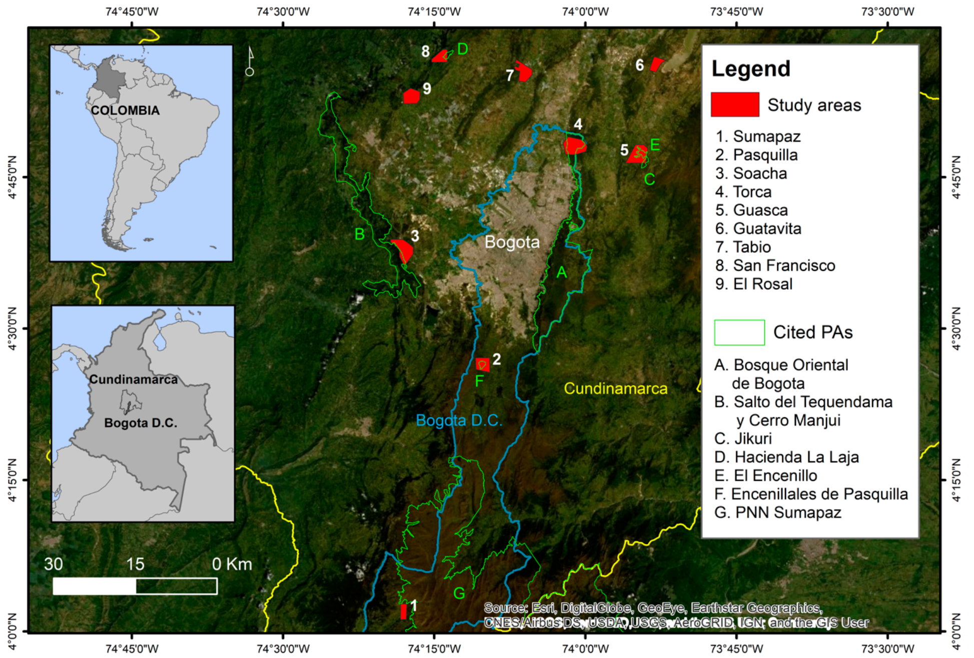

Figure 1. Study localities in the hinterland of Bogotá, in Cundinamarca department and Bogotá D.C., Colombia. Small map top left: Colombia; lower left: Cundinamarca department and Bogotá D.C. in Colombia. Cited protected areas (Cited PAs) in Legend refers to the reserves/natural parks cited and discussed in the text. Bogotá D.C. boundaries are outlined in blue, and Cundinamarca department borders are outlined in yellow.

2.2. Land Cover Mapping

2.2.1. Acquisition and Processing of Aerial Photos

A total of 71 aerial greyscale photos of the selected localities (Figure 1) was obtained from the Colombian Geographical Institute Agustín Codazzi (IGAC), covering a period from the 1940s up to the year 2007 (i.e., roughly one photo per decade and locality). The photos were scanned in high resolution and georeferenced in two consecutive steps using QGIS 2.18 [59]. To this aim, we used the thin plate spline as a transformation method for data interpolation, since it led to the highest precision among all the methods tested (first and second order polynomials). After a first georeferencing step, the overlapping areas were clipped to obtain a series of aerial scenes for each of the localities, which is equivalent in shape, size, and position (Figure 2a). A subsequent, second georeferencing step was performed to achieve the highest precision possible. All photos were resampled at 1 m pixel size. From the initial 71 scenes, we selected 41 that covered the very same area in each of the study localities through the time series (Table 1).

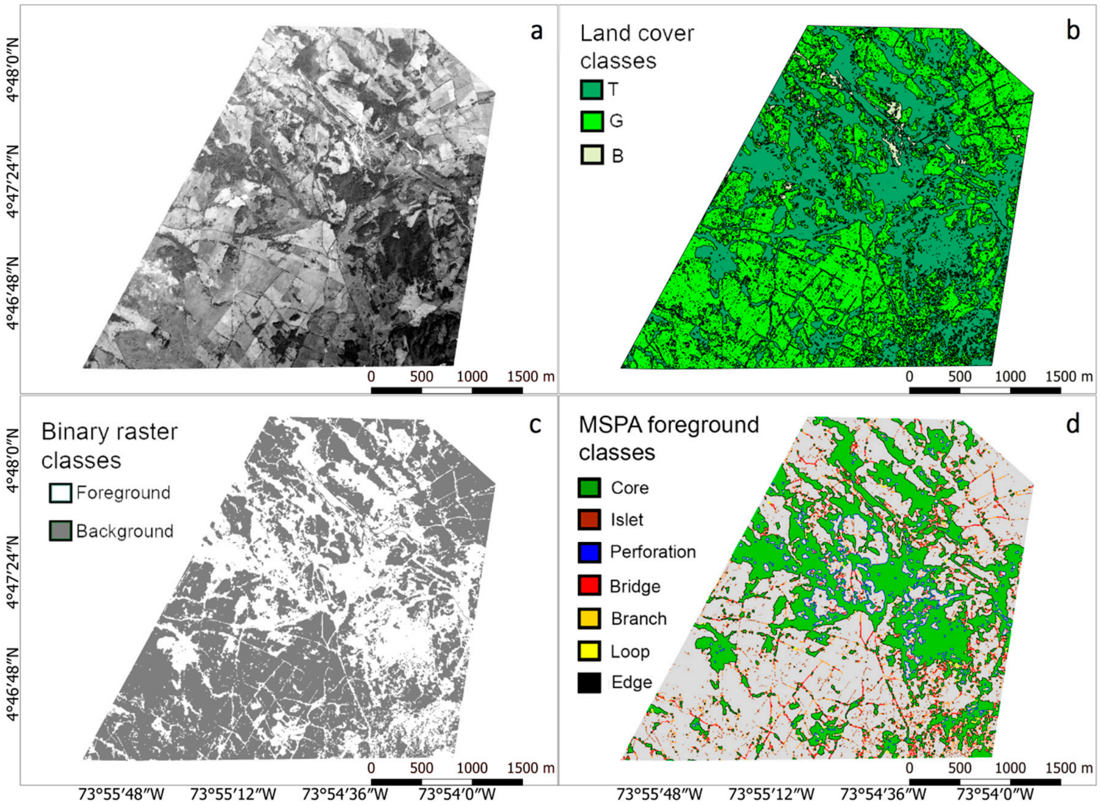

Figure 2. Example of the applied workflow (using data from the locality Guasca, 1985): (**a**) georeferenced, clipped, and resampled greyscale aerial photo; (**b**) derived land cover classification map (T = trees, high shrubs; G = grass, cultivated fields, and low shrubs; B = bare ground/built-up); (**c**) forest/non-forest binary raster (input for the Morphological Spatial Pattern Analysis, MSPA); (**d**) resulting map depicting MSPA classes.

Table 1. Information on the utilized aerial photo series for all study localities (1940–2007).

Locality/Decade	40s	50s	60s	70s	80s	90s	00s	No. of Scene	Area (ha)
Torca	1940	-	1962	1978	-	1993	2004	5	1081
Soacha	-	-	1962	-	1987	1996	-	3	1019
San Francisco	-	-	1962	1977	-	1993/98	2007	5	484
El Rosal	-	-	1962	1977	1987	1996	2007	5	720
Guasca	1940	1955	-	1978	1985	-	2007	5	987
Guatavita	1940	1958	1962	-	-	1997	2007	5	417
Tabio	1940	-	1961	-	-	1998	2007	4	711
Sumapaz	1948	-	1963	-	1987	1996	-	4	306
Pasquilla	1941	-	1961	-	1981	1993	2007	5	606

2.2.2. Texture and Object-Based Image Analysis

Traditionally, aerial photographs were classified through manual interpretation into land-cover/land-use categories. This required well trained specialists, and imposed numerous challenges [45]. In recent years, automated classification techniques have been used in interpreting aerial imagery [49,60–62]. Object-based classification is used to efficiently delineate homogeneous polygons of land-cover/land-use based on panchromatic aerial imagery [63]. Object-based approaches rely on grouping neighboring pixels of similar properties to form objects, a process known as segmentation, before carrying out further image-processing analysis [64]. Resulting objects can be classified using properties such as tone and color, size, shape, texture, and contextual relationships [45]. Texture analysis was performed to enhance the pixel classification of the greyscale pictures using the *glcm* package [65] in RStudio 1.0.153 [66]. A moving window size of 7 × 7 pixels was adopted as an average value in order to avoid the drawbacks of either too large or too small window sizes [67,68]. Texture metrics were calculated for the four directions and the generated raster layers were examined. Based on the most informative metrics to visually distinguish our land cover classes, we retained three metrics for classification purposes: entropy, mean and second moment [69]. Segmentation for the object-based image analysis (OBIA) was carried out using the 'Seeded Region Growing Algorithm' [70] on a layer stack of the selected three texture metrics and the greyscale original aerial picture with the OBIA module in SAGA GIS 2.1.4 [71] to enhance the image classification at the pixel level by reducing the within-class variability [72,73]. We specified 5 pixels as the minimum object size in accordance with the smallest recognizable entity, i.e., the approximate average width of a tree canopy in the high Andean forests under study.

2.2.3. Supervised Classification and Accuracy Assessment

In order to perform the supervised classification, we manually selected our training polygons among the ones generated by the segmentation algorithm. We distinguished three classes: B (bare ground/built-up including main and secondary roads, houses, and bare fields), G (grass, cultivated fields, and low shrubs), and T (trees and tall shrubs). We did not distinguish forest plantations and natural forests because the quality of the aerial imagery did not allow for it. Supervised classification was carried out with all the selected aerial photos using the maximum likelihood criterion in SAGA GIS 2.1.4. [71] (Figure 2b) due to its efficacy in performing a classification when there are well separated land cover classes, as was the case in our study [74].

An accuracy assessment was carried out to derive the overall accuracy (OA), class-specific user accuracy (UA) and the producer accuracy (PA). We used a balanced, random sampling response design to obtain a more accurate estimate of the user's accuracy for the proportionally smallest class B and allocated an adequate sample size to it [75]. The three land cover classes (B, G, T) were defined as strata and 100 validation points were randomly generated for each class. When object-based segmentation is used as a means to improve classification results, it is recommendable to adopt a pixel-based response sampling design, due to its simplicity and lack of specific boundary or structural quality control [76]. Thus, our response design was built of 300 blocks [77] of 3 × 3 pixels around the randomly generated points. Within the blocks, we applied a majority criterion. When a precise block-based class attribution was not possible due to the low quality of the greyscale picture, an additional visual interpretation of the land cover classes based on the neighboring pixels was carried out. Good practice recommendations stipulate that the reference classification should be of higher quality than the map classification [78]. For this reason, the visual validation was carried out on the original higher-resolution greyscale aerial picture. Stratified area estimators as well as the overall and class-specific accuracy were obtained following the equations proposed by Oloffson et al. [79]. The error matrices resulting from this response sampling design, all accuracy values, and class area statistics are presented in the Supplementary Material (Tables S2 and S3).

2.2.4. Morphological Spatial Pattern Analysis (MSPA)

In order to get some insights into the quality of the underlined forest recovery, we complemented the land cover classification with the morphological spatial pattern analysis (MSPA). In principle, a classification of forest fragments would also need data on the floristic composition and structure of the vegetation over time. However, by deriving MSPA classes from geometric patterns within the forest cover, we can infer the information on the structural features of the forest cover trends. We are well aware that other fragmentation metrics and frameworks exist and are available [80,81]. However, we chose to derive a limited set of robust indicators, which provides a simple interpretation of features in the landscape and which relates to the needs of wildlife populations and plant communities in the study area, while maintaining considerable sensitivity to pattern changes over time [82].

The classified images of all localities were analyzed for geometry and connectivity using the MSPA QGIS plugin [83]. The MSPA uses a series of mathematical morphological operators to describe the geometrical properties of raster binary maps, e.g., forest (or foreground) = 1, non-forest (or background) = 0. The MSPA returns a raster layer with a minimum of seven mutually exclusive feature classes (core, islet, loop, bridge, perforation, edge, and branch) [83] that trace the geometry and connectivity of the binary layer components' spatial arrangement [84]. We performed the MSPA focusing on the forest class (T) and thus defined the remaining two classes (B and G) as background.

The definition of each MSPA category is provided in Table 2. According to their morphology, these categories can be subdivided into four main groups: (i) core, (ii) islet, (iii) connectors and branches, and (iv) edge [80].

Table 2. Definition of the class groups and categories for the morphological spatial pattern analysis (MSPA) adapted from [85].

MSPA Class Group	MSPA Class Category	Definition
Core	Core	Internal forest pixels whose distance to the background is higher than a specified threshold value (here: 5 m)
Islet	Islet	Patch forest pixels that do not contain any core pixel, i.e., potentially vulnerable and isolated habitats
Connectors and branches	Bridge	Pixels that connect two or more disconnected core areas
	Loop	Pixels that connect a core area to itself
	Branch	Extensions of pixels in a core area that do not connect with other areas
Edge	Perforation	Pixels of the internal perimeter of a foreground object
	Edge	Pixels of the external perimeter of a foreground object

We produced forest/non-forest binary layers from the land cover imagery, removed the raster polygons smaller than the selected threshold size (50 pixels), and replaced them with the pixel value of the largest neighboring polygon (Figure 2c). Subsequently, we performed the MSPA by using the following parameterization: Foreground Connectivity = 4 pixels, Edge Width (s) = 5, Transition = 1, and Intext = 0. Foreground Connectivity was set to four pixels to constrain to cardinal directions only [84], but also to take into account the maps' high spatial resolution and to avert an overestimation of the connectivity in the connector's classes. Edge width was set to five meters, which we considered to be an adequate threshold in our particular study system, to distinguish between the fragment edge and core areas. Transition was set to one to illustrate all the detected connections [84]. The Intext value was set to zero, as opposed to the default Intext = 1, to avoid the subdivision of the internal background into the two categories core-opening and border-opening [84] (Figure 2d). The processing workflow is exemplified in Figure 2 and all the processing steps of the aerial imagery are summarized in the Supplementary Figure S4. Finally, an analysis of the correlation was performed to investigate the relationships between the class T area and MSPA groups defined in Table 2.

3. Results

The supervised land cover classification performed satisfactorily, returning good OA values (see Supplementary Tables S2 and S3 for the complete error matrices and accuracy indices of all the classes and localities through the time series). Regarding the class-specific accuracy values, the class T and G returned good values of UA and PA. Finally, the class B returned satisfactory values for UA but had low PA values in few cases indicating omission errors.

In the period between 1940 and 2007, we found an overall increasing proportion of forested surface in eight of the nine study localities (Figure 3 and Supplementary Table S5). The only exception with a net loss of forest cover was found in Pasquilla (−6.77 ha), while the highest increase was observed in Torca (+289.40 ha, Figures 3 and 4a–e). A consistent increase in forest cover was detected in Guasca and Guatavita (+141.19 ha and 115.61 ha, respectively), and also in Soacha (+106.88 ha) and Tabio (+99.64 ha; Figure 3 and Supplementary Table S5).

Based on the forest cover trends identified, the study localities can be divided into three groups: (i) Group 1 includes Guatavita, Soacha, Guasca, and Tabio. This group is characterized by a well defined increase in forest cover with no or very little decrease during the study period; (ii) Group 2 includes Torca, San Francisco, and Sumapaz, and is characterized by an initial increase in forest cover, followed by a decrease occurring around the 1990s and then, again, a final increase; (iii) Group 3 includes Pasquilla and El Rosal, which are characterized by an initial decrease of forest cover and a later increase that started in the 80ies.

The results of the Morphological Spatial Pattern Analysis (MSPA) are presented in Figure 5 and in the Supplementary Table S6. Overall, due to the peri-urban nature of the sampled area, the class background (i.e., non-forested areas corresponding to classes B and G) was the most abundant one in terms of percentage through time, except for El Rosal in 2007, Guatavita in 2007, and Torca from 1962 until 2004.

The MSPA category core was the second most abundant one. As shown in Figure 5, its net area share increased through time in all localities. A particularly high increase in the core area proportion was determined in Torca between 1940 and 1962 (+122%) as the most striking example here. In some localities, certain phases of decreasing core areas were found, e.g., in Pasquilla (1941–1961), Guatavita (1958–1962), El Rosal (1962–1977 and 1987–1996), San Francisco (1993–1998), and Torca (1978–1993). The proportion of islets, decreased through the time series in all the localities, with the exception of Sumapaz, where it increased slightly after the 1990s (+23%), and San Francisco as well as Tabio, where it increased markedly (+190% and +85%, respectively) in the 2000s.

The share of the connector group (loops, bridges, and branches), which includes the potential corridors for the species dispersal that connects the core areas [86], decreased noticeably through time only in Guasca and Pasquilla. The share of the edge group (perforations and edge MSPA classes), which is directly related to fragmentation [5,86,87], increased constantly through time in Guatavita and Tabio, and also slightly in Sumapaz.

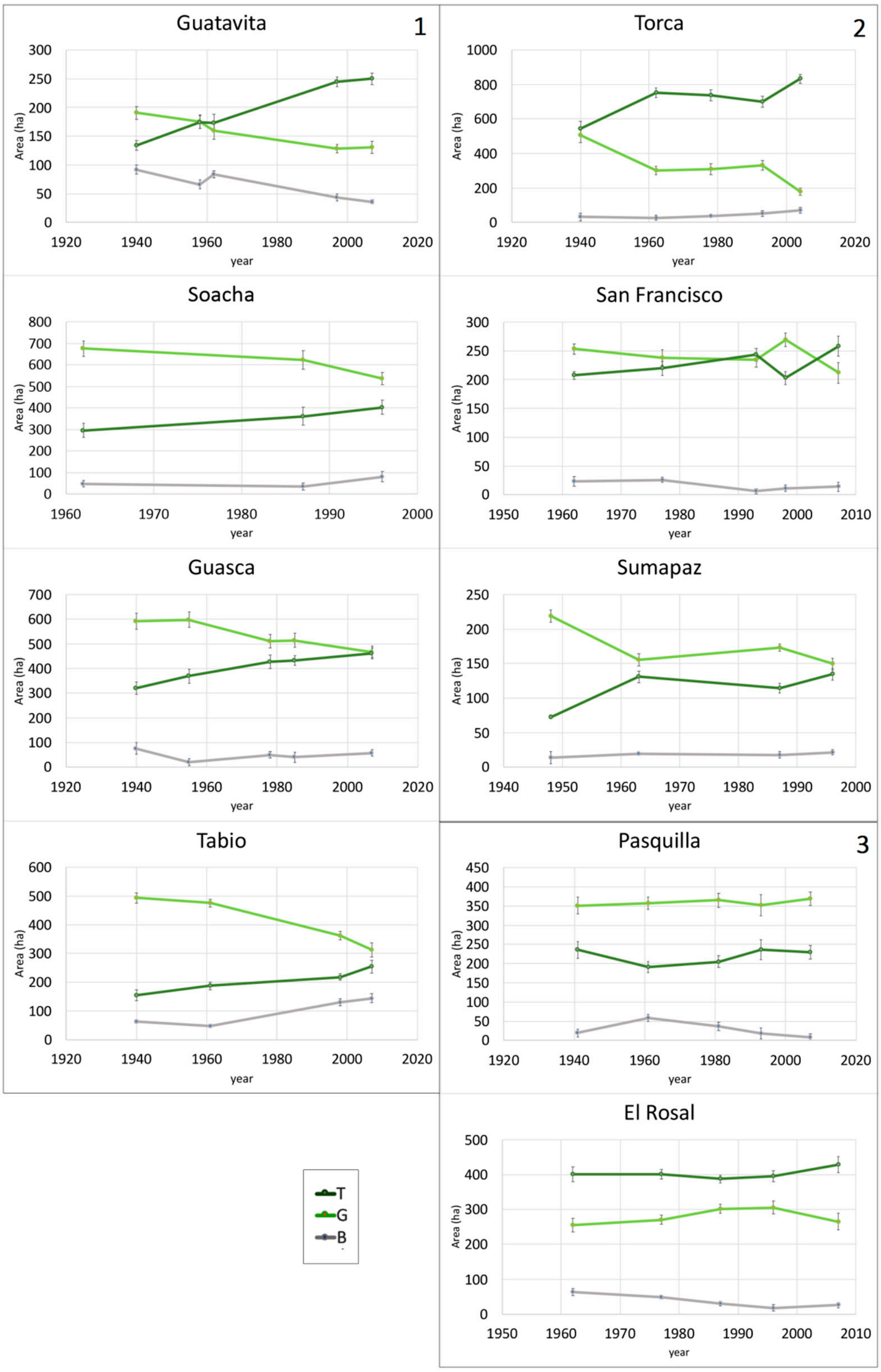

Figure 3. Forest cover change in the study localities (1940–2007). The distinguished groups of localities according to the general forest cover trend through time are marked with corresponding numbers: (**1**) well defined increase in forest cover, with no or very little decrease during the study period; (**2**) initial increase in forest cover, followed by a decrease around the 1990s and then, again, a final increase; (**3**) initial decrease in forest cover and then, an increase around 1980. B = bare ground/built up (including main and secondary roads, houses, and bare fields); G = grass/cultivated fields (including areas with low shrubs), and T = trees and tall shrubs (forest cover).

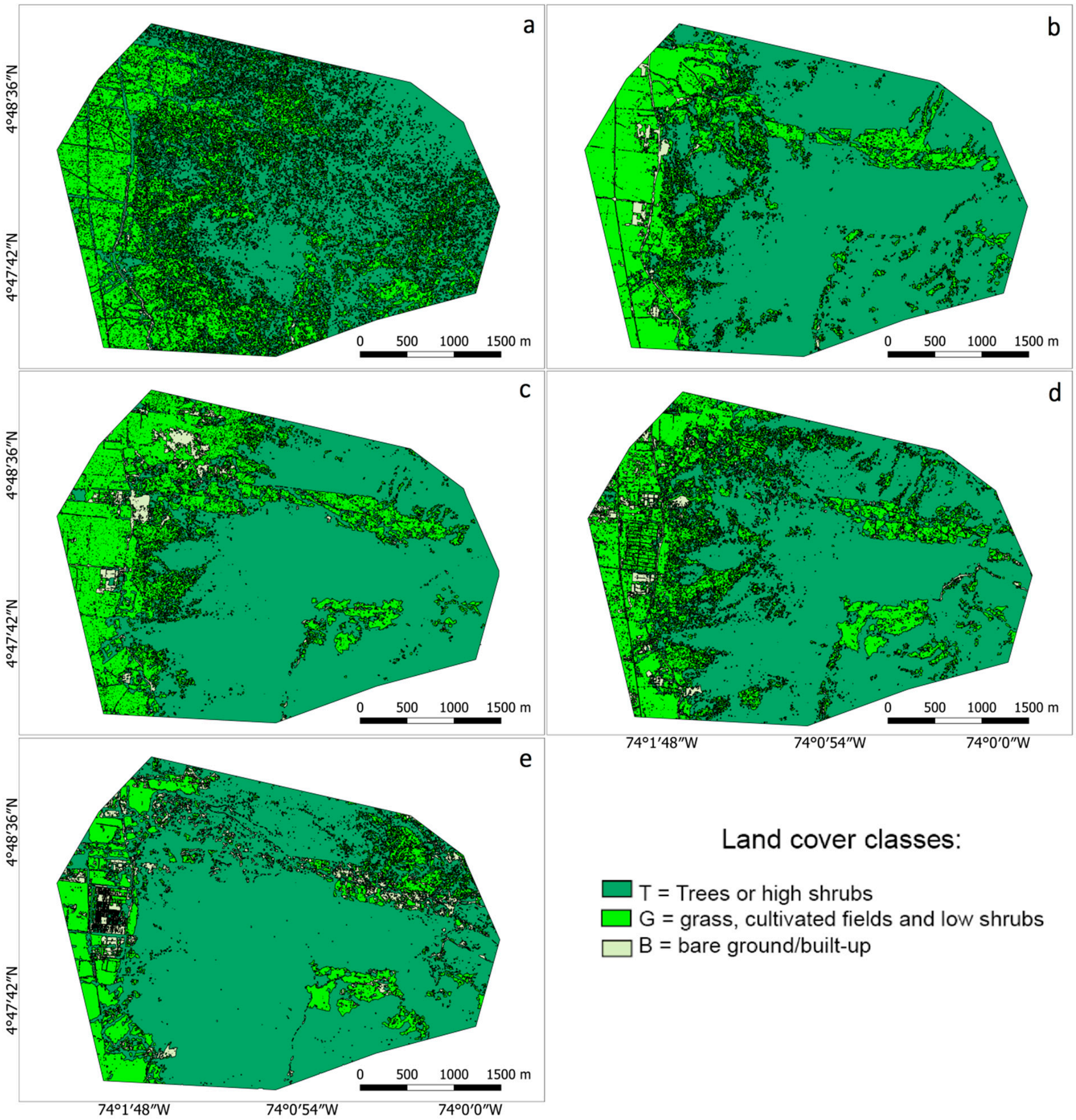

Figure 4. Map series depicting the land cover change in the locality Torca between 1940 and 2004: (**a**) 1940, (**b**) 1962, (**c**) 1978, (**d**) 1993, (**e**) 2004.

Considering all the localities, the correlation analysis carried out between the area of class T (trees or high shrubs) and MSPA groups, i.e., core, islet, connectors and edge (see Supplementary Table S7 for correlation coefficients and relative *p*-values), showed a significant positive correlation between the forest cover and the group core ($r = 0.97$, $p < 0.001$) and a slightly positive correlation with the group edge ($r = 0.59$, $p = 0.001$), which was often was stronger at an individual locality level (e.g., El Rosal: $r = 0.987$, $p = 0.02$; San Francisco: $r = 0.913$, $p = 0.031$; Tabio $r = 0.969$, $p = 0.031$). Only two localities that showed a positive correlation between the forest cover and core (Guasca: $r = 0.868$, $p = 0.057$; Torca: $r = 0.987$, $p = 0.002$), also showed a negative correlation between the forest cover and the group connectors (Guasca: $r = -0.858$, $p = 0.063$; Torca: $r = -0.904$, $p = 0.035$). Interestingly, the localities belonging to the first and second groups defined on general forest cover trends, had overall positive values of correlation with the group core (e.g., Guatavita: $r = 0.953$, $p = 0.012$; Torca $r = -0.987$, $p = 0.002$; Sumapaz: $r = 0.95$, $p = 0.046$) and negative values with the islet (e.g., Guatavita: $r = -0.924$, $p = 0.025$; Torca: $r = -0.983$, $p = 0.003$). The localities belonging to the third group did not show relevant correlation with the core, islet or connectors, but showed a positive correlation tendency with the group edge (e.g., El Rosal).

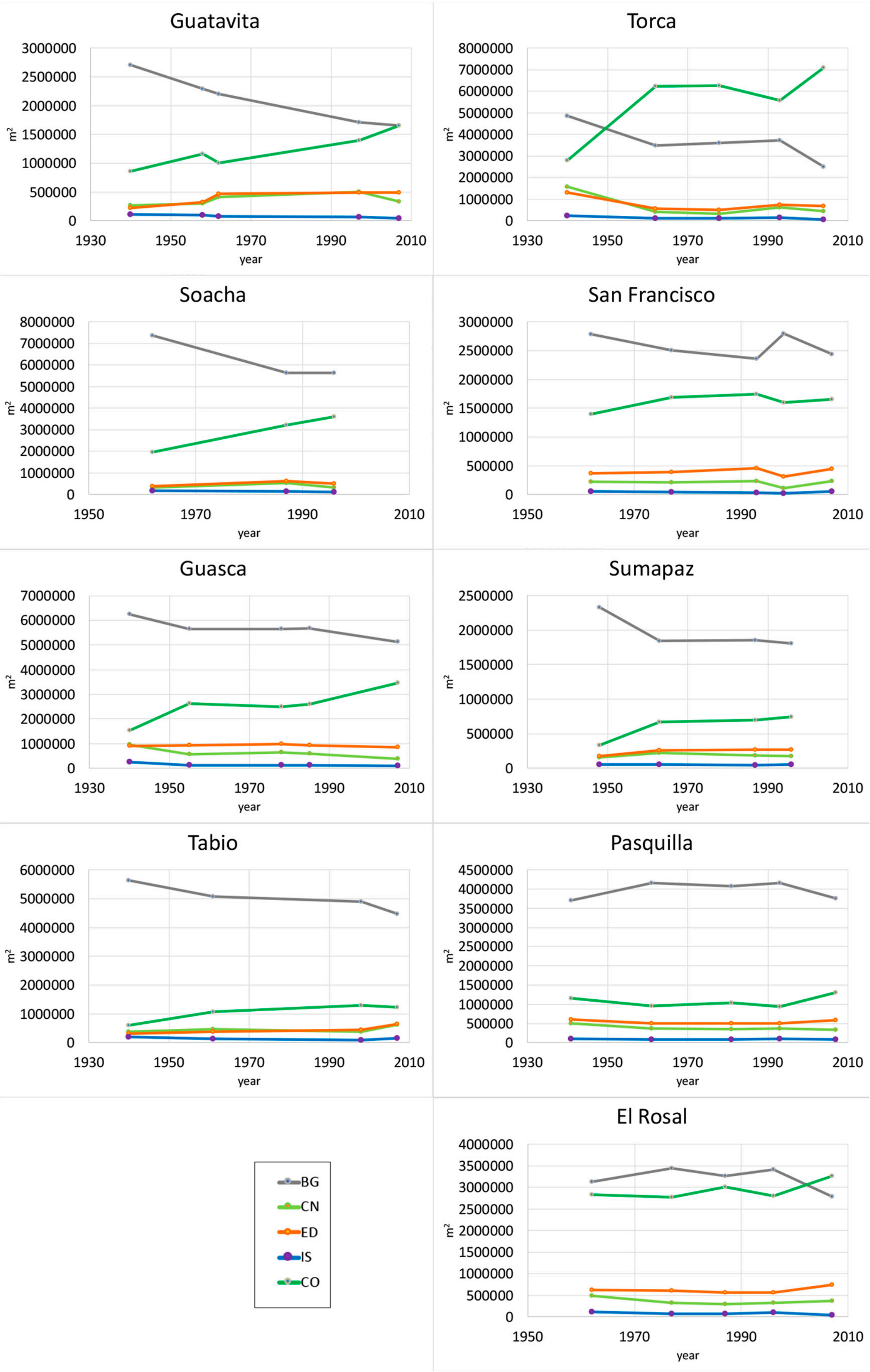

Figure 5. Changes in the relative share of MSPA classes in the study localities (1940–2007): BG = background, CN = connectors and bridges, ED = edges, IS = islets, CO = core (class definitions are presented in Table 2).

4. Discussion

4.1. Spatial Resolution Potential of Historical Aerial Imagery and Time Coverage

Our approach carries the advantage of analyzing a longer time series than normally allowed by mere satellite data at a very high spatial resolution. It allows tracking forest cover changes at a forest fragment scale, which becomes particularly useful for discussing the actual forest species composition and structural parameters, when related to vegetation assessment in the same sites.

On the other hand, the land cover classification generated by aerial images lacks multispectral information and thus limits classification performance. We found that this is particularly true for the accuracy of the rare class B. Even though OA, UA and PA values for classes T, G and B generally fulfilled a minimum threshold of goodness, some omission errors are noticeable for the PA values for class B in some of the aerial scenes. User's and producer's accuracy are sensitive to a number of factors, including the number of random validation points generated and the sampling method employed [88]. However, in our case the low values are most likely due to the relatively small proportion of class B (cf. Figure 2b). In some cases, the area's proportion of the mapped class (W), as incorporated in equations 1–5 of the accuracy calculations found in Oloffson et al. [79], was several times smaller in comparison to the other classes, which led to overall lower accuracy values for class B. Additionally, the lack of ground-truth data for past aerial scenes may have also influenced the goodness of selected training polygons. However, classes B and G were not in the focus of the present study.

Due to the unavailability of more recent, aerial photographs for our study area, our analysis stops in 2007. Our limited timeframe does not allow us to assume that general land cover trends have not changed in the more recent past (i.e., after 2007), considering that there are several urbanization and infrastructure development projects currently being planned or already implemented that may interfere with the recovery of the forests under study. For instance, there is evidence that forested areas close to El Rosal have been substantially decreasing between 2000 and 2015 [89]. Today, unfortunately, only a very little proportion of the study area in El Rosal (and contiguous Subachoque) is under some regime of protection, i.e., the nature reserve Hacienda la Laja, Subachoque, created in 2015 [90]. To the contrary, in Guasca, the suspension of mining activities in the 1990s culminating with the creation of the protected area "El Encenillo" in 2007, leading to a continuous recovery of the forest cover (Figure 3). In a few cases, the limitations to the interpretation of forest cover trends are caused by the incomplete time series of the aerial images, as in the case of Soacha, for which only three aerial scenes were available.

4.2. Individual History of Localities and Forest Cover Trends

The observed locality-specific variation in the forest cover trends appears to be connected to the individual history of each of the localities. In those rural localities that did not experience the worst effects of the country's five decade-long armed conflict between the government, the paramilitary groups and the guerrilla [91,92], and which possess a rather 'smooth' topography, at least within the analyzed area, as Guasca, Tabio, Soacha, San Francisco, El Rosal, and Guatavita, the general forest cover recovery identified here probably is related to a mix of abandonment of rural practices by those seeking better economic opportunities in urban conglomerates [22] and an increase in low-density settlements of secondary homes of people living in Bogotá, who allow forest regrowth within their properties [27], jointly with the widespread implementation of protection efforts since the 1970s [24]. Within this general outline, Torca is exceptional since it is contiguous to the main urbanization of Bogotá and hosts various highly diverse and partially well conserved forest fragments in its steeper parts [41,44]. During the past century, Torca experienced a considerable decrease in agriculture and animal husbandry in favor of an urban expansion, which attracted middle- and upper-class residents that do not engage in rural activities [93]. The latter, together with both the implementation of the protected area "Bosque Oriental de Bogotá" in the 1970s [94] and the harsh topography of a large portion of this area, played a key role in regulating land use conversion. The major part of forest recovery took place in areas of low elevation close to the main motorways, which used to be cleared regularly. However, recent plans to expand the motorways [95] and to build up a massive urbanization project [96] pose new threats to recovered forest fragments, especially at low elevations, where the topography is less pronounced.

The case of Pasquilla, as the only locality in our study with an overall net forest cover loss, can be illustrative of a well populated agricultural landscape in the close vicinity of Bogotá. During the 1940s, Pasquilla became heavily populated and agriculturally exploited, due to the increasing violence in the country and the migration towards the cities [57]. This is consistent with our observations of an initial decrease in forest cover in Pasquilla, right from the 1940s, followed by a phase of slow recovery from the 1980s. Between 1995 and 2009, the main land use shifted from agriculture to animal husbandry, especially affecting the forest cover and its ecological integrity [58]. This is visible in our results by the increased area of size class G (Figure 3). The land use shifts led to an expansion of human-induced azonal páramos and the opening of forest areas for cattle grazing, which affect both the margins and the interior of forest patches, leading to the perforation and size reduction of the fragments, altering the forest structure and its regenerative potential [31,97]. Finally, the considerable recovery of forest core areas in 2006 may be directly linked to the increased protection efforts, together with an emerging environmental commitment of the local population, culminating with the creation of the protected area "Los Encenillales" in 2004 [58]. The impact of the 1940s migrations on forest cover changes is also evident in Sumapaz, which is far from the city of Bogotá. In the mountainous region of Sumapaz, and the eastern portion of the Tolima department, the violence and the armed conflict started already in 1920 and caused the displacement of the population [98]. Consistently, we found an initial increase in forested areas during the 1950s and 1960s in the Sumapaz region, which may result from the rural depopulation that brought farmers from remote areas such as Sumapaz to Pasquilla and other localities considered safer. It may be noted that our study locality in Sumapaz is outside the limits of the National Park (PNN Sumapaz) and thus is not under any protection regime.

4.3. Insights from MSPA on Forest Cover Trends

Besides the core areas, a particularly relevant MSPA class for the dynamic of secondary forest fragments is islets. These correspond to patches of forest vegetation that are potentially vulnerable to disappearance due to their shape and size (i.e., they are small and/or elongated, thin, and isolated). Islets may also act as nuclei for forest growth by serving as stepping stones for pollination and plant dispersal [99,100]. A decrease in islets alone can be either interpreted as a sign of a re-gained connectivity between fragments and the inclusion of former stepping stones into a more extended forest fragment network or as a proof of a more stringent delimitation of cultivated areas, and therefore a more extensive exploitation of the land by the cutting of standing trees within pastures. In our sample, all the localities that recorded a decrease in the class islet for the last period of the time series were also characterized by an increase in the class core. This indicates that the observed islet decrease is mostly due to their inclusion into the forest fragment network and a general restoration of connectivity. Overall, we found a general positive correlation tendency between the forest cover and the core group, and a negative correlation tendency between the forest cover and islets. This was particularly significant for Soacha and Guatavita, where the islet decrease was constant through time, and for Torca, where the decrease trend was only interrupted in the year 1993, as underlined by the positive correlation of forested area with the group core (Guatavita: $r = 0.953$, $p = 0.012$; Torca: $r = 0.987$, $p = 0.002$) and its negative correlation with the group islet (Guatavita: $r = -0.924$, $p = 0.025$; Torca: $r = -0.983$, $p = 0.003$).

In the localities with increased islet values for the last period (Sumapaz, San Francisco, and Tabio) the interpretation is more complex: in Sumapaz, the final increase in islets was accompanied by a total gain in the forest class T (+18% in 1996, Supplementary Tables S5 and S6), a slight increase in core (+6%), a stationary edge (+0%), and a slight decrease in the background (−2%) and connectors (−5%). This indicates that new forest nuclei have formed, as there is no major change in any of the other classes. In San Francisco, the increase in islets was particularly high and it was accompanied by a total gain of forest (+27% in 2007), a slight decrease in background (−13%), a little increase in core (+4%), and a marked increase in connectors (+113%) and edges (+43%). This indicates that new tree nuclei have formed and then connected to other fragments, however, the high edge value implies that cores might be broken or changed in shape and so an increased fragmentation of the main forested area is assumed here and is supported by the positive correlation between the forested area and the edge group ($r = 0.913$, $p = 0.031$). In Tabio, the increase in islet is linked to an overall forest gain (+17% in 2007, Supplementary Table S6), a decrease in core (−6%) and background (−9%), and a marked increase in connectors (+64%) and edges (+4%). This indicates the formation of new tree nuclei in previous background areas, but also a certain degree of fragmentation at the borders of the major forest fragments. This interpretation is confirmed by an increase in edges and connectors, and a decrease in core and background, which is also underlined by the strong positive correlation of forested area and the edge group ($r = 0.969$, $p = 0.031$). The mountains of Tabio are included together with other portions of our study area in the special management area "Reserva Forestal Protectora Productora de la Cuenca Alta del Río Bogotá" [101] since the 1970s. This light protection status still allows for agricultural activities and infrastructure development, inevitably resulting in forest clearing to create pastures, and thus the fragmentation of the previously continuous forest cover. However, except for Guatavita and Tabio, the other localities covered by this special management area are also under other protection figures, and the limits of the Reserva overlap with protected areas with stricter regulations. For Guatavita, the establishment of the Reserva seems to have been beneficial in promoting forest cover and islet inclusion in the main core areas, even though the positive correlation between the forest cover and the edge group for this locality may indicate fragmentation. Conversely, our findings for Tabio underscore that a mild protection regime, extensive agricultural exploitation, and infrastructure development together can hamper the protection and regeneration of forests considerably. Thus, the hazards associated with urbanization and road construction, already reported as key drivers of deforestation in the area [27,30,31,57,58], should be taken into consideration when formulating forest management strategies.

4.4. Possible Factors Influencing Forest Recovery

Our results show a significant increase in forest cover and a general recovery of forest connectors in the examined localities between the 1940s and the early 2000s. Forest regeneration on abandoned agricultural lands, by enhancing landscape connectivity, can potentially contain the ecological damage of deforestation and land degradation [53,102,103]. Restored connectivity, together with the increase in size forest fragments is essential to guarantee the freedom of movement and availability of resources to local fauna populations [104–108].

