Assessing defaunation in the central Annamites ecoregion of Vietnam and Laos

Inaugural-Dissertation
to obtain the academic degree
Doctor rerum naturalium (Dr. rer. nat.)

submitted to the Department of Biology, Chemistry, Pharmacy
of Freie Universität Berlin

by

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Berlin, Germany

2020

Diese Dissertation wurde am Leibniz-Institut für Zoo- und Wildtierforschung in Berlin im Zeitraum vom September 2013 bis September 2017 unter der Leitung von Dr. Andreas Wilting und Prof. Dr. Heribert Hofer angefertigt und am Institut für Biologie der Freien Universität Berlin eingereicht.

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Disputation am: 19 November 2020

This dissertation is based on the following manuscripts:

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Andrew Tilker[1,2], Jesse F. Abrams[1], An Nguyen[1,2], Lisa Hörig[1], Jan Axtner, Julie Louvrier[1], Benjamin M. Rawson[6], Hoa Anh Quang Nguyen[6], Francois Guegan[7], Thanh Van Nguyen[1,10], Minh Le[10,11], Rahel Sollmann[4], & Andreas Wilting[1]. (2020). Identifying conservation priorities in a defaunated tropical biodiversity hotspot. *Diversity and Distributions*, 26(4), 426-440. https://doi.org/10.1111/ddi.13029

Andrew Tilker[1,2], An Nguyen[1,2], Tejas Bhagwat[1], Minh Le[10,11], Thanh Van Nguyen[1,10], Anh Tuan Nguyen[10], Jürgen Niedballa[1], Rahel Sollmann[4], & Andreas Wilting[1]. (2020). A little-known endemic caught in the South-east Asian extinction crisis: The Annamite striped rabbit *Nesolagus timminsi. Oryx*, 54(2), 178-187. https://doi.org/10.1017/S0030605318000534 §

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CONTENT

Zusammenfassung

Südostasien ist ein globaler Biodiversitäts-Hotspot. Anthropogene Bedrohungen führen jedoch derzeit zu einem starken Verlust größerer Wirbeltiere (*Defaunation*) in der gesamten Region. Sowohl Lebensraumveränderungen als auch eine nicht nachhaltige Bejagung haben zur *Defaunation* Südostasiens beigetragen. Im Truong-Son Gebirge in Vietnam und Laos ist die Lage besonders gravierend. Hier hat die weit verbreitete und wahllose Jagd mit Drahtschlingen für den illegalen Wildtierhandel die bodenbewohnende Säugetier- und Vogelarten stark dezimiert. Mehrere endemische Arten des Truong-Son Gebirges stehen bereits kurz vor der Ausrottung. Um wirksamere Strategien zum gezielten Schutz der biologischen Vielfalt in Südostasien zu entwickeln, ist es notwendig, den Prozess des Artenverlusts besser zu verstehen, sowie einen detaillierten Überblick über das derzeitige Artenvorkommen zu haben. Ziel dieser Arbeit war es, zu untersuchen wie sich die *Defaunation* auf die tropischen Artengemeinschaften Südostasiens – mit besonderem Augenmerk auf das zentrale Truong-Son Gebirge – auswirkt. Des Weiteren sollte diese Arbeit erste Informationen über das räumliche Vorkommen einiger stark bedrohter, endemischer Arten liefern, um somit gezieltere Schutzmaßnahmen zu unterstützen.

Zurzeit besteht nur eine unvollständige Kenntnis davon, wie sich verschiedene Faktoren die zur *Defaunation* beitragen, auf Artengemeinschaften in größeren räumlichen Maßstäben auswirken. Um dies zu untersuchen sammelten wir großskalig Kamerafallendaten aus zwei Regionen in Südostasien, die durch grundlegend unterschiedliche Einflussfaktoren bedroht werden (Kapitel 2): Im Malaysischen Teil von Borneo ist die Artengemeinschaft primär durch die Degradadirung des Regenwaldes bedroht, wohingegen im Truong-Son Gebirge die Jagd mit Drahtschlingen die Hauptbedrohung darstellt. Mit modernen *multi-species occupancy* Modellen und einem Defaunation-Index konnten wir feststellen, dass sowohl Walddegradation, als auch Wilderei negative Auswirkungen auf die Artengemeinschaften haben. Jedoch zeigten unsere Ergebnisse auch, dass Arten in den illegal bejagten Gebieten nicht nur ein deutlich höheres Aussterberisiko hatten, sondern auch, dass die Verbreitung der noch vorkommenden Arten durch die intensive Jagd viel stärker zurückgegangen ist, als

die Verbreitung ihrer Schwesterarten in den durch kommerzielle Forstwirtschaft degradierten Regenwäldern. Mit diesen Ergebnissen konnten wir sehr deutlich zeigen, dass die intensive, wahllose Wilderei im Vergleich zur Walddegradation momentan die schwerwiegendere Bedrohung für bodenlebende Säugetier- und Vogelarten darstellt.

Aufgrund begrenzter finanzieller und personeller Ressourcen für den Artenschutz ist es notwendig Maßnahmen gegen Wilderei gezielt dort einzusetzen, wo noch letzte Populationen der stark bedrohten Arten vorkommen. Dafür ist es wichtig die räumlichen Muster der *Defaunation* zu verstehen, was jedoch in tropischen Regenwäldern eine Reihe von Herausforderungen mit sich bringt. Um Vorkommensnachweise auch von besonders seltenen Arten zu bekommen, haben wir deshalb Kamerafallendaten und molekulargenetische Nachweise aus Umwelt-DNA-Proben (Blutegeln) kombiniert (Kapitel 3). Mittels *multi-species occupancy* Modellen konnten wir dann die räumliche Verteilung der Arten großflächig über fünf benachbarte Untersuchungsgebiete modellieren. Unsere Ergebnisse zeigten, dass trotz der starken Wilderei einige hochgradig bedrohte Arten noch immer im Untersuchungsgebiet vorkommen. Bedrohte und endemische Arten wurden vor allem in höheren Lagen und in entlegenen Gebieten gefunden. Unsere Ergebnisse lieferten unseren Naturschutzpartnern wichtige Informationen, um ihre Schutzpatrouillen gezielter einsetzen zu können.

Für die Entwicklung wirksamer Arterhaltungsstrategien ist es zudem wichtig zu verstehen, wie sich die *Defaunation* auf einzelne Arten auswirkt. Solche Informationen sind besonders für Arten wichtig, die nur wenig erforscht sind, jedoch in Gebieten vorkommen die besonders von Wilderei bedroht sind. Wir nutzten Kamerafallendaten des zentralen Truong-Son Gebirges, um die Ökologie und Verbreitung des Annamiten-Streifenkaninchens *Nesolagus timminsi* zu untersuchen (Kapitel 4). Es zeigte sich, dass sich das Vorkommen des Annamiten-Streifenkaninchens wahrscheinlich mit dem vergangenem Jagddruck erklären lässt und die Population durch diese intensive Wilderei mit Drahtschlingen bereits negativ beeinflusst wurde. Unsere Ergebnisse stellen den ersten großflächigen Referenzdatensatz über die Verbreitung des Annamiten-Streifenkaninchens dar und geben Hinweise auf Gebiete in denen bevorzugt und gezielt Drahtschlingen beseitigt werden sollten.

Summary

Southeast Asia is a global biodiversity hotspot, but anthropogenic threats are causing loss of larger vertebrate species (defaunation) across the region. Both habitat alteration and unsustainable hunting have contributed to defaunation in Southeast Asia. Defaunation is particularly severe in the Annamites ecoregion of Vietnam and Laos PDR, where widespread indiscriminate snaring for the illegal wildlife trade has decimated ground-dwelling mammal and bird species. Several Annamite endemics are now facing imminent extinction as a result of this snaring crisis. To develop more effective conservation strategies to protect biodiversity in Southeast Asia, it is necessary to better understand the defaunation process, and to have an accurate assessment of biodiversity in defaunated areas. The aim of this thesis was to improve our understanding of how defaunation impacts tropical faunal communities in Southeast Asia, with a specific focus on the Annamites ecoregion, thereby providing insights that can help inform conservation strategies to prevent further defaunation in tropical hotspots.

Scientists have an incomplete understanding of how different defaunation drivers impact faunal communities at large spatial scales. To investigate this issue, we collected landscape-scale camera-trapping data from two study areas with fundamentally different threats: habitat degradation (Malaysian Borneo) and indiscriminate snaring (Annamites). We used a defaunation index and occupancy models to assess how defaunation differentially impacts ground-dwelling mammal and bird communities in these regions (**chapter 2)**. We found that, while both defaunation drivers negatively impact faunal communities, the hunted sites had higher levels of functional extinction, lower species occupancies, and species distributions that were primarily influenced by anthropogenic- rather than habitat-based measures. We conclude that intensive, indiscriminate hunting may be a more severe short-term threat to terrestrial mammal and bird species than moderate levels of habitat degradation.

To optimize the use of limited conservation resources, it is often necessary to understand the spatial patterns of defaunation. However, accurately assessing biodiversity in defaunated tropical forests brings a unique set of challenges. We combined camera-trapping and leech-derived data from landscape-scale surveys with advanced statistical modelling techniques and innovative explanatory covariates to assess defaunation patterns in a central Annamites forest

complex that has been subjected to high levels of snaring pressure (**chapter 3**). Our findings show that, despite severe levels of defaunation, conservation-priority species still persist, albeit at extremely low occupancies. Threatened and endemic species were primarily found at higher elevations and in more remote areas. The results provide information that can be used to inform targeted enforcement efforts in this landscape.

Understanding how defaunation impacts individual species is important to developing effective conservation strategies. Such information is especially important for species that are understudied but occur in areas known to be under extreme anthropogenic pressure. We used data from landscape-scale camera-trapping in the central Annamites to investigate the ecology and distribution of the Annamite striped rabbit *Nesolagus timminsi* (**chapter 4**). We found that Annamite striped rabbit occupancy was best explained by a proxy for past hunting pressure, which likely indicates that populations have been negatively impacted by industrial snaring. We also found that that local abundance estimates were low at one site, and that the species is likely absent from a second site where hunting pressure appears to have been more intense. Our findings provide information on priority areas to target snare-removal efforts, and the first conservation baseline for the species.

Chapter 1

General introduction

Biodiversity of Southeast Asia and the Annamites

Southeast Asia (Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Timor-Leste, Thailand, and Vietnam) is a global biodiversity hotspot with exceptionally high levels of species richness and endemism (Sodi et al, 2004). The extraordinary biodiversity of Southeast Asia is largely the result of its complex geological history, in which fluctuating sea levels caused long periods of isolation for numerous island and archipelago species (Woodruff, 2010). This, coupled with the region's tropical climate, created an evolutionary cradle for speciation (De Bruyn et al, 2014). The region's mammal and bird communities are particularly diverse: Southeast Asia contains the highest mean proportion of country-endemic bird (9%) and mammal species (11%) when compared to the other tropical regions (Sodi et al, 2010). Moreover, new mammal and bird species are described on a regular basis (Ceballos & Ehrlich, 2009), many of which are likely endemic to the region.

Even within this biodiversity hotspot, species richness and endemism are not uniform. The Greater Annamites ecoregion, centered on a rugged mountain chain straddling the border of Vietnam and Lao PDR and arcing down into the Vietnamese central highlands (Fig. 1), has one of the highest concentrations of endemic mammal and bird species found anywhere in Southeast Asia (Baltzer et al, 2001; Tordoff et al, 2003; Sterling & Hurley, 2005). Biogeographers are still working to understand why the ecoregion has such high levels of endemism. The predominant theory is that the Annamites retained vast expanses of wet evergreen forests during otherwise dry glacial periods, and that these areas acted as long-term refugia for species adapted to wetter conditions (Schaller & Vbra, 1996; Surridge et al, 1999; Baltzer et al, 2001; but see Turvey et al, 2016). The exceptionally rugged terrain in the Annamites has given rise to diverse microhabitats, which have also probably contributed to its endemism. Although the dominant habitat type in the Annamites is broadleaf wet evergreen forest, habitat patterns across the ecoregion are incredibly complex, and also include areas of semi-evergreen, pine, karst, and xeric coastal scrub forest (Rundel, 1999).

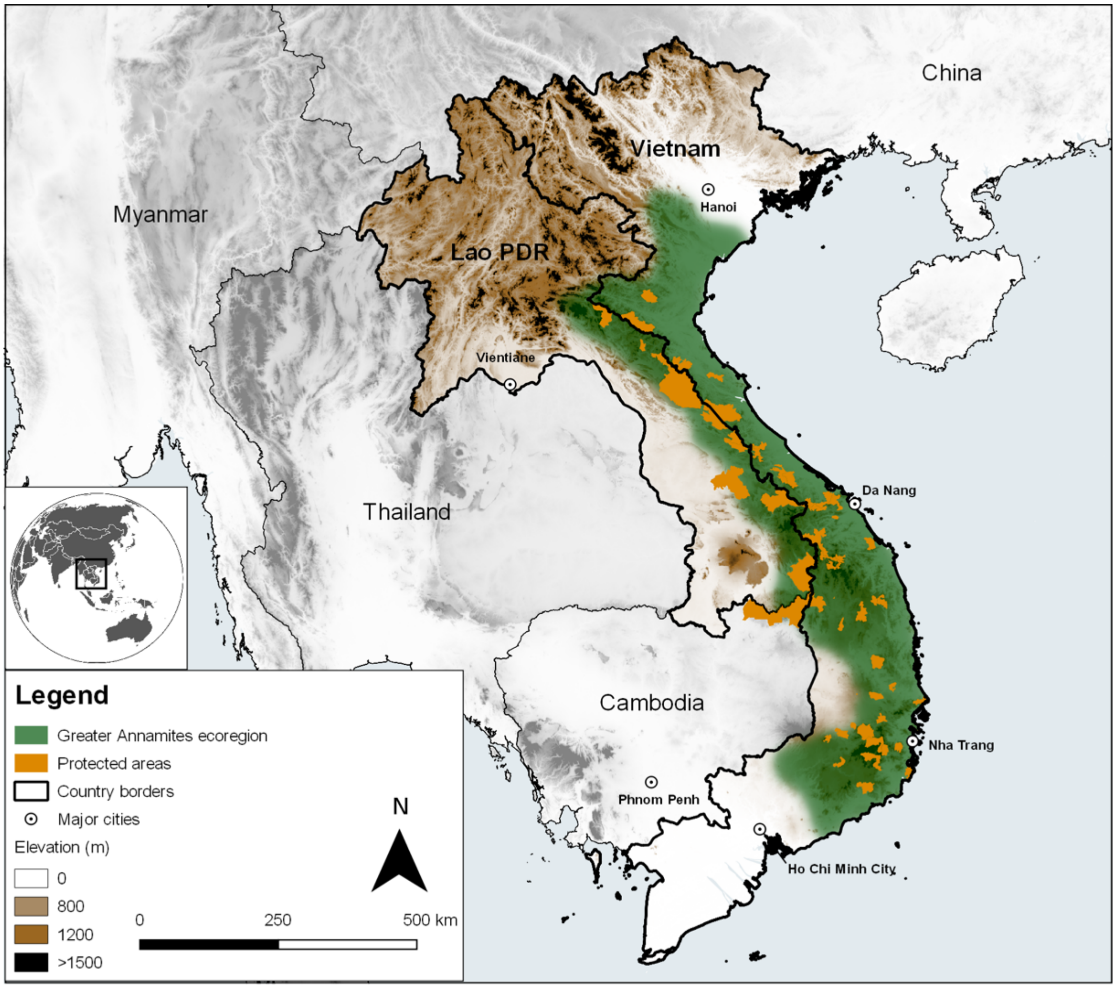

Figure 1. Greater Annamites ecoregion (green shaded area adapted from Baltzer et al, 2001). The ecoregion encompasses the Annamites mountain chain along the border of Vietnam and Lao PDR. It extends into the Vietnamese central highlands and marginally into extreme northeastern Cambodia. The main countries that comprise the Greater Annamites ecoregion (Vietnam and Lao PDR) are colored in the figure, while neighboring countries are shown in black and white.

Mammal and bird species restricted to the Greater Annamites ecoregion include the saola *Pseudoryx nghetinhensis*, the large-antlered muntjac *Muntiacus vuquangensis*, the Annamites dark muntjac species complex *Muntiacus rooseveltorum / truongsonensis* (species taxonomy unresolved [Timmins & Duckworth 2016a, Timmins & Duckworth 2016b]), Owston's civet *Chrotogale owstoni,* the Annamite striped rabbit *Nesolagus timminsi*, silver-backed chevrotain

Tragulus versicolor, red-shanked douc langur *Pygathrix nemaeus*, and Edwards's pheasant *Lophura edwardsi* (Tordoff et al, 2003; Fig. 2). Remarkably, the saola, large-antlered muntjac, and Annamite striped rabbit were only discovered by science within the past 25 years (Dung et al, 1993; Tuoc et al, 1994; Surridge et al, 1999; Averianov et al, 2000), and the silver-backed chevrotain was only described in the early 20th century (Thomas, 1910). These recent discoveries further highlight how little is known about the biodiversity of the ecoregion. In addition to its endemic species, the Annamites historically included many mammal and bird species typical of other parts of mainland Southeast Asia (Baltzer et al, 2001). Together, its high levels of endemism and richness make the Annamites one of the "hottest" areas within the Southeast Asian biodiversity hotspot.