The overall forest recovery, first described by Etter [47] for two localities in the Bogotá high plain for the period 1940–1996, was recently confirmed for the region north of Bogotá for the years 1985–2015 [27], and for the Colombian Andes in general, for the years 2001–2010 [52]. Our study, which incorporates localities in the southern part of the Bogotá high plain and evaluates a large time scale, further supports and extends these regional evidences.

However, the identified positive trend diverges from the high deforestation rates outlined for Andean lowlands [24] or the Amazon region [109,110]. It also differs from another locality in the Colombian high Andean department of Quindío, where a reduction in forest cover was reported for the period 1954–2009 [48]. The trend of forest recovery in the hinterland of Bogotá also differs from the results from other high Andean regions, such as southern Ecuador [111,112] and southeastern Bolivia [113], which experienced continuous forest loss. Nevertheless, forest recovery was also identified in other similar high Andean systems, such as in the San Martín department, in northern Peru [114].

As observed by Hecht [21], the patterns and drivers of deforestation are likely to vary between localities due to their individual history and accessibility. Dramatic deforestation takes place mainly in economic frontier zones [21] such as the Andean lowlands, the Amazon [24,109,110] or Southern

Ecuador [111,112], where population growth, the expansion of road networks, and the lack of protection favors timber extraction [112]. On the other hand, the hinterland of heavily populated cities, such as our study region, is a complex system, where the observed forest regrowth is mainly driven by rural–urban migration and population decline, eventually leading to the abandonment of rural activities [22,27,47,53]. These factors considerably contribute to forest regrowth together with the inaccessibility of steep and remote forested areas [27,47].

Even though forest cover dynamics are likely to be higher in peri-urban areas than in more remote forest fragments [27], the positive impacts of protected areas are evident in our study area, despite the proximity of the city. Conservation efforts through the establishment of protected areas appear to be effective at limiting deforestation and land-use change, as previously reported for Colombian montane forests [24,47], even without the rigorous and efficient implementation of conservation strategies in place and despite the transformation of areas inside national parks to some degree through anthropogenic activities [30].

5. Conclusions

The unique time coverage of the here employed, generally under-utilized, aerial imagery allowed us to provide a detailed reconstruction of vegetation dynamics at the landscape level, which in several cases clearly mirrors the historical changes that occurred during the occupation and exploitation of these rural areas. Forest recovery alone is expected to improve the systems' ecological conditions, but both the land cover types prior to a transition, and the land cover established by the transition, impact the ecosystem structure and functioning (see [115,116]). Accordingly, in the continuously intervened systems this study is focused on, it is highly likely that the legacy of centuries of land use is still relevant for todays' ecosystem remnants [117,118]. Similarly, when it comes to forest tree diversity and resilience, the effects from interventions in past centuries are likely to be relevant and noticeable even in a not-so-close future [119,120]. For this reason, generating locality-scale, longer-term information on land cover changes is key, considering that the majority of the studies focuses on broader geographical scales and employs satellite data with a shorter time-coverage. Moreover, elucidating not only the extent but also the nature of forest recovery as to its spatial configuration provides deep insights into forest fragment-related cover changes, and helps to understand the drivers and the processes shaping plant communities and the associated provision of ecosystem services [121].

Our findings of forest-recovery in the peri-urban region around Bogotá are encouraging. Nevertheless, they only apply to a limited sampling area. The aerial pictures that we used are available for all Colombia and are currently being georeferenced by the IGAC. Thus, an upscaling of the approach described in this study is possible and would be important to model the developments in adjacent administrative departments and high Andean forests ecosystems in general. This is very relevant, considering that the understanding of regional patterns of land use and land cover conversion in heavily populated high Andean systems is necessary to formulate sound land management plans that can potentially prevent broader scale, irreversible landscape degradation [113].

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/8/788/s1, Table S1: "Detailed information on study localities", Table S2: "Accuracy indices values for each class in each locality through time series", Table S3: "Error matrices for each locality through time series", Figure S4: "Processing steps of the aerial imagery", Table S5: "Forest cover extent and its changes in the study localities", Table S6: "MSPA classes groups percent change through time series in each locality", Table S7: "Correlation coefficients of forest cover and MSPA groups".

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References

1. Vitousek, P.M.; Mooney, H.A.; Lubchenco, J.; Melillo, J.M. Human domination of Earth's ecosystems. *Science* **1997**, *277*, 494–499. [CrossRef]
2. Newbold, T.; Hudson, L.N.; Hill, S.L.; Contu, S.; Lysenko, I.; Senior, R.A.; Börger, L.; Bennett, D.J.; Choimes, A.; Collen, B.; et al. Global effects of land use on local terrestrial biodiversity. *Nature* **2015**, *520*, 45–50. [CrossRef] [PubMed]
3. Pielke, R.A. Land use and climate change. *Science* **1995**, *310*, 1625–1626. [CrossRef]
4. Rodríguez Eraso, N.; Armenteras-Pascual, D.; Alumbreros, J.R. Land use and land cover change in the Colombian Andes: Dynamics and future scenarios. *J. Land Use Sci.* **2013**, *8*, 154–174. [CrossRef]
5. Cojoc, E.I.; Postolache, C.; Olariu, B.; & Beierkuhnlein, C. Effects of anthropogenic fragmentation on primary productivity and soil carbon storage in temperate mountain grasslands. *Environ. Monit. Assess.* **2016**, *188*, 653. [CrossRef] [PubMed]
6. Ziv, Y.; Davidowitz, G. When Landscape Ecology Meets Physiology: Effects of Habitat Fragmentation on Resource Allocation Trade-Offs. *Front. Ecol. Evol.* **2019**, *7*, 137. [CrossRef]
7. Ewers, R.M.; Thorpe, S.; Didham, R.K. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* **2007**, *88*, 96–106. [CrossRef]
8. Öckinger, E.; Lindborg, R.; Sjödin, N.E.; Bommarco, R. Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography* **2012**, *35*, 259–267. [CrossRef]
9. Brinck, K.; Fischer, R.; Groeneveld, J.; Lehmann, S.; De Paula, M.D.; Pütz, S.; Sexton, J.O.; Song, D.; Huth, A. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nat. Commun.* **2017**, *8*, 1–6. [CrossRef]
10. Billings, S.A. Soil organic matter dynamics and land use change at a grassland/forest ecotone. *Soil Biol. Biochem.* **2006**, *38*, 2934–2943. [CrossRef]
11. Fahrig, L. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst* **2003**, *34*, 487–515. [CrossRef]
12. Hubbell, S.P. The unified neutral theory of biodiversity and biogeography. *Monogr. Populat. Biol.* **2001**, *32*, 1–375. [CrossRef]
13. MacArthur, R.H.; Wilson, E.O. *The Theory of Island Biogeography*; Princeton University Press: Princeton, NJ, USA, 2001.
14. Brooks, T.M.; Mittermeier, R.A.; Mittermeier, C.G.; Da Fonseca, G.A.; Rylands, A.B.; Konstant, W.R.; Flick, P.; Pilgrim, J.; Oldfield, S.; Magin, G.; et al. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* **2002**, *16*, 909–923. [CrossRef]
15. Aynekulu, E.; Aerts, R.; Denich, M.; Negussie, A.; Friis, I.; Demissew, S.; Boehmer, H.J. Plant diversity and regeneration in a disturbed isolated dry Afromontane forest in northern Ethiopia. *Folia Geobot.* **2016**, *51*, 115–127. [CrossRef]
16. Olden, J.D. Biotic homogenization: A new research agenda for conservation biogeography. *J. Biogeogr.* **2006**, *33*, 2027–2039. [CrossRef]
17. Norden, N.; Chazdon, R.L.; Chao, A.; Jiang, Y.; Vílchez-Alvarado, B. Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecol. Lett.* **2009**, *12*, 385–394. [CrossRef] [PubMed]
18. Steinfeld, H.; Gerber, P.; Wassenaar, T.D.; Castel, V.; Rosales, M.; Rosales, M.; de Haan, C. *Livestock's Long Shadow: Environmental Issues and Options*; Food & Agriculture Org: Rome, Italy, 2006.

19. Wassenaar, T.; Gerber, P.; Verburg, P.H.; Rosales, M.; Ibrahim, M.; Steinfeld, H. Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. *Glob. Environ. Chang.* **2007**, *17*, 86–104. [CrossRef]
20. Rudel, T.K.; Defries, R.; Asner, G.P.; Laurance, W.F. Changing drivers of deforestation and new opportunities for conservation. *Conserv. Biol.* **2009**, *23*, 1396–1405. [CrossRef]
21. Hecht, S. The new rurality: Globalization, peasants and the paradoxes of landscapes. *Land Use Policy* **2010**, *27*, 161–169. [CrossRef]
22. Aide, T.M.; Grau, H.R. Globalization, migration, and Latin American ecosystems. *Science* **2004**, *305*, 1915. [CrossRef]
23. Grau, H.R.; Aide, T.M. Globalization and Land-Use Transitions in Latin America. *Ecol. Soc.* **2008**, *13*, 16. [CrossRef]
24. Armenteras, D.; Rodríguez, N.; Retana, J.; Morales, M. Understanding deforestation in montane and lowland forests of the Colombian Andes. *Reg. Environ. Chang.* **2011**, *11*, 693–705. [CrossRef]
25. Hecht, S.B.; Kandel, S.; Gomes, I.; Cuellar, N.; Rosa, H. Globalization, forest resurgence, and environmental politics in El Salvador. *World Dev.* **2006**, *34*, 308–323. [CrossRef]
26. Grau, H.R.; Aide, T.M.; Zimmerman, J.K.; Thomlinson, J.R.; Helmer, E.; Zou, X. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience* **2003**, *53*, 1159–1168. [CrossRef]
27. Rubiano, K.; Clerici, N.; Norden, N.; Etter, A. Secondary forest and shrubland dynamics in a highly transformed landscape in the Northern Andes of Colombia (1985–2015). *Forests* **2017**, *8*, 216. [CrossRef]
28. Cleef, A.M. Origen, evolución, estructura y diversidad biológica de la alta montaña colombiana. In *Visión socioecosistémica de los páramos y la alta montaña colombiana: Memorias del proceso de definición de criterios para la delimitación de páramos*; Cortés-Duque, J., Pinzón, C.E.S., Suárez Mejía, A.P., Eds.; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt: Bogotà, Colombia, 2013; pp. 3–21.
29. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; Da Fonseca, G.A.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853. [CrossRef]
30. Armenteras, D.; Gast, F.; Villareal, H. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biol. Conserv.* **2003**, *113*, 245–256. [CrossRef]
31. Etter, A.; Villa, L.A. Andean forests and farming systems in part of the Eastern Cordillera (Colombia). *Mt. Res. Dev.* **2000**, *20*, 236–246. [CrossRef]
32. Balthazar, V.; Vanacker, V.; Molina, A.; Lambin, E.F. Impacts of forest cover change on ecosystem services in high Andean mountains. *Ecol. Indic.* **2015**, *48*, 63–75. [CrossRef]
33. Etter, A.; McAlpine, C.; Wilson, K.; Phinn, S.; Possingham, H. Regional patterns of agricultural land use and deforestation in Colombia. *Agr. Ecosyst. Environ.* **2006**, *114*, 369–386. [CrossRef]
34. Cleef, A.M. The vegetation of the páramos of the Colombian Cordillera Oriental. *Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht* **1981**, *481*, 1–320.
35. Sturm, H.; Rangel-Ch., O. *Ecología de los páramos andinos: Una visión preliminar integrada*; Universidad Nacional de Colombia: Bogotà, Colombia, 1985.
36. Van der Hammen, T. *Plan ambiental de la cuenca alta del río Bogotá: Análisis y orientaciones para el ordenamiento territorial*; Corporación Autónoma Regional de Cundinamarca: Bogotá, Colombia, 1998.
37. Van der Hammen, T. *La Cordillera Oriental Colombiana Transecto Sumapaz vol. 7*; J. Cramer: Berlin, Germany, 2008.
38. Cortés, S. La vegetación boscosa y arbustiva de la cuenca alta del río Bogotá/Forest and shrub vegetation of the upper basin of the Bogotá river. In *La Cordillera Oriental Colombiana Transecto Sumapaz vol. 8*; J. Cramer: Berlin, Germany, 2008.
39. Acuña Cabanzo, A. Potencial de regeneración de rastrojos y bosques secundarios en la sabana de Bogotá. Bachelor's Thesis, Pontificia Universidad Javeriana: Bogotá, Colombia, 2013.
40. Muñoz-Camacho, J.C.; Hurtado, A.B.; Norden, N. *Composición florística de tres fragmentos de bosque altoandino en los alrededores de la sabana de Bogotá: Parcelas permanentes del Proyecto Rastrojos*; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt: Bogotá, Colombia, 2017.
41. Hurtado-Martilletti, A.B.; Echeverry-Galvis, M.A.; Salgado-Negret, B.; Muñoz, J.C.; Posada, J.M.; Norden, N. No trace of floristic homogenization in peri-urban Andean secondary forests despite high anthropogenic transformation. *J. Ecol.*. under review.

42. Rodríguez-Alarcón, S.; Rodríguez-Eraso, N.; Pineda-Rincón, I.; & López-Camacho, R. Effects of fragmentation on functional diversity associated with aboveground biomass in a high Andean forest in Colombia. *Landsc. Ecol.* **2018**, *33*, 1851–1864. [CrossRef]
43. Clerici, N.; Cote-Navarro, F.; Escobedo, F.J.; Rubiano, K.; Villegas, J.C. Spatio-temporal and cumulative effects of land use-land cover and climate change on two ecosystem services in the Colombian Andes. *Sci. Total Environ.* **2019**, *685*, 1181–1192. [CrossRef] [PubMed]
44. Calbi, M.; Fajardo-Gutiérrez, F.; Posada-Hostettler, J.; Lücking, R.; Brokamp, G.; Borsch, T. Seeing the wood despite the trees: Disentangling the impact of human disturbance on plant diversity, community structure, and standing biomass in fragmented high Andean forests. *Ecol. Evol.*. under review.
45. Morgan, J.L.; Gergel, S.E. Quantifying historic landscape heterogeneity from aerial photographs using object-based analysis. *Landsc. Ecol.* **2010**, *25*, 985–998. [CrossRef]
46. Morgan, J.L.; Gergel, S.E. Automated analysis of aerial photographs and potential for historic forest mapping. *Can. J. For. Res.* **2013**, *43*, 699–710. [CrossRef]
47. Etter, A. Multitemporal analysis (1940–1996) of land cover changes in the southwestern Bogotá highplain (Colombia). *Landscape Urban Plan.* **2002**, *59*, 147–158.
48. Quintero-Gallego, M.E.; Quintero-Angel, M.; Vila-Ortega, J.J. Exploring land use/land cover change and drivers in Andean mountains in Colombia: A case in rural Quindío. *Sci. Total Environ.* **2018**, *634*, 1288–1299. [CrossRef]
49. Lydersen, J.M.; Collins, B.M. Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography. *Ecosystems* **2018**, *21*, 1348–1363. [CrossRef]
50. Lindborg, R.; Eriksson, O. Historical landscape connectivity affects present plant species diversity. *Ecology* **2004**, *85*, 1840–1845. [CrossRef]
51. Anselm, N.; Brokamp, G.; Schütt, B. Assessment of Land Cover Change in Peri-Urban High Andean Environments South of Bogotá, Colombia. *Land* **2018**, *7*, 75. [CrossRef]
52. Sánchez-Cuervo, A.M.; Aide, T.M.; Clark, M.L.; Etter, A. Land cover change in Colombia: Surprising forest recovery trends between 2001 and 2010. *PLoS ONE* **2012**, *7*, e43943. [CrossRef] [PubMed]
53. Sánchez-Cuervo, A.M.; Aide, T.M. Consequences of the armed conflict, forced human displacement, and land abandonment on forest cover change in Colombia: A multi-scaled analysis. *Ecosystems* **2013**, *16*, 1052–1070. [CrossRef]
54. Vanwalleghem, T.; Gómez, J.A.; Amate, J.I.; de Molina, M.G.; Vanderlinden, K.; Guzmán, G.; Laguna, A.; Giráldez, J.V. Impact of historical land use and soil management change on soil erosion and agricultural sustainability during the Anthropocene. *Anthropocene* **2017**, *17*, 13–29. [CrossRef]
55. Waldner, L.S. The kudzu connection: Exploring the link between land use and invasive species. *Land Use Policy* **2008**, *25*, 399–409. [CrossRef]
56. Cortés, S.P.; Van der Hammen, T.; & Rangel-Ch, J.O. Comunidades vegetales y patrones de degradacion y sucesion en la vegetacion de los cerros occidentales de Chiacundinamarca-Colombia. *Revista Acad. Colomb. Ci. Exact.* **1999**, *23*, 529–555.
57. Julio, M.Á. Ciudad Bolívar: Gestión ambiente y territorio. Bachelor's Thesis, Universidad Nacional de Colombia, Bogotá, Colombia, 2003.
58. Hernández-Gómez, A.; Rojas-Robles, R.; Sánchez-Calderón, F.V. Cambios en el uso del suelo asociados a la expansión urbana y la planeación en el corregimiento de Pasquilla, zona rural de Bogotá (Colombia). *Cuad. Geogr. Rev. Colomb. Geogr.* **2013**, *22*, 257–271. [CrossRef]
59. QGIS Development Team. QGIS Geographic Information System, Version 2.18.14-Las Palmas. Open Source Geospatial Foundation. 2017. Available online: http://www.qgis.org/ (accessed on 20 January 2018).
60. Willhauck, G.; Schneider, T.; De Kok, R.; Ammer, U. Comparison of object oriented classification techniques and standard image analysis for the use of change detection between SPOT multispectral satellite images and aerial photos. In *Proceedings of XIX ISPRS Congress*; IAPRS: Amsterdam, Netherlands, 2000; Volume 33, pp. 35–42.
61. Varga, K.; Szabó, S.; Szabó, G.; Dévai, G.; Tóthmérész, B. Improved land cover mapping using aerial photographs and satellite images. *Open Geosci.* **2015**, *7*. [CrossRef]
62. Eitzel, M.V.; Kelly, M.; Dronova, I.; Valachovic, Y.; Quinn-Davidson, L.; Solera, J.; de Valpine, P. Challenges and opportunities in synthesizing historical geospatial data using statistical models. *Ecol. Inform.* **2016**, *31*, 100–111. [CrossRef]

63. Harb Rabia, A.; Terribile, F. Semi-automated classification of gray scale aerial photographs using geographic object based image analysis (GEOBIA) technique. In *EGU General Assembly Conference Abstracts*; EGU General Assembly: Vienna, Austria, 2013; Volume 15.
64. Blaschke, T.; Burnett, C.; Pekkarinen, A. Image segmentation methods for object-based analysis and classification. In *Remote Sensing Image Analysis: Including the Spatial Domain*; Springer: Dordrecht, Germany, 2004; pp. 211–236.
65. Zvoleff, A. *Package 'glcm'*. 2019. Available online: https://CRAN.R-project.org/package=glcm (accessed on 10 March 2019).
66. RStudio Team. *RStudio: Integrated Development for R*; RStudio, Inc.: Boston, MA, USA, 2016; Available online: http://www.rstudio.com/ (accessed on 20 January 2018).
67. Huang, Y.; Yue, A.; Wei, S.; Li, D.; Luo, M.; Jiang, Y.; Zhang, C. Texture feature extraction for land-cover classification of remote sensing data in land consolidation district using semi-variogram analysis. *WSEAS Trans. Comput.* **2008**, *7*, 857–866.
68. Wen, C.; Zhang, Y.; Deng, K. Urban area classification in high resolution SAR based on texture features. In Proceedings of the ISPRS 2009 Congress, Beijing, China, 14–16 September 2009; Zhang, J., Li, Z., Cheng, P., Yan, Q., Eds.; ISPRS: Sydney, Australia, 2009; pp. 281–285.
69. Hall-Beyer, M. GLCM texture: A tutorial. National Council on Geographic Information and Analysis Remote Sensing Core Curriculum v.3. 2000. Available online: https://ojskrede.github.io/inf4300/additional_resources/uc_calgary_glcm_tutorial.pdf (accessed on 3 March 2019).
70. Adams, R.; Bischof, L. Seeded region growing. *IEEE T. Pattern Anal.* **1994**, *16*, 641–647. [CrossRef]
71. Conrad, O.; Bechtel, B.; Bock, M.; Dietrich, H.; Fischer, E.; Gerlitz, L.M.; Wehberg, J.; Wichmann, V.; Böhner, J. System for Automated Geoscientific Analyses (SAGA) v.2.1.4. *Geosci. Model. Dev.* **2015**, *8*, 1991–2007. [CrossRef]
72. Blaschke, T. Object based image analysis for remote sensing. *ISPRS J. Photogramm.* **2010**, *65*, 2–16. [CrossRef]
73. Radoux, J.; Bogaert, P. Accounting for the area of polygon sampling units for the prediction of primary accuracy assessment indices. *Remot. Sens Environ.* **2014**, *142*, 9–19. [CrossRef]
74. Franklin, J.; Rogan, J.; Phinn, S.R.; Woodcock, C.E. Rationale and conceptual framework for classification approaches to assess forest resources and properties. In *Remote Sensing of Forest Environments*; Springer: Boston, MA, USA, 2003; pp. 279–300.
75. Stehman, S.V. Sampling designs for accuracy assessment of land cover. *Int. J. Remote. Sens.* **2009**, *30*, 5243–5272. [CrossRef]
76. Radoux, J.; Bogaert, P. Good practices for object-based accuracy assessment. *Remote Sens.* **2017**, *9*, 646. [CrossRef]
77. Stehman, S.V.; Wickham, J.D. Pixels, blocks of pixels, and polygons: Choosing a spatial unit for thematic accuracy assessment. *Remote Sens. Environ.* **2011**, *115*, 3044–3055. [CrossRef]
78. Olofsson, P.; Foody, G.M.; Herold, M.; Stehman, S.V.; Woodcock, C.E.; Wulder, M.A. Good practices for estimating area and assessing accuracy of land change. *Remote Sens. Environ.* **2014**, *148*, 42–57. [CrossRef]
79. Olofsson, P.; Foody, G.M.; Stehman, S.V.; Woodcock, C.E. Making better use of accuracy data in land change studies: Estimating accuracy and area and quantifying uncertainty using stratified estimation. *Remote Sens. Environ.* **2013**, *129*, 122–131. [CrossRef]
80. McGarigal, K. *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*; US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 1995.
81. Kindlmann, P.; Burel, F. Connectivity measures: A review. *Landsc. Ecol.* **2008**, *23*, 879–890. [CrossRef]
82. Vogt, P.; Riitters, K.H.; Estreguil, C.; Kozak, J.; Wade, T.G.; Wickham, J.D. Mapping spatial patterns with morphological image processing. *Landsc. Ecol.* **2007**, *22*, 171–177. [CrossRef]
83. Soille, P.; Vogt, P. Morphological segmentation of binary patterns. *Pattern Recognit. Lett.* **2009**, *30*, 456–459. [CrossRef]
84. Vogt, P.; Riitters, K. GuidosToolbox: Universal digital image object analysis. *Eur. J. Remote Sens.* **2017**, *50*, 352–361. [CrossRef]
85. Kang, S.; Choi, W. Forest cover changes in North Korea since the 1980s. *Reg. Environ. Chang.* **2014**, *14*, 347–354. [CrossRef]
86. Vogt, P.; Ferrari, J.R.; Lookingbill, T.R.; Gardner, R.H.; Riitters, K.H.; Ostapowicz, K. Mapping functional connectivity. *Ecolo. Indic.* **2009**, *9*, 64–71. [CrossRef]

87. De Paula, M.D.; Groeneveld, J.; Huth, A. The extent of edge effects in fragmented landscapes: Insights from satellite measurements of tree cover. *Ecol. Indic.* **2016**, *69*, 196–204. [CrossRef]
88. Araya, Y.H.; Cabral, P. Analysis and modeling of urban land cover change in Setúbal and Sesimbra, Portugal. *Remote Sens.* **2010**, *2*, 1549–1563. [CrossRef]
89. Garcia Guerrero, D.A.; Bejarano Rojas, G.A. Análisis de Cambios de Usos y Coberturas del Suelo en los Municipios El Rosal y Subachoque. Bachelor's Thesis, Universidad Distrital, Bogotá, Colombia, 2016.
90. RUNAP. 2020. Available online: http://runap.parquesnacionales.gov.co/ (accessed on 20 January 2020).
91. Dinámica Reciente de la Confrontación Armada en Cundinamarca. Available online: http://2014.derechoshumanos.gov.co/Observatorio/publicaciones/Paginas/estudiosregionales.aspx (accessed on 24 June 2020).
92. Panorama Actual de la Región del Sumapaz. Available online: http://2014.derechoshumanos.gov.co/Observatorio/publicaciones/Paginas/estudiosregionales.aspx (accessed on 24 June 2020).
93. Benavides Escobar, M.C. Una mirada a la gentrificación. El caso Bogotá. Ph.D. Thesis, Universidad Nacional de Colombia, Bogotá, Colombia, 2017.
94. Cerrosorientales.com. Available online: https://cerrosorientales.com/cronologia/ (accessed on 20 January 2020).
95. El Tiempo. 2018. Available online: https://www.eltiempo.com/bogota/comienza-la-ampliacion-de-la-autopista-norte-y-la-carrera-septima-213586 (accessed on 20 January 2020).
96. El Tiempo. 2018. Available online: https://www.eltiempo.com/bogota/como-sera-el-proyecto-lagos-de-torca-de-bogota-246476 (accessed on 20 January 2020).
97. Forman, R.T. *Land Mosaics: The Ecology of Landscapes and Regions 1995*; Cambridge University Press: Cambridge, MA, USA, 2014; p. 217.
98. Cadavid, E. Historia de la Guerrilla en Colombia. Universidad Federal de Juiz de Fora. Available online: www.ecsbdefesa.com.br/defesa/fts/HGC.pdf (accessed on 20 January 2020).
99. Latorre, L.F.L.; Arévalo, H.F.L. Comunidad de mamíferos no voladores en un área periurbana andina, Cundinamarca, Colombia. *Acta Biol. Colomb.* **2015**, *20*. [CrossRef]
100. Da Luz, N.B.; Garrastazu, M.C.; Doetzer Rosot, M.A.; Maran, J.C.; de Oliveira, Y.M.M.; Franciscon, L.; Cardoso, D.J.; de Freitas, J.V. Brazilian National Forest Inventory-a landscape scale approach to monitoring and assessing forested landscapes. *Brazil. J. For. Res.* **2018**, *38*. [CrossRef]
101. El Espectador. 2014. Available online: https://www.elespectador.com/noticias/bogota/reduccion-de-reserva-de-cuenca-alta-del-rio-bogota-articulo-473661 (accessed on 22 January 2020).
102. Guariguata, M.R.; Ostertag, R. Neotropical secondary forest succession: Changes in structural and functional characteristics. *For. Ecol. Manag.* **2001**, *148*, 185–206. [CrossRef]
103. Chazdon, R.L. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* **2008**, *320*, 1458–1460. [CrossRef] [PubMed]
104. Bierregaard, R.O.; Lovejoy, T.E.; Kapos, V.; dos Santos, A.A.; Huntchings, R.W. The biological dynamics of tropic rainforest fragments: A prospective comparison of fragments and continuous forest. *Bioscience* **1992**, *42*, 859–866. [CrossRef]
105. Dunning, J.; Danielson, B.; Pulliam, H. Ecological processes that affect populations in complex landscapes. *Oikos* **1992**, *65*, 169–175. [CrossRef]
106. Ferraz, G.; Nichols, J.D.; Hines, J.E.; Stouffer, P.C.; Bierregaard, R.O.; Lovejoy, T.E. A large scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* **2007**, *315*, 238–240. [CrossRef]
107. Aubad, J.; Aragón, P.; Rodríguez, M.A. Human access and landscape structure effects on Andean forest bird richness. *Acta Oecol.* **2010**, *36*, 396–402. [CrossRef]
108. Tinoco, B.A.; Astudillo, P.X.; Latta, S.C.; Strubbe, D.; Graham, C.H. Influence of patch factors and connectivity on the avifauna of fragmented Polylepis forest in the Ecuadorian Andes. *Biotropica* **2013**, *45*, 602–611. [CrossRef]
109. Armenteras, D.; Rudas, G.; Rodriguez, N.; Sua, S.; Romero, M. Patterns and causes of deforestation in the Colombian Amazon. *Ecol. Indic.* **2006**, *6*, 353–368. [CrossRef]
110. Etter, A.; McAlpine, C.; Phinn, S.; Pullar, D.; Possingham, H. Characterizing a tropical deforestation wave: A dynamic spatial analysis of a deforestation hotspot in the Colombian Amazon. *Global Change Biol.* **2006**, *12*, 1409–1420. [CrossRef]

111. Curatola Fernández, G.F.; Obermeier, W.A.; Gerique, A.; López Sandoval, M.F.; Lehnert, L.W.; Thies, B.; Bendix, J. Land cover change in the Andes of Southern Ecuador—Patterns and drivers. *Remote Sens.* **2015**, *7*, 2509–2542. [CrossRef]
112. Tapia-Armijos, M.F.; Homeier, J.; Espinosa, C.I.; Leuschner, C.; de la Cruz, M. Deforestation and forest fragmentation in South Ecuador since the 1970s–losing a hotspot of biodiversity. *PLoS ONE* **2015**, *10*, e0133701. [CrossRef] [PubMed]
113. Brandt, J.S.; Townsend, P.A. Land use–land cover conversion, regeneration and degradation in the high elevation Bolivian Andes. *Landsc. Ecol.* **2006**, *21*, 607–623. [CrossRef]
114. Kintz, D.B.; Young, K.R.; Crews-Meyer, K.A. Implications of land use/land cover change in the buffer zone of a national park in the tropical Andes. *Environ. Manag.* **2006**, *38*, 238–252. [CrossRef] [PubMed]
115. Farley, K. Grasslands to tree plantations: Forest transition in the Andes of Ecuador. *Ann. Assoc. Am. Geogr.* **2007**, *97*, 755–771. [CrossRef]
116. Hall, J.M.; Van Holt, T.; Daniels, A.E.; Balthazar, V.; Lambin, E.F. Trade-offs between tree cover, carbon storage and floristic biodiversity in reforesting landscapes. *Landsc. Ecol.* **2012**, *27*, 1135–1147. [CrossRef]
117. Foster, D.; Swanson, F.; Aber, J.; Burke, I.; Brokaw, N.; Tilman, D.; Knapp, A. The importance of land-use legacies to ecology and conservation. *BioScience* **2003**, *53*, 77–88. [CrossRef]
118. Bürgi, M.; Östlund, L.; Mladenoff, D.J. Legacy effects of human land use: Ecosystems as time-lagged systems. *Ecosystems* **2017**, *20*, 94–103. [CrossRef]
119. Flinn, K.M.; Marks, P.L. Agricultural legacies in forest environments: Tree communities, soil properties, and light availability. *Ecol.l Appl.* **2007**, *17*, 452–463. [CrossRef]
120. Comita, L.S.; Thompson, J.; Uriarte, M.; Jonckheere, I.; Canham, C.D.; Zimmerman, J.K. Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. *Ecol. Appl.* **2010**, *20*, 1270–1284. [CrossRef]
121. Eigenbrod, F. Redefining landscape structure for ecosystem services. *Curr. Landsc. Ecol. Rep.* **2016**, *1*, 80–86. [CrossRef]

Chapter 4. Modeling the potential present and future distribution of a tropical Andean treeline species using three different climate datasets

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ABSTRACT

Weinmannia fagaroides is a widespread tree species in biodiverse neotropical Andean treeline ecotones, especially in the Colombian cordilleras. For this reason, it is expected to represent a good indicator for mesoclimatic conditions and distribution shifts based on climate changes in High Andean forests. In this study, the current and potential future distribution of *W. fagaroides* in the forest belts of the northern high Andean region is modeled for the first time. Differences between three available climate datasets used for projecting the potential distribution of *W. fagaroides* were analyzed. By employing Generalized Linear Models (GLM), Random Forests (RF) and MaxEnt algorithms in the Biomod framework, we examined the environmental factors influencing the species current distribution. The predictive ability of climate data derived from different statistical methods as well as algorithm performances were evaluated. The climatic dataset and algorithms which retrieved higher evaluation scores were selected to calculate projections for the present and the future, averaging models from five different Global Circulation Models (GCMs). No statistically significant difference among climate datasets performances was detected. However, Chelsa 1.2 prediction of the current distribution of *W. fagaroides* retrieved slightly higher model evaluation metrics. The algorithms RF and MaxEnt offered a higher predictive power than the GLMs. Minimum coldest month temperature, mean annual precipitation, and bulk density were identified as main environmental drivers constraining the present distribution of *W. fagaroides*. Moreover, for the period 2060-2080, the distribution range of *W. fagaroides* is predicted to shrink by 38%, with a substantial elevational upward shift. Given that *W. fagaroides* can be a representative species for other high Andean treeline species, and that at present only around 23% of the modeled distribution area is situated in protected areas, we recommend that conservation efforts should aim at an expansion of protected areas in the high Andes to include forest/grasslands ecotones in adequate protection figures.

Keywords: *Weinmannia fagaroides*, Cunoniaceae, Biomod, environmental niche model, Chelsa, Worldclim, Climate Change

4.1. Introduction

High-elevation treelines are an easily detectable terrestrial ecotone, developing where closed canopy forests give way to open alpine shrub- and grasslands over a relatively short altitudinal range (Körner, 2012). Such abrupt ecotones - when not human-induced (Sarmiento, 2002; Di Pasquale et al., 2008) - are believed to be constrained by lower mean growing season temperatures, but also by wind and light exposure, which limit the establishment or growth of upright woody trees (Körner, 1998, 2008; Holtmeier and Broll, 2010; McIntire et al., 2016). High mountain environments are likely to undergo above-average warming rates (Schickhoff, 2011; IPCC, 2013), and so treelines are expected to move up to higher elevations (Harsch et al., 2009; Morueta-Holme et al., 2015; Gatti et al., 2019). Considering that species occur within a determined climatic range shaped by their climatic needs (Trivedi et al., 2008), treeline species are of particular interest because of their past and present histories as indicators of precise climatic conditions and environmental niche shifts (Körner, 2012).

In contrast to temperate treelines, treelines within tropical latitudes, as the ones occurring in the Northern and Central Andes, are not shaped by annual temperature extremes or seasonal snow or ice cover but instead, the growing season is spread across the entire year (Young & Leon, 2007). The temperature is rather mild, with small monthly (Jacob et al., 2015) and large diurnal variations, resulting in relatively warm days and freezing nights throughout the year (Körner & Paulsen, 2004; Hoch & Körner, 2005; Rehm & Feeley, 2013). Andean treelines are also much more diverse than their temperate counterparts (Young & Leon, 2007) and are affected by multiple ecological processes (*e.g.,* seed dispersal, seedling growth) (Young et al., 2017). In addition, the ecotone between forest, shrub- and grasslands has been modified through the centuries by anthropogenic pressure on the landscape, leading to shifts in treelines (Tovar et al. 2013). Previous studies found that Andean tree species are shifting their mean elevations upslope in response to climate warming, but at a slower pace than what predicted on the basis of changes in mean temperature alone (Feeley et al., 2011; Duque et al., 2015). However, also several relatively stationary tropical treelines have been reported (Harsch et al., 2009; Rehm and Feeley, 2015a, 2016). In general, our comprehension of how high Andean treelines and forests and associated tree species will respond to ongoing and future climate change is still quite sparse (Rehm & Feeley, 2015b), and species-specific responses are highly probable (Young & Leon, 2007).

Andean biodiversity developed mainly along two dimensions: latitudinal and altitudinal (Mutke et al., 2014). Accordingly, high Andean forests host an impressive biodiversity with many endemic and vulnerable species, which makes these ecosystems one of the global conservation priorities (Myers et al., 2000). Unfortunately, these ecosystems are in general mostly unprotected (Armenteras et al., 2003; Helmer et al., 2019). For this reason, modelling techniques examining the main environmental constraints underlying the distribution of distinctive high Andean ecotones species, thus their establishment and survival potential, can further our capacity to anticipate the future response of these highly diverse ecosystems (Pearson & Dawson, 2003). Moroever, these could ultimately provide the necessary baseline knowledge for relevant conservation strategies in the light of ongoing climate change (Cuykens et al., 2016).

Species Distribution Models (SDMs) originate back to the 1970s (Booth et al., 2014), but during the past two decades have become an increasingly important tool to explore many issues related to fundamental ecological and biogeographical research, evolution, conservation, and climate change and its detrimental effects on species and ecosystems (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Peterson et al., 2011). There are several challenges associated with SDMs, one of which is the difficulty of finding true absence points (Bobrowski & Schickhoff, 2017) to implement presence-absence models. Issues related to sampling bias and sampling effort, linked to spatial autocorrelation of species records and thus collinearity in environmental data (Araújo & Guisan, 2006; Loiselle et al., 2008; Naimi et al., 2011), can also contribute to levels of uncertainty (Veloz, 2009; Bobrowski & Schickhoff, 2017; Loiselle et al., 2008).

Most commonly, modeling approaches of species distributions link species occurrences with available climatic and topographic factors to characterize suitable habitat conditions (Soberon & Nakamura, 2009), aiming to explain existing patterns and/or making predictions (Elith & Leathwick, 2009) either in space or time. In this context, the choice of different environmental predictors may lead to different distribution maps for the same species (Luoto et al., 2007; Bobrowski & Schickhoff, 2017). Additionally, the the quantity and accuracy of the occurrence data and the selection of the modeling algorithm employed can also add uncertainties and biases to the model output (Elith et al., 2006; Araújo & New, 2007; Bobrowski & Schickhoff, 2017).

So far there have been very few efforts modeling andean treeline species distributions, mostly targeting *Polylepis* spp. (Rosaceae) (Cuyckens et al., 2016; Zutta & Rundel, 2017; Fajardo-Gutierrez et al., 2018; Caballero-Villalobos et al., subm.). Particularly, two studies projected the potential distribution of *P. tarapacana* and *P. quadrijuga* to a future scenario, highlighting a substantial reduction in the modeled area under climate change conditions (Cuyckens et al., 2016; and Caballero-Villalobos et al., subm.).

In this study we implement SDMs in order to characterize the suitable environmental conditions - or the “abiotically suitable distribution”- (Bobrowski et al., 2017; Peterson et al., 2011) of the treeline species *Weinmannia fagaroides* Kunth (Rehm & Feeley, 2015a) in northern Andean treeline ecotones, based on available environmental variables. Moreover, we hypothesise that the species' potential distribution will undergo a reduction of its area, as a result of ongoing climate change. Therefore, the specific objectives are: (*1)* to model the current distribution of the species; *(2)* to project the modeled distribution to the future, in order to make predictions in the context of climate change; and *(3)* to evaluate the efficacy of three different climate datasets and three different modelling algorithms in modeling the current species' distribution.

The comparison of different climate datasets and modeling algorithms adds an unprecedented testing dimension for this biogeographic area to our main task, that can provide data on the outcomes and performance of each datset and algorithm as a basis for future distribution modeling efforts in the Andes.

This study included a multi-step evaluation approach in parallel for the three climate datasets, with initial model calibration and subsequent evaluation of spatial prediction success and model accuracy. Specifically, we wanted to test the differences between three climatic datasets: Worldclim 1.4, Worldclim 2 and Chelsa 1.2, which are based on different downscaling methods. The Worldclim 1.4 datasets consist of interpolated climate data (Fick & Hijmans, 2017), with Worldclim 2 being a refined and expanded version of the dataset (Fick & Hijmans, 2017). In contrast, Chelsa 1.2 is based on a quasi-mechanistical statistical downscaling of the ERA-interim global circulation model with Global Precipitation Climatology Centre (GPCC) and Global Historical Climatology Network (GHCN) bias correction (for details see Karger et al., 2019). Therefore, it appears to perform better in mountainous areas (Bobrowski & Schickhoff, 2017). Finally, the distribution of *W. fagaroides* was projected under current and potential future climate scenarios and intersected with the current protected areas network to evaluate its protection status and assess potential target areas for the conservation of high Andean species and ecotones.