Biodiversity threats

Southeast Asia is also unique in the magnitude and diversity of anthropogenic pressures that threaten its biodiversity. Habitat loss in the region has been extensive. Southeast Asia's annual rate of deforestation is the highest of any tropical region in the world, and given current trends, will likely continue into the foreseeable future (Sodi et al, 2010; Wilcove et al, 2013). Although habitat loss is driven by myriad causes, agricultural conversion, especially for high-yield monoculture crops, remains one of the largest deforestation drivers (Wilcove & Koh, 2010).

Deforestation to plant oil palm has been particularly destructive. For example, between 1989 and 2013 oil palm conversion was responsible for 40% and 50% of deforestation in Malaysia and Indonesia, respectively (Vijay et al, 2016). Rubber is also emerging as a valuable commodity (Ahrends et al, 2015). By 2050, the area under rubber plantations is expected to more than triple, largely at the expense of existing primary forest (Ziegler et al, 2009). Finally, acacia plantations have become more widespread in recent years, and are particularly prevalent in Vietnam (Thulstrup et al, 2013). Forest degradation has also negatively impacted Southeast Asian biodiversity. While some degradation is the result of reduced-impact logging that uses carefully planned timber harvest regimes to minimize environmental impacts on tropical forests (Zimmerman & Kormos, 2012), much of Southeast Asia's forest degradation is a result of unsustainable logging – both legal and illegal – to supply lucrative regional and international timber markets (Mir & Fraser, 2003; Lang & Chan, 2006; Meyfroidt et al, 2009). Lack of robust environmental regulations, weak enforcement of existing laws, and high levels of corruption in many Southeast Asian countries has facilitated widespread unsustainable timber extraction (Laurance, 1999; Sodhi et al, 2004), even in protected areas (Curran et al, 2004). Illegal logging has proved difficult to counteract in countries with high levels of corruption, because large-scale illegal logging operations are often tied to powerful political and military groups (Koyuncu & Yilmaz, 2009).

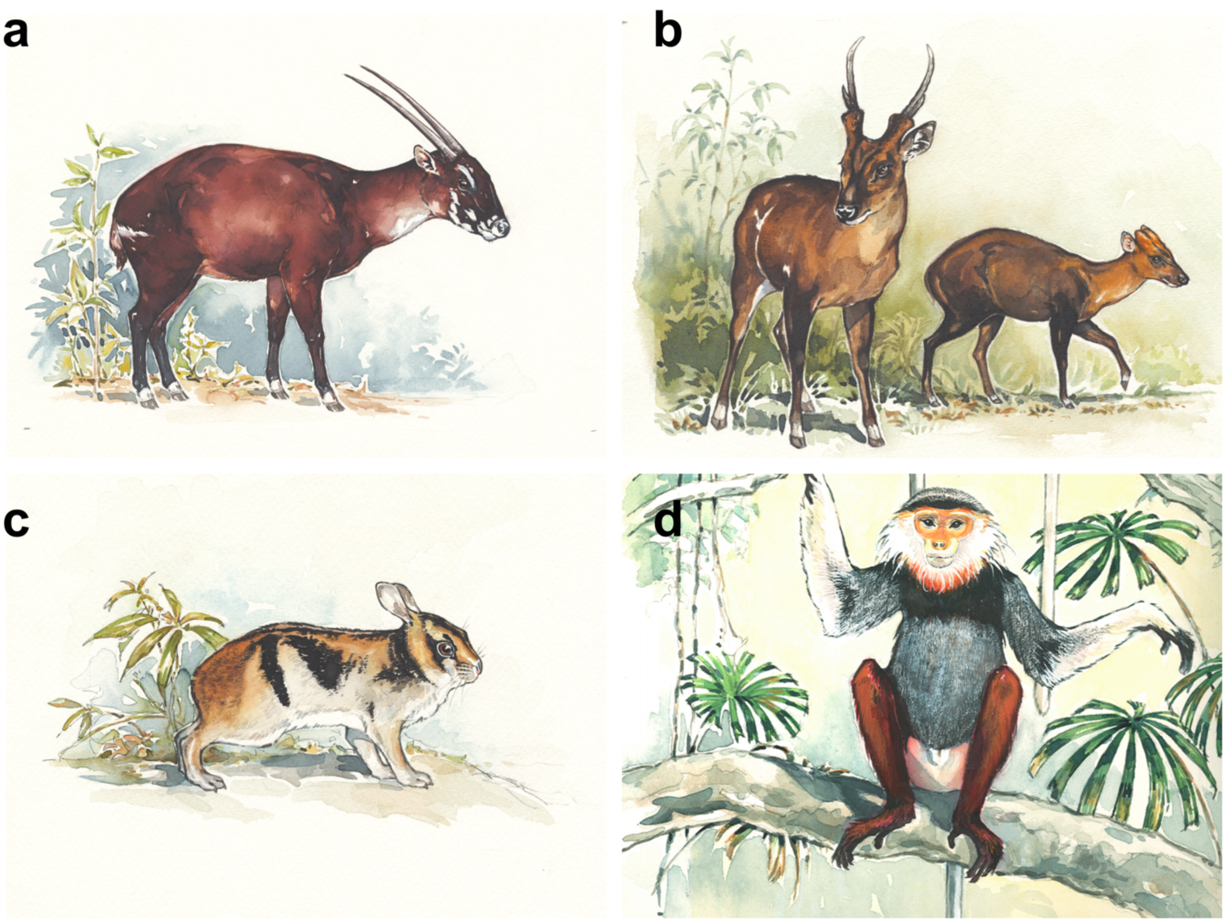

Figure 2. Annamite endemic mammal species. **(a)** saola *Pseudoryx nghetinhensis*; **(b)** large-antlered muntjac *Muntiacus vuquangensis* (left), Annamite dark muntjac species complex *Muntiacus rooseveltorum / truongsonensis* (right); **(c)** Annamite striped rabbit *Nesolagus timminsi*; **(d)** red-shanked douc *Pygathrix nemaeus.* Drawings by Joyce Powzyk, copyright AMNH.

In addition to habitat degradation, unsustainable hunting has also negatively impacted Southeast Asia's biodiversity (Corlett, 2007; Harrison et al, 2016). Wildlife is used both for consumption and medicinal purposes (Nooren & Claridge, 2001; Harrison et al, 2016), and poaching operations range from small-scale local activities for subsistence to highly-organized international crime syndicates (Sodhi et al, 2004). Although humans have hunted in Southeast Asia for millennia, higher population densities and thus greater meat consumption have led to unsustainable levels of offtake across large areas (Corlett, 2007). In many parts of Southeast Asia, bushmeat is used as a status symbol for burgeoning middle and upper classes (Van Song, 2008; Shairp et al, 2016), creating an almost limitless demand for a wide range of species. The medicinal trade is limited to a few high-value species, but the intensity of the trade has already driven some species close to extinction: Javan and Sumatran rhinoceroses' number less than 100 individuals each (Nardelli, 2014; Setiawan et al, 2018), and pangolins are rapidly disappearing from across the region (Heinrich et al, 2016).

None of these major threats operate in isolation. Deforestation and logging operations create roads, which improve accessibility, which invariably leads to higher levels of hunting pressure (Robinson et al, 1999; Clements et al, 2014; Harrison et al, 2016). Poachers often opportunistically extract high-value timber, and illegal loggers searching for these timber products often spend long periods in the forest during which time they subsist from wildlife. The fact that deforestation, degradation, and hunting are often linked is particularly concerning from a conservation perspective, because together they can have synergistically negative effects on biodiversity (Laurance & Useche, 2009).

Defaunation in Southeast Asia

Deforestation, habitat degradation, and unsustainable hunting have caused the widespread loss of larger vertebrate species (defaunation) across Southeast Asia, with myriad implications for ecological, evolutionary, and socio-economic processes (Dirzo et al, 2014). Indeed, there is mounting evidence in the scientific literature that, among global issues that have emerged from the Anthropocene, few have such diverse and potentially irremediable impacts on such a wide range of issues (Young et al, 2016).

Defaunation impacts numerous community- and ecosystem-level processes (Galetti & Dirzo, 2013). Declines in species occurrence can degrade ecological interactions (Valiente-Banuet et al, 2015), which in turn lead to cascading effects at multiple trophic levels (Jorge et al, 2013). Previous studies, for example, have shown that ungulate declines may reduce seed dispersal

(Wright et al, 2000; Beaune et al, 2013), which in turn impacts the composition of vegetation communities (Kurten, 2013). When compared to healthy tropical ecosystems, defaunated forests often have lower plant richness, higher dominance, lower diversity, and more homogenous spatial structure (Kurten, 2013). The impacts of these changes are more than theoretical: Bello et al (2015) recently showed that herbivore declines may ultimately erode carbon storage capacities in tropical rainforests. The loss of larger predators also has cascading effects on ecosystems. In the absence of apex predators, mesopredators may attain unnaturally high densities (Crooks & Soulé, 1999). This "mesopredator release" (Soulé et al, 1988) can have diverse consequences on a wide range of taxonomic groups (Brashares et al, 2010).