We further set out to answer four specific questions: *(i)* What are key environmental variables that constrain the current distribution of *W. fagaroides* in the northern Andes?; *(ii)* To what level do predictions based on different climate datasets differ and which algorithms perform better?; *(iii)* Which areas are predicted as potentially suitable for *W. fagaroides* under present and potential future climate scenarios?; *(iv)* Which fraction of the current and future modeled distribution is currently under some kind of protection regime and what are the implications for the conservation of *W. fagaroides*?

4.2 Materials and Methods

4.2.1. Study area

Our study area encompasses the Northern and Central Andes, ranging from Venezuela to Bolivia and including four isolated mountain systems in the north of South America, the *Sierra Nevada de Santa Marta* and the *Serranía de Perijá* in Colombia, and the *Cordillera del Norte* and *Cordillera de Mérida* in Venezuela (Fig. 1a). The southern part of the Colombian Andes, *i.e.*, the Western and Central Cordilleras, extend into Ecuador and further into the Western and Central Cordilleras of Perú and finally to the *Bolivian Yungas sensu* Hazzi et al. (2018). We selected the Northern and Central Andes as a biogeographic region, excluding the *Southern Yungas sensu* Hazzi et al. (2018), which does not correspond to the complete distribution area of *W. fagaroides* (reported to range from Honduras to Bolivia; see Morales, 2010), because we aimed for a homogeneous study area with a limited latitudinal gradient to address our research questions observing the conditions of environmental equilibrium and niche equality (Carretero & Sillero, 2016).

4.2.2. Target species

Weinmannia fagaroides, also referred to as *encenillo crespo* or *encino de hoja pequeña* (Fig. 1b), is a widespread, central to northern Andean and Central American treeline species (Harling, 1999; Morales, 2010). Within the complex genus *Weinmannia*, it is one of the few species for which a clear species delimitation is possible (Harling, 1999; Morales, 2010; Fajardo-Gutiérrez et al., 2020), facilitating its use for species distribution modeling based on occurrence data. *Weinmannia fagaroides* forms wind-dispersed shrubs or trees that grow at an elevation between 2,200 m and 4,000 m (Morales, 2010; Rehm & Freeley, 2015a; Bernal et al., 2016) in undisturbed or intervened High Andean forests. They can extend also into disturbed areas and ecotonal zones between grasslands and forests, suggesting that this species may be one of the future pioneer invaders of the grasslands above the treeline (Rehm & Feeley, 2016). Moreover, at times, they can be found as stunted shrubs in particularly harsh climatic conditions (Rehm & Feeley, 2016; Puetate-Huaca, 2017). It usually grows 5-10 m tall (Harling, 1999), but it can occasionally reach 25 m in mature forest fragments (Calbi et al., 2021). *Weinmannia fagaroides* is a heliophytic species that extends into the upper canopy or prefers open sites with little or no shadows (Tepán & Toledo , 2016; Whaley et al., 2010), requiring full exposition for optimal growth and development. Flowering shows a marked semestral pattern, as reported from Ecuador, with fruit production coinciding with the driest period of the year (Lozano, 2015). *Weinmannia fagaroides* has been traditionally used as a wood source and for dyeing, due to its high tannin content (Lozano, 2015). This species was found to be abundant in high Andean forest plots in Ecuador and Bolivia (Malizia et al., 2020), and characteristic of higher elevation high Andean fragments in Colombia (Calbi et al., 2021). In addition, *W. fagaroides* is ecologically important as phorophyte for a diverse array of epiphytes (Fajardo-Gutierrez et al., 2020, Calbi et al., 2021), as habitat for small forest mammals and birds (Calbi, *own observation*), its associations with endophytic fungi (Rojas-Jimenez et al., 2016), and for its role to prevent soil erosion and promote organic matter accumulation thanks to its deep and much branched root system (Puetate-Huaca, 2017; Restrepo, 2005).

4.2.3. Specimen data

Occurrence data were obtained from different sources. We retrieved a total of 1,369 georeferenced records from GBIF (1,336 out of the total of 1,690 for *W. fagaroides,* available at https://www.gbif.org/species/7333833 and 33 of the 34 records available for the orthographic variant "*W. fagarioides"*, https://www.gbif.org/species/9216702). In total, 33 records were added from revisions of physical and digitized herbarium collections (Jardín Botánico de Bogotá José Celestino Mutis - JBB, Herbario Universidad de Antioquia - HUA, Herbario Federico Meden Bogotá - FMB, Herbario Museo de La Salle Bogotá - BOG, Herbario Forestal de la Universidad Distrital UDBC). And finally, eight additional records were derived from field trips in the Eastern Cordillera of Columbia, totaling to 1,410 records. Since we aimed to model the biogeographical region of the Northern and Central Andes, which covers over 1.5 million km^2, from 11° N to 23° S, and elevations from around 600-800 m to up to 6,000 m a.s.l. (Herzog et al., 2011), we removed the records from Central America and from the Tepui areas of the Venezuelan Guayana shield, which harbor a peculiar population of *W. fagaroides*, initially described under the name *W. roraimensis* Cuatrec.

We then cleaned the remaining records, excluding those with georeferencing uncertainty above 1 km radius and those corresponding to elevations below 2,200 m, because they do not correspond with the elevational range reported for the species (Harling, 1999; Morales, 2010; Rehm & Freeley, 2015a; Bernal et al., 2016), and are likely the result of uncorrect species identification or georeferencing errors. We also removed spatial pseudo-replicates by keeping only one record for each 1 km^2 cell. We ended with 222 true presence records (Fig. 1a) and we randomly generated 1,000 pseudo-absence points within an internal buffer around the presence records of 20 km to avoid placing the pseudo-absences too close to the presence records, and an external buffer of 200 km, as recommended by Barbet-Massin et al. (2012) and Bobrowski et al. (2017).

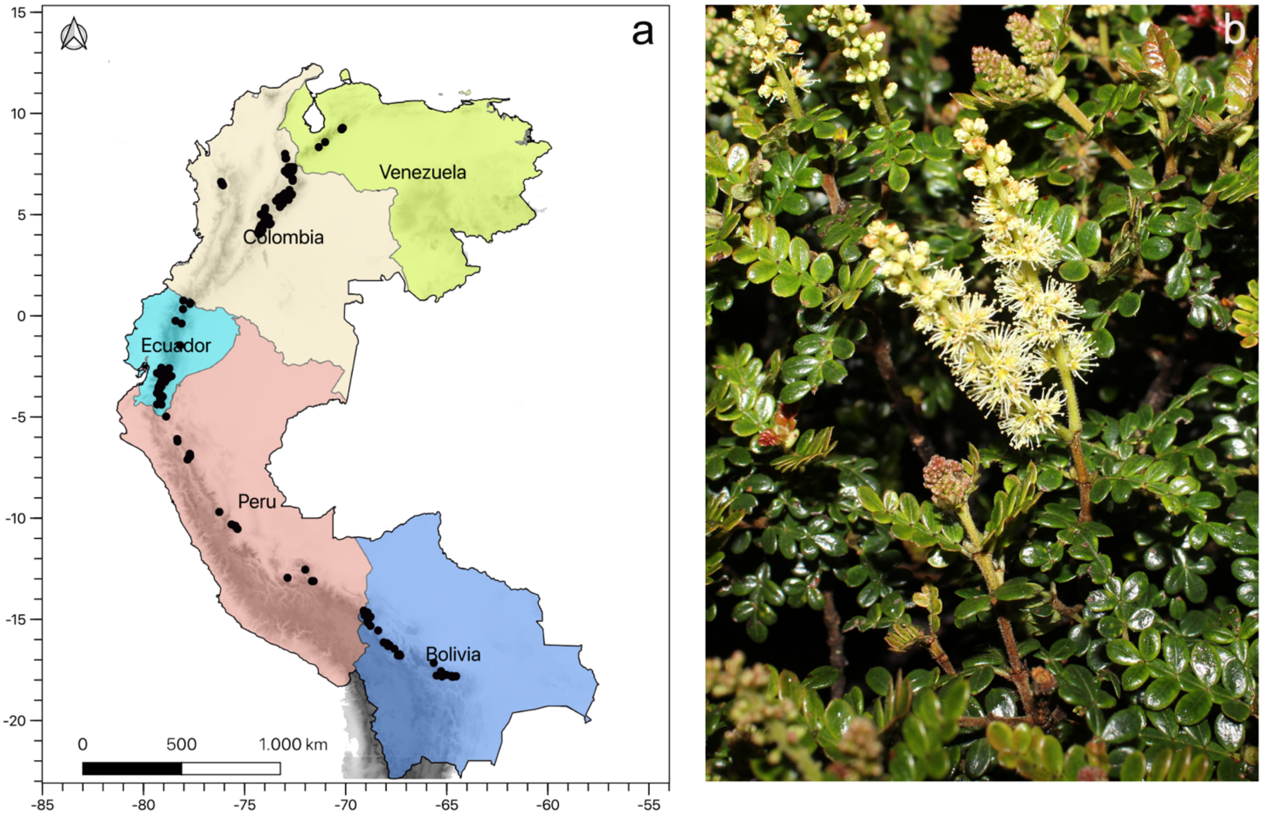

Figure 1: a) Study area with *W. fagaroides* occurrences used for the models in black. The Andean range is shown in light grey; b) flowers of *W. fagaroides.*

4.2.4. Climate datasets and selection of climatic variables

To model the current distribution of *W. fagaroides* in the Northern and Central Andes, we compared three different climate data sets: 1) Worldclim version 1.4 (Hijmans et al., 2005); 2) Worldclim version 2 (Fick & Hijmans, 2017); and 3) Chelsa version 1.2 (*herein* Chelsa) (Karger et al., 2019). Worldclim 1.4 is an interpolated climate data set, which uses latitude, longitude and elevation as predictor variables to regionalize monthly observations of precipitation and temperature with weighted linear regressions (Bobrowski et al., 2017; Hijmans et al., 2005). Worldclim 2 is a refined and expanded version of Worldclim 1, complemented with more climate stations, including a number of stations located at high latitudes and altitudes (Fick & Hijmans, 2017). Also, there is a substantial improvement of the estimates for areas with low station density and complex topography through the interpolation, which is done by a thin plate spline that includes covariates as topography, distance to the coast and satellite data (Fick & Hijmans, 2017).

On the other hand, to model temperature-related variables, Chelsa applies a statistical downscaling, while for rainfall a quasi-mechanistical statistical downscaling of the Era-Interim model is used, including covariates such as topography and winds, and validated using independent climatic stations (Karger et al., 2017, 2019; Osejo et al., 2019).

We downloaded 19 bioclimatic variables for each climate data set at a resolution of 30 arc sec (approximately 1 km). Additionally, we retrieved an Aster digital elevation model (DEM) of the study area (LP DAAC; https://lpdaac.usgs.gov/tools/data-pool, NASA/METI/AIST/Japan Spacesystems & U.S./Japan ASTER Science Team, 2009), which we utilized to calculate slope angle (SLOPE) and aspect (HILLSHADE) using QGIS v. 2.18 (QGIS Development Team, 2018). Furthermore, we downloaded three soil variables from the SoilGrids 250 m database (Hengl et al., 2017): soil type according to USDA categories (TAXOUSDA), soil pH value at 15 cm depth (PHIHOX), and bulk density (BLDFIE) at 15 cm depth. We also downloaded solar radiation (SOL_RAD) and direct normal irradiance (DNI) from the Global Solar Atlas (Global Solar Atlas, 2019). We then checked for multicollinearity among the variables in Worldclim 1.4 and 2 and Chelsa separately, using pairwise Spearman's rank correlations (correlation plots for each climatic dataset are available in the Supplementary Material S1). In this way we aimed at avoiding high inter-correlation which can lead to models with unsatisfying performance and possibly wrong interpretations (Dormann et al., 2007, 2013). We then gathered a consensus set of predictor variables that were uncorrelated in all three climate datasets (rs ≤ 0.7; Dormann et al.,2013) on which we performed Variance Inflation Factor (VIF) analysis (Miles, 2014), finally obtaining a set of ten predictors with VIF <10 that were used as input for the modelling algorithms.

4.2.5. Comparison of climate data sets and algorithms

To visualize geographical discordance between the two climate data sets, raster subtraction was calculated between current projected models of Chelsa, Worldclim 1.4 and Worldclim 2. Finally, we calculated and compared True Skill Statistic (TSS)

(Flueck, 1987) and Receiver Operating Characteristic (ROC) (Fielding and Bell, 1997) scores for each performed algorithm, as well as for the ensemble models generated for each dataset.

4.2.6. Modelling algorithms and evaluation criteria

We implemented Generalized Linear Models (GLMs) (McCullagh & Nelder, 1983), Random Forest (RF) (Breiman, 2001) and MaxEnt (Phillips et al., 2006) within the Biomod framework (Thuiller et al., 2016) in Rstudio v 1.3.1056 (RStudio Team, 2020). GLMs were fitted with a quadratic formula, binomial family (link = *logit*), and we did not specify interaction terms, as simpler models are believed to generate less diverging spatial predictions when projected to different conditions, - *i.e.* future climatic conditions - (Edwards et al. 2006, Elith et al. 2010; Merow et al., 2014). We specified the Bayesian Information Criterion (BIC) for the stepwise selection procedure as it results in more parsimonious models (Zhang et al., 2016). Control parameters were set to: epsilon = 1e-08 and maxit = 1,000. For the RF algorithm classification, 500 trees were generated, and node size was set to 5, corresponding to the default conditions of BIOMOD_ModelingOptions. MaxEnt settings were: 10,000 maximum iteration number, no threshold or hinge feature used and *beta_lqp* set to 0.95.

For model validation, all presence and pseudo-absence points were split randomly into training and testing data samples with a ratio of 70:30 and five cross-validation rounds. Prevalence was maintained at 0.5, making presences as important as absences in the model calibration. In this way, the impact of each pseudo-absence point was down-weighted allowing the sum of presence weights and the sum absence weights to be equal (Barbet-Massin et al., 2012). The number of permutation rounds to estimate variable importance was set to 3. Since none of the commonly used model evaluation measurement is universally valid, it is necessary to use more than one performance evaluation metric (Araujo & Guisan, 2006; Aguirre-Gutiérrez et al., 2013; Bobrowski & Schickhoff, 2017). As a threshold-independent evaluation metric, we selected the Receiver Operating Characteristic (ROC) (Fielding and Bell, 1997; Elith et al., 2002), while as threshold-dependent measure, we selected True Skill Statistics (TSS) (Flueck, 1987; first used in SDM by Allouche et al., 2006). Performance evaluation metrics were calculated applying test datasets. Variable importance was extracted and algorithm-specific response curves were generated. We obtained consensus ensemble models using a TSS-weighted average method to account for each model's predictive power. We only retained models with TSS > 0.8, discarding models with low predictive power. As part of the ensemble model evaluation, spatial predictions were transformed into binary distributions, according to autonomously calculated TSS and ROC maximizing cutoff values.

Ensemble models and single algorithm-models were compared in terms of TSS and ROC scores and the three models generated with each climatic dataset, and only selected algorithms were then projected in space to the present conditions. To quantify differences between TSS and ROC scores of the climate data sets, we applied Wilcoxon test statistics. Subtraction rasters between each pair of rasters generated on the basis of the three climate datasets were calculated and the output was classified into discrete pixel values difference classes (*e.g.* 0-5, 10-20, 20-50 pixel value difference etc.).

4.2.7. Spatial projection to present and future climatic conditions and intersection with Latin America protected areas network

After selecting the best performing climatic dataset model for the present, we projected it to the future (2060-2080), to five different CMIP5 General Circulation Models (GCMs) (ACCESS1-0, CCSM4, CESM1-CAM5, CSIRO-Mk3-6-0 and HAdGEM2-AO). These five future projections were averaged for the Representative Concentration Pathway (RCP) of greenhouse gas corresponding to a strong increase in global radiative forcing (RCP 8.5) (IPCC, 2013), as this represents a high-emission, fossil fuels-centered, business-as-usual scenario (Riahi et al., 2011) and we wanted to model the effects of the climate crisis under the worst-case scenario.

Finally, present and future predictions of the best performing climatic dataset and algorithms were projected into the geographical space and transformed to binary predictions using the cutoff value calculated for the ensemble models, that maximizes the TSS score. In our case it was 462 (for details on how this cutoff value is calculated, see Biomod 2 documentation, Thuiller et al., 2016). The predicted area was calculated and intersected with the IUCN Protected Areas Network shapefile of Latin America (retrieved from https://www.protectedplanet.net) to obtain the proportion of currently protected *W. fagaroides* populations in the species' projected distribution area.

4.3. Results

After checking for multicollinearity in each of the three datasets, the final consensus set of retained predictors used to build the models was composed of ten variables, including four bioclimatic variables (temperature seasonality: bio 4, minimum temperature of coldest month: bio 6, annual precipitation: bio 12, and precipitation seasonality: bio 15), three topographical variables (direct normal irradiance: DNI, slope: SLOPE, and hillshade: HILLSHADE), and three soil properties (soil type: TAXOUSDA, soil pH: PHIHOX, and bulk density: BLDFIE).

4.3.1. Comparison between climate datasets

Differences in minimum, maximum and mean values between the three different climate data sets for selected bioclimatic variables across the modeled area were evident (Table 1). For bio 4 and bio 6 the differences were more pronounced between Chelsa and Worldclim 1.4 and 2, whereas for bio 12 and 15, Worldclim 2 had very different values from both Chelsa and Worldclim 1.4, which were more similar among each other. Correlations between corresponding climate variables yielded quite high correlation coefficients, with highest correlation between the two Worldclim datasets (Table 2).

Table 1: Selected bioclimatic variables of the three climate datasets. Abbreviations - sd: standard deviation, min minimal value, max: maximal value.

Variable	Name	Unit	C. 1.2 max	C. 1.2 min	W. 1.4 max	W. 1.4 min	W. 2 max	W. 2 min
bio 4	Temperature Seasonality	C°	37.92	1.42	45.51	0.72	42.78	0.75
bio 6	Minimum Temperature of Coldest Month	C°	25.6	-16.3	23.9	-20.8	24.4	-18.7
bio 12	Annual Precipitation	mm	11522	2	11314	0	8029	0
bio 15	Precipitation Seasonality	mm	252	5	259	0	226	0

Table 2: correlation coefficients of corresponding variables from different climatic datasets. * = p<0.0001.

Paired datasets	bio 4	bio 6	bio 12	bio 15
Chelsa 1.2 and Worldclim 1.4	0.89 *	0.985 *	0.866 *	0.944 *
Chelsa 1.2 and Worldclim 2	0.884 *	0.987 *	0.873 *	0.926 *
Worldclim 1.4 and Worldclim 2	0.976 *	0.994 *	0.956 *	0.966 *

4.3.2. Model evaluation and comparison

The comparison of TSS and ROC scores of current projections by single algorithm and ensemble models (Table 3) yielded minimal differences but highlighted a slightly better performance of Chelsa as the best climatic data set to project the current distribution of *W. fagaroides*. However, none of the difference between climate datasets evaluation metrics was found to be statistically significant, according to the Wilcoxon statistics (Table 4). All datasets returned very high TSS and ROC scores. Chelsa obtained higher single algorithm and averaged ROC scores, while Worldclim 2 obtained higher TSS single algorithm and averaged scores. Nonetheless, the ensemble model scores indicated that Chelsa performed slightly better than the other datasets, obtaining a TSS average value of 0.905 and a ROC averaged value of 0.99. For this reason, and considering also the lack of future data at 30 arcsec resolution for Worldclim 2, we decided to proceed with the Chelsa database.

Table 3: ROC and TSS scores for three climate datasets and ensemble models, for the three algorithms employed: GLM, RF and MaxEnt.

Evaluation scores	Chelsa 1.2	Worldclim 1.4	Worldclim 2
ROC GLM	0.948	0.937	0.939
ROC RF	0.981	0.979	0.977
ROC MaxEnt	0.964	0.964	0.965
Mean ROC	**0.964**	0.960	0.960
Mean ROC of Ensemble Model	**0.99**	0.989	0.988
TSS GLM	0.813	0.814	0.822
TSS RF	0.888	0.896	0.897
TSS MaxEnt	0.854	0.861	0.865
Mean TSS	0.852	0.857	**0.861**
Mean TSS of Ensemble Model	**0.905**	0.900	0.903

Table 4: Wilcoxon statistics for single algorithm and ensemble models.

	W1.4 ROC	**W2 ROC**	**W1.4 TSS**	**W2 TSS**
C1.2 ROC	V = 5, p-value = 0.5	V = 5, p-value = 0.5		
W1.4 ROC		V = 3, p-value = 1		
C1.2 TSS			V = 0, p-value = 0.25	V = 0, p-value = 0.25
W1.4 TSS				V = 0, p-value = 0.25
	W1.4 ROC Ensemble	**W2 ROC Ensemble**	**W1.4 TSS Ensemble**	**W2 TSS Ensemble**
C1.2 ROC Ensemble	V = 6, p-value = 0.1736	V = 10, p-value = 0.09751		
W1.4 ROC Ensemble		V = 10, p-value = 0.09751		
C1,2 TSS Ensemble			V = 10, p-value = 0.125	V = 10, p-value = 0.125
W1.4 TSS Ensemble				V = 0, p-value = 0.3711

The projected ensemble models resulting separately from Chelsa, Worldclim 1.4 and 2 datasets, combining GLM, RF and MaxEnt (Fig. 2), showed some differences especially regarding the low probability areas. In particular, from North to South: Chelsa and Worldclim 2 predicted some high suitability pixels in the *Sierra Nevada de Santa Marta* and the *Serranía del Perijá*, where the species is known to occur (Tropicos.org), contrary to Worldclim 1.4. In the *Merida* Cordillera, Chelsa predicted a central area of higher suitability, while Worldclim 1.4 suitability was less concentrated and rather more spread throughout the mountain range. Worldclim 2 prediction was similar to Chelsa, but with a few more high suitability pixels in the southern part. In the Eastern Colombian Cordillera, Chelsa predicted considerably less suitable areas than Worldclim 1.4 and 2. The three different datasets-generated predictions agreed on the low suitability of the connecting branch of the Eastern to the Western Colombian Cordilleras, however, Worldclim 2 predicted a larger number of high suitability pixels. In the Northern part of the Central Colombian Cordillera, both Chelsa and Worldclim 1.4 predicted less suitable areas than Worldclim 2. In the southern part of the Central Colombian Cordillera Worldclim 2 predicted a much higher suitability than Chelsa and

Worldclim 1.4. In Ecuador Central and *Real* Cordilleras, Chelsa predicted less suitability than Worldclim 1.4 and Worldclim 2 that were very congruent among each other. All datasets retrieved a low probability area error in the middle of the Perúvian Amazon (*Loreto*), however, in Worldclim 2 the area was a lot less than Chelsa and Worldclim 1.4, likely an artifact driven only by the suitable bulk density values found in that area and the high importance of this variable in the GLM. In the sector north of the Peruvian Andes, all datasets predicted few areas of high suitability on both the Eastern and Western Cordilleras, especially in their northernmost portion. Most of the highly suitable areas were located on the Central Cordillera, with Worldclim 2 predicting more high suitability spots than Chelsa and Worldclim 1.4. In the central sector of Perúvian Andes, suitable areas were predicted on the Central and to a lesser extent on the Eastern Cordilleras, with again, Worldclim 2 predicting more high suitability pixels than Chelsa and Worldclim 1.4, especially in the zones close to the *'Nudo de Pasco'*. In the Southern sector, predicted suitability was in general very low, with Worldclim 2 predicting slightly higher values than Chelsa and then Worldclim 1.4. Worldclim 1.4 and 2 predicted some low-probability areas on the coast of Perú, contrary to Chelsa, which did not predict any. In Bolivia, predicted suitability was lower than in other portions of the Tropical Andes, with high suitability areas located only in the *Serranias del Norte* until the *'Codo de los Andes'*, for all datasets. Worldclim 2 predicted just one high suitability pixel in the southernmost part of the Bolivian Andes. Also, overall Worldclim 2 predicted more highly suitable pixels than Worldclim 1.4 and then Chelsa. Worldclim 2 also predicted a highly suitable pixel cluster around *'El Codo de los Andes'*. Moreover, the subtraction rasters of the continuous models underlined some more relevant discrepancies in the predictions generated by each dataset. The highest divergence was observed for the correlation rasters of Chelsa and Worldclim 1.4 and to a lesser extent for the one generated between Worldclim 1.4 and Worldclim 2. Overall, the geographical areas that seemed to be more affected were the North-East of Colombia, as well as the southern part of Venezuela, together with the Llanos de la Orinoquia in North-East Colombia. In North-West Bolivia, several discrepancies related to the Amazon region and bodies of water such as *'Titicaca'* lake and *'Salar de Uyuni'* were also noticeable. Additionally, across the Andean Range there were many uncorrelated spots between all datasets.

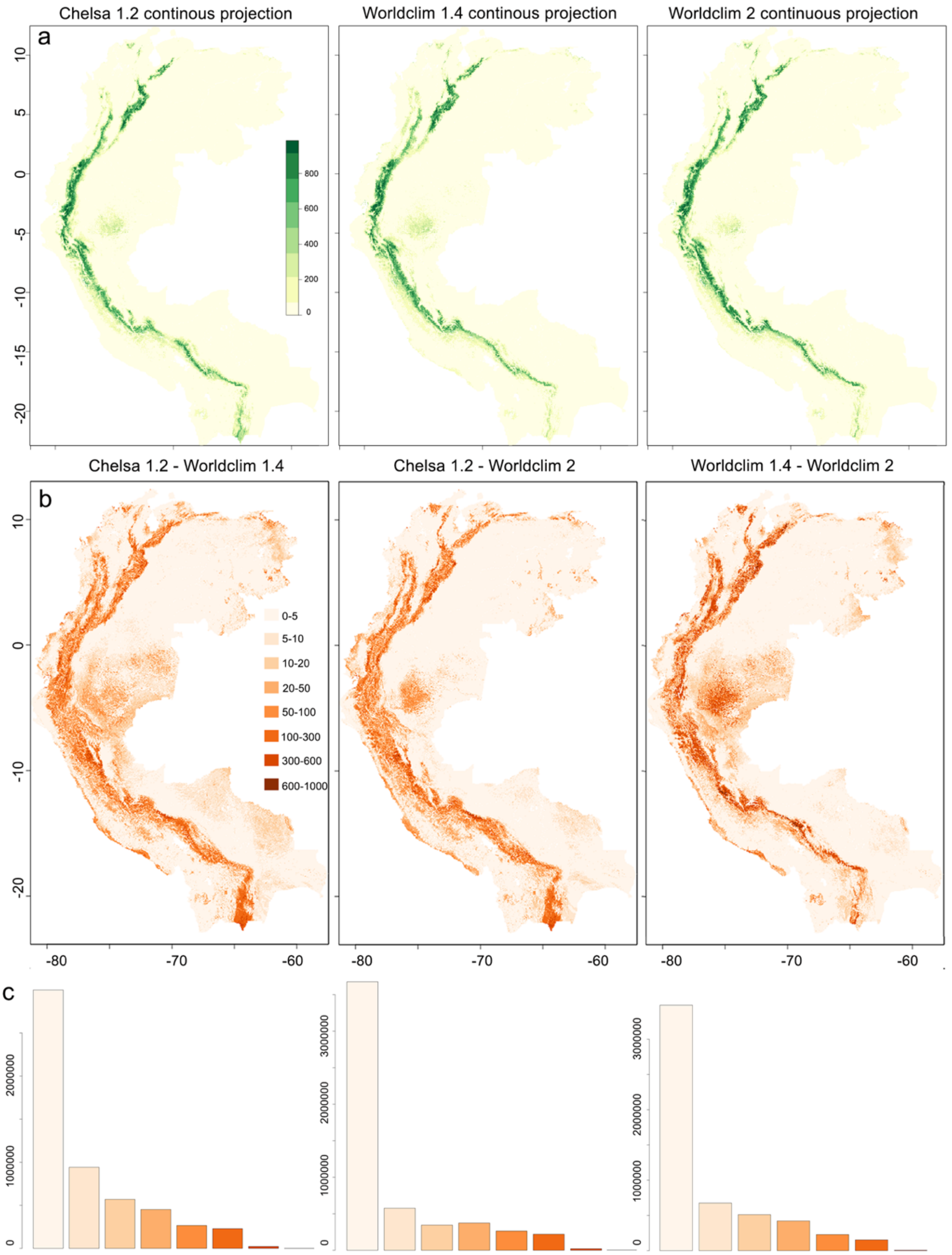

Figure 2: a) Current continuous projections of *W. fagaroides* distribution for Chelsa and Worldclim 1.4 and 2 with all 3 algorithms; b) rasters obtained through the subtraction of the continuous models of Chelsa 1.2 - Worldclim 1.4, Chelsa 1.2 - Worldclim 2 and Worldclim 1.4 - Worldclim 2 (the ones showed in a); negative and positive values were grouped by range of discrepancy (*e.g*. from 0 to 5 points of discrepancy etc.); c) pixel values frequency in subtraction rasters, the ranges of pxel value discrepancies are on the x axis, corresponding to the colorcode legend in b).

The variables showing the highest importance (Fig. 3) in the current model of Chelsa for the GLM algorithm were: bulk density, annual precipitation (bio 12) and minimum temperature of coldest month (bio 6); for the RF algorithm: bio 6 and bulk density and for the MaxEnt algorithm: bio 6, bio 12 and precipitation seasonality (bio 15). For the Worldclim 1.4 ensemble model the most important variables for the GLM algorithm were: bulk density and bio 12; for the RF algorithm: bio 6 and bulk density and for the MaxEnt algorithm only bio 6. For the Worldclim 2 ensemble model the variables with the highest importance for the GLM algorithm were: bulk density and bio 12; for the RF: bio 6 and bulk density and for MaxEnt again only bio 6.

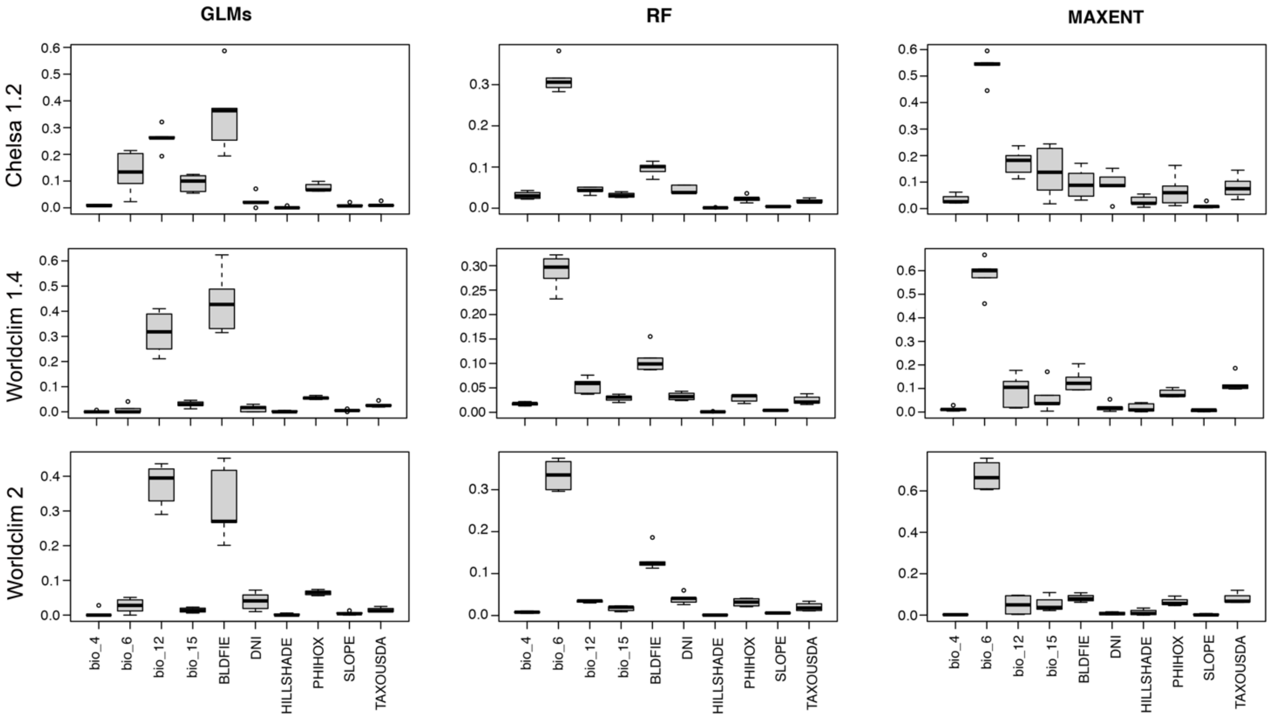

Figure 3: Variable importance for Chelsa, Worldclim 1.4 and Worldclim 2 by algorithm. on the y axis the variable importance value calculated in Biomod 2.

The response curves of GLMs, MaxEnt and RF (Fig. 4) highlighted that the optimum for the minimum temperature of the coldest month of *W.fagaroides* is around 5 ºC, with tolerance until 2 and up to around 8 ºC. For bulk density, the optimum of *W. fagaroides* was found to be around 1 g/cm^3, with tolerance until 1.1 g/cm^3. *Weinmannia fagaroides* optimum in terms of annual precipitation, ranged from very low values until about 1,600 mm, with tolerance until 2,000 mm. Lastly, regarding precipitation seasonality, the species optimum was found to be between very low values and about 50-60% of variation.

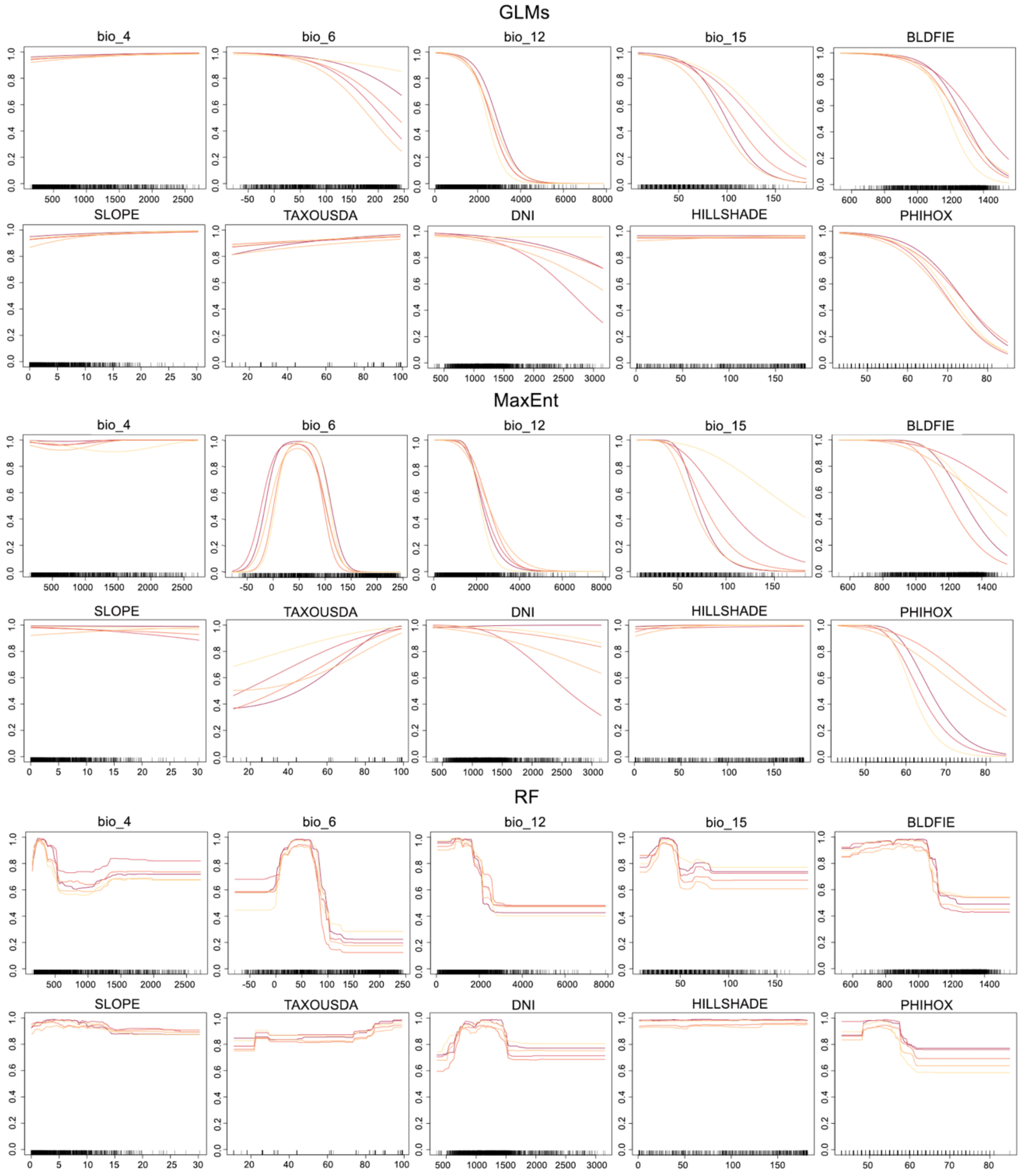

Figure 4: Species response curves of each algorithm for Chelsa 1.2 models. Each cross-validation round in shown in a different color.

As to the algorithms, RF and MaxEnt retrieved better TSS and ROC evaluation than GLMs scores. Also, by examining the geographic projections of each algorithm-generated model, we noticed that the GLMs models were retrieving a strange medium/low-suitability spot, with values well below the chosen threshold, in a lowland plain area in the northern part of Perú (Fig. 2). Thus, we kept only RF and Maxent algorithms, excluding GLMs from the final Chelsa ensemble model.

4.3.3. Modelling species present and future distribution and intersection with Protected Areas

According to the resulting binary projection, the modeled area of *W. fagaroides* was of ca. 109,752 km^2 (Fig. 5). After projecting the current Chelsa model to the five different selected GCMs for the year 2060-2080 (RCP 8.5), combining RF and MaxEnt, we averaged the generated ensemble models and applied the previously generated threshold value to the future geographical projection. As a result, the future modeled area was 68,220 km^2, representing a loss of 38% of the current area for the years 2060-2080. The future distribution seemed to shrink consistently across the whole Andean range, with more visible effects in the Eastern and Central Andean Cordilleras of Colombia, in Ecuador and at the southernmost end of the Bolivian Andean Range.