Declines in larger vertebrate species also have evolutionary consequences. Research into the evolutionary impacts of defaunation is still in its early stages. Nonetheless, some prescient studies have emerged in recent years. Research in the Brazilian Atlantic forest has shown that loss of large avian frugivores has resulted in the rapid evolutionary reduction of seed size in certain palm species (Galetti et al, 2013). Moreover, due to decreased dispersal, seeds in defaunated sites have also been shown to be more genetically similar than those found in forests with healthy frugivores populations, indicating that lower dispersal rates have already impacted gene flow (Carvalho et al, 2016). Although more research is needed to understand the evolutionary effects of defaunation, it is clear that the removal of vertebrates can cause fundamental shifts in evolutionary pathways. It is likely that such "evolutionary cascades" (Dirzo et al, 2014) will have numerous, perhaps unforeseen, ecological consequences.

While subsistence hunting is uncommon in Southeast Asia, it does occur in some areas, especially in regions that still have forest-dependent indigenous communities (Steinmetz et al, 2006). Because defaunation often results in depressed populations of game species (Benítez-López et al, 2017), the emptying of tropical forests could thus undermine long-term food security for these peoples (Bennett, 2002). Even when local people do not rely on bushmeat for subsistence, hunting often plays an important role in cultural traditions. Among the Katu people, an ethnic minority group from the central Annamites that historically led a semi-nomadic forest-dwelling way of life, hunting remains an integral part of social and religious life (Århem, 2015). For these peoples, the decline of wildlife in tropical forests may contribute to the erosion of traditional cultural values. To date, little research has focused on how defaunation impacts cultural erosion (but see Fernández-Llamazares et al, 2017).

Annamites snaring crisis

Within Southeast Asia, defaunation has been particularly severe in the Greater Annamites ecoregion. Habitat loss has been a major factor in these declines (Baltzer et al, 2001), particularly in Vietnam, where little primary forest remains (Cochard et al, 2016). However, deforestation rates in the Annamites have drastically declined in recent years and today large tracts of mature secondary forest remain. The main threat to terrestrial mammal and bird species in the Annamites is unsustainable hunting through the setting of indiscriminate wire snares (Gray et al, 2018). Snaring is almost ubiquitous across Annamites forests, even in protected areas, and reaches staggering magnitudes. For example, in a five-year timespan in two protected areas in central Vietnam, patrols removed more than 75,000 individual snares (Gray et al, 2016) – although, given the incomplete detection rates of snares by patrols (O'Kelly et al, 2018), it is almost certain that these snares represent a fraction of the total number of snares in the forest. There is little evidence that these snare removal efforts have been a major deterrent to continued snaring operations in these areas (Wilkinson, 2016).

Numerous social, cultural, and economic factors have contributed to the Annamites snaring epidemic. Consumption of bushmeat is widespread and socially acceptable to a large proportion of the Vietnamese and Lao populations (Drury, 2011; Sandalj et al, 2016). Demand is especially high in Vietnam. There are now more than 93 million people in Vietnam, a large proportion of which actively consume wildlife products or would if given the opportunity (Timmins et al, 2016a). Snares are also cheap and easy to set, potentially providing high reward for minimal initial investment (Gray et al, 2016). Most protected areas in the region are little more than "paper parks" with little or no active enforcement (Tilker et al, 2019). Finally, corruption and cronyism is widespread in Vietnam and Laos, and the protected area system has not been spared (Wikle & Le, 2013).

Not surprisingly, intensive snaring has severely depressed populations of ground-dwelling mammals and birds across the Annamites. Numerous forests in the region have lost a significant proportion of their faunal communities, and now are characterized by what Redford (1992) referred to as “empty forest”. In many protected areas, rodents and squirrels are the largest mammals present, and even these are being extracted as hunters target progressively smaller game. From a conservation perspective, this is a tragedy for all ground-dwelling mammal and bird species, but it is a catastrophe for the endemics because their extirpation from the Annamites equates to global extinction. The saola, large-antlered muntjac, and Edwards’s pheasant are listed as Critically Endangered on *The IUCN Red List for Threatened Species* (Timmins et al, 2016a; Timmins et al, 2016b; BirdLife International, 2018), and the Annamite striped rabbit and Owston’s civet as Endangered (Timmins et al, 2016c; Tilker et al, 2019). Among these species, the situation of the saola is particularly dire, and there is no doubt that extinction in the wild is imminent. Captive breeding is believed to be the last chance to save the species (Tilker et al, 2017).

Impacts of different defaunation drivers

There has been an increase in studies on defaunation in recent years. However, even with numerous insightful studies, several key questions remain unanswered. One of the most fundamental knowledge gaps relates to how different defaunation drivers impact faunal communities.

There has been considerable research into how habitat loss and degradation contribute to defaunation in tropical rainforests. Complete habitat conversion typically results in drastic reductions in species richness (Brook et al, 2003). Monoculture crops, for example oil palm, are unlikely to maintain significant components of vertebrate biodiversity: evidence from several studies indicates that most mammal species cannot adapt to landscapes characterized by homogenous agricultural systems (Jennings et al, 2015; Yue et al, 2015; Mendes-Oliveira et al, 2017). The effects of varying levels of habitat degradation, for example through selective logging, are more complex, and subsequently less well-understood. Research indicates that vertebrate responses are highly variable (Alroy, 2017), and that eurytopic species tend to be more tolerant to degradation than species with stenotopic traits (Burivalova et al, 2014). However, beyond these generalizations, relatively little is known about how species ecologies influence disturbance tolerance. Most studies on the topic have used nonsystematically-collected data or meta-analyses that rely on datasets with large sample sizes but are not well-suited for in-depth analyses (Meijaard et al, 2008). More research is needed to investigate how specific life history traits impact species responses to habitat degradation.

The impact of unsustainable hunting on tropical mammal and bird communities represents a more complex phenomenon than habitat degradation, and as such, the field has not been as well-developed. Most studies have focused on the consequences of gun-hunting on faunal communities (Peres, 2000; Di Bitetti et al, 2008; Flesher et al, 2013). Large mammal and bird species appear to be particularly vulnerable to gun-hunting, in part because these species are often targeted by hunters (Jerozolimski & Peres, 2003), in part because of life history characteristics that may make them more susceptible, such as lower population densities or longer generation times (Cardillo et al, 2005). The true consequences of more deleterious nonselective forms of hunting, such as snaring, have received far less attention, and it remains largely unknown how these methods impact mammalian and ground-dwelling bird community structure and composition. Given that snaring levels are expected to increase in developing countries as regional bushmeat industries becomes increasingly commercialized (Ripple et al, 2016), further research into the impacts of nonselective hunting is needed.

Challenges to assessing defaunation in Southeast Asia

Understanding the drivers and impacts of defaunation in Southeast Asia is critical to developing effective conservation strategies. However, because defaunation is a complex and multifaceted process, there are numerous challenges to rigorously assessing this phenomenon in tropical forests.

To assess the impacts of defaunation, it is first necessary to obtain robust information on the status and distribution of mammal and bird species. To do this, conservation scientists need data that can be analyzed within robust statistical frameworks, which in turn requires a systematic approach to data collection. Unfortunately, many biodiversity assessments in Southeast Asia still use *ad hoc* approaches, utilizing opportunistic sightings or focusing on the presence or absence of a small number of target species (Abrams et al 2018). In the Annamites, so-called expert-based assessments have been standard for at least 20 years, and are still employed by the most prominent biologists working in the region (e.g. Timmins, 2013). Systematic approaches require careful planning, often with the input of experts with statistical or modelling backgrounds, which may be one reason these approaches have not been more widely adopted.

Mammals and birds often occur at low densities in defaunated tropical communities, making it difficult to detect these species. Furthermore, even when these species are detected there is often too little data to use for rigorous statistical or modeling applications. The difficulty of gathering sufficient data on rare species in defaunation hotspots is a fundamental challenge to assessing this phenomenon. In recent years, conservation scientists have employed an increasingly sophisticated set of tools to help increase detection rates for rare tropical species and to maximize the usefulness of the datasets with low numbers of detections. For example, environmental DNA (eDNA) has been used to increase detection rates for some rare tropical mammals (Schnell et al, 2012), and Bayesian modeling techniques have been used to improve parameter estimates for data-poor species (Li et al, 2018).

Because defaunation processes typically occurs at landscape scales, it is also important for systematic surveys to be conducted at these scales. Surveys that occur over small areas may provide valuable information, but are unlikely to provide insight into how defaunation holistically impacts faunal communities. Currently, most biodiversity assessments in Southeast Asia tend to be conducted over relatively small extents (tens, rather than hundreds, of km^2; but see Canale et al, 2012) and often focus on less disturbed areas in an attempt to maximize quantity of data collected. There are good reasons why surveys over large spatial scales have not been more widely adopted: Landscape-scale approaches tend to be resource-intensive, require more manpower, and take longer to complete (Abrams et al, 2018). Nonetheless, it is likely that landscape-scale assessments are the only way to rigorously and comprehensively assess faunal impoverishment in tropical forests.