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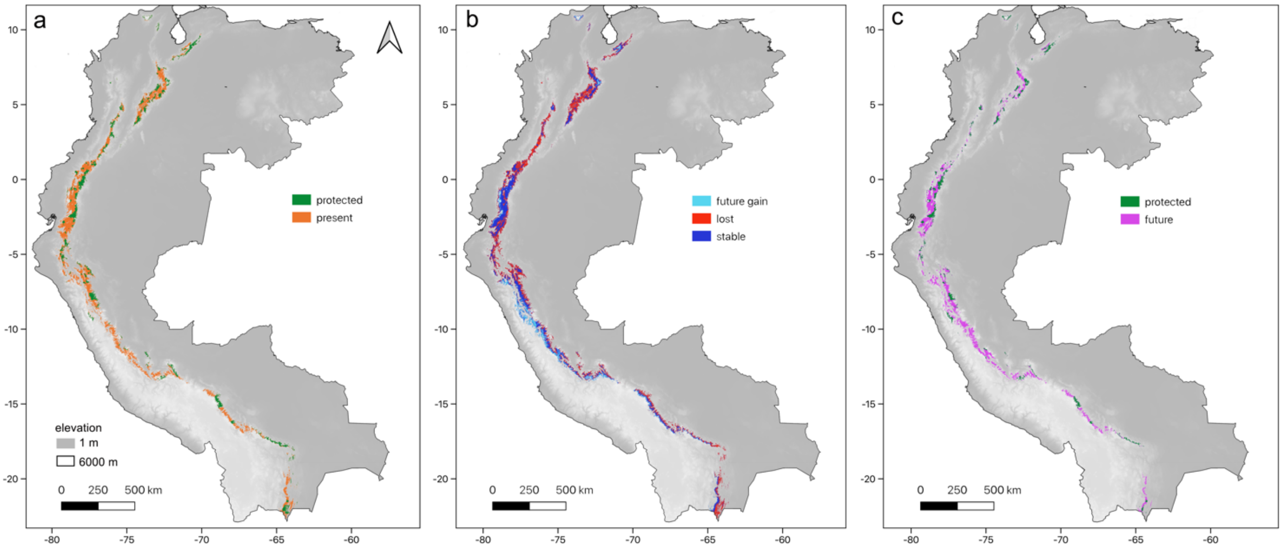

Figure 5: a) binary present and future projected distribution of *W. fagaroides* according to Chelsa ensemble model using RF and MaxEnt, b) binary present projected distribution overlapping with protected areas network

Additionally, an important elevational shift was noticeable by looking at the present and future elevation histograms (Fig. 6), where the frequency of values above around 3,700 m was notably higher for the 2060-2080 modeled area than for the modeled present distribution.

After intersecting the presence-absence current model with the Latin American Protected Areas (PAs) shapefile, we calculated that only 22.93% of the projected present distribution was under any protection regime across the Northern and Central Andean region. Of the modeled future distribution, 21.72% will be under protection if the PAs network remains unchanged. A total of 422 PAs across the study region encompass a portion of the modeled present distribution of *W. fagaroides,* with higher density in Colombia and Ecuador. Colombia has the highest number (283) and the biggest cumulative extension of PAs overlapping the modeled distribution, followed by Perú (63), Bolivia (26), Ecuador (26) and Venezuela (24). For the future scenario the number of PAs overlapping the projected binary distribution is down to 256 across the Tropical Andean range. Again, Colombia has the highest number (137), followed by Perú (62), Ecuador (26), Bolivia (18), and Venezuela (11).

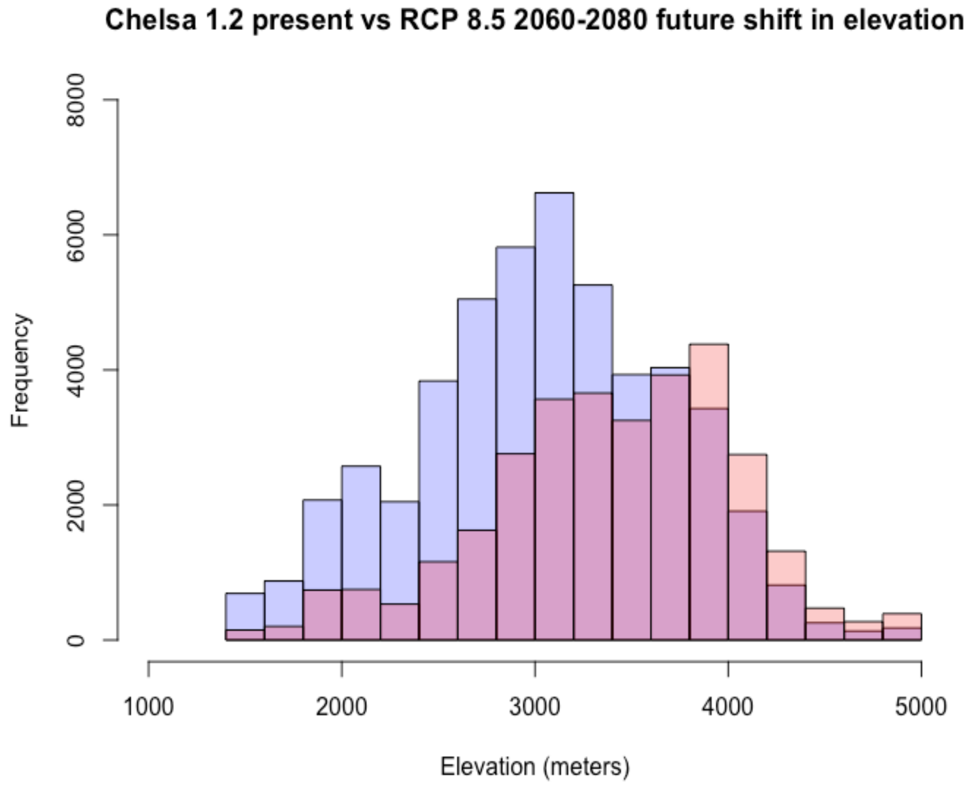

Figure 6: elevation shift in modeled present area (blue) vs future (orange), the intersection between the two histograms is showed in violet.

4.4. Discussion

4.4.1. The ecological niche of W. fagaroides

The distributional range of *W. fagaroides* was found to be primarily associated with one temperature-, one soil-, and one precipitation-related variable. Minimum temperature of the coldest month (bio 6) was the most important among the temperature-related variables. Bio 6 relates directly to trees freezing resistance. In areas like tropical Andean treelines, freezing temperatures occur almost on a daily basis (Wesche et al. 2008, Harsch and Bader 2011). Given that high-elevation tropical trees maintain their physiological activities all year round (Rehm and Freeley, 2015a), daily temperature extremes could damage active tissues, that are more sensitive to frost than dormant tissues (Rada et al. 1985, Sakai and Larcher 1987), therefore representing a constrain to recruitment, survival and persistence of tropical treeline species. According to the response curves of MaxEnt and RF, *W. fagaroides* is mainly found at relatively cool minimum temperature of the coldest month values. Also, according to our species records *W. fagaroides* is found in places with up to -5 ºC. One study (Rehm and Freeley, 2015a) showed that juveniles of *W. fagaroides* can withstand temperatures of up to -11.1 ºC, indicating that for *W. fagaroides*, freezing temperatures are not directly limiting the recruitment of the species. Then, treeline freezing events are in general not an immediate threat to recruitment for our species. However, temperatures tend to be much lower in open grasslands, 'outside' of treelines (Rehm and Freeley, 2015a), therefore extreme temperature value could be limiting the establishment of juveniles of *W. fagaroides* 'outside' of the treeline, as well as hampering its latter growth 'inside' the treeline.

It has been hypothesized that increasing mean temperatures and CO_2 concentrations could interfere negatively on tree photosynthetic capacity (Dusenge et al., 2015) and phenology, to a point of reducing their freezing resistance (Martin et al., 2010, Augspurger 2013). Also, it has been predicted that even if climate change leads to an increase in mean temperatures, low temperature extremes intensity and duration may remain somewhat constant (Vavrus et al., 2006, Kodra et al., 2011). One study focusing on several Andean *Weinmannia* species reported that ecosystem productivity in increasing temperatures in the Andes could be maintained only with the altitudinal migration of tree species (Rapp et al., 2012). Another study found that *W. fagaroides* survival was highest at mid-elevation with intermediate temperatures, and that survival was negatively affected by increasing mean temperature (Rehm and Freeley, 2016). A lower seedling survival at increased temperatures was also observed for the species *Weinmannia bangii* in Perú (Tito et al., 2020).

It is therefore possible that warming temperatures and rising CO_2 concentrations could push *W. fagaroides* upward on the mountains while compromising its response to freezing events, to a point where low temperatures become a limiting factor for this species. This possible upward shift is confirmed by our modeled future scenario 2060-2080 (RCP 8.5), where the distribution of *W. fagaroides* in the northern Andes undergoes a dramatic restriction together with a strong elevational shift.

The soil structure, nutrients composition and water balance are considered key ecological variables to explain the distribution of tree species (Piedallu et al., 2013; Walthert and Meier, 2017). Among the soil properties-related variables, we highlighted a high influence of bulk density (BLDFIE) on the modeled distribution of *W. fagaroides.* Soil bulk density is the weight of dry soil divided by its total volume, which may contain air or water, or both (Blake, 1965). According to the response curves of MaxEnt and RF, *W. fagaroides* prefers mid-low values of bulk density. Andisols (soils formed in volcanic ash, rich in organic matter), typical of the Andean Cordilleras, and particularly soils located at Andean timberlines, exhibit low bulk densities (< 0.85 g/cm^3) (Neall, 2009; Ponette-Gonzalez et al., 2016; de la Cruz-Amo et al., 2020), and therefore are intrinsically adequate for the growth of *W. fagaroides.* Bulk density is a good indicator of soil permeability and its suitability for root growth, which are two factors of vital importance for the soil-plant interface (Batey & McKenzie, 2006). While plant species optimal values are usually lower than <1.5 g/cm^3, bulk densities greater than 1.6 g/cm^3 tend to restrict root growth (Soilquality.org.au, 2020), although it may vary with soil type (Hunt and Gilkes, 1992). Not only sandy soils and deeper soils (Cresswell and Hamilton, 2002), but also compacted agricultural soils, which undergo machinery impacts and increased animal trampling (Binkley et al., 2003; Brevik et al., 2002; Steffens et al., 2008; Wiesmeier et al., 2012), are prone to higher bulk density values. Complementary, Hofstede (1995) reported that paramo tropical alpine grasslands reach a higher bulk density and a lower moisture content after long-term heavy grazing. In this context, the peculiar bulk density preference of *W. fagaroides* could imply that the species would not be able to establish new populations in climatically suitable areas where the soils are too compacted by cattle trampling or agricultural practices, both strongly present activities in the Andean timberlines, where the presence of human settlements and soil exploitation has a long history and rural activities are still strongly present (Etter et al., 2006; Armenteras et al., 2003).

We found a high influence of annual precipitation among the precipitation-related variables to predict the climatic space of *W. fagaroides*. Tropical Andean treelines and paramos have in general a cold and wet climate, with a large spatial variability (Herzog et al., 2011). Precipitation normally ranges from around 1,000 mm up to more than 4,000 mm (Luteyn, 1999; Hofstede et al., 2003), with extremely high values over the Eastern slope of the Andes, due to the water vapor transport from the Amazon (Insel et al., 2010). Besides, in the Andes, precipitation is highly influenced by both, the Pacific and the Amazon basin. This, combined with the irregular topography and the large differences in slope, aspect and elevation, results in a very complex pattern of precipitation, often strongly varying at local level (Buytaert et al., 2006; Urrutia & Vuille, 2009).

According to the response curves of MaxEnt and RF, *W. fagaroides* does not seem to be a drought-sensitive species, which is also partially supported by Palomeque et al. (2020) who found that *W. fagaroides* seeds exhibit prolonged tolerance to desiccation, and also by the fact that efficient seed dispersal needs relatively dry conditions (Lozano, 2015). Thus, it appears that high values of precipitation are a limit to *W. fagaroides* establishment and persistence, indicating that this species may prefer relatively dry paramos and Andean forests to rather humid ones or alternatively, that other wet tolerant species might outcompete it in more humid areas.

Increases and decreases, but also no correlation of total annual rainfall and net precipitation with elevation has been reported for Andean high mountain environments (Padrón et al., 2015; Veneklaas and Van Ek, 1990; Buytaert et al., 2006; Garreaud, 2009). The lack of a general scheme is justified as local precipitation regimes largely depend on complex topographical features that increase variability in rain shading and strong winds (Buytaert et al., 2006). Moreover, ongoing and future variations in precipitation patterns and their sign depend on the geographical subregion under consideration (Dore, 2005).

However, the observed trends in annual precipitation for the period 1964-2008 point towards a general decrease of mean annual precipitations across the tropical

Andes through time, with the exception of some sites in the Western Cordillera of the Colombian Andes, in the southern Andes of Ecuador, and a few localities in the southern highlands of Perú (Herzog et al., 2011). We hypothesized that overall *W. fagaroides* distribution would not be directly endangered by the predicted lower annual precipitation rates of the near future. Nevertheless, in Latin America, climate change is also causing long periods with relatively wetter or drier conditions (Dore, 2005), that may be more relevant for plant survival than any unidirectional trends themselves. Such largely unpredictable shifts in precipitation patterns at a local scale, especially when bringing wetter conditions, may hamper *W. fagaroides* populations and thus many Tropical Andean treelines in general.

Another possible scenario for *W. fagaroides* future distribution could consider the interaction of temperature and precipitation. It has been stipulated that other *Weinmannia* species may tolerate higher precipitation if and when this might help to offset the effects of warming on moisture balance. This capacity of balancing physiological processes may in turn help to prevent a too strong up-ward shift, facilitating the species persistence (Crimmins et al., 2011).

4.4.2. Present and future spatial projection, protected areas and implication for conservation measures

A dramatic loss of 38% of the modeled *W. fagaroides* present distribution is predicted for the future scenario (2060-2080), together with a substantial upward shift in elevation. In our results, an upward shift is noticeable in any modeled mountain massif and major losses of area occur across the Tropical Andean Range. The most heavily impacted areas are located at both ends of the *Merida* Cordillera, in the southern part of the Eastern Colombian Cordillera, especially at lower elevations of the *Cundiboyacense* highplain, and in the Western Colombian Cordillera. In the latter a relevant strong impact is noticeable on the paramo of Frontino and also on the paramo complex of *'Noroccidente Medio Antioqueno'*, where respectively an almost complete and a complete loss of area are predicted. Major area losses occur also in the mountains surrounding the department of Nariño, Colombia, and therefore also in the northern part of the Ecuadorian Andean Cordilleras, and at the southernmost end of the Bolivian Andes, especially in and around the National Park Amboró, and the Fauna and Flora Natural Reserve of Tariqua, close to the Border with Argentina.

Tropical Andean treelines are shaped by both human and climatic processes (Morueta-Holme 2015; Fadrique et al. 2018; Baltazar et al., 2015), therefore permanent but also transitorial land use change is also an important constraint to be considered when projecting the adaptability of *W. fagaroides* future response to a changing environment. In this context, protected areas could play an important role to limit tree species extraction, land use change and soil deterioration at higher elevations. So far only around the 23% of the predicted current distribution of *W. fagaroides* is under any protection regime. This figure is set to proportionally decrease in the future, as the percent value remains more or less unchanged while the actual distribution shrinks, underpinning the urgent need to protect effectively tropical high mountain ecosystems.

More work is still needed to address and incorporate relevant aspects of *W. fagaroides* ecology, as well as information about its interactions with other Andean species. Besides, *W. fagaroides* populations are also suffering pressure from human disturbance and its impact on tree communities has rarely been addressed in high Andean forests (Calbi et al., 2021). Thus, it is urgent to identify hotspots of vulnerability as well as regeneration and possible resilient patches. Additionally, genetic diversity studies may help in understanding population dynamics in order to better protect their biodiversity in the light of climate change. In our knowledge there is no sustainable management strategy that has been proposed so far. Thus, *W. fagaroides* treelines and this could be the occasion to implement precise conservation measures for this species and high Andean treeline species in general.

Lastly, we would like to point out some areas where the presence of the species is well documented and high suitability values were retrieved for the present and future projections of the species ecological niche. In these areas we therefore recommend the implementation of protection efforts for the conservation of *W. fagaroides* treelines that should aim to strenghten the focus of local efforts on Andean treelines and adjacent *paramo* or *puna* grasslands and to monitor and assist the possible altitudinal migration of the species, while studying and restoring soil properties. These areas are the Venezuelan *Merida* Cordillera, the paramos *'Almorzadero'*, *'Sierra Nevada del Cocuy'*, *'Guantivá -La Rusia'*, '*Chingaza*' and '*Sumapaz*' in the Colombian Eastern Cordillera, and the National Natural Park *Los Nevados* in the Central Colombian Cordillera; the Western Cordillera and the *'Cordillera Real'* in Ecuador and the eastern slopes of the Andes, especially in the ecotone between the *‘Yungas’* and the *‘Puna’* in Perú and Bolivia.

4.4.3. Comparison between datasets and algorithms

The comparison of different climate datasets when modelling a species present distribution is an increasingly common practice to quantify the uncertainty of approaches and to derive a better idea of the potential range of results (e.g. Soria-Auza et al., 2010; Bobrowski et al. 2017; Kalan et al., 2017; Morales-Barbero & Vega-Álvarez, 2018; Lembrechts et al., 2019; Milanesi et al., 2020). Comparative analysis between climate datasets in species distribution modeling, as in Bobrowski et al. (2017), were never carried out for our target region, the Northern and Central Andes, where it could be particularly useful for species inhabiting areas with high topographic complexity. High-elevation climate stations are fairly rare in such mountainous environments (Condom et al., 2020), which limits the precision of interpolated climate data sets in predicting the condition of high mountains areas compared to lowland areas, where more stations are located (Condom et al., 2020). Temperature is usually strongly negatively correlated with elevation, and so for temperature-related variables there should be no major variation between different climate data sets, at least at a regional-scale (Soria-Auza et al., 2010; Karger et al., 2017). Previous comparison of temperature-related variables from different climate data sets indicated that Chelsa was able to compete with Worldclim 1 (Karger et al., 2017). However, one recent study located in Colombia affirmed that regarding temperature-related variables, Worldclim 2 predictions were better than Chelsa (Osejo et al. 2019).

In contrast to temperatures, precipitation patterns are influenced by many topographic and wind related factors, as well as by solar radiation cycles in less predictable ways. This results in patterns of precipitation that are not correlated with altitude or latitude, especially in high elevation environments. Since Chelsa includes covariates as topography and winds (Karger et al., 2017; Osejo et al., 2019), it should be able to better address the topographic heterogeneity in local patterns of precipitation than Worldclim 1.4 (Karger et al., 2017). Worldclim 1 ignores most of the small-scale atmospheric processes that are necessary to predict site-specific topoclimatic conditions (Bobrowski et al., 2017). However, Osejo et al. (2019) showed that Chelsa and Worldclim 2 performed equally good in predicting precipitation patterns, probably since the upgraded interpolation of Worldlclim 2 also takes into account covariates as topography, distance to the coast and satellite data (Fick & Hijmans. 2017).

To date, there is no available study modelling the distribution of *Weinmannia fagaroides.* Additionally, few modelling studies focusing on treeline species have been conducted in the Andean region. These include *Polylepis tarapacana* (Cuyckens et al., 2016), *Polylepis* spp. (Zutta & Rundel, 2017; Fajardo-Gutierrez et al., 2018) and *Polylepis quadrijuga* (Caballero-Villalobos et al., subm.), but also *Alnus acuminata* (Wicaksono et al., 2017) and *Podocarpus parlatorei* (Quiroga et al., 2018). However, many efforts in investigating the vulnerability of Andean species to climate change have been carried out (Morueta-Holme et al., 2015; Cuesta et al., 2020; Valencia et al., 2020). Even though both Worldclim and Chelsa climate data have been used separately to model Andean species ecological niches (Fajardo-Gutierrez et al., 2018; Caballero-Villalobos et al., in prep), no comparative analysis exists to date.

Although some differences between climate datasets were evident in both temperature and precipitation-related variables, and the models of *W. fagaroides* showed a slightly better performance (although not significantly different) and prediction power of the Chelsa dataset, the three data sets did not result in notable differences in the model evaluation metrics. Therefore, there is no real argument from the modeling performed here to prefer one or another data set. Accordingly, our results alone do not provide a test of the quality of the different climate data sets. Such test would require a ground proofing approach, comparing the interpolated and the actually measured variables (Karger et al., 2017; Osejo et al., 2019), or to model a species with an exactly known distribution.

Nevertheless, our results indicate that both Chelsa and Worldclim 2 are able to efficiently predict the current distribution of *W. fagaroides*, retrieving models with very high evaluation scores. However, given that there is no high-resolution future data available at the moment for Worldclim 2, and that Chelsa had overall slightly better TSS and ROC scores, we selected the latter for our final model projection in the geographical space and in time.

As to variable importance, the two ensemble models generated with Worldclim 1.4 and 2 retrieved the same set of important variables for each algorithm. For Chelsa, however, the addition of minimum temperature of the coldest month (bio 6) for the GLMs, and of mean annual precipitation (bio 12) and precipitation seasonality (bio 15) for MaxEnt were the most noticeable changes. Notably, precipitation-related variables were more important in the Chelsa generated model, possibly indicating their higher precision in mountain environments and therefore a higher predictive value, as already stipulated by Karger et al. (2017).

Finally, coming to the single algorithm performances, regarding TSS and ROC values, RF and MaxEnt returned the best scores, as already pointed out in other studies (Kaky et al., 2020; Hernandez et al., 2008), whereas GLMs had much lower model evaluation metrics values. Also, by plotting separately the spatial projection generated by each algorithm, we were able to identify that GLMs were responsible for the introduction of the aforementioned error area in the Perúvian Amazon, likely an artifact generated by the high importance value of the bulk density variable in the GLMs models.

4.4.4. Limitations of our approach

Our results should be interpreted with caution, since our study is based on species records that are in part obtained by data repositories as GBIF. Biodiversity repository data is susceptible to both, species determination and geolocalization errors (see for example Anderson et al., 2016). Also, spatial sampling is often biased, with some areas being sampled more often than others, due to their higher accessibility or easier sampling conditions (Daru et al., 2018). Such geographical bias can of course lead to a sampling bias in the species environmental space, which may lead to biased models (Veloz, 2009; Anderson and Gonzalez, 2011). To avoid geographical sampling bias, we applied a geographical filtering on occurrence points (retaining only one record for each grid cell). Additionally, even though *W. fagaroides* is reported also in Central America, up to Mexico, we decided to model only the Tropical Andean distribution. The Central America distribution and the Andean one are in fact disjunct, with the *Darien* acting as a biogeographical barrier. The tropical Andean distribution maintains a spatial continuity throughout the ranges, and we assumed that *W. fagaroides* Tropical Andean ecological niche to be homogeneous. Also, we wanted to avoid including such a big latitudinal gradient in our models. Lastly, we neither considered ecological interactions of our study species, nor land use change constraints that affect Andean treeline species spatial distributions (Morueta-Holme 2015; Fadrique et al. 2018; Baltazar et al., 2015).

4.5. Conclusions

In this study, we characterized for the first time the ecological niche of the Andean treeline-forming species *W. fagaroides.* We also contributed to the growing evidence of the good performance of the Chelsa dataset in high mountain environments. The environmental space for *W. fagaroides* was defined accurately by the performed environmental niche model, as reflected by the high values of testing dataset evaluation metrics. The main variables shaping the current distribution of *W. fagaroides* were found to be minimum temperature of the coldest month, mean annual precipitation and bulk density. Moreover, our results point toward a substantial decrease of suitable area for the period 2060-2080 (RCP 8.5). Considering that *W. fagaroides* could be indicative of the treeline ecotones in the Northern Andes, we provide relevant insights into underlying environmental constraints that may drive the assemblage of treeline-forming tree species of the Northern Andes and give decision-makers relevant priorities to make conservation strategies more efficient.

4.6. References

Aguirre-Gutiérrez, J., Carvalheiro, L. G., Polce, C., van Loon, E. E., Raes, N., Reemer, M., & Biesmeijer, J. C. (2013). Fit-for-purpose: species distribution model performance depends on evaluation criteria–Dutch hoverflies as a case study. *PloS one*, 8(5), e63708.

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology, 43*(6), 1223-1232.

Anderson R. P., Araújo M., Guisan A., Lobo J. M., Martínez Meyer E., Peterson T., Soberón J. (2016). *Final report of the task group on GBIF data fitness for use in distribution modelling - are species occurrence data in global online repositories fit for modeling species distributions? The case of the Global Biodiversity Information Facility (GBIF)*. GBIF, Copenhagen, Denmark.

Anderson, R. P., & Gonzalez Jr, I. (2011). Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. *Ecological Modelling*, *222*(15), 2796-2811.

Araujo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of biogeography*, *33*(10), 1677-1688.

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in ecology & evolution*, *22*(1), 42-47.

Armenteras, D., Gast, F., & Villareal, H. (2003). Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological conservation, 113*(2), 245-256.

Augspurger, C. (2013). Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology 94*:41–50.

Balthazar, V., Vanacker, V., Molina, A., & Lambin, E. F. (2015). Impacts of forest cover change on ecosystem services in high Andean mountains. *Ecological indicators*, *48*, 63-75.

Batey, T., McKenzie, D. C. (2006). Soil compaction: identification directly in the field. *Soil Use and Management, 22*(2), 123-131.

Bernal, R., Gradstein, S. R., Celis, M. (2016). La flora de Colombia en cifras. *Catálogo de plantas y líquenes de Colombia*, 1, 115-136.

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many?. *Methods in ecology and evolution, 3*(2), 327-338.

Batey, T., & McKenzie, D. C. (2006). Soil compaction: identification directly in the field. *Soil Use and Management, 22*(2), 123-131.

Binkley, D., Singer, F., Kaye, M., & Rochelle, R. (2003). Influence of elk grazing on soil properties in Rocky Mountain National Park. *Forest Ecology and Management, 185*(3), 239-247.

Blake GR (1965) Bulk density. In: Black C.A. (Ed) *Methods of soil analysis. Part 3 Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling*. American Society of Agronomy and Soil Science Society of America, Madison, pp 374–390.

Bobrowski, M., Schickhoff, U. (2017). Why inputs matter: Selection of climatic variables for species distribution modelling in the Himalayan region. *Ecological modelling, 359*, 92-102.

Bobrowski, M., Gerlitz, L., & Schickhoff, U. (2017). Modelling the potential distribution of Betula utilis in the Himalaya. Global ecology and conservation, 11, 69-83.

Breiman, L. (2001). Random forests. *Machine learning*, *45*(1), 5-32.

Brevik, E., Fenton, T., & Moran, L. (2002). Effect of soil compaction on organic carbon amounts and distribution, South-Central Iowa. *Environmental Pollution, 116*, S137-S141.

Booth, T.H., Nix, H.A., Busby, J.R. and Hutchinson, M.F. (2014). BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions, 20*(1), pp.1-9.

Buytaert, W., Celleri, R., Willems, P., Bièvre, B. D., & Wyseure, G. (2006). Spatial and temporal rainfall variability in mountainous areas: A case study from the south Ecuadorian Andes. *Journal of Hydrology, 329*(3-4), 413–421. doi:10.1016/j.jhydrol.2006.02.031

Caballero-Villalobos, L., Fajardo-Gutiérrez, F., Calbi, M., Silva-Arias, G.A. (subm.) Climate change can drive significant loss of suitable habitat for Polylepis quadrijuga, a treeline species in the sky islands of the northern Andes.

Calbi, M., Fajardo-Gutiérrez, F., Posada, J. M., Lücking, R., Brokamp, G., & Borsch, T. (2021). Seeing the wood despite the trees: Exploring human disturbance impact on plant diversity, community structure, and standing biomass in fragmented high Andean forests. *Ecology and Evolution, 11*(5), 2110-2172.

Carretero, M. A., & Sillero, N. (2016). Evaluating how species niche modelling is affected by partial distributions with an empirical case. *Acta Oecologica, 77*, 207-216.

Condom, T., Martínez, R., Pabón, J. D., Costa, F., Pineda, L., Nieto, J. J., ... & Villacis, M. (2020). Climatological and Hydrological Observations for the South American Andes: In situ Stations, Satellite, and Reanalysis Data Sets. *Frontiers in Earth Science, 8,* 92.

Cresswell, H. P., Hamilton (2002) Particle Size Analysis. In: *Soil Physical Measurement and Interpretation For Land Evaluation.* (Eds. NJ McKenzie, HP Cresswell and KJ Coughlan) CSIRO Publishing: Collingwood, Victoria. pp 224-239.

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum Elevations. *Science, 331*(6015), 324–327.

Cuesta, F., Tovar, C., Llambí, L. D., Gosling, W. D., Halloy, S., Carilla, J., ... & Yager, K. (2020). Thermal niche traits of high alpine plant species and communities across the tropical Andes and their vulnerability to global warming. *Journal of Biogeography, 47*(2), 408-420.

Cuyckens, G. A. E., Christie, D. A., Domic, A. I., Malizia, L. R., & Renison, D. (2016). Climate change and the distribution and conservation of the world's highest elevation woodlands in the South American Altiplano. *Global and Planetary Change*, 137, 79-87.

Daru, B. H., Park, D. S., Primack, R. B., Willis, C. G., Barrington, D. S., Whitfeld, T. J., ... & Davis, C. C. (2018). Widespread sampling biases in herbaria revealed from large-scale digitization. *New Phytologist, 217*(2), 939-955.

de la Cruz-Amo, L., Bañares-de-Dios, G., Cala, V., Granzow-de la Cerda, Í., Espinosa, C. I., Ledo, A., ... & Cayuela, L. (2020). Trade-Offs Among Aboveground, Belowground, and Soil Organic Carbon Stocks Along Altitudinal Gradients in Andean Tropical Montane Forests. *Frontiers in Plant Science, 11*, 106.

Di Pasquale, G., Marziano, M., Impagliazzo, S., Lubritto, C., De Natale, A., & Bader, M. Y. (2008). The Holocene treeline in the northern Andes (Ecuador): first evidence from soil charcoal. *Palaeogeography, Palaeoclimatology, Palaeoecology, 259*(1), 17-34.

Dore, M. H. I. (2005). Climate change and changes in global precipitation patterns: What do we know? *Environment International, 31*(8), 1167–1181.

Dormann, C. F., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., ... & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography, 30*(5), 609-628.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27-46.

Dusenge, M. E., Wallin, G., Gårdesten, J., Niyonzima, F., Adolfsson, L., Nsabimana, D., & Uddling, J. (2015). Photosynthetic capacity of tropical montane tree species in relation to leaf nutrients, successional strategy and growth temperature. *Oecologia, 177*(4), 1183-1194.

Duque, A., Stevenson, P. R., & Feeley, K. J. (2015). Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences, 112*(34), 10744-10749.

Edwards Jr, T. C., Cutler, D. R., Zimmermann, N. E., Geiser, L., & Moisen, G. G. (2006). Effects of sample survey design on the accuracy of classification tree models in species distribution models. *Ecological modelling, 199*(2), 132-141.

Elith, J., Burgman, M. A., & Regan, H. M. (2002). Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecological modelling, 157*(2-3), 313-329.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., ... & Li, J. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography, 29*(2), 129-151.

Elith, J., Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics, 40*, 677-697.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in ecology and evolution, 1*(4), 330-342.

Etter, A., McAlpine, C., Wilson, K., Phinn, S., & Possingham, H. (2006). Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, ecosystems & environment, 114*(2-4), 369-386.

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., ... & Feeley, K. J. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature, 564*(7735), 207-212.

Fajardo-Gutiérrez, F., Infante-Betancour, J., & Cabrera-Amaya, D. M. (2018). Modelling the potential distribution of the genus Polylepis occurring in Colombia with conservation considerations. *Ecología Austral, 28*(01bis), 202-215.

Fajardo-Gutiérrez, F., Olaya, T. L., & Calbi, M. (2020). Flora de Bogotá: Cunoniaceae. *Pérez-Arbelaezia, 21*(1), 185-223.

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., ... & Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography, 38*(4), 783-791.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology, 37*(12), 4302-4315.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation*, 38-49.

Flueck, J.A. (1987). *A study of some measures of forecast verification*. Reprints, 10th Conference on Probability and Statistics in Atomaspheric Sciences. Edmonton, AB, Canada, American Meteorological Society, pp. 69-73.

Garreaud, R. D. (2009). The Andes climate and weather. *Advances in Geosciences, 22*, 3.

Gatti, R. C., Callaghan, T., Velichevskaya, A., Dudko, A., Fabbio, L., Battipaglia, G., & Liang, J. (2019). Accelerating upward treeline shift in the Altai Mountains under last-century climate change. *Scientific reports, 9*(1), 1-13.

Global Solar Atlas; The World Bank, SolarGIS (2017). http://globalsolaratlas.info. Accessed on 10th November 2019.

Guisan, A., Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology letters, 8*(9), 993-1009.

Guisan, A., Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological modelling, 135*(2-3), 147-186.

Harling, G. (1999). 78. Cunoniaceae, in G. Harling & L. Andersson (eds), *Flora of Ecuador no. 61*. Council of Nordic Publications in Botany, Copenhagen.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology letters, 12*(10), 1040-1049.

Harsch, M. A., and M. Y. Bader. (2011). Treeline form—a potential key to understanding treeline dynamics. *Global Ecology and Biogeography 20*:582–596.

Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences*, *115*(31), 7985-7990.

Helmer, E. H., Gerson, E. A., Baggett, L. S., Bird, B. J., Ruzycki, T. S., & Voggesser, S. M. (2019). Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. *PloS one, 14*(4), e0213155.

Hengl, T., De Jesus, J.M., Heuvelink, G.B.M., Gonzalez, M.R., Kilibarda, M., Blagotić, ... & Kempen, B. (2017). SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE 12*(2), e0169748.

Hernandez, P. A., Franke, I., Herzog, S. K., Pacheco, V., Paniagua, L., Quintana, H. L., ... & Young, B. E. (2008). Predicting species distributions in poorly-studied landscapes. *Biodiversity and conservation, 17*(6), 1353-1366.

Herzog, S. K., Martínez, R., Jørgensen, P. M., & Tiesse, H. (2011). *Climate change and biodiversity in the tropical Andes*. Inter-American Institute for Global Change Research, International Council of Scientific Unions, Scientific Committee on Problems of the Environment (SCOPE), p. 348.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology, 25*, 1965–1978.

Hoch, G., & Körner, C. (2005). Growth, demography and carbon relations of Polylepis trees at the world's highest treeline. *Functional Ecology,* 941-951.

Hofstede, R. G. (1995). The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant and Soil, 173*(1), 111-132.

Hofstede, R., Segarra P., Mena P. (2003). *Los páramos del mundo*. Global Peatland Initiative/NC-IUCN/EcoCiencia, Quito, Ecuador, 85 pp.

Holtmeier, F. K., & Broll, G. (2010). Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Physical Geography, 31*(3), 203-233.

Hunt N and Gilkes R (1992) *Farm Monitoring Handbook*. The University of Western Australia, Nedlands, WA.

Insel, N., Poulsen, C. J., & Ehlers, T. A. (2010). Influence of the Andes Mountains on South American moisture transport, convection, and precipitation. *Climate Dynamics, 35*(7-8), 1477-1492.

IPCC (2013). *Climate change 2013: The physical science basis*. Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5). New York.

Jacob, M., Annys, S., Frankl, A., De Ridder, M., Beeckman, H., Guyassa, E., & Nyssen, J. (2015). Tree line dynamics in the tropical African highlands–identifying drivers and dynamics. *Journal of Vegetation Science, 26*(1), 9-20.

Kaky, E., Nolan, V., Alatawi, A., & Gilber, F. (2020). A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: A case study with Egyptian medicinal plants*. Ecological Informatics, 101150.*

Kalan, K., Ivović, V., Glasnović, P., & Buzan, E. (2017). Presence and potential distribution of Aedes albopictus and Aedes japonicus japonicus (Diptera: Culicidae) in Slovenia. *Journal of medical entomology, 54*(6), 1510-1518.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific data, 4*, 170122.

Karger, D. N., & Zimmermann, N. E. (2019). *Climatologies at High Resolution for the Earth Land Surface Areas CHELSA V1. 2: Technical Specification*. Swiss Federal Research Institute WSL, Switzerland.

Kodra, E., Steinhaeuser, K., Ganguly, A.R. (2011). Persisting cold extremes under 21st-century warming scenarios. *Geophysical Research Letters 38*:L08705.

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia, 115*(4), 445-459.

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of biogeography, 31*(5), 713-732.

Körner, C. (2008). Winter crop growth at low temperature may hold the answer for alpine treeline formation. *Plant Ecology & Diversity, 1*(1), 3-11.

Körner, C. (2012). *Alpine treelines: functional ecology of the global high elevation tree limits*. Springer Science & Business Media. 220 p.

Lembrechts, J. J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider, S., … Nijs, I. (2019). Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography, 28*(11), 1578-1596.

Loiselle, B. A., Jørgensen, P. M., Consiglio, T., Jiménez, I., Blake, J. G., Lohmann, L. G., & Montiel, O. M. (2008). Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes?. *Journal of Biogeography, 35*(1), 105-116.

Lozano, P. (2015). Especies forestales arbóreas y arbustivas de los bosques montanos del Ecuador. Ministerio del Ambiente, Programa FAO.

Luoto, M., Virkkala, R., & Heikkinen, R. K. (2007). The role of land cover in bioclimatic models depends on spatial resolution. *Global ecology and biogeography, 16*(1), 34-42.

Luteyn, J. L. (1999). *Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature*. New York Botanical Garden Press, 278 pp.

Malizia, A., Blundo, C., Carilla, J., Osinaga Acosta, O., Cuesta, F., Duque, A., ... & Young, K. R. (2020). Elevation and latitude drives structure and tree species composition in Andean forests: Results from a large-scale plot network. *PloS one, 15*(4), e0231553.

Martin, M., K. Gavazov, C. Körner, S. Haettenschwiler, and C. Rixen. (2010). Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO2. *Global Change Biology 16*:1057–1070.

McCullagh, P., & Nelder, J. A. (1983). Log-linear models. In *Generalized linear models* (pp. 127-148). Springer US.

McIntire, E. J., Piper, F. I., & Fajardo, A. (2016). Wind exposure and light exposure, more than elevation-related temperature, limit tree line seedling abundance on three continents. *Journal of Ecology, 104*(5), 1379-1390.

Merow, C., Smith, M. J., Edwards Jr, T. C., Guisan, A., McMahon, S. M., Normand, S., ... & Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models?. *Ecography, 37*(12), 1267-1281.

Milanesi, P., Della Rocca, F., & Robinson, R. A. (2020). Integrating dynamic environmental predictors and species occurrences: Toward true dynamic species distribution models. *Ecology and Evolution, 10*(2), 1087-1092.

Miles, J. (2014). Tolerance and Variance Inflation Factor. Wiley StatsRef: Statistics Reference Online. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1002/9781118445112.stat06593.

Morales, J. F. (2010). Sinopsis del género Weinmannia (Cunoniaceae) en México y Centroamérica. *Annals of the Missouri Botanical Garden, 67*(2), 137-155.

Morales-Barbero, J., & Vega-Álvarez, J. (2018). Input matters matter: bioclimatic consistency to map more reliable species distribution models. *Methods in Ecology and Evolution, 10*, 212– 224.

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J. D., Segnitz, R. M., & Svenning, J. C. (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences, 112*(41), 12741-12745.

Mutke, J., Jacobs, R., Meyers, K., Henning, T., & Weigend, M. (2014). Diversity patterns of selected Andean plant groups correspond to topography and habitat dynamics, not orogeny. *Frontiers in genetics, 5*, 351.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*(6772), 853-858.

Naimi, B., Skidmore, A. K., Groen, T. A., & Hamm, N. A. (2011). Spatial autocorrelation in predictors reduces the impact of positional uncertainty in occurrence data on species distribution modelling. *Journal of Biogeography, 38*(8), 1497-1509.

NASA/METI/AIST/Japan Spacesystems, and U.S./Japan ASTER Science Team (2009). ASTER Global Digital Elevation Model [Data set]. NASA EOSDIS Land Processes DAAC. Retrieved from https://lpdaac.usgs.gov/products/astgtmv002/.

Neall, V. E. (2009). Volcanic soils. *Land use, land cover and soil sciences, 7*, 23-45.

Osejo, B. B., Vargas, T. B., & Martinez, J. A. (2019). Spatial distribution of precipitation and evapotranspiration estimates from WorldClim and Chelsa datasets: Improving long-term water balance at the watershed-scale in the Urabá region of Colombia. *International Journal of Sustainable Development and Planning, 14*(2), 105-117.

Padrón, R. S., Wilcox, B. P., Crespo, P., & Célleri, R. (2015). Rainfall in the Andean Páramo: new insights from high-resolution monitoring in Southern Ecuador. *Journal of Hydrometeorology, 16*(3), 985-996.

Palomeque, X., Uyaguari, C. P., Marín, F., Palacios, M., & Stimm, B. (2020). Effects of storage on seed germination and viability for three native tree species of Ecuador. *Trees, 34*(6), 1487-1497.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?. *Global ecology and biogeography, 12*(5), 361-371.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., & Araújo, M. B. (2011). *Ecological niches and geographic distributions* (MPB-49) (Vol. 49). Princeton University Press.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological modelling, 190*(3-4), 231-259.

Piedallu, C., Gégout, J. C., Perez, V., & Lebourgeois, F. (2013). Soil water balance performs better than climatic water variables in tree species distribution modelling. *Global Ecology and Biogeography*, 22(4), 470-482.

Ponette-González, A. G., Ewing, H. A., Fry, M., & Young, K. R. (2016). Soil and fine root chemistry at a tropical Andean timberline. *Catena, 137*, 350-359.

https://www.protectedplanet.net, Accessed on 21th November 2020.

Puetate-Huaca, G. (2017). Translocación de plántulas de: Weinmannia Rollottii, Weinmannia Fagaroides, Prunus Huantensis y Ocotea Infrafaveolata, en un área degradada en la parroquia el Carmelo, provincia del Carchi (Bachelor's thesis, Universidad Técnica del Norte, Ibarra, Ecuador). Retrieved from http://repositorio.utn.edu.ec/handle/123456789/6722?locale=en.

QGIS Development Team. (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available at http://qgis.osgeo.org.

Quiroga, M. P., Premoli, A. C., & Kitzberger, T. (2018). Niche squeeze induced by climate change of the cold-tolerant subtropical montane Podocarpus parlatorei. *Royal Society open science, 5*(11), 180513.

Rada, F., G. Goldstein, A. Azocar, and F. Meinzer. (1985). Daily and seasonal osmotic changes in a tropical treeline species. *Journal of Experimental Botany 36*:989–1000.

Rapp, J. M., Silman, M. R., Clark, J. S., Girardin, C. A., Galiano, D., & Tito, R. (2012). Intra-and interspecific tree growth across a long altitudinal gradient in the Perúvian Andes. *Ecology, 93*(9), 2061-2072.

Rehm, E. M., & Feeley, K. J. (2013). Forest patches and the upward migration of timberline in the southern Perúvian Andes. *Forest Ecology and Management, 305*, 204-211

Rehm, E. M., & Feeley, K. J. (2015a). Freezing temperatures as a limit to forest recruitment above tropical Andean treelines. *Ecology, 96*(7), 1856-1865.

Rehm, E. M., & Feeley, K. J. (2015b). The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. *Ecography, 38*(12), 1167-1175.

Rehm, E. M., & Feeley, K. J. (2016). Seedling transplants reveal species-specific responses of high-elevation tropical treeline trees to climate change. *Oecologia, 181*(4), 1233-1242.

Restrepo, A. J. D. (2005). Los sedimentos del río Magdalena: reflejo de la crisis ambiental. Universidad Eafit.

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., ... & Rafaj, P. (2011). RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Climatic Change, 109*(1-2), 33.

Rojas-Jimenez, K., Hernandez, M., Blanco, J., Vargas, L. D., Acosta-Vargas, L. G., & Tamayo, G. (2016). Richness of cultivable endophytic fungi along an altitudinal gradient in wet forests of Costa Rica. *Fungal Ecology, 20*, 124-131.

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. Available at http://www.rstudio.com/.

Sakai, A., and W. Larcher. (1987). Frost survival of plants. Page 321 in W. Billings, F. Golley, O. Lange, J. Olson, and H. Remmert, editors. *Ecological studies 62*. Springer-Verlag, Berlin, Germany.

Sarmiento, F. O., & Frolich, L. M. (2002). Andean cloud forest tree lines. *Mountain Research and Development, 22*(3), 278-287.

Schickhoff, U. (2011). *Dynamics of mountain ecosystems. Handbook of Biogeography*. Sage Publications, London, 313-337.

Soberón, J., & Nakamura, M. (2009). Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences, 106*(Supplement 2), 19644-19650.

Soilquality.org.au, available at: http://soilquality.org.au/factsheets/bulk-density-measurement. Accessed on 10 December 2020.

Soria-Auza, R. W., Kessler, M., Bach, K., Barajas-Barbosa, P. M., Lehnert, M., Herzog, S. K., & Böhner, J. (2010). Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia. *Ecological Modelling, 221*(8), 1221-1229.

Steffens, M., Kölbl, A., Totsche, K. U., & Kögel-Knabner, I. (2008). Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (PR China). *Geoderma, 143*(1-2), 63-72.

Tepán, B. V., & Toledo, C. A. (2016). *Diversidad y estructura en bosques secundarios andinos del cantón Cuenca, provincia del Azuay*. Universidad de Cuenca, Cuenca.

Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package ‘biomod2’. Species distribution modeling within an ensemble forecasting framework. *Ecography, 32*, 369-373.

Tito, R., Vasconcelos, H. L., & Feeley, K. J. (2020). Multi-population seedling and soil transplants show possible responses of a common tropical montane tree species (Weinmannia bangii) to climate change. *Journal of Ecology*, 109 (1): 62-37.

Tovar C, Arnillas CA, Cuesta F, Buytaert W (2013). Diverging Responses of Tropical Andean Biomes under Future Climate Conditions. *PLoS ONE 8*(5): e63634.

Trivedi, M. R., Berry, P. M., Morecroft, M. D., & Dawson, T. P. (2008). Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology, 14*(5), 1089-1103.

Tropicos.org. Missouri Botanical Garden. Available at http://www.tropicos.org/Specimen/1248764 and http://www.tropicos.org/Specimen/3278575. Accessed on 9 January 2021.

Urrutia, R., & Vuille, M. (2009). Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research: Atmospheres*, 114(D2).

Valencia, J. B., Mesa, J., León, J. G., Madriñán, S., & Cortés, A. J. (2020). Climate vulnerability assessment of the Espeletia complex on Páramo sky islands in the northern Andes. *Frontiers in Ecology and Evolution, 8*, 309.

Vavrus, S., J. E. Walsh, W. L. Chapman, and D. Portis. (2006). The behavior of extreme cold air outbreaks under greenhouse warming. *International Journal of Climatology 26*:1133– 1147.

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography, 36*(12), 2290-2299.

Veneklaas, E. J., & Van Ek, R. (1990). Rainfall interception in two tropical montane rain forests, Colombia. *Hydrological Processes, 4*(4), 311–326.

Walthert, L., & Meier, E. S. (2017). Tree species distribution in temperate forests is more influenced by soil than by climate. *Ecology and evolution*, 7(22), 9473-9484.

Weinmannia fagaroides Kunth in GBIF Secretariat (2019). GBIF Backbone Taxonomy. Checklist dataset https://doi.org/10.15468/39omei. Accessed via GBIF.org on 13 February 2019.

Wesche, K., A. Cierjacks, Y. Assefa, S. Wagner, M. Fetene, and I. Hensen. (2008). Recruitment of trees at tropical alpine treelines: Erica in Africa versus Polylepis in South America. *Plant Ecology and Diversity 1*:35–46.

Whaley, O. (2010). *Plantas y vegetación de Ica, Perú: un recurso para su restauración y conservación*. Royal Botanic Gardens, Kew.

Wicaksono, C. Y., Aguirre-Guiterrez, J., Nouhra, E., Pastor, N., Raes, N., Pacheco, S., & Geml, J. (2017). Contracting montane cloud forests: a case study of the Andean alder (*Alnus acuminata*) and associated fungi in the Yungas. *Biotropica*, 49(2), 141-152.

Wiesmeier, M., Spörlein, P., Geuß, U., Hangen, E., Haug, S., Reischl, A., ... & Kögel-Knabner, I. (2012). Soil organic carbon stocks in southeast Germany (Bavaria) as affected by land use, soil type and sampling depth. *Global Change Biology, 18*(7), 2233-2245.

Young, K. R., & Leon, B. (2007). Tree-line changes along the Andes: implications of spatial patterns and dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1478), 263-272.

Young, K. R., Ponette-González, A. G., Polk, M. H., & Lipton, J. K. (2017). Snowlines and treelines in the tropical Andes. *Annals of the American Association of Geographers, 107*(2), 429-440.

Zhang, Z. (2016). Variable selection with stepwise and best subset approaches. *Annals of translational medicine, 4*(7).

Zutta, B. R., & Rundel, P. W. (2017). Modeled shifts in Polylepis species ranges in the Andes from the Last Glacial Maximum to the present. *Forests, 8*(7), 232.

Chapter 5. General conclusions

5.1. Main conclusions from the previous chapters in relation to the formulated research questions

This project incorporated different analytical tools and different spatial scales to characterize in space and time high Andean forest plant communities in the heavily populated region of Bogotá. Multi-scalar approaches as the one presented in this dissertation, can further the holistic understanding of regional patterns of species diversity, and the impact of land use and land cover change history, together with predicted climatic-driven shifts in the vegetation composition of endangered high Andean ecosystems.

5.1.1 What is the current state of high-Andean forests in the surrounding area of Bogotá in terms of plant species diversity, above-ground biomass, fragment age and forest cover fragmentation?

Overall, the study presented in Chapter 2 on the taxonomic, phylogenetic, functional diversity and above-ground biomass in disturbed high Andean forest in the surrounding of Bogotá, yielded the characterization of six tree layer and five understory types of communities. The specific composition of each locality showed little regional floristic homogenization, similarly to what reported by Hurtado-Martilletti et al. (2020), underlining a high beta-diversity of the area.

Overall, 98 taxa of trees were recorded, belonging to 64 genera and 41 families. Asteraceae, Melastomataceae, Ericaceae, Primulaceae, Lauraceae, and Rosaceae were the most diverse families in the study area. For the understory, 326 taxa were recorded, belonging to 174 genera and 82 families. Orchidaceae, Asteraceae, and Polypodiaceae were the most diverse families.

Regarding, plot-specific diversity indicators, the number of tree species per plot varied from 10 to 24 and Pielou's evennes values for the tree layer ranged from 0.42 to 0.86. The number of understory species per plot varied from 18 to 38 with Pielou's evenness ranging from 0.53 to 0.84. The variability in Pielou's evenness values indicates that in the study area, both fragments with an heterogeneous species composition and fragments dominated by few species are present (i.e. secondary growths with highly abundant *Cavendishia bracteata* or *Miconia squamulosa*).

Moreover, the standardized phylogenetic diversity metrics calculated for the tree layer returned mostly values below zero, meaning that the majority of plot species assemblages are mostly composed by few, relatively closely related families (in terms of their evolutionary history). In fact, most of the sampled tree species belong to not many Angiosperms orders, namely Laurales, Myrtales, Asterales, Ericales, Rosales and Oxalidales. The situation was different for understory phylogenetic diversity, with around half of plot assemblages displaying values above zero. This indicates that many of the understory species assemblages that were found in the plots belonged to less closely related families than the tree layer species (*i.e.* the understories where Lycophytes, Monocots, Piperales and Eudicots are well represented).

In terms of above-ground biomass, the study plots ranged from about 47 to 495 Mg/ha, averaging 149 Mg/ha. Moreover, the minimum fragment age obtained through the analysis of the aerial imagery presented in Chapter 3, retrieved values spanning from 18 years to 78 years for the studied forest fragments. These varying values of both above-ground biomass and minimum fragment age remark the presence of an heterogeneous stand structure across the study range, a sign of the complex history of these landscapes. Lastly, despite the general recovery of forest cover and connectivity during the last decades reported in Chapter 3, all the landscape fragmentation metrics calculated in Chapter 2 portrayed a heavily fragmented forest cover around the study locations. This, together with the sensitivity of plant communities to the proximity of human activities evaluated in Chapter 2, ultimately point towards a high vulnerability of the studied high Andean forests.

5.1.2. What are the aspects of anthropic disturbance that have the most impact on vegetation composition and structure and which variables can be used as indicators of disturbance ?

The results of Chapter 2 underscored the complexity and singularity of interactions between disturbance drivers and plant communities. The impact of anthropic disturbance, which is usually considered to have a negative effect on native biodiversity and carbon storage, was visible through the lower tree layer diversity and the lower aboveground biomass in relation to increasing disturbance. Moreover, besides the regional/topographical small scale processes and environmental gradients, identified tree and understory communities proved to be shaped by anthropic disturbance factors. In fact, the compositionally based clustering of local communities was largely correlated with landscape diversity, distance to roads, minimum fragment age, proximity to cultivated fields, edge density, and distance from main roads.

A negative impact of human disturbance was not directly apparent through all the other diversity metrics employed, and a mixed effect of human disturbance on understory diversity metrics emerged. Nevertheless, the anthropic-related factors that were most significantly correlated with trees and understory diversity metrics and biomass were: minimum fragment age, distance to houses, forest edge effect, presence or proximity of cattle and cultivated fields, and forest patch size. All these anthropic factors relate directly with the well documented land use conversion from forests to farmlands or the undisciplined peri-urban expansion that took place during the last decades in the densely populated area of Bogotá (Etter, 2002; Rubiano et al., 2016; Anselm et al., 2018; Clerici et al., 2019).

Additionally, as result of the characterization of the main environmental drivers of the distribution of the high Andean tree *Weinmannia fagaroides* in Chapter 4, an important role of soil bulk density was underscored. Bulk density relates with soil compaction, water availability and organic matter content. *Weinmannia fagaroides* was observed to prefer lower values, thus less compacted soils, likely with a higher organic matter content. This connects to the evidence that uncontrolled, intensive agriculture and farming in the area could exacerbate soil condition, leaving deteriorated soils and representing yet another potential impediment to the establishment of high Andean species in the study area, especially in the eventuality of climate-driven distributional shifts.

Finally, in the course of the study presented in Chapter 2, two variables emerged as possibile effective indicators of human disturbance in high Andean forests around Bogotá: tree layer above-ground biomass and the abundance of late successional tree species. These two indicators can be assessed relatively easily (*i.e.* even remotely estimated through the analysis of multispectral satellite imagery as in the case of above-ground biomass) and serve as immediate proxies of the status of high Andean forests, rather than diversity measures themselves. Diversity indexes calculation is often laborious, and these metrics seldom reacted ambiguously to the effects of disturbance or fragmentation (Fahrig et al., 2003).

5.1.3. How has forest cover and forest connectivity developed through time?

Thanks to the unique time coverage of the under-utilized aerial imagery, employed in the analysis of forest cover trends for the period 1940-2000, presented in Chapter 3, a detailed reconstruction of vegetation dynamics at the landscape level was possibile. Overall, the forest cover increased in all localities except one, and it was found to be positively correlated with a general restoration of forest core areas and connectivity. Moreover, based on the forest cover trends, we identified three groups of localities displaying: (i) a well defined increase in forest cover with no or very little decrease during the studied period; (ii) an initial increase in forest cover, followed by a decrease occurring around the 1990s and then, again, a final increase; (iii) an initial decrease of forest cover and a later increase that started in the 80ies.

The evaluation of the relationship between forest cover trends and forest connectivity metrics, led to a meaningful interpretation of each locality's forest cover trend, which in several cases clearly mirrored past changes in the occupation and exploitation history of the analysed rural areas. Especially in those rural localities that did not experience the worst effects of the armed conflict and which possess a rather ‘smooth’ topography, the underlined forest cover recovery is probably related to a mix of abandonment of rural practices, an increase in low-density settlements of secondary homes of people living in Bogotá, and the effectiveness of regional protection efforts implemented since the 1970s.

5.1.4. How will climate change affect the distribution and the successful establishment of a representative high Andean species found in our permanent plots network?

According to the results of the study presented in Chapter 4, the main environmental constraits shaping the current distribution of *Weinmannia fagaroides* were found to be related with minimum temperature of the coldest month, mean annual precipitation and soil bulk density. The binary projection of the modeled current distribution of the species retrieved an area of roughly 110,000 km^2. However, the projected future modeled area ecompassed only about 68,000 km^2, highlighting a loss of ca. 38% of the current area for the years 2060-2080. The future distribution narrowed consistently across the entire Northern and Central Andean range shifting towards higher elevations, especially in the Eastern and Central Andean Cordilleras of Colombia, in Ecuador and at the southernmost end of the Bolivian Andean Range. It is possible that in the context of climate change, warming temperatures and rising CO_2 concentrations could push *W. fagaroides* upward on the mountains, while compromising its response to freezing events, to a point where low temperatures become a limiting factor for this species. This effect may be noticeable in the limited upward elevational shift underscored by the generated binary distribution maps. In addition, even if *W. fagaroides* was not found to be a drought-sensitive species and its distribution should not be directly endangered by the lower annual precipitation rates of the near future, largely unpredictable climate change-driven shifts in precipitation patterns at a local scale may also hamper *W. fagaroides* populations, as well as Tropical Andean treelines in general (Helmer et al., 2019).

Lastly, a substantial lack of protection efforts targeting *W. fagaroides* and high andean treelines in general was highlighted in Chapter 3, as only about 23% of the potential current distribution was found to be under any protection regime. This, together with the current high fragmentation and detrimental effects of anthropic distrurbance reported for high Andean forests around Bogotá in Chapter 2, adds urgency to the development of effective conservation strategies targeting *bosques altoandinos,* especially in the light of climate change mitigation.

5.2. Implications of the present study for the understanding of high Andean forest fragments in the surroundings of Bogotá

The area of Bogotá, and the high Andean ecosystems of the Northern and Central Andes in general, have undergone anthropic disturbance for centuries, with continuous agropastoral activities and subsequent land cover change (Grau & Aide, 2008; Sánchez-Cuervo & Aide, 2013). In this context, our findings of a general recover of forest cover and connectivity are encouraging. Moreover, the presence of some well preserved forest fragments can be interpreted as a positive sign of resilience at a regional scale, and the fact that the area hosts a high beta-diversity with strong compositional turnover across the landscape, points towards a high conservation value of these regrowing forests (de Castro Solar et al., 2015; Hurtado-Martilletti et al., 2020). Maintaining both old-growth forests and species-rich secondary forests becomes crucial for biodiversity conservation in human-modified tropical landscapes (Rozendaal et al., 2019).

Secondary forest cover is increasing globally and especially in the neotropics (Hansen et al., 2013; Arroyo-Rodríguez et al., 2017), where it often represents a frequent or even dominant type of natural vegetation (Chazdon et al., 2009; Gardner et al., 2009; Arroyo-Rodríguez et al., 2017). Thus, there is the need to fully recognize the importance of the relatively isolated secondary fragments of high Andean forests that were object of this study, that can still represent potential repositories for montane forest species within the human-modified landscape matrix (Arroyo- Rodríguez et al., 2017; van Breugel et al., 2019; Hurtado-Martilletti et al., 2020), while being a source of essential ecosystem functions and services (Melo et al., 2013; Ferraz et al., 2014; Gilroy et al., 2014).

Therefore, secondary forest patches, have to be included as key elements of conservation planning (Arroyo-Rodríguez et al., 2017) and efforts to implement forest connectivity and corridors and to guarantee land-use continuity, even in partially forested areas, should become priorities for local decision-makers. Successful conservation strategies require a sound understanding of community and ecosystem dynamics and the understanding of temporal changes in floristic composition. The predictors and indicators of disturbance that were identified in this research, could help to improve the management strategies for the passive or active restoration and protection of the remaining forest fragments in the surroundings of Bogotá.

Nonetheless, we have to consider that here presented results are relative to a limited sampling area and also that in the continuously intervened systems this study is focused on, it is highly likely that the legacy of centuries of land use is still relevant for todays' ecosystem remnants (Foster et al. 2003; Bürgi et al., 2017). It is known that landscape and matrix heterogeneity, together with intermediate levels of disturbance, may add uncertainty to natural successional pathways (Arroyo-Rodríguez et al., 2015), and that the effects on species assemblages that could even be visible in a not-so-close future (Flinn et al., 2007), overall reducing the potential to deliver ecosystem functions and services (Arroyo-Rodríguez et al., 2015)

The very low values of above-ground biomass, the absence of the forest ecosystem's late successional species and the high fragmentation reported for some of the studied localities should be a warning signal that should impulse protection efforts and restoration measures. Particularly, the sensitivity of a distinctive high

Andean species to potentially anthropic-driven soil compaction highlighted here, underscored how some of the potential detrimental -and not readily apparent- effects of human disturbance may be hampering the establishement of forest species. In this framework, the notion of forest degradation imply that the capacity for regeneration is reduced or lost, recovery is arrested, essential ecological interactions are disrupted, and that human intervention is necessary to impulse trajectory of recovery (Ghazoul & Chazdon, 2017). Thus, the implementation of efficient land and biodiversity management strategies that can prevent broader scale, irreversible landscape degradation (Brandt & Townsend, 2006; Comita et al., 2010) is strongly needed in the study area.

Lastly, with the recent unprecedented effort to restore forests at large scales on deforested or degraded land brought about by a renewed political and social engagement (Brancalion & Chazdon, 2017), the area of Bogotá and Colombia is experiencing an increase in ecological or agroecological restoration projects (Aguilar-Garavito & Ramírez 2015; Rivera, 2021; El Espectador, 2021). Ecological and agroecological restoration have a great potential to address climate mitigation, conservation, environmental justice and sustainable development (Erbaugh et al., 2020). To this aim, more comprehensive multi-layer characterizations of the vegetation in different stadia of intervention and succession, as the one performed in this study, are much needed to generate fine-scale baseline data for restoration projects.

5.3. Future perspectives and approaches integration

The need to strengthen our understanding of the resilience of highly transformed landscapes was highlighted throughout this project. Accordingly, with the work presented in Chapter 2, a first approximation to disentangling the relationship between natural and human-induced causes of species diversity patterns and loss and their underlying mechanisms, was achieved through an exploratory approach. Moreover, a test of the effectiveness of relevant drivers and indicators of disturbance identified in the literature, was performed with a large number of variables considered simultaneously. Nevertheless, the here considered study area was quite circumscribed. Therefore, this exercise may be relevant as a prior analysis step or to be included in similar studies and the undelying methodology should be tested on a broader scale or on different ecosystems or case studies. Moreover, modelling efforts targeting vulnerable high Andean species should be perfomed more frequently (*e.g.* late successional species identifyied in Chapter 2), as they are efficient tools for making predictions on species response to climate change, thus ecosystem resilience.

Additionally, it is recommendable that future research aims to expand further the network of permanent plots in the area of Bogotá to improve the monitoring of this fragile ecosystems in relation to urban expansion processes. Tracking forest fragment-related species composition changes would help to understand better the factors shaping plant communities and to assess spatial and temporal patterns of associated ecosystem services provision to the neighboring city. Plot-based work should be implemented together with the generation of fine scale and long-term information on land cover and landscape connectivity changes. Lastly, as current environmental challenges require the incusion of study ecosystems within their socioeconomic context, an upscaling of the approach described in Chapter 3, where the observed forest cover trend was interpreted in the light of the individual locality's history, is possibile and would be highly beneficial to gain a more comprehensive understanding of ecosystem dynamics in other Andean Colombian departments or high Andean ecosystems in general.

References

Acuña, C. A. (2013). *Potencial de regeneración de rastrojos y bosques secundarios en la sabana de Bogotá* (Master's thesis, Pontificia Universidad Javeriana, Bogotá, Colombia). Retrieved from https://repository.javeriana.edu.co/handle/10554/17925.

Agudelo Valencia, M. (2010). *Evaluación del estado actual de la vegetación en parcelas enmendadas con biosólidos en la antigua arenera Juan Rey, Bogotá DC* (Bachelor's thesis, Pontificia Universidad Javeriana, Bogotá, Colombia). Retrieved from https://repository.javeriana.edu.co/handle/10554/8518.

Aguilar-Garavito, M. & W. Ramírez. (2015). *Monitoreo a procesos de restauración ecológica aplicado a ecosistemas terrestres*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.

Aide, T. M. (2004). ECOLOGY: Enhanced: Globalization, Migration, and Latin American Ecosystems. *Science, 305*(5692), 1915–1916.

Anderson, E. P., Marengo, J., Villalba, R., Halloy, S., Young, B., Cordero, D., ... & Ruiz, D. (2011). Consequences of climate change for ecosystems and ecosystem services in the tropical Andes. *Climate change and biodiversity in the tropical Andes, 1*, 1-18.

Andrade, M. G. (2011). Estado del conocimiento de la biodiversidad en Colombia y sus amenazas. Consideraciones para fortalecer la interacción ciencia-política. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales, 35*(137), 491-508.

Andrade, G. I., Remolina, F., & Wiesner, D. (2013). Assembling the pieces: a framework for the integration of multi-functional ecological main structure in the emerging urban region of Bogotá, Colombia. *Urban ecosystems, 16*(4), 723-739.

Anselm, N., Brokamp, G., & Schütt, B. (2018). Assessment of land cover change in peri-urban high andean environments South of Bogotá, Colombia. *Land, 7*(2), 75.

Arellano, H. (2009). *Caracterización de Comunidades Vegetales identificadas en la microcuenca de la quebrada La Taza, área priorizada por la subdirección científica*. Informe Final del Contrato 1011-2008. Subdirección Científica. Jardín Botánico de Bogotá.

Armenteras, D., Gast, F., & Villareal, H. (2003). Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological conservation, 113*(2), 245-256.

Arroyo-Rodríguez, V., Melo, F. P., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., ... & Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews, 92*(1), 326-340.

Ataroff, M. (2003). Selvas y bosques de montaña. In: Aguilera, M., Azócar, A., González Jiménez, E. (Eds.). *Biodiversidad de Venezuela, Tomo II*, pp. 762-810. Fundación Polar, Ministerio de Ciencia y Tecnología, Fondo Nacional para la Ciencia, Tecnología e Innovación (FONACIT). Editorial ExLibris, Caracas, Venezuela.

Avella, A., Torres, S., Gómez, W., & Pardo, M. (2014). Los páramos y bosques altoandinos del pantano de Monquentiva o pantano de Martos (Guatavita, Cundinamarca, Colombia): Caracterización ecológica y estado de conservación. *Biota Colombiana, 15*(1), 3–39.

Correa Ayram, C. A., Etter, A., Díaz-Timoté, J., Buriticá, S.R., Ramírez, W., & Corzo, G. (2020). Spatiotemporal evaluation of the human footprint in Colombia: Four decades of anthropic impact in highly biodiverse ecosystems. *Ecological Indicators*, *117*, 106630.

Bader, M. (1999). *A study on the distribution of vascular epiphytes in a secondary cloud forest, Central Cordillera, Colombia*. (Doctoral thesis, Wageningen University and Research Center, Wageningen, Netherlands).

Baptiste, B., Pinedo-Vasquez, M., Gutierrez-Velez, V. H., Andrade, G. I., Vieira, P., Estupiñán-Suárez, L. M., ... & Lee, T. M. (2017). Greening peace in Colombia. *Nature Ecology & Evolution, 1*(4), 1-3.

Beltrán, H. E., & Barrera-Cataño, J. I. (2014). Caracterización de invasiones de Ulex europaeus L. de diferentes edades como herramienta para la restauración ecológica de bosques altoandinos, Colombia. *Biota Colombiana*, *15*.

Bernal, R., Gradstein, S. R., & Celis, M. (2015). *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia. Bogotá.

Boron V. Payán, E., MacMillan, D. & Tzanopoulos, J. (2016). Achieving sustainable development in rural areas in Colombia: Future scenarios for biodiversity conservation under land use change. *Land Use Policy 59*, 27–37.

Borrelli, P., Armenteras, D., Panagos, P., Modugno, S., & Schütt, B. (2015). The implications of fire management in the andean paramo: A preliminary assessment using satellite remote sensing. *Remote Sensing, 7*(9), 11061-11082.

Bovendorp, R. S., Brum, F. T., McCleery, R. A., Baiser, B., Loyola, R., Cianciaruso, M. V., & Galetti, M. (2019). Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. *Ecography, 42*(1), 23–35.

Brancalion, P. H., & Chazdon, R. L. (2017). Beyond hectares: four principles to guide reforestation in the context of tropical forest and landscape restoration. *Restoration Ecology, 25*(4), 491-496.

Brandt, J. S.; Townsend, P. A. (2006). Land use–land cover conversion, regeneration and degradation in the high elevation Bolivian Andes. *Landsc. Ecol. 21*, 607–623.

Braun-Blanquet, J. (1932) *Plant sociology. The study of plant communities*. McGraw Hill, London.

Bubb P, May I, Miles L, Sayer J. (2004). *Cloud Forest Agenda*. UNEP-World Conservation Monitoring Centre: Cambridge, UK.

Bürgl, H. (1961). Historia geológica de Colombia. *Revista de la Academia Colombiana de Ciencias, 11*, 137–191.

Bürgi, M.; Östlund, L.; Mladenoff, D. J. (2017). Legacy effects of human land use: Ecosystems as time-lagged systems. *Ecosystems, 20,* 94–103.

Buytaert, W., Célleri, R., De Bièvre, B., Cisneros, F., Wyseure, G., Deckers, J., & Hofstede, R. (2006). Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews, 79*(1-2), 53–72.

Caballero-Villalobos, L., Fajardo-Gutiérrez, F., Calbi, M., Silva-Arias, G. A. (subm.) Climate change can drive significant loss of suitable habitat for Polylepis quadrijuga, a treeline species in the sky islands of the northern Andes. Submitted to *Frontiers in Ecology and Evolution*.

Cantillo Higuera, E. E., & Gracia, C. M. (2013). Diversidad y caracterización florística de la vegetación natural en tres sitios de los cerros orientales de Bogotá D. C. *Colombia Forestal, 16*(2), 228.

Cardozo G, H., & Schnetter, M. L. (1976). Estudios ecológicos en el Páramo de Cruz Verde, Colombia. III. La biomasa de tres asociaciones vegetales y la productividad de Calamagrostis effusa (HBK) Steud. y Paepalanthus columbiensis Ruhl. en comparacion con la concentracion de clorofila. *Caldasia*, 69-83.

Castellanos-Castro, C., & Bonilla, M. A. (2011). Grupos funcionales de plantas con potencial uso para la restauración en bordes de avance de un bosque altoandino. *Acta Biológica Colombiana*, *16*(1), 153-174.

Chazdon, R. L., Harvey, C. A., Komar, O., Griffith, D. M., Ferguson, B. G., Martínez-Ramos, M., ... & Philpott, S. M. (2009). Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica, 41*(2), 142-153.

Chazdon, R. L. (2014). Second growth: the Promise of Tropical Forest Regeneration in an Age of Deforestation. University of Chicago Press, Chicago.

Chisacá L. (2005). Adelantar el Estudio Corológico de Seis (6) Especies Andinas y Realizar Mínimo Cinco (5) Levantamientos de Vegetación en Áreas Relevantes para la Estructura Ecológica Principal del Distrito. Informe Final del Contrato No. 249-2005. Subdirección Científica. Jardín Botánico José Celestino Mutis.

Chaves, M. E., & Arango, N. (1998). *Informe nacional sobre el estado de la biodiversidad: Diversidad biológica (Vol. 1).* Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.

Cleef, A. M. (1979). *Secuencia altitudinal de la vegetación de los páramos de la cordillera Oriental, Colombia*. Actas del IV Simposio internacional de Ecología Tropical. Panamá.

Cleef, A. M. (1981). The vegetation of the páramos of the Colombian Cordillera Oriental. *Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht, 481*(1), 1-320.

Cleef, A. M. y H. Hooghiemstra. (1984). Present vegetation of the high plain of Bogotá. In H. Hooghiemstra, Vegetational and climatic history of the high plain of Bogotá, Colombia. *Dissertationes Botanicae. 78*: 42-76.

Clerici, N., Rubiano, K., Abd-Elrahman, A., Posada Hoestettler, J. M., & Escobedo, F. J. (2016). Estimating aboveground biomass and carbon stocks in periurban Andean secondary forests using very high resolution imagery. *Forests, 7*(7), 138.

Clerici, N., Salazar, C., Pardo-Díaz, C., Jiggins, C. D., Richardson, J. E., & Linares, M. (2019a). Peace in Colombia is a critical moment for Neotropical connectivity and conservation: Save the northern Andes–Amazon biodiversity bridge. *Conservation Letters, 12*(1), e12594.

Clerici, N., Cote-Navarro, F., Escobedo, F. J., Rubiano, K., & Villegas, J. C. (2019b). Spatio-temporal and cumulative effects of land use-land cover and climate change on two ecosystem services in the Colombian Andes. *Science of the Total Environment, 685*, 1181-1192.

Clerici, N., Armenteras, D., Kareiva, P., Botero, R., Ramírez-Delgado, J. P., Forero-Medina, G., ... & Biggs, D. (2020). Deforestation in Colombian protected areas increased during post-conflict periods. *Scientific reports, 10*(1), 1-10.

Comita, L. S.; Thompson, J.; Uriarte, M.; Jonckheere, I.; Canham, C. D.; Zimmerman, J. K. (2010). Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. *Ecological Applications 20*, 1270–1284.

Cortés-Duque, J., & Sarmiento Pinzón, C. E. (2013). *Visión socioecosistémica de los páramos y la alta montaña colombiana. Memorias del proceso de definición de criterios para la delimitación de páramos.* Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.

Cortés-Sánchez. S. P., Van der Hammen, T. y Rangel J. O. (1999). Comunidades vegetales y patrones de degradación y sucesión en la vegetación de los cerros occidentales de Chía, Cundinamarca, Colombia. *Revista de la Academia Colombiano de Ciencias Exactas, Fisicas y Naturales 13*, 89.

Cortés-Sánchez, S. P. (2003). Estructura de la vegetación arbórea y arbustiva en el costado oriental de la Serranía de Chiía(Cundinamarca, Colombia)/Structure of the arboreal and shrubby vegetation of the Eastern flank of the Serranía de Chía (Cundinamarca, Colombia). *Caldasia*, 119-137.

Cortés-Sánchez, S. P. (2006). *Identificación y Caracterización de las Comunidades Vegetales Presentes en las Áreas Rurales Del D.C. y La Región*. Informe final contrato 048-2006. Subdirección Científica. Jardín Botánico de Bogotá José Celestino Mutis.

Cortés-Sánchez, S. P. (2007). *Generar modelos estructurales que permitan la representación de comunidades vegetales de acuerdo con las diferentes características físicas y bióticas del distrito y realizar la caracterización de mínimo cuatro (4) comunidades vegetales*. Informe final contrato 089-2007. Subdirección Científica. Jardín Botánico de Bogotá José Celestino Mutis.

Cortés-Sánchez, S. P. (2008). La vegetación boscosa y arbustiva de la cuenca alta del río Bogotá. In: T. van der Hammen, A.P. Preciado & P.P. E (Eds.), *Studies on tropical Andean ecosystems 7*. J. Cramer, Berlin, Stuttgart.

Cortés-Sánchez, S. P. (2011). *Caracterización fisionómica, estructural y florística de algunas comunidades vegetales en la cuenca media del río Tunjuelo*. Subdirección Científica. Jardín Botánico de Bogotá José Celestino Mutis

Cortés-Sánchez, S. P. (2018). Identificación y cuantificación de los procesos de cambio de las coberturas sobre el territorio de la cuenca alta del río Bogotá, entre 1977 y 2015, *Ciudad. Estados Política, 5*(2), 17–32.

Cuatrecasas, J. (1934). *Observaciones geobotánicas en Colombia*. Trabajos del Museo Nacional de Ciencias Naturales. Serie Botánica 27. 143p, Madrid.

Cuatrecasas, J. (1958). Aspectos de la vegetación natural de Colombia. *Revista de la Academia Colombiano de Ciencias Exactas, Fisicas y Naturales, 10*(40): 221-264.

Cuesta, F., Peralvo, M., & Valarezo, N. (2009). *Los bosques montanos de los Andes Tropicales. Una evaluación regional de su estado de conservación y de su vulnerabilidad a efectos del cambio climático*. Serie investigación y sistematización, 5. Programa Regional ECOBONA–INTERCOOPERATION, Quito.

de Castro Solar, R. R., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., … Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters, 18*, 1108–1118. doi: 10.1111/ele.12494.

Diaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution, 16*(11), 646–655.

Duvier, J. A. I. (2019). Composición florística y formas de vida de las macrófitas acuáticas de la serranía de La Lindosa (Guaviare), Guayana Colombiana/Floristic composition and life forms of aquatic macrophytes of serrania La Lindosa (Guaviare), Colombian Guiana. *Caldasia, 41*(2).

El Espectador. Redacción Medio Ambiente (2021, January 2). Los nuevos compromisos climáticos de Colombia. *El Espectador*. Retrieved from https://www.elespectador.com/noticias/medio-ambiente/los-nuevos-compromisos-climaticos-de-colombia/.

Erbaugh, J. T., Pradhan, N., Adams, J., Oldekop, J. A., Agrawal, A., Brockington, D., ... & Chhatre, A. (2020). Global forest restoration and the importance of prioritizing local communities. *Nature Ecology & Evolution, 4*(11), 1472-1476.

Escobedo, F. J., Clerici, N., Staudhammer, C. L., & Corzo, G. T. (2015). Socio-ecological dynamics and inequality in Bogotá, Colombia's public urban forests and their ecosystem services. *Urban Forestry & Urban Greening, 14*(4), 1040-1053

Etter, A., & Villa, L. A. (2000). Andean forests and farming systems in part of the Eastern Cordillera (Colombia). *Mountain Research and Development, 20*(3), 236-245.

Etter, A. (2002). Multitemporal analysis (1940–1996) of land cover changes in the southwestern Bogota highplain (Colombia). *Landscape and urban planning, 59*(3), 147-158.

Etter, A., McAlpine, C., Wilson, K., Phinn, S., & Possingham, H. (2006). Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, Ecosystems & Environment, 114*(2-4), 369–386.

Etter, A., McAlpine, C., Pullar, D., & Possingham, H. (2006). Modelling the conversion of Colombian lowland ecosystems since 1940: Drivers, patterns and rates. *Journal of environmental management, 79*(1), 74-87.

Eufemia, L., Bonatti, M., Castro-Nunez, A., Lana, M., Morales, H., & Sieber, S. (2019). Colombia's inadequate environmental goals. *Science (New York, N.Y.), 364*(6439), 444–445.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, *34*(1), 487-515.

Fajardo-Gutiérrez, F. (2013). *Análisis de la riqueza y diversidad de las especies vegetales para la identificación de cambios en la composición, estructura y distribución de especies.* Informe final contrato No 1014/2012. Subdirección Científica. Jardín Botánico de Bogotá.

Fajardo-Gutiérrez, F., Infante-Betancour, J., & Cabrera-Amaya, D. M. (2018). Modelización de la distribución potencial del género Polylepis en Colombia y consideraciones para su conservación. *Ecología Austral, 28*(1-bis), 202-215.

Fandiño, M.C., Ferreira P., (1998). *Colombia biodiversidad siglo XXI: propuesta técnica para la formulación de un plan de acción nacional en biodiversidad*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Ministerio del Medio Ambiente y Departamento Nacional de Planeación, Bogotá, Colombia.

Ferraz, S. F., Ferraz, K. M., Cassiano, C. C., Brancalion, P. H. S., da Luz, D. T., Azevedo, T. N., ... & Metzger, J. P. (2014). How good are tropical forest patches for ecosystem services provisioning?. *Landscape ecology, 29*(2), 187-200.

Fjeldså, J., Álvarez, M. D., Lazcano, J. M., & León, B. (2005). Illicit crops and armed conflict as constraints on biodiversity conservation in the Andes region. *ambio: a Journal of the Human Environment, 34*(3), 205-211.

Flinn, K. M.; Marks, P. L. (2007). Agricultural legacies in forest environments: Tree communities, soil properties, and light availability. *Ecological Applications, 17*, 452–463.

Forero, E. (1965). *Estudio fitosociológico de un bosque subclimácico en el Altiplano de Bogotá.* (Bachelor's thesis, Universidad Nacional de Colombia, Departamento de Biología, Bogotá).

Foster, D.; Swanson, F.; Aber, J.; Burke, I.; Brokaw, N.; Tilman, D.; Knapp, A. (2003). The importance of land-use legacies to ecology and conservation. *BioScience, 53*, 77–88.