The erosion of faunal communities often occurs through multiple processes that result in complex patterns of defaunation within landscapes (Benítez-López et al, 2019). Understanding these patterns is central to assessing defaunation, and as a result, spatial analyses are a key component in defaunation research. It is important that these spatial analyses incorporate proxies that capture the underlying defaunation process. Proxies for habitat loss and degradation can be obtained through remote sensing (Niedballa et al, 2015). The advent of high-resolution satellite imagery and LIDAR point-cloud data, in particular, has enabled fine-scale measures of forest degradation (Bush et al, 2017). Capturing the relevant aspects of hunting-driven defaunation is more challenging. Because hunting cannot be directly observed through remote-sensing, scientists are often forced to rely on indirect proxies that might influence hunting pressure, such as measures of accessibility. While these indirect proxies have proven useful in some situations (Koerner et al, 2017), their ability to fully capture the complexities of hunting behavior varies. Developing accurate proxies for hunting pressure is essential to obtain a deeper understanding of the defaunation process.

Linking defaunation research to applied conservation

Research into defaunation is more than an academic exercise – understanding the patterns and processes of faunal decline has real-world implications for biodiversity conservation. Assessing patterns of defaunation in a landscape, for example, can help stakeholders prioritize areas for conservation interventions. Such assessments could help conservation managers deploy anti-poaching teams to protect areas of high biodiversity (Tilker et al, *submitted*), or conversely, identify areas for future re-wilding efforts (Seddon et al, 2014). Regardless of the specific objectives, identifying areas for targeted actions is an important part of optimizing the use of limited conservation resources. Modern statistical analyses can play an important role in assessing defaunation patterns for conservation prioritization (Benítez-López et al, 2019). If the factors influencing defaunation patterns can be identified, then predictive models can be built that allow conservation scientists to predict species distributions to unsampled regions in the study landscape (Sollman et al, 2017). The resulting maps can provide conservation managers with an informative and intuitive visual representation of biodiversity occurrence patterns.

To prevent continued pantropical defaunation, it is imperative that conservation stakeholders focus resources on the most pressing biodiversity threats. Within this context, understanding the impacts of different defaunation drivers can provide information to guide higher-level conservation strategies. In situations in which there are multiple biodiversity threats, for example, it may be prudent to focus conservation actions on the defaunation drivers that are more likely to have the most immediate and deleterious impact on mammal and bird communities. Such considerations are applicable at local scales, where conservation stakeholders must make decisions regarding protected area management, as well as regional and even international scales, where governments and non-governmental organizations (NGOs) must make decisions regarding programmatic focuses.

Research into the effects of defaunation can also help guide species-specific conservation strategies. Different defaunation drivers impact species in different ways (Brodie et al, 2015). Assessing how these drivers impact individual species, and how they are likely to affect future population trends, is a critical component in the development of evidence-based conservation strategies (Pullin & Knight, 2003). Such research is especially important for species that are little-known and understudied. Bland et al (2015) predicted the probable extinction threat for 313 mammal species listed as Data Deficient on *The IUCN Red List for Threatened Species* and found that most (64%) are likely at risk of extinction. Information on how defaunation drivers impact these species is an important first step towards species conservation planning.

Aims of the study

Understanding how defaunation impacts tropical mammal and bird communities is critical to the development of effective conservation strategies, and yet, even after several decades of studies on the topic, fundamental knowledge gaps remain. Scientists still have an incomplete understanding of how different defaunation drivers impact faunal communities, or how to model complex spatial patterns of defaunation. In a more applied context, there are countless tropical mammal and bird species that are impacted by defaunation drivers in ways that are at best poorly understood, at worst unknown. As one of the most biodiverse and threatened tropical regions in the world, Southeast Asia represents an ideal place to address these knowledge gaps. Within Southeast Asia, biodiversity and threat levels reach their pinnacle in the Annamites ecoregion, where overhunting has created vast areas of "empty forest" (Redford, 1992) and driven several endemic species to the brink of extinction (Timmins et al, 2016a; Timmins et al, 2016b; Tilker et al, 2019). From a conservation perspective, the Annamites is therefore not only an ideal place to study defaunation, but more importantly, it is one of the highest priority areas for applied research that can be used to help guide urgent conservation actions. The main objectives of this thesis were to:

(1) Establish a landscape-scale systematic survey methodology for evaluating occurrence patterns of terrestrial mammal and bird species, as a first step to robustly assessing defaunation patterns and processes at large spatial scales.

(2) Investigate how two main defaunation drivers (habitat degradation in Malaysian Borneo, unsustainable hunting in the Annamites) differentially impact tropical terrestrial mammal and bird communities in Southeast Asia. An improved understanding of how different defaunation drivers effect tropical faunal communities can be used to guide conservation strategies designed to mitigate these threats.

(3) Assess spatial patterns of defaunation in a forest complex in the central Annamites landscape characterized by severe levels of faunal impoverishment. Mapping species distributions and biodiversity hotspots gives conservation stakeholders information needed to target anti-poaching activities to protect conservation-priority species.

(4) Use the Annamite striped rabbit as a case study of a little-known species caught in the Southeast Asian extinction crisis to show how rigorous assessments of defaunation patterns and processes can be used to make explicit recommendations for species-specific conservation strategies.

Structure of the dissertation

Following the general introduction (Chapter 1), the dissertation is structured into four chapters:

Chapter 2: Scientists have an incomplete understanding of how different defaunation drivers impact tropical faunal communities. The chapter "**Habitat degradation and unsustainable hunting differentially impact faunal communities in the Southeast Asian tropical biodiversity hotspot**" assesses the how two fundamental defaunation drivers impact terrestrial mammal and bird communities. The unique study design – with moderately degraded but unhunted sites in Malaysian Borneo, and structurally intact but overhunted sites in the Annamites – provides an ideal setup for the first landscape-scale comparative study on the impacts of different defaunation drivers. Defaunation is evaluated at three hierarchical levels: species functional extinction, species occurrence, and factors that influence of species occurrence. The last two levels were evaluated using Bayesian community occupancy models. The findings show that, while both defaunation drivers result in impoverished faunal communities, unsustainable hunting may be the more immediate threat to Southeast Asian mammal and bird species.

Chapter 3: Understanding the spatial patterns of defaunation is critical to informing on-the-ground conservation efforts. The chapter "**Identifying conservation priorities in a defaunated tropical biodiversity hotspot**" combines camera-trapping and leech-derived data from landscape-scale surveys with advanced statistical modelling techniques to assess defaunation patterns in a central Annamites forest complex that has been subjected to high levels of industrial snaring. The findings indicate that, despite severe levels of defaunation, priority species still occur in the study sites, primarily in areas that are more remote and at higher elevations. The study provides information that can be used to prioritize areas for targeted conservation actions, both at the landscape level and within individual protected areas.

Chapter 4: Research into how defaunation impacts individual species is critical to develop effective conservation strategies. This information is especially important for species that are understudied, but occur in areas that are known to be under threat. The chapter "**A little-known endemic caught in the South-east Asian extinction crisis: the Annamite striped rabbit *Nesolagus timminsi***" provides the first insights into the status and distribution of a mammal that occurs in a region characterized by high levels of defaunation but for which, prior to this study, little was known. To model Annamite striped rabbit occurrence, an innovative covariate is developed that is used as a proxy for past snaring intensity. Local abundance estimates indicate that the species occurs at low densities at one site, and likely absent from the second site where hunting appears to have been more severe. The results provide information on priority areas for targeted anti-poaching efforts and give the first conservation baseline for the species.

Chapter 5: This chapter (**general discussion**) provides a summary of the major results of this dissertation. Key findings from the previous chapters are discussed within the broader context of defaunation in the central Annamites. This chapter highlights implications that these findings have for ongoing and future conservation efforts in this biodiversity hotspot.

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Chapter 2

Habitat degradation and indiscriminate hunting differentially impact faunal communities in the Southeast Asian tropical biodiversity hotspot.

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Author contributions

Survey design and data collection protocols: RS, AW, JN, AT; fieldwork: AT, AN, AM, STW; data analysis: JFA, AT, AN, AM; remote-sensing data preparation: TB; manuscript preparation: AT, JFA, AW; revision of article: all authors.

Abstract

Habitat degradation and hunting have caused the widespread loss of larger vertebrate species (defaunation) from tropical biodiversity hotspots. However, these defaunation drivers impact vertebrate biodiversity in different ways and, therefore, require different conservation interventions. We conducted landscape-scale camera-trap surveys across six study sites in Southeast Asia to assess how moderate degradation and intensive, indiscriminate hunting differentially impact tropical terrestrial mammals and birds. We found that functional extinction rates were higher in hunted compared to degraded sites. Species found in both sites had lower occupancies in the hunted sites. Canopy closure was the main predictor of occurrence in the degraded sites, while village density primarily influenced occurrence in the hunted sites. Our findings suggest that intensive, indiscriminate hunting may be a more immediate threat than moderate habitat degradation for tropical faunal communities, and that conservation stakeholders should focus as much on overhunting as on habitat conservation to address the defaunation crisis.