Franco P. & Betancur J. (2000). *Ambiente biótico. Guía ambiental para la localidad de Sumapaz*. Alcaldía mayor de Bogotá-Universidad Nacional de Colombia. Bogotá.

Garavito, N. T., Álvarez, E., Caro, S. A., Murakami, A. A., Blundo, C., Espinoza, T. B., ... & León, B. (2012). Evaluación del estado de conservación de los bosques montanos en los Andes tropicales. *Revista Ecosistemas, 21*(1-2).

García, D. M. & M. R. Mayorga. (2009). *Caracterización florística y estructural de los relictos de vegetación natural presentes en tres sitios de los cerros orientales de Bogotá D.C. Parque Nacional Enrique Olaya Herrera II etapa, Los Soches y Quebrada la Vieja*. Convenio 545-2005 Universidad Distrital-Jardín Botánico de Bogotá.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology letters, 12*(6), 561-582.

Gentry, A. H. (1982). Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny?. *Annals Missouri Botanical Garden 69*:557-593.

Gentry, A. H. (1995). Patterns of diversity and floristic composition in Neotropical montane forests. In: Churchill, S. P.; Balslev, H.; Forero, E. & Luteyn, J. L. (Eds.), *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden, New York.

Ghazoul, J., & Chazdon, R. (2017). Degradation and recovery in changing forest landscapes: a multiscale conceptual framework. *Annual Review of Environment and Resources, 42*, 161-188.

Gíl Amaya, K. S. (2012). *Evaluación del estado de conocimiento y conservación de la familia orchidaceae, a través de colecciones ex situ en el departamento de Cundinamarca, Colombia.* (Bachelor's thesis, Pontificia Universidad Javeriana, Bogotá, Colombia). Retrieved from https://repository.javeriana.edu.co/handle/10554/8984.

Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Baptiste, B. L., Uribe, C. A. M., ... & Edwards, D. P. (2014). Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. *Nature Climate Change, 4*(6), 503-507.

Giraldo, C. (2007). *Patrones de distribución o Corología de seis especies andinas prioritarias y su relación con las condiciones físico bióticas, los gradientes ecológicos y la alteración antrópica a una escala de 1:25.000 a 1:10.000*. Informe Final de contrato 141-2007. Subdirección Científica. Jardín Botánico de Bogotá.

Giraldo-Cañas, D. (2010). Distribution and invasion of C3 and C4 grasses (Poaceae) along an altitudinal gradient in the Andes of Colombia. *Caldasia, 32*(1), 65-86.

Givnish, T. J., Barfuss, M. H., Van Ee, B., Riina, R., Schulte, K., Horres, R., ... & Winter, K. (2014). Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Molecular phylogenetics and evolution, 71*, 55-78.

Gómez, M. A. B. (Ed.). (2005). *Estrategias Adaptativas de plantas del páramo y del bosque altoandino en la cordillera Oriental de Colombia*. Universidad Nacional de Colombia. Bogotá.

Gonzalez-Salazar, M. A., Venturini, M., Poganietz, W. R., Finkenrath, M., & Leal, M. R. L. (2017). Combining an accelerated deployment of bioenergy and land use strategies: Review and insights for a post-conflict scenario in Colombia. *Renewable and Sustainable Energy Reviews, 73*, 159-177.

Gradstein, S. R. (2008). Epiphytes of tropical montane forests—Impact of deforestation and climate change. In Gradstein, S. R., Homeier, J., & Gansert, D. (Eds.), *Biodiversity and ecology series. The tropical mountain forest—Patterns and processes in a biodiversity hotspot* (Vol. 2, pp. 51–62). Göttingen Centre for Biodiversity and Ecology, Göttingen, Germany.

Grau, H. R., Aide, M., 2008. Globalization and land-use transitions in Latin America. *Ecology and Society 13* (2), 16.

Gregory-Wodzicki, K. M. (2000). Uplift history of the Central and Northern Andes: a review. *Geological society of America bulletin, 112*(7), 1091-1105.

Grimm, N. B., Chapin, F. S., Bierwagen, B. , Gonzalez, P. , Groffman, P. M., Luo, Y. , Melton, F. , 725 Nadelhoffer, K. , Pairis, A. , Raymond, P. A., Schimel, J. and Williamson, C. E., (2013). The impacts 726 of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment, 727* 11: 474-482.

Grubb, P. J., Lloyd, J. R., Pennington, T. D., & Whitmore, T. C. (1963). A comparison of montane and lowland rain forest in Ecuador I. The forest structure, physiognomy, and floristics. *The Journal of Ecology,* 567-601.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... & Townshend, J. (2013). High-resolution global maps of 21st-century forest cover change. *Science, 342*(6160), 850-853.

Hartshorn, G. S. (1980). Neotropical forest dynamics. *Biotropica*, 23-30.

Helmer, E. H., Gerson, E. A., Baggett, L. S., Bird, B. J., Ruzycki, T. S., & Voggesser, S. M. (2019). Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. *PloS one, 14*(4), e0213155.

Hernández-Camacho, J., Hurtado, A., Ortiz, R., & Walschburger, T. (1992). Centros de endemismo en Colombia. *La Diversidad Biológica de Iberoamérica, 1,* 175-190.

Hernández, N. (2010). *Caracterización de Comunidades Vegetales identificadas en la microcuenca de la quebrada La Fucha, área priorizada por la subdirección científica.* Informe Final del Contrato Nº 786-2009. Subdirección Científica. Jardín Botánico de Bogotá.

Herzog, S. K., Martínez, R., Jørgensen, P. M., & Tiesse, H. (2011). *Climate change and biodiversity in the tropical Andes.* Inter-American Institute for Global Change Research, International Council of Scientific Unions, Scientific Committee on Problems of the Environment (SCOPE).

Hofstede, R. G. M., Wolf, J. H. D., Benzing, D. H. (1993) Epiphytic biomass and nutrient status of a Colombian upper montane rain forest. *Selbyana 14*: 37–45.

Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences, 103*(27), 10334-10339.

Hurtado-Martilletti, A. B., Echeverry-Galvis, M. Á., Salgado-Negret, B., Muñoz, J. C., Posada, J. M., & Norden, N. (2020). Little trace of floristic homogenization in peri-urban Andean secondary forests despite high anthropogenic transformation. *Journal of Ecology, 09*(3),1468-1478.

IAvH (1998) *Informe nacional sobre el estado de la biodiversidad Colombia 1997 vol Tomo I: Diversidad Biológica.* Instituto Humboldt, PNUMA, Ministerio del Medio Ambiente, Santa Fe de Bogotá.

IGAC. (2015). *Suelos y Tierras de Colombia*. Subdirección de Agrología. Instituto Geográfico Agustín Codazzi, Bogotá.

Isaacs, P. (2012). *Determinar los patrones espaciales de distribución, extensión, pérdida, fragmentación y representatividad de las coberturas vegetales priorizadas en el distrito capital así como definir las alternativas de conectividad ecológica*. Infome Final de Contrato Nº 863 – 2012. Subdirección Científica. Jardín Botánico de Bogotá José Celestino Mutis.

Irving, E. M. (1975) *Structural evolution of the Northernmost Andes, Colombia*. US Geological Survey, Washington DC.

Jardín Botánico de Bogotá - Universidad Distrital Francisco José de Caldas. 2001. *Caracterización Fisonómica, Estructural y Florística de las unidades de vegetación presentes en las áreas Rurales del Distrito Capital.-Específicamente Páramo de Sumapaz.* Convenio Interadministrativo 026-2001. Informe final.

Jardín Botánico José Celestino Mutis - Universidad Distrital Francisco José de Caldas. 2002. *Caracterización Fisonómica, Estructural y Florística de las unidades de vegetación presentes en las áreas Rurales del Distrito Capital. Fase II Específicamente Páramo De Sumapaz*. Convenio interadministrativo 042-2002. Informe final.

Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences, 110(*28), E2602-E2610.

Jørgensen, P. M., Ulloa Ulloa, C., León, B., León-Yánez, S., Beck, S. G., Nee, M., ... & Gradstein, R. (2011). *Regional patterns of vascular plant diversity and endemism. Climate Change and Biodiversity in the Tropical Andes.* Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE).

Kappelle, M., & Brown, A. D. (2001). *Bosques nublados del neotrópico*. Instituto Nacional de la Biodiversidad. Santo Domingo, Heredia, Costa Rica.

Kattan, G. H., Franco, P., Rojas, V., & Morales, G. (2004). Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography, 31*(11), 1829-1839.

Kessler, M. (2000). Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant ecology, 149*(2), 181-193.

La Torre, M. D. L. Á., Herrando-Pérez, S., & Young, K. R. (2007). Diversity and structural patterns for tropical montane and premontane forests of central Peru, with an assessment of the use of higher-taxon surrogacy. *Biodiversity and Conservation, 16*(10), 2965-2988.

Lai, G. Y., Liu, H. C., Kuo, A. J., & Huang, C. Y. (2020). Epiphytic bryophyte biomass estimation on tree trunks and upscaling in tropical montane cloud forests. *PeerJ, 8*, e9351.

Lessmann, J., Fajardo, J., Bonaccorso, E., & Bruner, A. (2019). Cost-effective protection of biodiversity in the western Amazon. *Biological Conservation, 235*, 250–259.

León, O. A., Cadena-Vargas, C. E., & Acosta-Ortiz, M. S. (2011). El preocupante estado de Centronia mutisii (Melastomataceae). *Universitas Scientiarum*, *16*(3), 243-253.

Lozano, G. y Schnetter, R. (1976). Estudios ecológicos en el Páramo de Cruz Verde. Colombia II. Las comunidades vegetales. *Caldasia. 11*(54):53-68.

Madriñán, S., Cortés, A. J., & Richardson, J. E. (2013). Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in genetics, 4*, 192.

Melo, F. P., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., & Tabarelli, M. (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends in ecology & evolution, 28*(8), 462-468.

Mendoza, J. E., & Etter, A. (2002). Multitemporal analysis (1940–1996) of land cover changes in the southwestern Bogotá highplain (Colombia). *Landscape and Urban Planning, 59*(3), 147–158.

Minambiente. (2017). Estrategia Integral de Control a la deforestación y gestión de los bosques (EICDGB). Working paper. Bogotá. Retrieved from https://www.minambiente.gov.co/images/EICDGB_1.0_AGOSTO_9_2017.pdf.

Mittermeier, R. A., Myers, N., Mittermeier, C. G., & Robles Gil, P. (1999). *Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions*. CEMEX, SA, Agrupación Sierra Madre, SC.

Mora-Osejo, L. E., & Sturm, H. (1994). *Estudios ecológicos del páramo y del bosque altoandino cordillera oriental de Colombia*. Academia Colombiana de Ciencias Exactas, Físicas y Naturales, Santafé de Bogotá (Colombia).

Morales, L., (2017). Peace and environmental protection in Colombia. *Proposals for sustainable rural development.* Inter-Am. Dialogue [online]. Retrieved from http://www. thedialogue.org/wp-content/uploads/2017/01/Envt-Colombia-Eng_Web-Res_Finalfor-web.pdf.

Moreno, R. A. A., Vargas, C. E. C., Morales, G. M., Peña, N., & Pérez, B. (2011). Conservación integral de" Dicksonia sellowiana" Hook., en Bogotá DC y su área de influencia. *Revista de la Academia Colombiana de ciencias exactas, físicas y naturales*, *35*(134), 79-96.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*(6772), 853.

Ocampo-Zuleta, K., & Solorza-Bejarano, J. (2017). Banco de semillas de retamo espinoso Ulex europaeus L. en bordes del matorral invasor en un ecosistema zonal de bosque altoandino, Colombia. *Biota Colombiana*, *18*(1 Sup), 89-98.

Ordóñez-Blanco, J. C., & Parrado-Rosselli, Á. (2017). Relación fenología-clima de cuatro especies de orquídeas en un bosque altoandino de Colombia. *Lankesteriana*, *17*(1), 1-15.

Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters, 5*(3), 402–411.

Pizano, C., y García, H. (Eds.). (2014). *El bosque seco tropical en Colombia.* Instituto de investigación de recursos biológicos Alexander von Humboldt (IAvH). Bogotá.

Poos, M. S., Walker, S. C., & Jackson, D. A. (2009). Functional-diversity indices can be driven by methodological choices and species richness. *Ecology, 90*(2), 341–347.

Potapov, P., Hansen, M. C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., ... & Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science advances, 3*(1), e1600821.

Pulido, C. R. M. (2011). Estado del conocimiento en Weinmannia tomentosa Lf (encenillo) y algunas propuestas de estudio sobre su regeneración. *The Journal of Agricultural and Environmental Research, 2*(1), 45-53.

Rangel, J.O. (1991). *Vegetación y ambiente en tres gradientes montañosos de Colombia*. (Doctoral Tesis, University of Amsterdam, Amsterdam).

Rangel, J.O. (1997a) *Diversidad de la flora de Colombia. Informe Nacional sobre el estado de la biodiversidad, tomo I* (Chaves, M. E and Arango, N. Eds.). Instituto de Investigación de Recursos Biológicos A.von Humboldt, Bogotá, Colombia.

Rangel, J.O. (1997b) Diversidad de la fauna de Colombia. Informe Nacional sobre el estado de la biodiversidad, tomo I (ed. by M.E. Chaves and N. Arango), pp. 337–365. Instituto de Investigación de Recursos Biológicos A. von Humboldt, Bogotá.

Rangel, J.O., and H. Arellano-P. (2010). Bosques de Polylepis: un tipo de vegetación condenado a la extinción. In Rangel-Ch, J. O. (Ed.). *Colombia Diversidad Biótica X. Cambio Global (Natural) y Climático (Antrópico) en el páramo colombiano*. Instituto de Ciencias Naturales-Facultad de Ciencias-Universidad Nacional de Colombia. Bogotá.

Ramírez-Morán, N. A., Leon-Gomez, M., & Lücking, R. (2016). Use of lichen biotypes as bioindicators of perturbation in fragments of high Andean forest (" Encenillo" Biological Reserve, Colombia). *Caldasia, 38*(1), 31-52.

Restrepo-Abadía, J. F. (2016). *Caracterización vegetal del bosque altoandino en diferentes estados sucesionales de la reserva biológica Encenillo, Guasca-Cundinamarca* (Bachelor's thesis, Pontificia Universidad Javeriana, Bogotá, Colombia). Retrieved from https://repository.javeriana.edu.co/handle/10554/19536.

Rippstein, G. (2001). *Agroecología y biodiversidad de las sabanas en los Llanos Orientales de Colombia (No. 322).* Ciat, Cali, Colombia.

Rivera, M. (2021, February 27). Los cambios que vienen para la Van der Hammen. *El Espectador.* Retrieved from https://www.elespectador.com/noticias/Bogotá/los-cambios-que-vienen-para-la-reserva-van-der-hammen/?outputType=amp.

Rodríguez-Alarcón, S., Rodríguez-Eraso, N., Pineda-Rincón, I., & López-Camacho, R. (2018). Effects of fragmentation on functional diversity associated with aboveground biomass in a high Andean forest in Colombia. *Landscape Ecology, 33*(11), 1851–1864.

Rodríguez Eraso, N., Armenteras-Pascual, D., Alumbreros, J. R. (2013). Land use and land cover change in the Colombian Andes: Dynamics and future scenarios. *Journal of Land Use Science, 8,* 154–174.

Rodriguez, M., Bodini, A., Escobedo, F. J., & Clerici, N. (2021). Analyzing socio-ecological interactions through qualitative modeling: Forest conservation and implications for sustainability in the peri-urban Bogotá (Colombia). *Ecological Modelling, 439*, 109344.

Rojas, S. L. (2017). Estructura y composición florística de la vegetación en proceso de restauración en los Cerros Orientales de Bogotá (Colombia). *Caldasia*, *39*(1), 124-139.

Romero, J. F. G., Fernandez, D. C. G., & de Restrepo, M. C. (2004). Incidencia de las micorrizas arbusculares y vesículo arbusculares como estrategia adaptativa de especies de páramo y selva altoandina, cordillera oriental de Colombia. *Colombia forestal*, *8*(17), 43-59.

Rozendaal, D. M., Bongers, F., Aide, T. M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., ... & Poorter, L. (2019). Biodiversity recovery of Neotropical secondary forests. *Science advances, 5*(3), eaau3114.

Rubiano, K., Clerici, N., Norden, N., & Etter, A. (2017). Secondary forest and shrubland dynamics in a highly transformed landscape in the Northern Andes of Colombia (1985–2015). *Forests, 8*(6), 216.

Sánchez, R. & Rangel, J. O. (1990). Estudios ecológicos en la cordillera Oriental Colombiana V. Análisis fitosociológicos de la vegetación de los depósitos turbosos paramunos de los alrededores de Bogotá. *Caldasia, 16* (77): 155-192.

Sánchez-Cuervo, A. M., Aide, T. M., Clark, M. L., & Etter, A. (2012). Land cover change in Colombia: Surprising forest recovery trends between 2001 and 2010. *PLoS One, 7*(8), e43943.

Sánchez-Cuervo, A. M., Aide, T. M., (2013). Consequences of the Armed Conflict, Forced Human Displacement, and Land Abandonment on Forest Cover Change in Colombia: a Multi-scaled Analysis. *Ecosystems 16*, 1052–1070.

Schnetter, M. L., & Cardozo-G, H. (1976). *Ecological studies in Paramo de Cruz Verde, Colombia. IV. The biological activity of the soil in different plant associations*. Caldasia, Bogotá.

Sistema de Información sobre Biodiversidad de Colombia. (2021). *Las cifras de biodiversidad en Colombia*. Retrieved from http://www.sibcolombia.net/web/sib/cifras.

SIAC. (2017). Sistema de Información Ambiental de Colombia. Retrieved from https://181.225.72.78/Portal-SIAC-web/faces/Dashboard/Biodiversidad2/bosques/estadoCifrasBosques.xhtml?tematica=Cambio+de+superficie&anio=2016&entidad=IDEAM&instituto=IDEAM.

Simpson, B. B. (1983). An historical phytogeography of the high Andean flora. *Revista Chilena de Historia Natural, 56*, 109–122.

Stadtmüller, T. *Cloud Forest in the Humid Tropics: A Bibliographic Review*. (1987). United Nations University Press, Tokyo, Japan.

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R*. Springer.

Trujillo L. (2010). *Caracterización de Comunidades Vegetales identificadas enlas microcuencas de las quebradas de Suate, Chiguaza, Aleñadero y Guangua, áreas priorizadas por la subdirección científica.* Informe final contrato No 238/2010. Subdirección Científica. Jardín Botánico de Bogotá.

Trujillo L. (2011). *Caracterización de Comunidades Vegetales identificadas enla microcuenca de la quebrada Curubital, áreas priorizadas por la subdirección científica*. Informe final contrato No 292/2011. Subdirección Científica. Jardín Botánico de Bogotá.

Trujillo L. (2012a). *Caracterización de Comunidades Vegetales identificadas enla microcuenca del río Chisacá, áreas priorizadas por la subdirección científica*. Informe final contrato No 811/2012. Subdirección Científica. Jardín Botánico de Bogotá.

Trujillo L. (2012b). *Informe final contrato 096-2012. Desarrollar la caracterización florística y estructural, distribución y espacialización de comunidades vegetales para actualizar el mapa de cobertura vegetal en áreas priorizadas por el jardín botánico para la conservación en Bogotá D.C. y la región*. Subdirección Científica. Jardín Botánico de Bogotá.

Tschanz, C. M., Marvin, R. F., Cruzb, J., Mehnert, H. H., Cebula, G. T., (1974). Geologic evolution of Sierra-Nevada-de-Santa-Marta, northeastern Colombia. *Bulletin of the Geolical Society of America, 85*, 273–284.

Valencia, J. B., Mesa, J., León, J. G., Madriñán, S., & Cortés, A. J. (2020). Climate vulnerability assessment of the espeletia complex on Páramo Sky Islands in the Northern Andes. *Frontiers in Ecology and Evolution, 8*, 309.

van Breugel, M., Craven, D., Lai, H. R., Baillon, M., Turner, B. L., & Hall, J. S. (2019). Soil nutrients and dispersal limitation shape compositional variation in secondary tropical forests across multiple scales. *Journal of Ecology, 107*(2), 566–581.

Van der Hammen, T., & González, E. (1960). Upper pleistocene and holocene climate and vegetation of the “Sabana de Bogota”(Colombia, South America). *Leidse Geologische Mededelingen, 25*(1), 261-315.

Van der Hammen, T. (1974). The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, 3-26.

Van Der Hammen, T., & Rangel, J. O. (1997). El estudio de la vegetación en Colombia (Recuento histórico-tareas futuras). *Colombia diversidad biótica II*, 17-57.

Van der Hammen, T. (1998). *Plan Ambiental de la cuenca alta del Río Bgotá. Análisis de la problemática y soluciones recomendadas*. Corporación Autónoma Regional de Cundinamarca, CAR, Bogotá.

Van der Hammen T. (2008). *La Cordillera Oriental colombiana. Transecto Sumapaz. Ecoandes. Estudios de Ecosistemas Tropandinos* (Vol. 7). J.Cramer, Berlín-Stuttgart.

Vanwalleghem, T.; Gómez, J.A.; Amate, J. I.; de Molina, M. G.; Vanderlinden, K.; Guzmán, G.; Laguna, A.; Giráldez, J. V. Impact of historical land use and soil management change on soil erosion and agricultural sustainability during the Anthropocene (2017). *Anthropocene, 17*, 13–29.

Vargas, J. O. (1986). Estudios ecológicos en un relicto de bosque de Weinmannia tomentosa y Drimys granadensis en la región de Monserrate. *Perez-Arbelaezia, 1*(3), 338-356.

Vargas, O., Díaz, A., Trujillo, L., Velasco, P., Díaz, R., León, O. & Montenegro, A. (2007). *Barreras para la Restauración Ecológica*. Universidad Nacional de Colombia –Colciencias, Bogotá.

Veneklaas, E. J., Zagt, R. J., Van Leerdam, A., Van Ek, R., Broekhoven, A. J., & Van Genderen, M. (1990). Hydrological properties of the epiphyte mass of a montane tropical rain forest, Colombia. *Vegetatio, 89*(2), 183-192.

Young, K. R., & León, B. (1999). *Peru's humid eastern montane forests: An overview of their physical settings, biological diversity, human use and settlement, and conservation needs*. Centre for Research on the Cultural and Biological Diversity of Andean Rainforests (DIVA).

Young, B., Young, K. R., & Josse, C. (2011). *Vulnerability of tropical Andean ecosystems to climate change. Climate change and biodiversity in the tropical Andes*. SCOPE, IAI.

Waldner, L.S. The kudzu connection: Exploring the link between land use and invasive species. (2008). *Land Use Policy, 25*, 399–409

WWF. Choco-Darien Moist Forests. (2016). Retrieved from http://wwf.panda.org/about_our_earth/ecoregions/chocodarien_moist_forests.cfm

List of publications and own contributions

Chapter 2

Calbi, M., Fajardo-Gutierrez, F., Lucking, R., Posada, J. M., Brokamp, G., Borsch, T. (2021) Seeing the wood despite the trees: exploring the impact of human disturbance on plant diversity, community structure, and standing biomass in fragmented high Andean forests. *Ecology and Evolution*, 11(1).

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Own contribution: Performed field work, data acquisition and analyses and wrote the manuscript.

Chapter 3

Calbi, M., Clerici, N., Borsch, T., & Brokamp, G. (2020). Reconstructing long term high Andean forest dynamics using historical aerial imagery: A case study in Colombia. *Forests*, *11*(8), 788.

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Own contribution: Performed data acquisition and analyses and wrote the manuscript.

Appendices

Supporting information to Chapter 2

Table S1: Complete table of all fitted GLMs. Response vs predictors and responses vs secondary predictors.

Response				**Coefficients:**				**Pseudo.R.squared**			**Likelihood Ratio test**			
TSR	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	TSR~slope+north+ logg+house_dist	Gaussian	(Intercept)	2,764	0,039	71,300	<2e-16	0,045	0,265	0,266	-4	-6,410	12,821	0.0122
			slope	-0,106	0,041	-2,562	0,016							
			north	0,079	0,041	1,941	0,063							
			logg	-0,091	0,044	-2,042	0,051							
			house_dist	-0,069	0,038	-1,843	0,076							
Tpielou	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	TPIELOU~slope+mean_T+ house_dist +median_patch	Gaussian	(Intercept)	-0,309	0,019	-16,237	<0.0001	-0,283538	0,414305	-0,0740139	-4	-8,5593	17,1190	0.002
			slope	-0,051	0,020	-2,525	0,018							
			mean_T	-0,039	0,021	-1,865	0,073							
			house_dist	-0,029	0,020	-1,480	0,151							
			median_patch	0,032	0,019	1,670	0,107							
HSR	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HSR~cattle+cult_50m+ house_dist+median_patch	Gaussian	(Intercept)	3,458	0,037	93,706	<2e-16	0,0637122	0,35315	0,353529	-4	-6,9703	13,9410	0,007
			cattle	0,062	0,041	1,523	0,140							
			cult_50m	-0,086	0,045	-1,932	0,064							
			house_dist	-0,042	0,036	-1,157	0,257							
			median_patch	-0,123	0,053	-2,338	0,027							
Hpielou	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HPIELOU~logg + mean_prec+age+path_dis	Gaussian	(Intercept)	-0,337	0,021	-16,315	<0.0001	-0,231828	0,35264	-0,0638177	-4	-6,9577	13,9150	0,008
			logg	0,044	0,023	1,943	0,063							
			mean_prec	0,041	0,024	1,694	0,102							
			age	-0,052	0,021	-2,462	0,021							
			path_dist	-0,026	0,027	-0,976	0,338							
Tshann	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	Tshann ~slope+mean_T+ house_dist+cult_50	Gaussian	(Intercept)	0,704	0,025	27,699	<2e-16	0,75299	0,414253	0,814632	-4	-8,5579	17,1160	0.002
			slope	-0,087	0,027	-3,211	0,003							
			mean_T	-0,027	0,029	-0,935	0,358							
			house_dist	-0,047	0,026	-1,822	0,080							
			cult_50m	-0,040	0,029	-1,395	0,174							
Hshann	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	Hshann~track_dist+ mean_prec+age+house_dist	Gaussian	(Intercept)	0,896	0,022	40,441	<2e-16	0,669964	0,440919	0,759986	-4	-9,3034	18,6070	0.001
			track_dist	0,069	0,029	2,379	0,025							
			mean_prec	0,088	0,029	3,061	0,005							
			age	-0,104	0,024	-4,389	0,000							
			house_dist	-0,034	0,023	-1,523	0,139							

TsesPD	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	TsesPD ~cult_50m+	Gaussian	(Intercept)	0,898	0,068	13,296	<0.0001	0.152870	0.348572	0.371054	-4	-6,8574	13,7150	0.008
	mean_prec+protected+track_dist		cult_50m	-0,093	0,095	-0,986	0,333							
			mean_prec	-0,023	0,078	-0,296	0,770							
			protected	-0,274	0,119	-2,301	0,029							
			track_dist	0,106	0,116	0,919	0,366							

HsesPD	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HsesPD~edge+	Gaussian	(Intercept)	1,023	0,066	15,437	<0.0001	0,104383	0,269437	0,283442	-4	-5,0230	10,0460	0.040
	track_dist+mean_prec+mean_T		edge	-0,107	0,071	-1,501	0,145							
			track_dist	-0,149	0,092	-1,619	0,117							
			mean_prec	-0,081	0,084	-0,966	0,342							
			mean_T	-0,230	0,078	-2,947	0,007							

TsesMPDABU	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	TsesMPDABU~slope+	Gaussian	(Intercept)	0,926	0,057	16,383	<0.0001	0,12214	0,252624	0,278275	-4	-4,6590	9,3180	0.054
	mean_T +cattle_100+path_dist		slope	-0,070	0,066	-1,054	0,301							
			mean_T	-0,139	0,087	-1,601	0,121							
			cattle_100	-0,182	0,088	-2,078	0,047							
			path_dist	0,067	0,065	1,036	0,310							

HsesMPDABU	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HsesMPDABU ~slope +	Gaussian	(Intercept)	0,833	0,080	10,434	<0.0001	0,172752	0,415291	0,43475	-4	-8,5862	17,1720	0.002
	logg+house_dist+age		slope	0,142	0,074	1,920	0,065							
			logg	0,089	0,075	1,179	0,249							
			house_dist	-0,235	0,078	-3,006	0,006							
			age	0,207	0,090	2,309	0,029							

TsesMNTDABU	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	TsesMNTDABU~cult_50m+	Gaussian	(Intercept)	0,922	0,067	13,830	<0.0001	0.127567	0.302391	0.321500	-4	-5,7615	11,5230	0.021
	track_dist +cattle_100+slope		cult_50m	-0,189	0,103	-1,832	0,078							
			track_dist	0,133	0,085	1,556	0,131							
			cattle_100	-0,149	0,080	-1,876	0,072							
			slope	-0,150	0,076	-1,964	0,060							

HsesMNTDABU	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HsesMNTDABU~edge +	Gaussian	(Intercept)	0,666	0,107	6,211	0,000	0.139841	0.359632	0.375118	-4	-7,1314	14,2630	0.007
	cattle_100+cult_50m+protected		edge	-0,313	0,126	-2,478	0,020							
			cattle_100	0,223	0,102	2,191	0,037							
			cult_50m	0,193	0,109	1,768	0,088							
			protected	-0,348	0,152	-2,289	0,030							

FDiv	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	FDiv~north+mean_prec+logg+house_dist	Gaussian	(Intercept)	-0,193	0,016	-12,426	<0.0001	-0,241602	0,396379	-0,0559837	-4	-8,0769	16,1540	0,003
			north	-0,024	0,016	-1,519	0,140							
			mean_prec	-0,026	0,016	-1,602	0,121							
			logg	0,031	0,015	2,010	0,055							
			house_dist	-0,044	0,016	-2,767	0,010							

FRic	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	FRic~slope+north+cult_50m+ house_dist	Gaussian	(Intercept)	-4,073	0,056	-73,037	<2e-16	-0,126904	0,589519	-0,0005292	-4	-14,2470	28,4940	<0,0001
			slope	-0,217	0,048	-4,477	0,000							
			north	0,154	0,053	2,882	0,008							
			cult_50m	-0,095	0,059	-1,597	0,122							
			house_dist	-0,120	0,049	-2,454	0,021							

FEve	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	FEve~logg+age+mean_T+protected	Gaussian	(Intercept)	-0,474	0,020	-23,296	<2e-16	-0,125731	0,253105	-0,0275516	-4	-4,6693	9,3386	0,053
			logg	-0,060	0,028	-2,110	0,044							
			age	0,031	0,023	1,326	0,196							
			mean_T	-0,055	0,028	-1,982	0,058							
			protected	-0,029	0,023	-1,266	0,216							

FDis	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	FDis~edge+slope+house_dist+median_patch	Gaussian	(Intercept)	-1,441	0,016	-92,074	<2e-16	-0,137523	0,45849	-0,0053616	-4	-9,8143	19,6290	0,001
			edge	0,034	0,020	1,711	0,099							
			slope	-0,044	0,019	-2,295	0,030							
			house_dist	-0,025	0,016	-1,591	0,123							
			median_patch	0,023	0,016	1,378	0,180							

AGBplot	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	AGBplot~slope+age+cattle+cult_50m	Gamma	(Intercept)	1,715	0,072	23,734	<2e-16	0,150415	0,52161	0,525516	-4	-11,7970	23,5950	<0,0001
			slope	-0,172	0,078	-2,219	0,035							
			age	0,317	0,078	4,058	0,000							
			cattle	0,232	0,098	2,370	0,025							
			cult_50m	-0,231	0,096	-2,395	0,024							

Response				**Coefficients:**				**Pseudo.R.squared**			**Likelihood Ratio test**			
HSR	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HSR~FDis+FDiv+	Gaussian	(Intercept)	3,463	0,03867	89,542	<2e-16	0,0451143	0,265434	0,265719	-4	-4,936	9,871	0,043
	FRic+n_sp.10DBH		FDis	-0,08331	0,05329	-1,563	0,13							
			FDiv	0,10275	0,04743	2,167	0,039							
			FRic	0,0848	0,05236	1,619	0,117							
			n_sp.10DBH	0,03145	0,04589	0,685	0,499							
Hpielou	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HPIELOU~FDis+	Gaussian	(Intercept)	-0,33664	0,02152	-15,640	<0.000	-0,18688	0,295693	-0,0535119	-4	-5,609	11,217	0.024
	n_FST_ind_T+n_stems+		FDis	-0,03134	0,02338	-1,341	0,191							
	TsesMPD		n_FST_ind_T	0,03408	0,02516	1,355	0,187							
			n_stems	0,04537	0,02347	1,933	0,064							
			TsesMPD	0,05124	0,02495	2,054	0,05							
Hshann	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	Hshann~FDis+FRic+	Gaussian	(Intercept)	0,89802	0,02507	35,825	<2e-16	0.370602	0.275045	0.474078	-4	-5,146	10,293	0.036
	n_stems+ n_inv_sp_		FDis	-0,07597	0,03485	-2,180	0,038							
			FRic	0,07827	0,03082	2,540	0,017							
			n_stems	0,031	0,02455	1,262	0,218							
			n_inv_sp_T	-0,0474	0,02916	-1,626	0,116							
HsesPD	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HsesPD~FDis+FRic+	Gaussian	(Intercept)	1,007	0,06489	15,525	<0.000	0,149233	0,361625	0,380422	-4	-7,181	14,363	0.006
	n_FST_ind_T+		FDis	-0,22282	0,07203	-3,094	0,005							
	TsesMPDABU		FRic	0,17464	0,07007	2,492	0,019							
			n_FST_ind_T	0,15244	0,07016	2,173	0,039							
			TsesMPDABU	0,18361	0,07453	2,463	0,02							
HsesMPDABU	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HsesMPDABU~FDiv+FRic+	Gaussian	(Intercept)	0,82655	0,07123	11,605	<0.000	0,261149	0,555694	0,581732	-4	-12,980	25,960	<0,0001
	n_sp.10DBH+		FDiv	0,24527	0,08248	2,974	0,006							
	TsesMPDABU		FRic	-0,2625	0,08501	-3,088	0,005							
			n_sp.10DBH	0,12922	0,079	1,636	0,114							
			TsesMPDABU	0,15706	0,05962	2,634	0,014							
HsesMNTDABU	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	HsesMNTDABU~n_sp.10DBH+	Gaussian	(Intercept)	0,6697	0,1065	6,288	<0.000	0,127161	0,333223	0,347572	-4	-6,485	12,970	0,011
	n_trees+FRic +n_FST_ind		n_sp.10DBH	0,3259	0,1146	2,844	0,008							
			n_trees	0,2584	0,1172	2,206	0,036							
			FRic	-0,2239	0,1126	-1,989	0,057							
			n_FST_ind_T	0,2397	0,1056	2,269	0,031							

AGBplot	*best model*	*family*	*variable*	*Estimate*	*Std. Err.*	*t value*	*Pr(>|t|)*	*McFadden*	*Cox and Snell*	*Nagelkerke*	*Df.diff*	*LogLik.diff*	*Chisq*	*p.value*
	AGBplot~TsesMPD+ n_large_trees+n_trees+ X.n_CON_sp_T	Gamma	(Intercept)	1,7140	0,07467	22,955	<2e-16	0,151863	0,524993	0,528924	-4	-12	24	<0,0001
			TsesMPD	-0,06882	0,11824	-0,582	0,565							
			n_large_trees	0,3635	0,112	3,246	0,003							
			n_trees	0,22454	0,10409	2,157	0,04							
			X.n_CON_sp_T	0,29929	0,1142	2,621	0,014							

Supporting information to Chapter 3

Table S1: Detailed information on study localities.

Study locality	Area (ha)	Dominant Land cover at the start of analyzed time series	Relief	Proximity to closer town/main urban area (km)	Percentage of protected area within study site	Name of PA (year of establishment)
Torca	1081	T/G	mountainous	0	68%	Reserva Forestal Protectora Nacional Bosque Oriental de Bogotà (1976)
Soacha	1019	G	flat/hilly	8	14%	Distrito Regional de Manejo Integrado Sector Salto del Tequendama y Cerro Manjuí (1999)
San Francisco	484	G	mountainous/hilly	7	11%	Reserva Natural de la Sociedad Civil Hacienda la Laja (2015)
El Rosal	720	T	hilly	10	0%	-
Guasca	987	G	hilly	9	22%	Reserva Natural de la Sociedad Civil El Encenillo (2007) Reserva Natural de la Sociedad Civil Jikuri (2014)
Guatavita	417	G	hilly	4	0%	-
Tabio	711	G	hilly/mountainous	0	0%	-
Sumapaz	306	G	mountainous	21	0%	-
Pasquilla	606	G	montainous	6	10%	Encenillales de Pasquilla (2004)

T = Trees or high shrubs; G = grass, cultivated fields and low shrubs; B = bare ground/built-up. Proximity to closer town/main urban area was measured as a line distance between the centroid of the analyzed area and the closest point of the closer town or city; when 0 it indicates that the analyzed area includes parts of the town or city.