Keywords

Annamites, Borneo, defaunation, habitat degradation, hunting, multi-species occupancy, Southeast Asia, tropical rainforest

Introduction

Global biodiversity is decreasing at an alarming rate (Buchart et al, 2010), with the most rapid declines occurring in tropical rainforests (Bradshaw et al, 2009). Two overarching threats, habitat alteration (Achard et al, 2002) and hunting (Benítez-López et al, 2017), have led to the widespread loss of larger vertebrate species (defaunation) from tropical biodiversity hotspots. Both defaunation drivers result in impoverished and homogenized faunal communities, with myriad ecological, evolutionary, and socio-economic consequences (Dirzo et al, 2014). Defaunation drives population declines (Redford, 1992) and species extinctions (Tilker et al, 2017), alters community- and ecosystem-level processes (Galetti & Dirzo, 2013), changes the trajectory of evolutionary pathways (Galetti et al, 2013), and threatens livelihoods for forest-dependent peoples (Nasi et al, 2011). There is mounting evidence in the scientific literature that, among global issues that have emerged from the Anthropocene, few have such diverse and potentially irremediable impacts (Young et al, 2016). To protect biodiversity and preserve ecosystem functions in the world's remaining tropical rainforests, it is therefore imperative that conservation stakeholders devise effective solutions to address ever-increasing rates of habitat alteration and hunting.

Although both defaunation drivers cause species declines and alter mammal and bird communities, the mechanisms through which they operate are fundamentally different. Habitat alteration impacts ecological suitability by altering forest structure. Habitat alteration occurs along a gradient of degradation, ranging from forest conversion that results in the complete loss of suitable habitat (Margono et al, 2014), to reduced impact selective logging that maintains overall forest structural integrity (Imai et al, 2012). The extent of habitat loss in tropical rainforests through conversion (*1*Hansen et al, 2013), and its effects on faunal communities (Yue et al, 2015), have been well documented. Because complete habitat loss typically results in severe declines in vertebrate richness (Alroy, 2017), and has been linked to numerous local extinction events (Brooks et al, 2002), preventing deforestation has become a central theme of global conservation efforts focused on biodiversity protection in tropical rainforests. The impact of less extreme forms of habitat alteration on faunal communities is more complex, as different logging regimes result in varying levels of degradation. Several studies indicate that while levels of habitat degradation have a holistically negative impact on tropical mammal and bird communities, species-specific responses can vary substantially (Cleary et al, 2018; Meijaard &

Sheil, 2008, Brodie et al, 2015). For example, forest specialists may decline with habitat degradation, leading to an overall decrease in species richness, even while some generalists benefit (Burivalova et al, 2014). Even with several insightful studies on this topic in recent years, further research is needed to understand how mammal and bird communities respond to different levels of degradation and, more generally, the role of habitat degradation in pantropical faunal declines.

In addition to habitat degradation, there is increasing evidence that widespread and intensive hunting across the tropics has resulted in faunal declines (Benítez-López et al, 2017). However, the true extent of overhunting, and its specific impacts on faunal communities, remains poorly understood. This lack of information is partly due to the fact that hunting is linked to a diverse set of socio-economic and cultural drivers (Bennet et al, 2000), which tend to be manifested in regionally-specific patterns of wildlife exploitation. In this respect, hunting represents a more complex phenomenon than habitat degradation. Some patterns do however appear to be consistent across sites. Larger mammals appear to be particularly susceptible to overhunting, both because they are targeted by hunters (Ripple et al, 2016) and often have lower population densities (Cardillo et al, 2005). There is also evidence that more eurytopic species show greater resilience to hunting pressure, as indicated by the survival of some generalist species in faunally impoverished systems (Bogoni et al, 2016). Notably, much of the information in the scientific literature on the effects of hunting comes from sites where gun hunting is the predominant method of wildlife exploitation (Cullen et al, 2001, Di Betti et al, 2008, Flesher et al, 2013). As a selective method, gun hunting is unlikely to directly impact entire faunal communities. The true consequences of more deleterious forms of hunting, such as indiscriminate snaring, have received far less attention and thus it remains largely unknown how overhunting by snaring impacts mammalian and ground dwelling bird community structure and composition. Given that snaring levels are expected to increase in developing countries as regional bushmeat industries becomes increasingly commercialized (Brashares et al, 2011), further research into the impacts of nonselective hunting is needed.

Among the world's tropical biodiversity hotspots, Southeast Asia is unique, both because of its exceptionally high levels of species richness and endemism, and the magnitude of the anthropogenic threats that it faces (Sodhi et al, 2004). However, even within this hotspot, biodiversity and threat levels are not uniform. The island of Borneo and the Annamite Mountains of Vietnam and Laos stand out as sub-regional centers of endemism, especially for the region's mammals and birds (De Bruyn et al, 2014). At least three small carnivores, one muntjac, and five galliforms are found only on Borneo (Phillipps, 2011; Phillipps, 2016). The Annamites ecoregion contains similarly high concentrations of endemic mammals and birds (Baltzer et al, 2001). Remarkably, several species restricted to this ecoregion were only recently discovered by science, including the saola *Pseudoryx nghetinhensis* (Van Dung et al, 1993), the large-antlered muntjac *Muntiacus vuquangensis* (Tuoc et al, 1994), and the Annamite striped rabbit *Nesolagus timminsi* (Surridge et al, 1999, Averianov et al, 2000). The two regions face significant, although fundamentally different, anthropogenic pressures. The primary threat to faunal communities in many parts of Borneo is widespread habitat alteration. Over the past forty years, Borneo's forests have had one of the highest rates of commercial logging of any tropical region in the world, with much of its remaining rainforests degraded (Gaveau et al, 2014). Although hunting is an issue in certain parts of Borneo (Bennet et al, 2000), all available evidence indicates that levels of hunting pressure in most parts of Borneo are significantly lower than the levels of industrial-scale exploitation found in mainland Southeast Asia. In contrast, hunting pressure is extremely high in the Annamites, where intensive hunting is predominantly accomplished by the setting of indiscriminate wire snares (Gray et al, 2018). Snaring is almost ubiquitous across Annamites forests, even in protected areas (Gray et al, 2018), and has led to precipitous declines in the populations of the region's terrestrial mammals and birds.

Understanding the impacts of indiscriminate hunting and habitat degradation on tropical mammal and bird communities is essential to the development of effective mitigation strategies. Knowledge on the effects of specific defaunation drivers allows conservation stakeholders to make more informed management decisions, which can in turn optimize the efficacy of limited conservation resources. Although several studies have focused on the impacts of each driver, often focusing on one or two species of particular concern (Hearn et al, 2026; Briceño-Méndez, 2016), there have been no comprehensive, systematic, large-scale studies comparing how hunting and habitat degradation differentially impact tropical faunal communities. To address this question, we conducted landscape-scale systematic camera-trapping across six study sites in Southeast Asia that are characterized by different defaunation drivers. In Sabah, Malaysian Borneo, we surveyed three active or former logging concessions. The concessions have undergone varying levels of logging intensity, ranging from conventional logging to reduced impact sustainably-managed programs, resulting in a gradient of habitat degradation (Ong et al, 2012; Sollmann et al, 2017; Brozovic et al, 2018). In contrast to most other areas in Southeast Asia, none of the areas have been subjected to significant past or current hunting pressure. In the Annamites, we surveyed two forest blocks (Bach Ma National Park [NP] and Hue / Quang Nam Saola Nature Reserves [SNRs]) in Vietnam and one block in Laos (consisting of Eastern Xe Sap National Protected [NPA] area and Palé watershed protection forest). Although these areas experienced extensive degradation during and shortly after the American-Vietnam war, habitat degradation over the last 30 years has been minimal (Meyfroidt & Lambin, 2008), and the areas are predominantly characterized by mature secondary forest. Unlike Malaysian Borneo, both past and current levels of hunting pressure are high, with most hunting accomplished by indiscriminate snaring (Gray et al, 2018; Wilkinson, 2016; Tilker, 2014).

Here, we investigated how moderate habitat degradation and intensive, indiscriminate hunting differentially impact tropical faunal communities, with the ultimate goal of providing information that can support the development of more effective conservation strategies. We assessed defaunation in both hunted and degraded sites, and at three hierarchical levels: species' functional extinction, species' occurrence, and drivers of species' occurrence. In all our hunting sites there is widespread, industrial snaring. Although our most degraded study site was subject to intensive conventional logging, altogether the degraded sites have experienced moderate levels of habitat disturbance, in the context that none were clear-cut. We used a defaunation index (Giocomini & Galetti, 2013) and Bayesian community occupancy models (Dorazio & Royle, 2005) to evaluate defaunation at each level. Our setup, with three degraded but unhunted sites, and three sites that are overhunted but structurally intact, provides a unique opportunity to assess the differential effects of these defaunation drivers on faunal communities at landscape scales.