Table S2: Accuracy indices values for each class in each locality through time series

		User's accuracy (UA)	95% CI UA	Producer's accuracy (PA)	95% CI PA	Overall accuracy (OA)	95% CI OA
El Rosal							
1962	B	0.840	0.072	0.896	0.060	0.936	0.048
	G	0.940	0.047	0.899	0.059		
	T	0.950	0.043	0.966	0.035		
1977	B	0.810	0.077	1.000	0.000	0.961	0.038
	G	0.940	0.047	0.989	0.020		
	T	1.000	0.000	0.937	0.048		
1987	B	0.890	0.061	0.901	0.059	0.980	0.027
	G	0.990	0.020	0.965	0.036		
	T	0.980	0.027	0.998	0.008		
1996	B	0.920	0.053	0.634	0.094	0.962	0.038
	G	0.930	0.050	0.987	0.022		
	T	0.990	0.020	0.957	0.040		
2007	B	0.980	0.027	0.801	0.078	0.938	0.047
	G	0.930	0.050	0.898	0.059		
	T	0.940	0.047	0.970	0.033		
Guasca							
1940	B	0.910	0.056	0.651	0.093	0.924	0.052
	G	0.960	0.038	0.918	0.054		
	T	0.870	0.066	0.998	0.008		
1955	B	0.980	0.027	0.453	0.098	0.933	0.049
	G	0.980	0.027	0.908	0.057		
	T	0.870	0.066	1.000	0.000		
1978	B	0.860	0.068	0.811	0.077	0.946	0.044
	G	0.950	0.043	0.958	0.039		
	T	0.950	0.043	0.946	0.044		
1985	B	0.740	0.086	0.465	0.098	0.952	0.042
	G	0.940	0.047	0.980	0.028		
	T	0.980	0.027	0.965	0.036		
2007	B	0.790	0.080	0.840	0.072	0.954	0.041
	G	0.980	0.027	0.941	0.046		
	T	0.950	0.043	0.981	0.027		
Guatavita							
1940	B	0.930	0.050	0.926	0.051	0.940	0.047
	G	0.970	0.033	0.904	0.058		
	T	0.910	0.056	1.000	0.000		
1958	B	0.960	0.038	0.867	0.067	0.937	0.048

	G	0.960	0.038	0.911	0.056		
	T	0.910	0.056	0.990	0.019		
1962	B	0.940	0.047	0.961	0.038	0.899	0.059
	G	0.960	0.038	0.797	0.079		
	T	0.840	0.072	0.962	0.037		
1997	B	0.920	0.053	0.914	0.055	0.968	0.035
	G	0.960	0.038	0.964	0.036		
	T	0.980	0.027	0.979	0.028		
2007	B	0.940	0.047	0.965	0.036	0.961	0.038
	G	0.950	0.043	0.925	0.052		
	T	0.970	0.033	0.980	0.028		
Pasquilla							
1941	B	0.800	0.078	0.570	0.097	0.915	0.055
	G	0.930	0.050	0.938	0.047		
	T	0.900	0.059	0.910	0.056		
1961	B	0.800	0.078	0.907	0.057	0.939	0.047
	G	0.970	0.033	0.942	0.046		
	T	0.930	0.050	0.943	0.045		
1981	B	0.780	0.081	0.798	0.079	0.940	0.047
	G	0.950	0.043	0.960	0.038		
	T	0.950	0.043	0.928	0.051		
1993	B	0.920	0.053	0.233	0.083	0.902	0.058
	G	0.860	0.068	0.999	0.005		
	T	0.990	0.020	0.809	0.077		
2007	B	0.970	0.033	0.271	0.087	0.948	0.043
	G	0.960	0.038	0.962	0.038		
	T	0.930	0.050	0.952	0.042		
San Francisco							
1962	B	0.860	0.068	0.685	0.091	0.974	0.031
	G	0.970	0.033	0.993	0.016		
	T	0.990	0.020	0.983	0.025		
1977	B	0.930	0.050	0.913	0.055	0.953	0.041
	G	0.980	0.027	0.925	0.052		
	T	0.930	0.050	0.989	0.021		
1993	B	0.890	0.061	0.619	0.095	0.964	0.036
	G	0.970	0.033	0.957	0.040		
	T	0.960	0.038	0.979	0.028		
1998	B	0.890	0.061	0.763	0.083	0.964	0.036
	G	0.970	0.033	0.969	0.034		
	T	0.960	0.038	0.969	0.034		
2007	B	1.000	0.000	0.482	0.098	0.917	0.054
	G	0.870	0.066	0.966	0.036		

	T	0.960	0.038	0.900	0.059		
Soacha							
1962	B	0.920	0.053	0.798	0.079	0.931	0.050
	G	0.940	0.047	0.962	0.037		
	T	0.910	0.056	0.880	0.064		
1987	B	0.950	0.043	0.567	0.097	0.869	0.066
	G	0.960	0.038	0.828	0.074		
	T	0.760	0.084	0.970	0.033		
1996	B	0.770	0.082	0.595	0.096	0.913	0.055
	G	0.980	0.027	0.908	0.057		
	T	0.860	0.068	0.983	0.025		
Sumapaz							
1948	B	0.920	0.053	0.350	0.093	0.962	0.038
	G	0.960	0.038	0.989	0.020		
	T	0.970	0.033	0.996	0.012		
1963	B	0.900	0.059	1.000	0.000	0.949	0.043
	G	0.940	0.047	0.971	0.033		
	T	0.970	0.033	0.917	0.054		
1987	B	0.970	0.033	0.728	0.087	0.965	0.036
	G	0.990	0.020	0.977	0.029		
	T	0.930	0.050	0.984	0.025		
1996	B	0.750	0.085	0.929	0.050	0.935	0.048
	G	0.930	0.050	0.955	0.041		
	T	0.980	0.027	0.914	0.055		
Tabio							
1940	B	0.860	0.068	0.952	0.042	0.946	0.044
	G	0.970	0.033	0.963	0.037		
	T	0.910	0.056	0.891	0.061		
1961	B	0.790	0.080	1.000	0.000	0.950	0.043
	G	1.000	0.000	0.936	0.048		
	T	0.890	0.061	0.974	0.031		
1998	B	0.870	0.066	0.974	0.031	0.953	0.042
	G	0.990	0.020	0.937	0.047		
	T	0.950	0.043	0.967	0.035		
2007	B	0.920	0.053	0.900	0.059	0.897	0.060
	G	0.910	0.056	0.874	0.065		
	T	0.870	0.066	0.924	0.052		
Torca							
1940	B	1.000	0.000	0.157	0.071	0.907	0.057
	G	0.940	0.047	0.881	0.063		
	T	0.880	0.064	0.974	0.031		
1962	B	0.980	0.027	0.721	0.088	0.959	0.039

	G	0.910	0.056	0.974	0.031		
	T	0.980	0.027	0.961	0.038		
1978	B	0.900	0.059	1.000	0.000	0.947	0.044
	G	0.900	0.059	0.921	0.053		
	T	0.970	0.033	0.955	0.040		
1993	B	0.920	0.053	0.727	0.087	0.949	0.043
	G	0.930	0.050	0.926	0.051		
	T	0.960	0.038	0.977	0.030		
2004	B	0.950	0.043	0.855	0.069	0.964	0.036
	G	0.900	0.059	0.946	0.044		
	T	0.980	0.027	0.978	0.029		

Table S3: Error matrices for each locality through time series

El Rosal 1962

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	84	14	2	100	66,9559	0,09306065
G	1	94	5	100	244,2104	0,33942309
T	1	4	95	100	408,3204	0,56751626
total	86	112	102	300	719,4867	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,07817095	0,01302849	0,00186121	0,09306065
G	0,00339423	0,31905771	0,01697115	0,33942309
T	0,00567516	0,02270065	0,53914045	0,56751626
total	0,08724034	0,35478685	0,55797281	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,1757E-05	1,0532E-05	1,7146E-06
G	1,1521E-05	6,5634E-05	5,5277E-05
T	3,2207E-05	0,00012493	0,00015453
total	5,5485E-05	0,00020109	0,00021152
SE area	0,00744884	0,01418069	0,01454379

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,84	0,07	0,89604129	0,06	0,9363691	0,05
G	0,94	0,05	0,89929406	0,06		
T	0,95	0,04	0,96624859	0,04		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	62,768	5,359	10,504
G	255,264	10,203	19,998
T	401,454	10,464	20,510
total	719,4867		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

El Rosal 1977

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	81	5	14	100	58,7797	0,08169368
G	0	94	6	100	284,9359	0,39601194
T	0	0	100	100	375,7978	0,52229437
total	81	99	120	300	719,5134	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,06617188	0,00408468	0,01143712	0,08169368
G	0	0,37225123	0,02376072	0,39601194
T	0	0	0,52229437	0,52229437
total	0,06617188	0,37633591	0,55749221	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,0375E-05	3,2021E-06	8,1165E-06
G	0	8,9343E-05	8,9343E-05
T	0	0	0
total	1,0375E-05	9,2545E-05	9,7459E-05
SE area	0,003221	0,00962004	0,00987216

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,81	0,08	1	0,00	0,96071748	0,04
G	0,94	0,05	0,98914617	0,02		
T	1	0,00	0,93686399	0,05		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	47,612	2,318	4,542
G	270,779	6,922	13,567
T	401,123	7,103	13,922
total	719,5134		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

El Rosal 1987

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	89	9	2	100	30,0829	0,04181058
G	1	99	0	100	294,5663	0,40940161
T	0	2	98	100	394,8553	0,54878781
total	90	110	100	300	719,5045	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,03721142	0,00376295	0,00083621	0,04181058
G	0,00409402	0,40530759	0	0,40940161
T	0	0,01097576	0,53781206	0,54878781
total	0,04130543	0,4200463	0,53864827	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,7287E-06	1,4462E-06	3,4609E-07
G	1,6761E-05	1,6761E-05	0
T	0	5,9625E-05	5,9625E-05
total	1,849E-05	7,7832E-05	5,9971E-05
SE area	0,00429996	0,00882226	0,00774411

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,89	0,06	0,90088432	0,06	0,98033106	0,03
G	0,99	0,02	0,96491171	0,04		
T	0,98	0,03	0,99844757	0,01		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	29,719	3,094	6,064
G	302,225	6,348	12,441
T	387,560	5,572	10,921
total	719,5045		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

El Rosal 1996

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	92	1	7	100	12,2241304	0,01698614
G	2	93	5	100	324,908717	0,45147958
T	0	1	99	100	382,520335	0,53153428
total	94	95	111	300	719,653182	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,01562725	0,00016986	0,00118903	0,01698614
G	0,00902959	0,41987601	0,02257398	0,45147958
T	0	0,00531534	0,52621894	0,53153428
total	0,02465684	0,42536121	0,54998194	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	2,145E-07	2,8853E-08	1,8973E-07
G	4,0355E-05	0,00013404	9,7799E-05
T	0	2,8253E-05	2,8253E-05
total	4,0569E-05	0,00016232	0,00012624
SE area	0,00636942	0,0127404	0,01123573

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,6337896	0,09	0,9617222	0,04
G	0,93	0,05	0,9871046	0,02		
T	0,99	0,02	0,95679311	0,04		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	17,744	4,584	8,984
G	306,113	9,169	17,971
T	395,796	8,086	15,848
total	719,6532		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

El Rosal 2007

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	98	2	0	100	20,99264	0,02915569
G	2	93	5	100	256,1821	0,35579921
T	0	6	94	100	442,844	0,6150451
total	100	101	99	300	720,01874	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,02857257	0,00058311	0	0,02915569
G	0,00711598	0,33089327	0,01778996	0,35579921
T	0	0,03690271	0,5781424	0,6150451
total	0,03568856	0,36837909	0,59593236	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,6829E-07	1,6829E-07	0
G	2,5063E-05	8,3245E-05	6,0739E-05
T	0	0,00021551	0,00021551
total	2,5231E-05	0,00029892	0,00027624
SE area	0,00502306	0,01728925	0,0166206

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,98	0,03	0,80060879	0,08	0,93760824	0,05
G	0,93	0,05	0,89824118	0,06		
T	0,94	0,05	0,97014768	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	25,696	3,617	7,089
G	265,240	12,449	24,399
T	429,082	11,967	23,456
total	720,0187		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guasca 1940

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	91	8	1	100	53,9362	0,054650543
G	4	96	0	100	565,3345	0,572821913
T	1	12	87	100	367,6582	0,372527545
total	96	116	88	300	986,9289	1

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,049731994	0,00437204	0,000546505	0,05465054
G	0,022912877	0,54990904	0	0,57282191
T	0,003725275	0,04470331	0,324098964	0,37252754
total	0,076370146	0,59898438	0,324645469	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	2,4708E-06	2,2204E-06	2,98668E-07
G	0,000127273	0,00012727	0
T	1,38777E-05	0,00014803	0,000158542
total	0,000143621	0,00027752	0,000158841
SE area	0,011984206	0,01665898	0,012603199

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,91	0,06	0,65119679	0,09	0,92373999	0,05
G	0,96	0,04	0,91806907	0,05		
T	0,87	0,07	0,99831661	0,01		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	75,372	11,828	23,182
G	591,155	16,441	32,225
T	320,402	12,438	24,379
total	986,929		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guasca 1955

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	98	2	0	100	9,3492	0,00947295
G	2	98	0	100	553,6963	0,56102537
T	0	13	87	100	423,8908	0,42950168
total	100	113	87	300	986,9363	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,009283493	0,000189459	0	0,00947295
G	0,011220507	0,54980486	0	0,56102537
T	0	0,055835219	0,37366646	0,42950168
total	0,020504	0,605829537	0,37366646	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,77661E-08	1,77661E-08	0
G	6,2314E-05	6,2314E-05	0
T	0	0,000210745	0,00021074
total	6,23318E-05	0,000273077	0,00021074
SE area	0,007895049	0,016525034	0,01451706

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,98	0,03	0,45276496	0,10	0,93275482	0,05
G	0,98	0,03	0,90752402	0,06		
T	0,87	0,07	1	0,00		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	20,236	7,792	15,272
G	597,915	16,309	31,966
T	368,785	14,327	28,082
total	986,9363		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guasca 1978

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	86	9	5	100	46,8769	0,04748682
G	1	95	4	100	515,1937	0,52189689
T	1	4	95	100	425,0855	0,43061629
total	88	108	104	300	987,1561	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,040838662	0,004273813	0,002374341	0,04748682
G	0,005218969	0,495802047	0,020875876	0,52189689
T	0,004306163	0,017224652	0,409085478	0,43061629
total	0,050363794	0,517300512	0,432335694	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	2,74244E-06	1,8655E-06	1,08194E-06
G	2,72376E-05	0,000130686	0,000105649
T	1,8543E-05	7,19245E-05	8,89691E-05
total	4,85231E-05	0,000204476	0,0001957
SE area	0,006965854	0,014299498	0,013989285

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,86	0,07	0,81087342	0,08	0,94572619	0,04
G	0,95	0,04	0,95844105	0,04		
T	0,95	0,04	0,94622184	0,04		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	49,717	6,876	13,478
G	510,656	14,116	27,667
T	426,783	13,810	27,067
tot	987,1561		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guasca 1985

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	74	8	18	100	25,2182	0,02555197
G	4	94	2	100	536,4892	0,54358984
T	0	2	98	100	425,2301	0,43085819
total	78	104	118	300	986,9375	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,01890846	0,00204416	0,00459936	0,02555197
G	0,02174359	0,51097445	0,0108718	0,54358984
T	0	0,00861716	0,42224102	0,43085819
total	0,04065205	0,52163577	0,43771217	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	1,2689E-06	4,8539E-07	9,7342E-07
G	0,00011461	0,00016834	5,8501E-05
T	0	3,6753E-05	3,6753E-05
total	0,00011588	0,00020558	9,6227E-05
SE area	0,0107649	0,01433799	0,00980955

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,74	0,09	0,46512927	0,10	0,95212393	0,04
G	0,94	0,05	0,97956175	0,03		
T	0,98	0,03	0,96465451	0,04		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	40,121	10,624	20,824
G	514,822	14,151	27,735
T	431,995	9,681	18,976
total	986,9375		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guasca 2007

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	79	14	7	100	61,4426	0,06225602
G	1	98	1	100	448,8519	0,4547941
T	1	4	95	100	476,6398	0,48294988
total	81	116	103	300	986,9343	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,04918225	0,00871584	0,00435792	0,06225602
G	0,00454794	0,44569822	0,00454794	0,4547941
T	0,0048295	0,019318	0,45880238	0,48294988
total	0,05855969	0,47373206	0,46770825	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	6,4949E-06	4,7136E-06	2,5486E-06
G	2,0684E-05	4,095E-05	2,0684E-05
T	2,3324E-05	9,0469E-05	0,00011191
total	5,0503E-05	0,00013613	0,00013514
SE area	0,00710653	0,01166758	0,01162501

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,79	0,08	0,83986529	0,07	0,95368286	0,04
G	0,98	0,03	0,94082343	0,05		
T	0,95	0,04	0,98095851	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	57,795	7,014	13,747
G	467,542	11,515	22,570
T	461,597	11,473	22,487
total	986,9343		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guatavita 1940

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	93	7	0	100	91,493103	0,21960898
G	3	97	0	100	177,595675	0,42627918
T	1	8	91	100	147,529445	0,35411184
total	97	112	91	300	416,618223	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,20423635	0,01537263	0	0,21960898
G	0,01278838	0,41349081	0	0,42627918
T	0,00354112	0,02832895	0,32224177	0,35411184
total	0,22056585	0,45719238	0,32224177	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	3,1714E-05	3,1714E-05	0
G	5,3413E-05	5,3413E-05	0
T	1,254E-05	9,3223E-05	0,00010374
total	9,7666E-05	0,00017835	0,00010374
SE area	0,00988261	0,01335476	0,01018509

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,93	0,05	0,92596545	0,05	0,93996893	0,05
G	0,97	0,03	0,90441316	0,06		
T	0,91	0,06	1	0,00		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	91,892	4,117	8,070
G	190,475	5,564	10,905
T	134,252	4,243	8,317
total	416,6182		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guatavita 1958

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	96	4	0	100	59,79784	0,14353543
G	3	96	1	100	166,640011	0,39999347
T	2	7	91	100	190,168978	0,4564711
total	101	107	92	300	416,606829	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,13779401	0,00574142	0	0,14353543
G	0,0119998	0,38399373	0,00399993	0,39999347
T	0,00912942	0,03195298	0,4153887	0,4564711
total	0,15892324	0,42168813	0,41938864	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	7,9912E-06	7,9912E-06	0
G	4,7029E-05	6,2059E-05	1,5999E-05
T	4,1252E-05	0,00013702	0,00017238
total	9,6272E-05	0,00020707	0,00018837
SE area	0,00981184	0,01438979	0,01372497

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,96	0,04	0,8670476	0,07	0,93717644	0,05
G	0,96	0,04	0,91061073	0,06		
T	0,91	0,06	0,99046246	0,02		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	66,209	4,088	8,012
G	175,678	5,995	11,750
T	174,720	5,718	11,207
total	416,6068		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guatavita 1962

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	94	3	3	100	85,803504	0,20597688
G	1	96	3	100	132,137841	0,31720546
T	1	15	84	100	198,627273	0,47681766
total	96	114	90	300	416,568619	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,19361827	0,00617931	0,00617931	0,20597688
G	0,00317205	0,30451724	0,00951616	0,31720546
T	0,00476818	0,07152265	0,40052683	0,47681766
total	0,2015585	0,3822192	0,4162223	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	2,417E-05	1,2471E-05	1,2471E-05
G	1,0062E-05	3,9028E-05	2,9576E-05
T	2,2736E-05	0,00029281	0,00030865
total	5,6968E-05	0,0003443	0,0003507
SE area	0,00754769	0,01855545	0,01872695

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,94	0,05	0,96060582	0,04	0,89866234	0,06
G	0,96	0,04	0,79670839	0,08		
T	0,84	0,07	0,96229066	0,04		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	83,963	3,144	6,162
G	159,221	7,730	15,150
T	173,385	7,801	15,290
total	416,5686		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guatavita 1997

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	92	5	3	100	43,1964308	0,10370656
G	1	96	3	100	129,175584	0,31012645
T	1	1	98	100	244,153521	0,58616699
total	94	102	104	300	416,525536	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,09541004	0,00518533	0,0031112	0,10370656
G	0,00310126	0,29772139	0,00930379	0,31012645
T	0,00586167	0,00586167	0,57444365	0,58616699
total	0,10437297	0,30876839	0,58685864	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	7,9957E-06	5,1603E-06	3,1613E-06
G	9,6178E-06	3,7306E-05	2,8271E-05
T	3,4359E-05	3,4359E-05	6,8024E-05
total	5,1973E-05	7,6825E-05	9,9456E-05
SE area	0,00720921	0,00876499	0,00997277

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,9141259	0,05	0,96757508	0,03
G	0,96	0,04	0,96422238	0,04		
T	0,98	0,03	0,97884501	0,03		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	43,474	3,003	5,886
G	128,610	3,651	7,156
T	244,442	4,154	8,142
total	416,5255		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Guatavita 2007

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	94	6	0	100	36,9438919	0,08867547
G	1	95	4	100	127,339905	0,30565068
T	0	3	97	100	252,33529	0,60567386
total	95	104	101	300	416,619087	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,08335494	0,00532053	0	0,08867547
G	0,00305651	0,29036814	0,01222603	0,30565068
T	0	0,01817022	0,58750364	0,60567386
total	0,08641145	0,31385889	0,59972967	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	4,4797E-06	4,4797E-06	0
G	9,3422E-06	4,4824E-05	3,6237E-05
T	0	0,00010783	0,00010783
total	1,3822E-05	0,00015713	0,00014407
SE area	0,00371779	0,01253525	0,01200273

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,94	0,05	0,96462845	0,04	0,96122672	0,04
G	0,95	0,04	0,92515508	0,05		
T	0,97	0,03	0,9796141	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	36,001	1,549	3,036
G	130,760	5,222	10,236
T	249,859	5,001	9,801
total	416,6191		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Pasquilla 1941

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	80	19	1	100	13,7553	0,02269126
G	1	93	6	100	353,7313	0,5835285
T	2	8	90	100	238,7071	0,39378024
total	83	120	97	300	606,1937	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,01815301	0,00431134	0,00022691	0,02269126
G	0,00583528	0,5426815	0,03501171	0,5835285
T	0,0078756	0,03150242	0,35440222	0,39378024
total	0,0318639	0,57849526	0,38964084	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	8,3215E-07	8,0043E-07	5,1489E-08
G	3,4051E-05	0,00022391	0,00019398
T	3,0699E-05	0,00011528	0,00014097
total	6,5582E-05	0,00033999	0,000335
SE area	0,00809827	0,01843875	0,01830308

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,8	0,08	0,56970458	0,10	0,91523673	0,05
G	0,93	0,05	0,93809153	0,05		
T	0,9	0,06	0,90956127	0,06		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	19,316	4,909	9,622
G	350,680	11,177	21,908
T	236,198	11,095	21,747
total	606,1937		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Pasquilla 1961

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	80	14	6	100	65,6544383	0,10827682
G	1	97	2	100	346,825661	0,57198236
T	1	6	93	100	193,877169	0,31974082
total	82	117	101	300	606,357269	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,08662146	0,01515876	0,00649661	0,10827682
G	0,00571982	0,55482289	0,01143965	0,57198236
T	0,00319741	0,01918445	0,29735896	0,31974082
total	0,09553869	0,58916609	0,31529522	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,8948E-05	1,4258E-05	6,6791E-06
G	3,2716E-05	9,6166E-05	6,4772E-05
T	1,0223E-05	5,8243E-05	6,7227E-05
total	6,1887E-05	0,00016867	0,00013868
SE area	0,00786686	0,01298718	0,01177615

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,8	0,08	0,90666366	0,06	0,93880331	0,05
G	0,97	0,03	0,94170879	0,05		
T	0,93	0,05	0,94311282	0,05		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	57,931	4,770	9,349
G	357,245	7,875	15,435
T	191,182	7,141	13,995
total	606,3573		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Pasquilla 1981

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	78	12	10	100	37,3243147	0,06155533
G	2	95	3	100	369,186054	0,60886235
T	0	5	95	100	199,843525	0,32958232
total	80	112	108	300	606,353893	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,04801316	0,00738664	0,00615553	0,06155533
G	0,01217725	0,57841923	0,01826587	0,60886235
T	0	0,01647912	0,31310321	0,32958232
total	0,06019041	0,60228498	0,33752461	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	6,5677E-06	4,0417E-06	3,4446E-06
G	7,3394E-05	0,00017787	0,00010897
T	0	5,2118E-05	5,2118E-05
total	7,9961E-05	0,00023403	0,00016453
SE area	0,00894212	0,01529794	0,01282691

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,78	0,08	0,79768791	0,08	0,93953559	0,05
G	0,95	0,04	0,96037465	0,04		
T	0,95	0,04	0,92764556	0,05		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	36,497	5,422	10,627
G	365,198	9,276	18,181
T	204,659	7,778	15,244
total	606,3539		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Pasquilla 1993

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	92	5	3	100	4,69923266	0,00774932
G	3	86	11	100	408,826942	0,6741806
T	1	0	99	100	192,879505	0,31807008
total	96	91	113	300	606,40568	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,00712938	0,00038747	0,00023248	0,00774932
G	0,02022542	0,57979531	0,07415987	0,6741806
T	0,0031807	0	0,31488938	0,31807008
total	0,03053549	0,58018278	0,38928173	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	4,4645E-08	2,8813E-08	1,7652E-08
G	0,0001336	0,00055277	0,00044947
T	1,0117E-05	0	1,0117E-05
total	0,00014376	0,0005528	0,0004596
SE area	0,01199011	0,02351166	0,02143837

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,23347832	0,08	0,90181407	0,06
G	0,86	0,07	0,99933217	0,01		
T	0,99	0,02	0,80889844	0,08		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	18,517	7,271	14,251
G	351,826	14,258	27,945
T	236,063	13,000	25,481
total	606,4057		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Pasquilla 2007

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	97	3	0	100	2,31665657	0,00382038
G	1	96	3	100	369,293674	0,60899909
T	1	6	93	100	234,784126	0,38718053
total	99	105	96	300	606,394456	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,00370577	0,00011461	0	0,00382038
G	0,00608999	0,58463913	0,01826997	0,60899909
T	0,00387181	0,02323083	0,36007789	0,38718053
total	0,01366756	0,60798457	0,37834786	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	4,2901E-09	4,2901E-09	0
G	3,7088E-05	0,00014386	0,00010902
T	1,4991E-05	8,5403E-05	9,8576E-05
total	5,2083E-05	0,00022926	0,00020759
SE area	0,00721687	0,01514144	0,01440807

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,97	0,03	0,27113592	0,09	0,94842279	0,04
G	0,96	0,04	0,96160192	0,04		
T	0,93	0,05	0,95171118	0,04		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	8,288	4,376	8,577
G	368,678	9,182	17,996
T	229,428	8,737	17,124
total	606,3945		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

San Francisco 1962

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	86	9	5	100	18,3679935	0,03796691
G	2	97	1	100	259,313521	0,5360048
T	1	0	99	100	206,108036	0,42602829
total	89	106	105	300	483,78955	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,03265154	0,00341702	0,00189835	0,03796691
G	0,0107201	0,51992466	0,00536005	0,5360048
T	0,00426028	0	0,42176801	0,42602829
total	0,04763192	0,52334168	0,4290264	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,7531E-06	1,1925E-06	6,9162E-07
G	5,688E-05	8,4449E-05	2,873E-05
T	1,815E-05	0	1,815E-05
total	7,6783E-05	8,5642E-05	4,7572E-05
SE area	0,00876259	0,00925428	0,00689723

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,86	0,07	0,68549706	0,09	0,97434421	0,03
G	0,97	0,03	0,99347076	0,02		
T	0,99	0,02	0,98308171	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	23,044	4,239	8,309
G	253,187	4,477	8,775
T	207,558	3,337	6,540
total	483,7896		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

San Francisco 1977

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	93	6	1	100	25,4498988	0,05260321
G	1	98	1	100	224,848504	0,46474655
T	0	7	93	100	233,510469	0,48265024
total	94	111	95	300	483,808871	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,04892098	0,00315619	0,00052603	0,05260321
G	0,00464747	0,45545162	0,00464747	0,46474655
T	0	0,03378552	0,44886473	0,48265024
total	0,05356845	0,49239333	0,45403822	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,8196E-06	1,5764E-06	2,7671E-07
G	2,1599E-05	4,2762E-05	2,1599E-05
T	0	0,00015318	0,00015318
total	2,3419E-05	0,00019752	0,00017506
SE area	0,00483927	0,01405422	0,01323098

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,93	0,05	0,91324249	0,06	0,95323733	0,04
G	0,98	0,03	0,9249752	0,05		
T	0,93	0,05	0,98860559	0,02		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	25,917	2,341	4,589
G	238,224	6,800	13,327
T	219,668	6,401	12,546
total	483,8089		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

San Francisco 1993

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	89	2	9	100	4,23012545	0,00874285
G	1	97	2	100	231,536411	0,47854094
T	0	4	96	100	248,071717	0,51271621
total	90	103	107	300	483,838253	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,00778114	0,00017486	0,00078686	0,00874285
G	0,00478541	0,46418471	0,00957082	0,47854094
T	0	0,02050865	0,49220756	0,51271621
total	0,01256655	0,48486821	0,50256524	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	7,5588E-08	1,5133E-08	6,3235E-08
G	2,29E-05	6,7313E-05	4,5338E-05
T	0	0,00010196	0,00010196
total	2,2976E-05	0,00016929	0,00014737
SE area	0,0047933	0,01301124	0,01213943

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,89	0,06	0,61919454	0,10	0,96417341	0,04
G	0,97	0,03	0,95734201	0,04		
T	0,96	0,04	0,97939039	0,03		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	6,080	2,319	4,546
G	234,598	6,295	12,339
T	243,160	5,874	11,512
total	483,8383		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

San Francisco 1998

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	89	2	9	100	9,71523311	0,02008256
G	1	97	2	100	269,315374	0,55670745
T	0	4	96	100	204,734022	0,42320999
total	90	103	107	300	483,764629	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,01787348	0,00040165	0,00180743	0,02008256
G	0,00556707	0,54000623	0,01113415	0,55670745
T	0	0,0169284	0,40628159	0,42320999
total	0,02344055	0,55733628	0,41922317	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	3,9883E-07	7,9847E-08	3,3365E-07
G	3,0992E-05	9,1099E-05	6,1359E-05
T	0	6,9472E-05	6,9472E-05
total	3,1391E-05	0,00016065	0,00013116
SE area	0,00560278	0,01267478	0,01145268

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,89	0,06	0,76250244	0,08	0,9641613	0,04
G	0,97	0,03	0,96890558	0,03		
T	0,96	0,04	0,96912962	0,03		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	11,340	2,710	5,312
G	269,620	6,132	12,018
T	202,805	5,540	10,859
total	483,7646		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

San Francisco 2007

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	100	0	0	100	6,61673597	0,01368321
G	2	87	11	100	235,224505	0,48643714
T	1	3	96	100	241,724849	0,49987965
total	103	90	107	300	483,56609	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,01368321	0	0	0,01368321
G	0,00972874	0,42320031	0,05350809	0,48643714
T	0,0049988	0,01499639	0,47988447	0,49987965
total	0,02841075	0,4381967	0,53339255	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	0	0	0
G	4,6846E-05	0,00027032	0,00023399
T	2,4988E-05	7,3449E-05	9,6923E-05
total	7,1834E-05	0,00034377	0,00033091
SE area	0,0084755	0,01854107	0,01819107

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	1	0,00	0,48162086	0,10	0,91676799	0,05
G	0,87	0,07	0,96577704	0,04		
T	0,96	0,04	0,89968348	0,06		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	13,738	4,098	8,033
G	211,897	8,966	17,573
T	257,931	8,797	17,241
total	483,5661		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Soacha 1962

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	92	6	2	100	41,9288	0,04113989
G	1	94	5	100	691,1691	0,67816448
T	1	8	91	100	286,0783	0,28069562
total	94	108	98	300	1019,1762	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,0378487	0,00246839	0,0008228	0,04113989
G	0,00678164	0,63747461	0,03390822	0,67816448
T	0,00280696	0,02245565	0,25543302	0,28069562
total	0,0474373	0,66239866	0,29016404	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,2583E-06	9,6421E-07	3,3508E-07
G	4,5991E-05	0,00026201	0,00022066
T	7,879E-06	5,8575E-05	6,5181E-05
total	5,5128E-05	0,00032155	0,00028618
SE area	0,00742482	0,01793173	0,01691681

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,79786791	0,08	0,93075633	0,05
G	0,94	0,05	0,96237305	0,04		
T	0,91	0,06	0,88030556	0,06		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	48,347	7,567	14,832
G	675,101	18,276	35,820
T	295,728	17,241	33,793
total	1019,1762		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Soacha 1987

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	95	5	0	100	21,1175	0,02073153
G	2	96	2	100	537,0428	0,52722725
T	1	23	76	100	460,457	0,45204121
total	98	124	78	300	1018,6173	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,01969496	0,00103658	0	0,02073153
G	0,01054455	0,50613816	0,01054455	0,52722725
T	0,00452041	0,10396948	0,34355132	0,45204121
total	0,03475992	0,61114422	0,35409587	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	2,0622E-07	2,0622E-07	0
G	5,5032E-05	0,00010782	5,5032E-05
T	2,0434E-05	0,00036554	0,00037648
total	7,5673E-05	0,00047357	0,00043152
SE area	0,00869899	0,02176162	0,02077295

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,95	0,04	0,56659971	0,10	0,86938444	0,07
G	0,96	0,04	0,82818122	0,07		
T	0,76	0,08	0,97022121	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	35,407	8,861	17,367
G	622,522	22,167	43,447
T	360,688	21,160	41,473
total	1018,6173		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Soacha 1996

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	77	20	3	100	62,2769	0,06110439
G	1	98	1	100	496,7053	0,48735362
T	6	8	86	100	460,2065	0,451542
total	84	126	90	300	1019,1887	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,04705038	0,01222088	0,00183313	0,06110439
G	0,00487354	0,47760655	0,00487354	0,48735362
T	0,02709252	0,03612336	0,38832612	0,451542
total	0,07901643	0,52595078	0,39503278	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	6,6793E-06	6,0343E-06	1,0975E-06
G	2,3751E-05	4,7023E-05	2,3751E-05
T	0,00011616	0,00015158	0,00024796
total	0,00014659	0,00020464	0,00027281
SE area	0,01210728	0,01430511	0,01651703

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,77	0,08	0,59545053	0,10	0,91298304	0,06
G	0,98	0,03	0,9080822	0,06		
T	0,86	0,07	0,9830225	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	80,533	12,340	24,186
G	536,043	14,580	28,576
T	402,613	16,834	32,995
total	1019,1887		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Sumapaz 1948

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	92	3	5	100	5,2725	0,01725245
G	4	96	0	100	225,5024	0,73787952
T	0	3	97	100	74,8338	0,24486803
total	96	102	102	300	305,6087	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,01587226	0,00051757	0,00086262	0,01725245
G	0,02951518	0,70836434	0	0,73787952
T	0	0,00734604	0,23752199	0,24486803
total	0,04538744	0,71622795	0,23838461	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	2,2128E-07	8,749E-08	1,4281E-07
G	0,00021119	0,00021119	0
T	0	1,7625E-05	1,7625E-05
total	0,00021141	0,0002289	1,7768E-05
SE area	0,01453988	0,01512941	0,00421515

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,34970596	0,09	0,96175858	0,04
G	0,96	0,04	0,98902079	0,02		
T	0,97	0,03	0,99638138	0,01		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	13,871	4,444	8,709
G	218,885	4,624	9,062
T	72,852	1,288	2,525
total	305,6087		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Sumapaz 1963

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	90	4	6	100	21,5464	0,07053748
G	0	94	6	100	160,3593	0,52497591
T	0	3	97	100	123,5546	0,40448661
total	90	101	109	300	305,4603	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,06348373	0,0028215	0,00423225	0,07053748
G	0	0,49347736	0,03149855	0,52497591
T	0	0,0121346	0,39235201	0,40448661
total	0,06348373	0,50843346	0,42808281	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	4,5232E-06	1,9299E-06	2,8345E-06
G	0	0,00015701	0,00015701
T	0	4,8091E-05	4,8091E-05
total	4,5232E-06	0,00020703	0,00020793
SE area	0,00212679	0,01438852	0,01441992

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,9	0,06	1	0,00	0,9493131	0,04
G	0,94	0,05	0,97058396	0,03		
T	0,97	0,03	0,91653296	0,05		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	19,392	0,650	1,273
G	155,306	4,395	8,614
T	130,762	4,405	8,633
total	305,4603		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Sumapaz 1987

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	97	2	1	100	13,3933	0,04383197
G	0	99	1	100	171,0428	0,55976811
T	4	3	93	100	121,124	0,39639992
total	101	104	95	300	305,5601	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,04251701	0,00087664	0,00043832	0,04383197
G	0	0,55417043	0,00559768	0,55976811
T	0,015856	0,011892	0,36865193	0,39639992
total	0,058373	0,56693907	0,37468793	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	5,6473E-07	3,8037E-07	1,9212E-07
G	0	3,1334E-05	3,1334E-05
T	6,0949E-05	4,6188E-05	0,00010333
total	6,1513E-05	7,7902E-05	0,00013485
SE area	0,00784304	0,00882621	0,01161262

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,97	0,03	0,72836764	0,09	0,96533937	0,04
G	0,99	0,02	0,97747794	0,03		
T	0,93	0,05	0,98389059	0,02		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	17,836	2,397	4,697
G	173,234	2,697	5,286
T	114,490	3,548	6,955
total	305,5601		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Sumapaz 1996

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	75	16	9	100	26,5987	0,08705193
G	1	93	6	100	153,402	0,50205237
T	0	2	98	100	125,5491	0,4108957
total	76	111	113	300	305,5498	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,06528895	0,01392831	0,00783467	0,08705193
G	0,00502052	0,4669087	0,03012314	0,50205237
T	0	0,00821791	0,40267779	0,4108957
total	0,07030947	0,48905492	0,44063561	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,4352E-05	1,0288E-05	6,2691E-06
G	2,5206E-05	0,00016575	0,0001436
T	0	3,3426E-05	3,3426E-05
total	3,9558E-05	0,00020946	0,00018329
SE area	0,00628952	0,01447273	0,0135385

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,75	0,08	0,92859392	0,05	0,93487544	0,05
G	0,93	0,05	0,95471629	0,04		
T	0,98	0,03	0,91385668	0,05		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	21,483	1,922	3,767
G	149,431	4,422	8,667
T	134,636	4,137	8,108
total	305,5498		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Tabio 1940

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	86	11	3	100	69,6494	0,09798909
G	0	97	3	100	489,9275	0,68927441
T	2	7	91	100	151,2104	0,2127365
total	88	115	97	300	710,7873	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,08427062	0,0107788	0,00293967	0,09798909
G	0	0,66859618	0,02067823	0,68927441
T	0,00425473	0,01489155	0,19359021	0,2127365
total	0,08852535	0,69426654	0,21720812	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	1,1677E-05	9,4952E-06	2,8224E-06
G	0	0,00013965	0,00013965
T	8,9599E-06	2,976E-05	3,744E-05
total	2,0637E-05	0,00017891	0,00017991
SE area	0,00454284	0,01337555	0,01341315

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,86	0,07	0,95193772	0,04	0,94645701	0,04
G	0,97	0,03	0,96302522	0,04		
T	0,91	0,06	0,89126601	0,06		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	62,923	3,229	6,329
G	493,476	9,507	18,634
T	154,389	9,534	18,686
total	710,7873		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Tabio 1961

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	79	13	8	100	60,6345	0,08527447
G	0	100	0	100	445,7916	0,62694743
T	0	11	89	100	204,6249	0,28777809
total	79	124	97	300	711,051	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,06736683	0,01108568	0,00682196	0,08527447
G	0	0,62694743	0	0,62694743
T	0	0,03165559	0,2561225	0,28777809
total	0,06736683	0,66968871	0,26294446	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,2186E-05	8,3074E-06	5,4061E-06
G	0	0	0
T	0	8,1896E-05	8,1896E-05
total	1,2186E-05	9,0203E-05	8,7302E-05
SE area	0,0034908	0,00949755	0,00934356

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,79	0,08	1	0,00	0,95043677	0,04
G	1	0,00	0,9361774	0,05		
T	0,89	0,06	0,97405552	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	47,901	2,482	4,865
G	476,183	6,753	13,236
T	186,967	6,644	13,022
total	711,0510		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Tabio 1998

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	87	8	5	100	145,783	0,20502476
G	1	99	0	100	343,6656	0,48332081
T	0	5	95	100	221,6021	0,31165443
total	88	112	100	300	711,0507	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,17837154	0,01640198	0,01025124	0,20502476
G	0,00483321	0,4784876	0	0,48332081
T	0	0,01558272	0,29607171	0,31165443
total	0,18320475	0,5104723	0,30632295	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	4,8022E-05	3,125E-05	2,0168E-05
G	2,336E-05	2,336E-05	0
T	0	4,6602E-05	4,6602E-05
total	7,1382E-05	0,00010121	6,677E-05
SE area	0,00844878	0,01006043	0,00817132

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,87	0,07	0,97361854	0,03	0,95293085	0,04
G	0,99	0,02	0,93734292	0,05		
T	0,95	0,04	0,96653454	0,04		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	130,268	6,008	11,775
G	362,972	7,153	14,021
T	217,811	5,810	11,388
total	711,0507		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Tabio 2007

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	92	7	1	100	141,2756	0,19865856
G	3	91	6	100	300,2159	0,42215683
T	2	11	87	100	269,6563	0,37918461
total	97	109	94	300	711,1478	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,18276588	0,0139061	0,00198659	0,19865856
G	0,0126647	0,38416271	0,02532941	0,42215683
T	0,00758369	0,04171031	0,32989061	0,37918461
total	0,20301427	0,43977912	0,3572066	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	2,934E-05	2,5951E-05	3,9465E-06
G	5,2385E-05	0,00014743	0,00010153
T	2,8466E-05	0,00014218	0,00016426
total	0,00011019	0,00031557	0,00026973
SE area	0,01049716	0,01776424	0,0164236

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,90026122	0,06	0,8968192	0,06
G	0,91	0,06	0,87353559	0,07		
T	0,87	0,07	0,92352886	0,05		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	144,373	7,465	14,631
G	312,748	12,633	24,761
T	254,027	11,680	22,892
total	711,1478		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Torca 1940

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	100	0	0	100	4,8801	0,00451397
G	3	94	3	100	474,6435	0,43903357
T	2	10	88	100	601,5862	0,55645245
total	105	104	91	300	1081,1098	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,00451397	0	0	0,00451397
G	0,01317101	0,41269156	0,01317101	0,43903357
T	0,01112905	0,05564525	0,48967816	0,55645245
total	0,02881403	0,46833681	0,50284917	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	0	0	0
G	5,6657E-05	0,00010981	5,6657E-05
T	6,1302E-05	0,00028149	0,00033028
total	0,00011796	0,0003913	0,00038694
SE area	0,01086091	0,0197813	0,01967076

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	1	0,00	0,15665885	0,07	0,90688369	0,06
G	0,94	0,05	0,88118541	0,06		
T	0,88	0,06	0,97380724	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	31,151	11,742	23,014
G	506,324	21,386	41,916
T	543,635	21,266	41,682
total	1081,1098		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Torca 1962

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	98	2	0	100	19,4348	0,01797613
G	0	91	9	100	323,2774	0,29901403
T	1	1	98	100	738,4324	0,68300984
total	99	94	107	300	1081,1446	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,01761661	0,00035952	0	0,01797613
G	0	0,27210276	0,02691126	0,29901403
T	0,0068301	0,0068301	0,66934964	0,68300984
total	0,02444671	0,27929239	0,69626091	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	6,3975E-08	6,3975E-08	0
G	0	7,3966E-05	7,3966E-05
T	4,665E-05	4,665E-05	9,2358E-05
total	4,6714E-05	0,00012068	0,00016632
SE area	0,00683478	0,01098545	0,01289667

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,98	0,03	0,72061277	0,09	0,95906902	0,04
G	0,91	0,06	0,97425773	0,03		
T	0,98	0,03	0,96134888	0,04		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	26,430	7,389	14,483
G	301,955	11,877	23,279
T	752,759	13,943	27,329
total	1081,1446		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Torca 1978

Error matrix of sample counts

Class	B	G	T	total	mapped area (ha)	W
B	90	7	3	100	38,7852	0,0358748
G	0	90	10	100	316,5724	0,29281714
T	0	3	97	100	725,769	0,67130806
total	90	100	110	300	1081,1266	

Error matrix expressed in terms of proportion of area

Class	B	G	T	total
B	0,03228732	0,00251124	0,00107624	0,0358748
G	0	0,26353543	0,02928171	0,29281714
T	0	0,02013924	0,65116882	0,67130806
total	0,03228732	0,2861859	0,68152678	1

Error matrix espressed in terms of standard errors

Class	B	G	T
B	1,17E-06	8,463E-07	3,783E-07
G	0	7,7947E-05	7,7947E-05
T	0	0,00013247	0,00013247
total	1,17E-06	0,00021126	0,00021079
SE area	0,00108167	0,01453474	0,01451863

Accuracy indices values

Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,9	0,06	1	0,00	0,94699156	0,04
G	0,9	0,06	0,92085397	0,05		
T	0,97	0,03	0,95545596	0,04		

Area estimates and 95% CI

Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	34,907	1,169	2,292
G	309,403	15,714	30,799
T	736,817	15,696	30,765
total	1081,1266		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Torca 1993

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	92	8	0	100	39,6332	0,03665856
G	2	93	5	100	328,9052	0,30421946
T	1	3	96	100	712,6061	0,65912198
total	95	104	101	300	1081,1445	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,03372587	0,00293268	0	0,03665856
G	0,00608439	0,2829241	0,01521097	0,30421946
T	0,00659122	0,01977366	0,6327571	0,65912198
total	0,04640148	0,30563045	0,64796807	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	9,9906E-07	9,9906E-07	0
G	1,8323E-05	6,0858E-05	4,4405E-05
T	4,3444E-05	0,0001277	0,00016851
total	6,2766E-05	0,00018956	0,00021292
SE area	0,00792251	0,01376797	0,01459163

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,92	0,05	0,72682751	0,09	0,94940707	0,04
G	0,93	0,05	0,92570654	0,05		
T	0,96	0,04	0,97652512	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	50,167	8,565	16,788
G	330,431	14,885	29,175
T	700,547	15,776	30,920
total	1081,1445		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Torca 2004

Error matrix of sample counts						
Class	B	G	T	total	mapped area (ha)	W
B	95	2	3	100	63,1713	0,05845142
G	1	90	9	100	186,6035	0,17266132
T	1	1	98	100	830,9739	0,76888725
total	97	93	110	300	1080,7487	

Error matrix expressed in terms of proportion of area				
Class	B	G	T	total
B	0,05552885	0,00116903	0,00175354	0,05845142
G	0,00172661	0,15539519	0,01553952	0,17266132
T	0,00768887	0,00768887	0,75350951	0,76888725
total	0,06494434	0,16425309	0,77080257	1

Error matrix espressed in terms of standard errors			
Class	B	G	T
B	1,6393E-06	6,7641E-07	1,0043E-06
G	2,9812E-06	2,7102E-05	2,4663E-05
T	5,9119E-05	5,9119E-05	0,00011704
total	6,3739E-05	8,6897E-05	0,00014271
SE area	0,00798368	0,00932185	0,01194613

Accuracy indices values						
Class	UA	95% CI UA	PA	95% CI PA	OA	95% CI OA
B	0,95	0,04	0,85502222	0,07	0,96443355	0,04
G	0,9	0,06	0,94607163	0,04		
T	0,98	0,03	0,97756486	0,03		

Area estimates and 95% CI			
Class	stratified estimator area (ha)	SE Area (ha)	95% CI (ha)
B	70,189	8,628	16,912
G	177,516	10,075	19,746
T	833,044	12,911	25,305
total	1080,7487		

B = bare ground/built-up (including main and secondary roads, houses, and bare fields); G = grass/ cultivated fields (including areas with low shrubs), and T = Trees and tall shrubs (forest cover).W= proportion of the mapped class . UA= User's accuracy; PA= Producer's accuracy; OA= Overall accuracy. CI= confidence interval; SE= standard error.