Methods

Study areas and design

We used systematic camera trapping to collect data on the ground-dwelling mammal and bird communities in six study areas in Southeast Asia. Stations were spaced approximately 2.5

kilometers apart (Annamites: $\bar{x}$ = 2.47 ± 0.233 km; Malaysian Borneo: $\bar{x}$ = 2.46 ± 0.220 km, Figure 1a). At each station two white-flash camera traps (Reconyx® Hyperfire Professional PC850; Reconyx, Holmen, USA) were set facing in different directions. Cameras were placed along trails, ridgelines, and water sources to maximize detections of mammals and ground-dwelling birds. All cameras were placed 20 – 40 cm above the ground, were operational 24 hours per day, and were left in the field for a minimum of 60 days.

Systematic camera trapping in the Annamites was conducted between November 2014 and December 2016 (Supplementary Table 5) in a continuous forest across Vietnam and Laos. In total the survey areas cover more than 1,000 km^2 of broadleaf evergreen lowland and upland dipterocarp tropical rainforest, split into three study sites. In Vietnam, we surveyed: Bach Ma NP (approximately 340 km^2) and the Hue and Quang Nam SNRs (together approximately 275 km^2). In Laos, we surveyed the eastern section of Xe Sap and the adjacent Palé area (together approximately 300 km^2). The Forest is categorized as a watershed protection forest. The two study sites in Vietnam are surrounded by densely-populated human-modified areas that contain permanent settlements, plantations, and agricultural fields. By contrast, the Lao site does not contain extensive human-modified areas, and population density is low. However, the eastern part of Xe Sap NPA and the Palé areas are heavily utilized by Vietnamese poachers and gold mining operations (*49*). Poaching, primarily accomplished by the setting of wire snares, occurs in all sites. Because snaring pressure is related to a complex set of factors, further complicated by different management regimes among the sites, we did not make *a priori* assumptions into the underlying gradient of hunting pressure across the sites.

Systematic camera trapping in Malaysian Borneo was conducted between October 2014 and July 2016 (Supplementary Table 5). We used the same survey design as in the Annamites, with two camera traps set in different directions at each station, and stations spaced approximately 2.5 km apart. As with the study sites in the Annamites, the Malaysian Borneo sites contain wet evergreen lowland and upland dipterocarp tropical rainforest. We surveyed three logging concessions that form a contiguous forest block: Deramakot FR, Tangkulap-Sungai Talibu FR, and Northern Kuamut FR. The concessions have been subjected to varying levels of habitat degradation from both past and current logging. From the 1950s to 1989, Deramakot FR (approximately 550 km^2) was licensed to a private logging company (Ong et al, 2012; Sollmann et al, 2017; Brozovic et al, 2018). In 1989, management of the forest passed to the Sabah Forestry Department and logging activities stopped. Reduced-impact logging was initiated in 1995 (Ong et al, 2012; Sollmann et al, 2017; Brozovic et al, 2018). Deramakot FR uses a 40-year logging cycle to allow forests to regenerate before harvest (Ong et al, 2012; Sollmann et al, 2017; Brozovic et al, 2018). In 1997, the concession obtained Forest Stewardship Council (FSC) certification, Dermakot FR is promoted as the flagship of the Sabah Forestry Department for sustainable forest management (Lagan et al, 2007). From the 1970s to 2002, Tangkulap FR (approximately 501 km^2) was managed by a private logging company, and was repeatedly logged using conventional logging techniques (Brozovic et al, 2018). Logging stopped in 2001, and in 2011 the reserve received FSC certification (Brozovic et al, 2018). Although the forest has regenerated during this interim, it remains moderately degraded due to the intensity of past conventional logging activities (Brozovic et al, 2018). In 2015, Tangkulap FR was reclassified as a protected area, except for 2,000 ha of industrial timber plantation area that remains as production forest. Kuamut FR (approximately 695 km^2) was intensively logged using conventional techniques between 2004 and 2012, and the forest is highly degraded (Ong et al, 2012; Sollmann et al, 2017; Brozovic et al, 2018). In 2016, Kuamut FR was reclassified as a class 1 protected area in Sabah. Overall, Kuamut FR is the most degraded of the three areas, followed by Tangulap FR, then Deramakot FR (Ong et al, 2012; Sollmann et al, 2017; Brozovic et al, 2018).. There are a small number of villages around the periphery of the three sites. However, there is little evidence that villagers engage in routine hunting inside the study sites (Brozovic et al, 2018).

To avoid any confounding effects due to greater visibility around camera-trap stations, our data collection procedure was standardized prior to field work. We have developed detailed field protocols for camera-trap setup (see Abrams et al., 2018). The camera-trap setup protocols include the removal of vegetation to ensure that the area surveyed by the camera-trap is comparable for all sampling stations and, therefore, among the different study sites. We note that, in contrast to previous studies that combine data *post hoc*, our study was conceptually planned as a part of one project, with regular interactions between the field teams before and during the fieldwork to ensure the standardization of data collection procedures. Finally, because detectability can also be influenced local factors such as different movements or abundances, species detection rates can vary between hunted (Annamites) and degraded

(Malaysian Borneo) study sites. We therefore modeled detectability differently between the hunted and degraded sites (see full model description below).

Occupancy covariates

We modeled species occurrence using occupancy models that account for imperfect detection (Dorazio & Royle, 2005). We used covariates to assess the factors that influence species occurrence, and to improve model fit. We included two covariates in our models: canopy closure and village density. We expect that canopy closure would have more influence on species occurrence in the three degraded sites, and that village density would have more influence in the three hunted sites.

We used canopy closure as a measure of forest degradation. We consider higher canopy closure values to indicate more intact forest, and lower values to indicate more degraded forest (Asner et al, 2004). Canopy closure was assessed *in situ*. In the field we established a 20 x 20 m grid at each station, with the centerpoint halfway between the two camera traps. The grid was positioned along the north-south, east-west axes. We used a handheld GPS (Garmin® model 62sc, Garmin Ltd, 107 Canton of Schaffhausen, Switzerland) to take canopy photographs at the centerpoint and the corners of the grid (northwest, northeast, southeast, and southwest). Coordinates were recorded for each photograph, and the Waypoint Averaging function was used to minimize GPS error. Canopy photographs were manually converted to black and white using the open source GNU Image Manipulation Program (GIMP team, 2017), producing a raster file with black areas representing vegetation and white areas representing open sky. We then used R *v. 3.4.0* (R Core Team, 2018) to calculate percentage canopy closure for each image. Finally, canopy closure values were averaged across the five rasters to give a single mean canopy closure value for each camera-trap station. Detailed information on canopy data collection protocols can be found in Abrams et al (2018). Canopy closure values are given as a percentage, with higher values indicating a more intact canopy, and more structurally intact forest. The canopy closure values show that the sites in Malaysian Borneo are more degraded than the sites in the Annamites ($\bar{x}_{\text{Borneo}}$ = 0.77 ± 0.2, $\bar{x}_{\text{Annamites}}$= 0.83 ± 0.05). Among the degraded sites in Malaysian Borneo, canopy closure values were highest for Deramakot FR ($\bar{x}_{\text{Deramakot}}$ = 0.84 ± 0.12), followed by Tangkulap FR ($\bar{x}_{\text{Tangkulap}}$ = 0.73 ± 0.22), followed by Kuamut ($\bar{x}_{\text{Kuamut}}$ = 0.71 ± 0.23). The canopy closure values for the Malaysian Borneo sites reflect the degradation levels that would be expected based both on historical logging patterns and observations made *in situ*. The three sites in the Annamites had similar canopy closure values.

We used village density as a proxy for hunting at the local scale. Hunting pressure is often related to accessibility (Benítez-López et al, 2017), and several studies in other tropical regions have demonstrated a defaunation gradient around local villages (Muchaal & Ngandjui, 1999; Abrahams et al, 2017; Koerner et al, 2017). To calculate village density we first created a heatmap in QGIS *v. 2.18.9* (QGIS Development Team, 2019) using a village shapefile as the input point layer. We used the default quartic kernel decay function and set the radius to 15 km. The village density radius was chosen so that all individual sampling stations in our study landscape fell within the “hunting halo” in the final heatmap. Observations while conducting fieldwork in the Annamites indicate that all camera-trap stations, even those in the most remote areas of the Palé area, were subject to some level of hunting pressure, as evidenced by the presence of wire snares. To be consistent among sites, we also used the same village density radius for the study sites in Malaysian Borneo. After creating the heatmap, we used the extract function in the *raster* package (*86*) to obtain village density values for each station. The village density covariate is unitless, with higher values indicating areas closer to a higher number of villages, and lower values indicating areas that are more remote. Consistent with observations made *in situ*, in the Annamites, Bach Ma NP had the highest density of surrounding villages, followed by the Saola NRs, followed by Xe Sap / Palé. The sites in Malaysian Borneo had low village density values, reflecting the low number of villages in their vicinity.