Figure S4: Processing steps of the aerial imagery

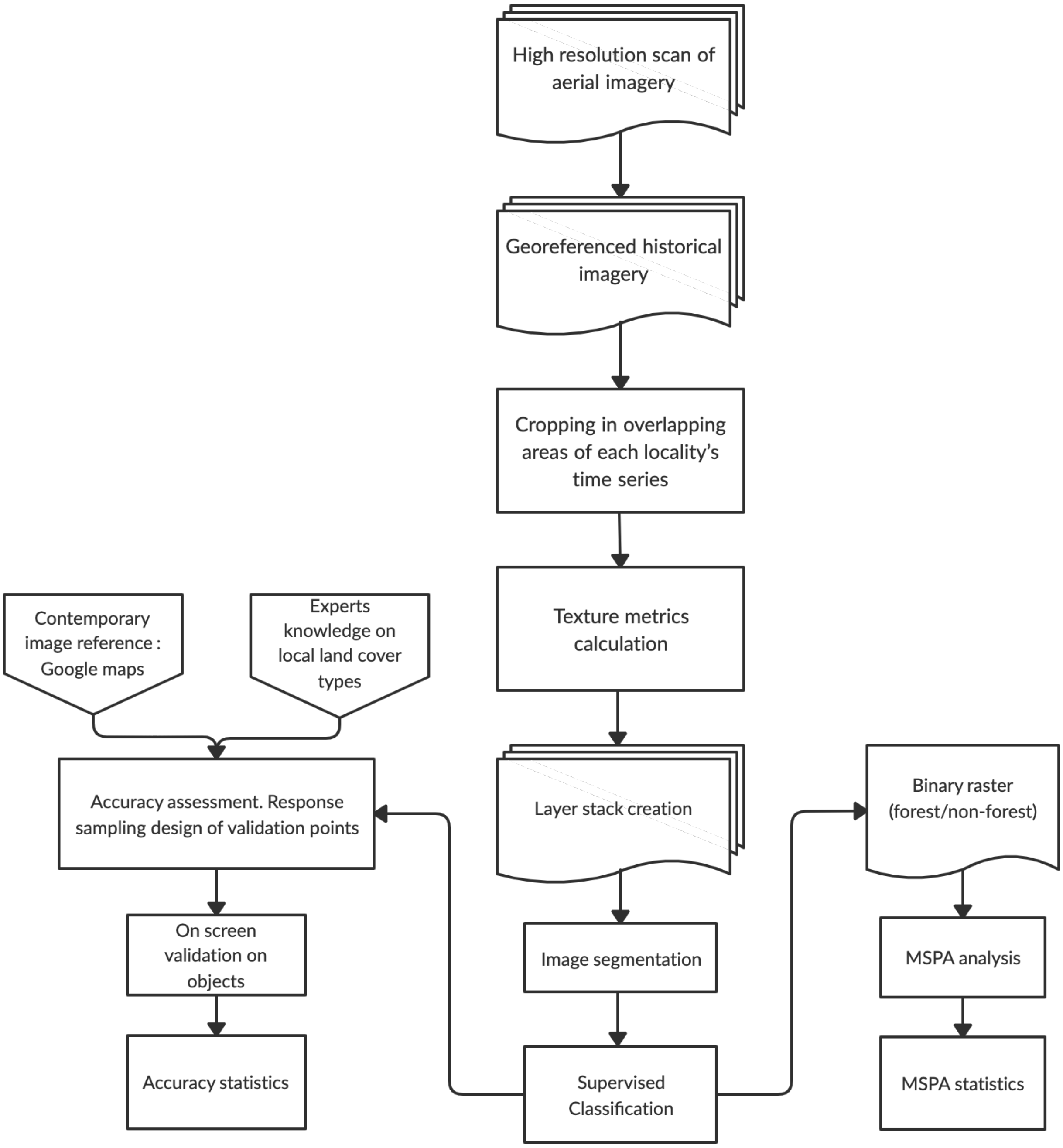


Table S5: Forest cover extent and its changes in the study localities. Forest cover extent (T) and its changes (ΔT) in the study localities (1940-2007) and corresponding confidence intervals.

Locality	Year	Area size (T) [ha]	Confidence Interval (95%)	Change of area size (ΔT) [ha]	Change of area size (ΔT) [%]	Overall forest cover gain [ha]
El Rosal	1962	401.45	20.51	-	-	
	1977	401.12	13.92	-0.33	0.08%	
	1987	387.56	10.92	-13.56	-3.38%	
	1996	395.80	15.85	8.24	2.13%	
	2007	429.08	23.46	33.29	8.41%	27.64
Guasca	1940	320.40	24.38	-	-	
	1955	368.78	28.08	48.38	15.10%	
	1978	426.78	27.07	58.00	15.72%	
	1985	431.99	18.98	5.21	1.22%	
	2007	461.60	22.49	29.60	6.85%	141.19
Guatavita	1940	134.25	8.32	-	-	
	1958	174.72	11.21	40.47	30.15%	
	1962	173.39	15.29	-1.34	-0.77%	
	1997	244.44	8.14	71.06	40.98%	
	2007	249.86	9.80	5.42	2.22%	115.61
Pasquilla	1941	236.20	21.75	-	-	
	1961	191.18	14.00	-45.02	-19.06%	
	1981	204.66	15.24	13.48	7.05%	
	1993	236.06	25.48	31.40	15.34%	
	2007	229.43	17.12	-6.63	-2.81%	-6.77
San Francisco	1962	207.56	6.54	-	-	
	1977	219.67	12.55	12.11	5.83%	
	1993	243.16	11.51	23.49	10.69%	
	1998	202.81	10.86	-40.35	-16.59%	
	2007	257.93	17.24	55.13	27.18%	50.38
Soacha	1962	295.73	33.79	-	-	
	1987	360.69	41.47	64.96	21.97%	
	1996	402.61	32.99	41.92	11.62%	106.88
Sumapaz	1948	72.85	2.52	-	-	
	1963	130.76	8.63	57.91	79.49%	
	1987	114.49	6.95	-16.27	-12.44%	
	1996	134.64	8.11	20.15	17.60%	61.79
Tabio	1940	154.39	18.69	-	-	
	1961	186.97	13.02	32.58	21.10%	
	1998	217.81	11.39	30.84	16.49%	
	2007	254.03	22.89	36.22	16.63%	99.64
Torca	1940	543.64	41.68	-	-	
	1962	752.76	27.33	209.12	38.47%	
	1978	736.82	30.77	-15.94	-2.12%	
	1993	700.55	30.92	-36.27	-4.92%	
	2004	833.04	25.31	132.50	18.91%	289.40

Table S6: MSPA classes groups percent change through time series in each locality

Locality	Year	MSPA category					% change in forest class area
		BG	CN	ED	IS	CO	
EL ROSAL	1962	NA	NA	NA	NA	NA	
	1977	10%	-34%	-3%	-48%	-2%	0%
	1987	-5%	-8%	-8%	0%	9%	-3%
	1996	4%	11%	2%	51%	-7%	2%
	2007	-18%	14%	30%	-55%	16%	8%
GUASCA	1940	NA	NA	NA	NA	NA	
	1955	-9%	-41%	4%	-56%	70%	15%
	1978	0%	14%	7%	10%	-5%	16%
	1985	0%	-11%	-7%	6%	4%	1%
	2007	-9%	-36%	-9%	-36%	34%	7%
GUATAVITA	1940	NA	NA	NA	NA	NA	
	1958	-15%	11%	48%	-16%	35%	30%
	1962	-4%	40%	44%	-17%	-14%	-1%
	1997	-22%	21%	5%	-16%	39%	41%
	2007	-4%	-35%	2%	-41%	18%	2%
PASQUILLA	1941	NA	NA	NA	NA	NA	
	1961	12%	-25%	-17%	-15%	-18%	-19%
	1981	-2%	-5%	2%	-2%	9%	7%
	1993	2%	3%	-1%	11%	-10%	15%
	2007	-10%	-7%	15%	-10%	40%	-3%
SAN FRANCISCO	1962	NA	NA	NA	NA	NA	
	1977	-10%	-4%	5%	-37%	21%	6%
	1993	-6%	11%	20%	-14%	3%	11%
	1998	18%	-53%	-33%	-43%	-8%	-17%
	2007	-13%	113%	43%	190%	4%	27%
SOACHA	1962	NA	NA	NA	NA	NA	

	1987	-23%	67%	71%	-7%	64%	22%
	1996	0%	-39%	-20%	-29%	12%	12%
SUMAPAZ	1948	NA	NA	NA	NA	NA	
	1963	-21%	42%	48%	6%	97%	79%
	1987	1%	-16%	3%	-29%	5%	-12%
	1996	-2%	-5%	0%	23%	6%	18%
TABIO	1940	NA	NA	NA	NA	NA	
	1961	-10%	24%	20%	-36%	79%	21%
	1998	-3%	-19%	23%	-32%	20%	16%
	2007	-9%	64%	44%	85%	-6%	17%
TORCA	1940	NA	NA	NA	NA	NA	
	1962	-29%	-74%	-57%	-49%	122%	38%
	1978	4%	-17%	-12%	-18%	0%	-2%
	1993	3%	87%	47%	47%	-11%	-5%
	2004	-33%	-28%	-6%	-55%	27%	19%

MSPA categories groups: BG= Background, CN= Connectors and bridges, ED= Edges, IS= Islets, CO= Core

Table S7: Correlation coefficients of forest cover and MSPA groups

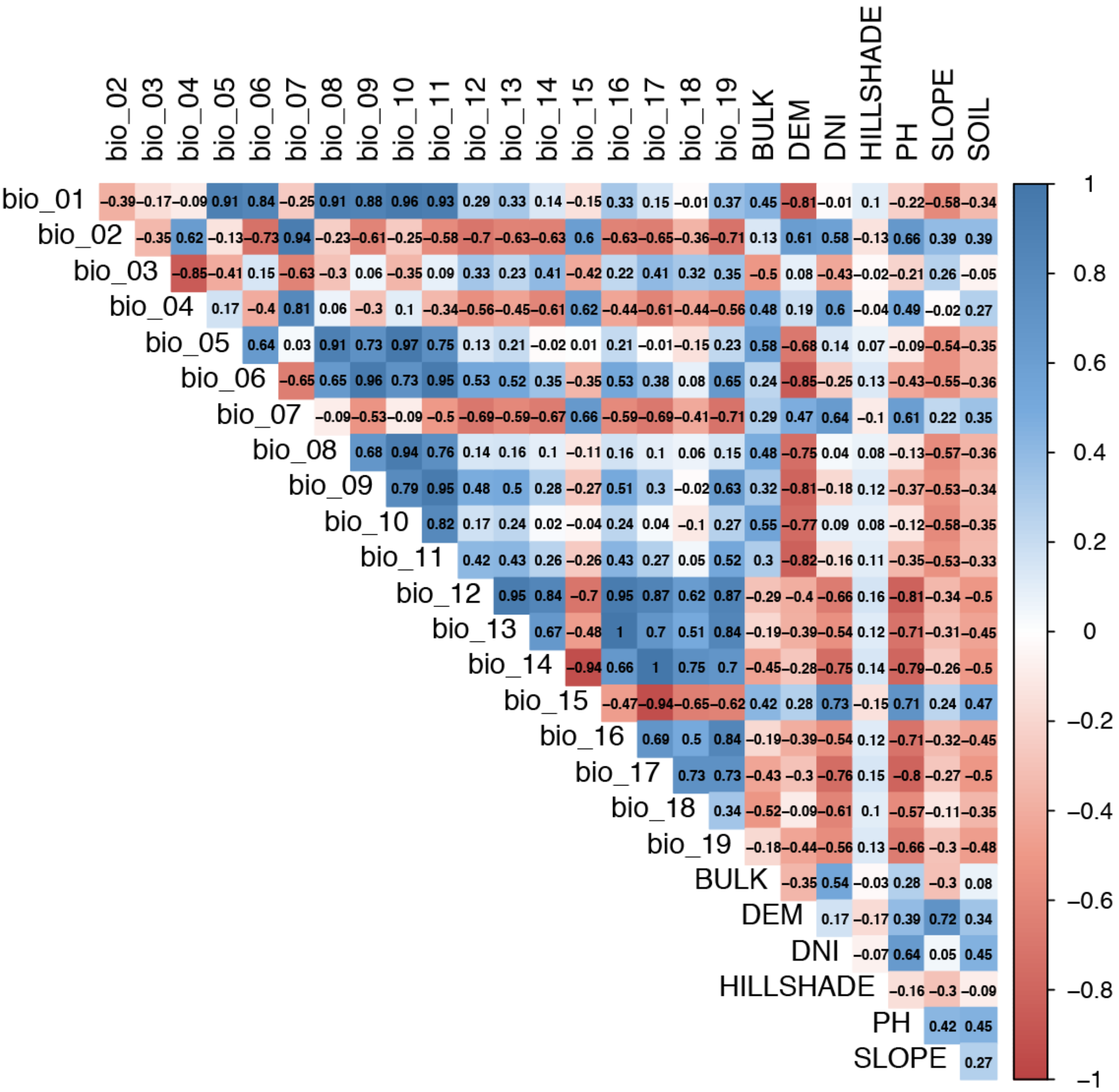
Locality/ MSPA group	CORE	p-value	ISLET	p-value	CONN.	p-value	EDGE	p-value
All localities	0,972	0,000	0,267	0,819	0,379	0,173	0,593	0,001
EL ROSAL	0,684	0,203	-0,444	0,453	0,307	0,615	0,987	0,002
GUASCA	0,868	0,057	-0,832	0,080	-0,858	0,063	-0,091	0,884
GUATAVITA	0,953	0,012	-0,924	0,025	0,574	0,311	0,847	0,070
PASQUILLA	0,412	0,491	0,633	0,252	0,370	0,540	0,627	0,258
SAN FRANCISCO	0,591	0,294	0,295	0,630	0,670	0,216	0,913	0,031
SOACHA	0,986	0,108	-0,905	0,280	0,150	0,904	0,611	0,581
SUMAPAZ	0,950	0,046	-0,087	0,913	0,688	0,312	0,939	0,061
TABIO	0,849	0,151	-0,392	0,608	0,743	0,257	0,969	0,031
TORCA	0,987	0,002	-0,983	0,003	-0,904	0,035	-0,839	0,076

*CONN. = CONNECTORS

Supporting information to Chapter 4

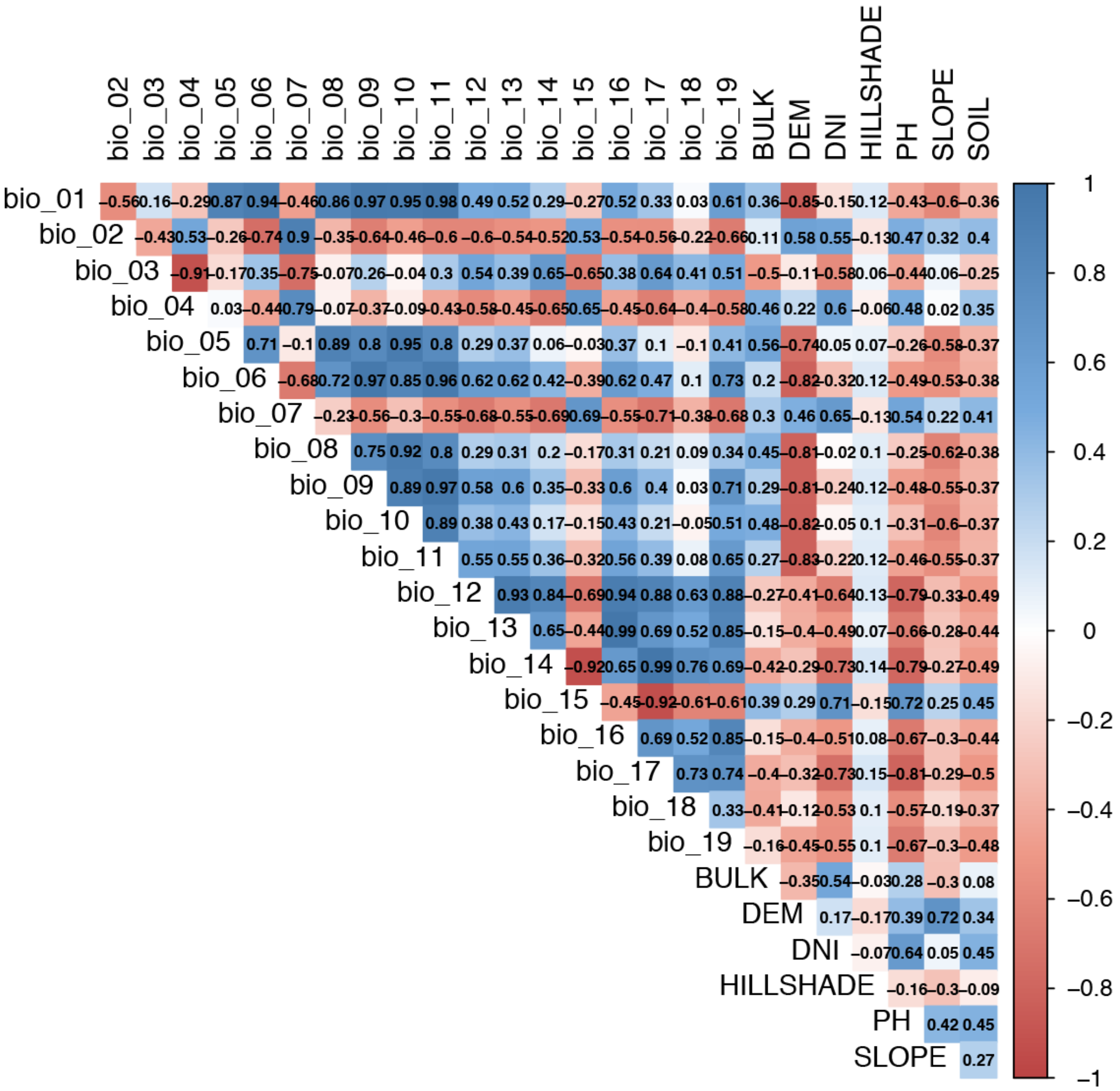
Figure S1: Correlation plots for each climatic dataset

Chelsa 1.2



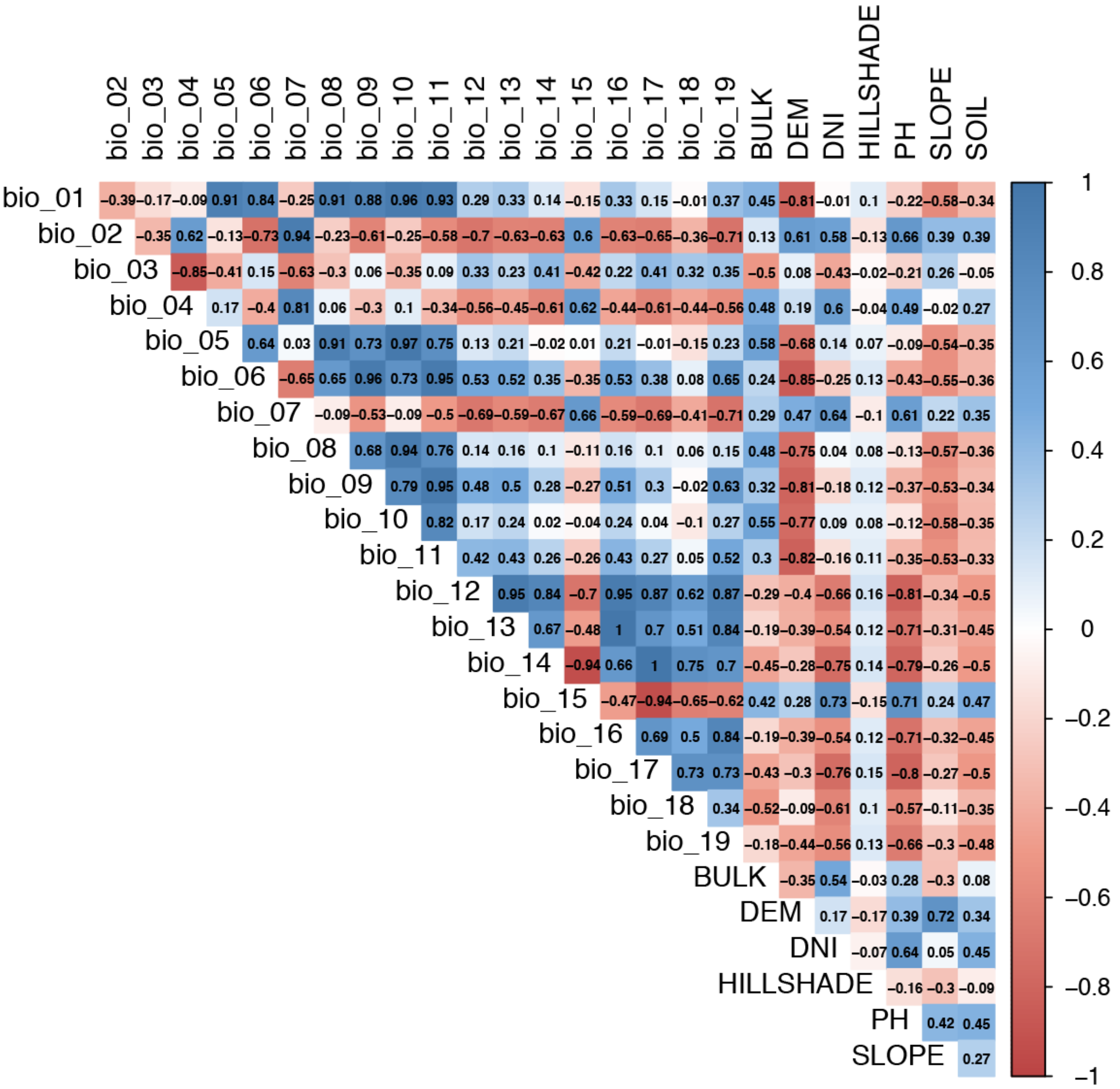
	bio_02	bio_03	bio_04	bio_05	bio_06	bio_07	bio_08	bio_09	bio_10	bio_11	bio_12	bio_13	bio_14	bio_15	bio_16	bio_17	bio_18	bio_19	BULK	DEM	DNI	HILLSHADE	PH	SLOPE	SOIL
bio_01	−0.39	−0.17	−0.09	0.91	0.84	−0.25	0.91	0.88	0.96	0.93	0.29	0.33	0.14	−0.15	0.33	0.15	−0.01	0.37	0.45	−0.81	−0.01	0.1	−0.22	−0.58	−0.34
bio_02		−0.35	0.62	−0.13	−0.73	0.94	−0.23	−0.61	−0.25	−0.58	−0.7	−0.63	−0.63	0.6	−0.63	−0.65	−0.36	−0.71	0.13	0.61	0.58	−0.13	0.66	0.39	0.39
bio_03			−0.85	−0.41	0.15	−0.63	−0.3	0.06	−0.35	0.09	0.33	0.23	0.41	−0.42	0.22	0.41	0.32	0.35	−0.5	0.08	−0.43	−0.02	−0.21	0.26	−0.05
bio_04				0.17	−0.4	0.81	0.06	−0.3	0.1	−0.34	−0.56	−0.45	−0.61	0.62	−0.44	−0.61	−0.44	−0.56	0.48	0.19	0.6	−0.04	0.49	−0.02	0.27
bio_05					0.64	0.03	0.91	0.73	0.97	0.75	0.13	0.21	−0.02	0.01	0.21	−0.01	−0.15	0.23	0.58	−0.68	0.14	0.07	−0.09	−0.54	−0.35
bio_06						−0.65	0.65	0.96	0.73	0.95	0.53	0.52	0.35	−0.35	0.53	0.38	0.08	0.65	0.24	−0.85	−0.25	0.13	−0.43	−0.55	−0.36
bio_07							−0.09	−0.53	−0.09	−0.5	−0.69	−0.59	−0.67	0.66	−0.59	−0.69	−0.41	−0.71	0.29	0.47	0.64	−0.1	0.61	0.22	0.35
bio_08								0.68	0.94	0.76	0.14	0.16	0.1	−0.11	0.16	0.1	0.06	0.15	0.48	−0.75	0.04	0.08	−0.13	−0.57	−0.36
bio_09									0.79	0.95	0.48	0.5	0.28	−0.27	0.51	0.3	−0.02	0.63	0.32	−0.81	−0.18	0.12	−0.37	−0.53	−0.34
bio_10										0.82	0.17	0.24	0.02	−0.04	0.24	0.04	−0.1	0.27	0.55	−0.77	0.09	0.08	−0.12	−0.58	−0.35
bio_11											0.42	0.43	0.26	−0.26	0.43	0.27	0.05	0.52	0.3	−0.82	−0.16	0.11	−0.35	−0.53	−0.33
bio_12												0.95	0.84	−0.7	0.95	0.87	0.62	0.87	−0.29	−0.4	−0.66	0.16	−0.81	−0.34	−0.5
bio_13													0.67	−0.48	1	0.7	0.51	0.84	−0.19	−0.39	−0.54	0.12	−0.71	−0.31	−0.45
bio_14														−0.94	0.66	1	0.75	0.7	−0.45	−0.28	−0.75	0.14	−0.79	−0.26	−0.5
bio_15															−0.47	−0.94	−0.65	−0.62	0.42	0.28	0.73	−0.15	0.71	0.24	0.47
bio_16																0.69	0.5	0.84	−0.19	−0.39	−0.54	0.12	−0.71	−0.32	−0.45
bio_17																	0.73	0.73	−0.43	−0.3	−0.76	0.15	−0.8	−0.27	−0.5
bio_18																		0.34	−0.52	−0.09	−0.61	0.1	−0.57	−0.11	−0.35
bio_19																			−0.18	−0.44	−0.56	0.13	−0.66	−0.3	−0.48
BULK																				−0.35	0.54	−0.03	0.28	−0.3	0.08
DEM																					0.17	−0.17	0.39	0.72	0.34
DNI																						−0.07	0.64	0.05	0.45
HILLSHADE																							−0.16	−0.3	−0.09
PH																								0.42	0.45
SLOPE																									0.27

Worldclim 1.4



	bio_02	bio_03	bio_04	bio_05	bio_06	bio_07	bio_08	bio_09	bio_10	bio_11	bio_12	bio_13	bio_14	bio_15	bio_16	bio_17	bio_18	bio_19	BULK	DEM	DNI	HILLSHADE	PH	SLOPE	SOIL
bio_01	−0.56	0.16	−0.29	0.87	0.94	−0.46	0.86	0.97	0.95	0.98	0.49	0.52	0.29	−0.27	0.52	0.33	0.03	0.61	0.36	−0.85	−0.15	0.12	−0.43	−0.6	−0.36
bio_02		−0.43	0.53	−0.26	−0.74	0.9	−0.35	−0.64	−0.46	−0.6	−0.6	−0.54	−0.52	0.53	−0.54	−0.56	−0.22	−0.66	0.11	0.58	0.55	−0.13	0.47	0.32	0.4
bio_03			−0.91	−0.17	0.35	−0.75	−0.07	0.26	−0.04	0.3	0.54	0.39	0.65	−0.65	0.38	0.64	0.41	0.51	−0.5	−0.11	−0.58	0.06	−0.44	0.06	−0.25
bio_04				0.03	−0.44	0.79	−0.07	−0.37	−0.09	−0.43	−0.58	−0.45	−0.65	0.65	−0.45	−0.64	−0.4	−0.58	0.46	0.22	0.6	−0.06	0.48	0.02	0.35
bio_05					0.71	−0.1	0.89	0.8	0.95	0.8	0.29	0.37	0.06	−0.03	0.37	0.1	−0.1	0.41	0.56	−0.74	0.05	0.07	−0.26	−0.58	−0.37
bio_06						−0.68	0.72	0.97	0.85	0.96	0.62	0.62	0.42	−0.39	0.62	0.47	0.1	0.73	0.2	−0.82	−0.32	0.12	−0.49	−0.53	−0.38
bio_07							−0.23	−0.56	−0.3	−0.55	−0.68	−0.55	−0.69	0.69	−0.55	−0.71	−0.38	−0.68	0.3	0.46	0.65	−0.13	0.54	0.22	0.41
bio_08								0.75	0.92	0.8	0.29	0.31	0.2	−0.17	0.31	0.21	0.09	0.34	0.45	−0.81	−0.02	0.1	−0.25	−0.62	−0.38
bio_09									0.89	0.97	0.58	0.6	0.35	−0.33	0.6	0.4	0.03	0.71	0.29	−0.81	−0.24	0.12	−0.48	−0.55	−0.37
bio_10										0.89	0.38	0.43	0.17	−0.15	0.43	0.21	−0.05	0.51	0.48	−0.82	−0.05	0.1	−0.31	−0.6	−0.37
bio_11											0.55	0.55	0.36	−0.32	0.56	0.39	0.08	0.65	0.27	−0.83	−0.22	0.12	−0.46	−0.55	−0.37
bio_12												0.93	0.84	−0.69	0.94	0.88	0.63	0.88	−0.27	−0.41	−0.64	0.13	−0.79	−0.33	−0.49
bio_13													0.65	−0.44	0.99	0.69	0.52	0.85	−0.15	−0.4	−0.49	0.07	−0.66	−0.28	−0.44
bio_14														−0.92	0.65	0.99	0.76	0.69	−0.42	−0.29	−0.73	0.14	−0.79	−0.27	−0.49
bio_15															−0.45	−0.92	−0.61	−0.61	0.39	0.29	0.71	−0.15	0.72	0.25	0.45
bio_16																0.69	0.52	0.85	−0.15	−0.4	−0.51	0.08	−0.67	−0.3	−0.44
bio_17																	0.73	0.74	−0.4	−0.32	−0.73	0.15	−0.81	−0.29	−0.5
bio_18																		0.33	−0.41	−0.12	−0.53	0.1	−0.57	−0.19	−0.37
bio_19																			−0.16	−0.45	−0.55	0.1	−0.67	−0.3	−0.48
BULK																				−0.35	0.54	−0.03	0.28	−0.3	0.08
DEM																					0.17	−0.17	0.39	0.72	0.34
DNI																						−0.07	0.64	0.05	0.45
HILLSHADE																							−0.16	−0.3	−0.09
PH																								0.42	0.45
SLOPE																									0.27

Worldclim 2



	bio_02	bio_03	bio_04	bio_05	bio_06	bio_07	bio_08	bio_09	bio_10	bio_11	bio_12	bio_13	bio_14	bio_15	bio_16	bio_17	bio_18	bio_19	BULK	DEM	DNI	HILLSHADE	PH	SLOPE	SOIL
bio_01	−0.39	−0.17	−0.09	0.91	0.84	−0.25	0.91	0.88	0.96	0.93	0.29	0.33	0.14	−0.15	0.33	0.15	−0.01	0.37	0.45	−0.81	−0.01	0.1	−0.22	−0.58	−0.34
bio_02		−0.35	0.62	−0.13	−0.73	0.94	−0.23	−0.61	−0.25	−0.58	−0.7	−0.63	−0.63	0.6	−0.63	−0.65	−0.36	−0.71	0.13	0.61	0.58	−0.13	0.66	0.39	0.39
bio_03			−0.85	−0.41	0.15	−0.63	−0.3	0.06	−0.35	0.09	0.33	0.23	0.41	−0.42	0.22	0.41	0.32	0.35	−0.5	0.08	−0.43	−0.02	−0.21	0.26	−0.05
bio_04				0.17	−0.4	0.81	0.06	−0.3	0.1	−0.34	−0.56	−0.45	−0.61	0.62	−0.44	−0.61	−0.44	−0.56	0.48	0.19	0.6	−0.04	0.49	−0.02	0.27
bio_05					0.64	0.03	0.91	0.73	0.97	0.75	0.13	0.21	−0.02	0.01	0.21	−0.01	−0.15	0.23	0.58	−0.68	0.14	0.07	−0.09	−0.54	−0.35
bio_06						−0.65	0.65	0.96	0.73	0.95	0.53	0.52	0.35	−0.35	0.53	0.38	0.08	0.65	0.24	−0.85	−0.25	0.13	−0.43	−0.55	−0.36
bio_07							−0.09	−0.53	−0.09	−0.5	−0.69	−0.59	−0.67	0.66	−0.59	−0.69	−0.41	−0.71	0.29	0.47	0.64	−0.1	0.61	0.22	0.35
bio_08								0.68	0.94	0.76	0.14	0.16	0.1	−0.11	0.16	0.1	0.06	0.15	0.48	−0.75	0.04	0.08	−0.13	−0.57	−0.36
bio_09									0.79	0.95	0.48	0.5	0.28	−0.27	0.51	0.3	−0.02	0.63	0.32	−0.81	−0.18	0.12	−0.37	−0.53	−0.34
bio_10										0.82	0.17	0.24	0.02	−0.04	0.24	0.04	−0.1	0.27	0.55	−0.77	0.09	0.08	−0.12	−0.58	−0.35
bio_11											0.42	0.43	0.26	−0.26	0.43	0.27	0.05	0.52	0.3	−0.82	−0.16	0.11	−0.35	−0.53	−0.33
bio_12												0.95	0.84	−0.7	0.95	0.87	0.62	0.87	−0.29	−0.4	−0.66	0.16	−0.81	−0.34	−0.5
bio_13													0.67	−0.48	1	0.7	0.51	0.84	−0.19	−0.39	−0.54	0.12	−0.71	−0.31	−0.45
bio_14														−0.94	0.66	1	0.75	0.7	−0.45	−0.28	−0.75	0.14	−0.79	−0.26	−0.5
bio_15															−0.47	−0.94	−0.65	−0.62	0.42	0.28	0.73	−0.15	0.71	0.24	0.47
bio_16																0.69	0.5	0.84	−0.19	−0.39	−0.54	0.12	−0.71	−0.32	−0.45
bio_17																	0.73	0.73	−0.43	−0.3	−0.76	0.15	−0.8	−0.27	−0.5
bio_18																		0.34	−0.52	−0.09	−0.61	0.1	−0.57	−0.11	−0.35
bio_19																			−0.18	−0.44	−0.56	0.13	−0.66	−0.3	−0.48
BULK																				−0.35	0.54	−0.03	0.28	−0.3	0.08
DEM																					0.17	−0.17	0.39	0.72	0.34
DNI																						−0.07	0.64	0.05	0.45
HILLSHADE																							−0.16	−0.3	−0.09
PH																								0.42	0.45
SLOPE																									0.27