Historical defaunation index

We used the defaunation index proposed by Giacomini and Galetti (2013) to calculate historical defaunation for each study area. This defaunation index is a weighted measure of dissimilarity between an assemblage of interest and a reference assemblage representing a historical or less disturbed site. The defaunation index is given by the equation:

$$D(r,f) = \frac{\sum_{k=1}^{S} \omega_k \left(N_{k,r} - N_{k,f}\right)}{\sum_{k=1}^{S} \omega_k \left(N_{k,r} + N_{k,r}\right)}$$

where D is the index of defaunation of focal assemblage f with respect to a reference assemblage r; S is the total number of species in the focal (f) and reference (r) assemblages; k is the identification of a species; $N_{k,r}$ is presence or absence of species k in the reference assemblage; $N_{k,f}$ is presence or absence of species k in the focal assemblage; and ω_k is the weight assigned to species k. When comparing a more defaunated assemblage to a reference assemblage, D ranges from 0 to 1. It is also important to note that D can assume negative values if the focal assemblage is less defaunated than the reference assemblage. It is therefore possible for D to range from -1 to 1, with positive values indicating more defaunation, and negative values indicating less defaunation.

To construct the historical reference assemblage, we used IUCN range maps to document ground-dwelling mammal and terrestrial bird species that historically occurred in each study area. We included mammal and terrestrial bird species > 500g in our analyses for two reasons. First, smaller species are unlikely to be impacted by snaring (*57*). Second, many smaller mammals (rodents, squirrels) and birds (partridges) are difficult to identify to species level using camera trap photographs. We excluded highly arboreal species in our analysis – for example, the red-shanked douc langur *Pygathrix nemaeus* in the Annamites, the dusky langur *Presbytis rubicunda* in Malaysian Borneo, and all large Sciuridae from both landscapes – as these species are unlikely to be reliably detected by camera-traps placed at ground level. We also excluded riverine habitat specialist species, for example all otter species (*Lutra* spp., *Lutrogale perspicillata*, and *Aonyx cinerea*), because the majority of our camera stations were not located on streams or rivers and, as a result, we believe that it is possible that our study would not have recorded these species even if present. Finally, we did not include weasel species for either study area (*Mustela kathiah* in the Annamites, *Mustela nudipes* in Malaysian Borneo), as these species may be routinely under-recorded by camera-trapping (Abramov et al, 2008; Supparatvikorn et al, 2012). Species that could not be confidently identified to species level using camera-trap images were grouped at the genus level. In the Annamites, Chinese pangolin *Manis pentadactyla* and Sunda pangolin *M. javanica* were grouped as *Manis* spp., and the large-toothed ferret badger *Melogale personata* and small-toothed ferret badger *M. moschata* were grouped as *Melogale* spp. We also grouped all images of Annamite dark muntjac *Muntiacus rooseveltorum / truongsonensis*, as the taxonomy for this species complex is currently unresolved (*90,91*). In Malaysian Borneo, the greater mousedeer *Tragulus napu* and lesser mousedeer *Tragulus kanchil* were grouped as

Tragulus spp. The final historical reference assemblages provide a validated list of terrestrial mammal and bird species that historically occurred at each site.

For the historical defaunation analysis, we compiled a list of species that were recorded in < 2.5% of our total camera-trap locations at each study site, and considered these species as functionally extinct. We chose to use a measure of functional extinction as defined by an occupancy-based metric, rather than a measure of complete extinction defined by species recorded or not recorded during our study, for two reasons. First, even if a species was not recorded during our surveys, it would be incorrect to infer species absence. Second, using a functionally extinct definition allows for the possibility that a species may be present but not in numbers that constitute an ecologically functional population. Because the number of stations was different between the sites in the Annamites and Malaysian Borneo, we decided to use 2.5% of all stations instead of a fixed number of minimum stations. 2.5% of total stations represents two stations for Bach Ma NP, two stations for the Saola NRs, and one station for Xe Sap / Palé. 2.5% of stations represents two stations for Deramakot FR, two stations for Tangkulap FR, and two stations for Kuamut FR. We believe that this low number of stations is a conservative estimate for a species to exist in the landscape and remain ecologically functional. Therefore, the final current species assemblage therefore gives a conservative estimate of functionally extinct mammals and terrestrial birds in our study sites .

To assign species weights in the historical defaunation index, we followed the methods presented by Giacomini and Galetti (2013). We used three species weights: equal weighting, threatened status as an indication of conservation priority, and average body mass (2013). We derived threat status by assigning values for each species using *The IUCN Red List of Threatened Species* (assessed as of February 1st, 2019). Weights were given as follows: Least Concern = 1; Near Threatened = 2; Vulnerable = 3; Endangered = 4; and Critically Endangered = 5. We did not have any species in our dataset classified as Extinct or Extinct in the Wild. Two species from the sites in the Annamites (Annamite dark muntjac species complex *Muntiacus rooseveltorum / truongsonensis* and Annamite striped rabbit *Nesolagus timminsi*) were listed as Data Deficient. We assigned these two species a mean value of 2.5. We also assigned species weights based on average body mass. Average body mass was taken from natural history books and regional field guides (Phillipps, 2011; Baltzer et al, 2001; Francis, 2019). If this information was not available for a species, we used the average body mass for a similar species as an approximation. Following Giacomini and Galetti (2013), we raised the body mass to the power of ¾ to better reflect species functions based on body size.

Community occupancy analysis

We adopted the hierarchical formulation of occupancy models by Royle and Dorazio (2005) and extended this to a community occupancy model by linking the species-specific models by assuming that species-specific parameters come from a common underlying distribution, governed by community hyperparameters. To assess the impacts of defaunation on species occurrence, we ran community occupancy models for 15 phylogenetically closely-related terrestrial mammal and galliform species or species pairs. Species pairs were restricted to species that occur in both the Annamites and Malaysian Borneo. For example, we could not use serow *Capricornis milneedwardsii* in the analyses because the species occurs in the Annamites but not in Borneo, and we could not include the Bornean orangutan *Pongo pygmaeus* because the species occurs in Borneo but not in the Annamites. Similarly, we could not include binturong *Arctictis binturong* because, while the species range includes both Borneo and the Annamites, we did not record it in our surveys in the Annamites. All species pairs represent taxa that are approximately the same body size and in the same feeding guild. While we acknowledge that there may be site-specific differences in the ways in which species or species pairs respond to anthropogenic pressures, given the functional similarities between the pairs, we believe that responses are likely to be generally similar.

Our minimum camera-trapping period was 60 days ($\bar{x}$ = 68.8 days) and spacing was approximately 2.5 km (see Study areas and design section above). We consider our trapping period to satisfy occupancy closure and independence assumptions (MacKenzie et al, 2017). To establish species encounter histories, we pooled camera-trap data into 10-day occasions, resulting in at least six sampling occasions for all stations, and determined for each site and occasion whether a given species was detected or not. A 10-day occasion length was chosen to maximize the number of occasions while simultaneously avoiding zero-inflation in the encounter history dataset.

We ran separate Bayesian community occupancy analyses for each study site. We modeled occupancy probability as having a species-specific random intercept. We modeled the effect on occupancy of two covariates: canopy closure (x_{canopy}) and village density ($x_{village}$). Covariate values were normalized. We accounted for varying camera-trapping effort within the 10-day occasion as the only covariate on detection probability (p). The full community occupancy model had the following parameterization:

$$z_{ij} \sim Bernoulli(\psi_{ij})$$

$$logit(\psi_{ij}) = \alpha_{i[site]} + \beta 1_i * \text{canopy}_j + \beta 2_i * \text{village density}_j$$

$$\alpha_i \sim Normal(\mu_\alpha, \sigma_\alpha)$$

$$\beta 1_i \sim Normal(\mu_{\beta 1}, \sigma_{\beta 1})$$

$$\beta 2_i \sim Normal(\mu_{\beta 2}, \sigma_{\beta 2})$$

$$y_{ijk} \sim Bernoulli(p_{ijk})$$

$$logit(p_{ijk}) = \alpha.p_i + \beta.\text{r}_i * \text{Effort}_{jk}$$

$$\alpha.p_i \sim Normal(\mu.p_{\alpha.p}, \sigma.p_{\alpha.p})$$

$$\beta.r_i \sim Normal(\mu.p_{\beta.r}, \sigma.p_{\beta.r})$$

in which z_{ij} is the true occupancy state (0 or 1) of species i at camera trap station j; ψ_{ij} is the respective occupancy probability; α is the intercept of the logit-linear predictor of occupancy probability, and $\beta 1$- $\beta 2$ are the coefficients for canopy coverage and village density, respectively. In our model, y_{ijk} are the observations (0 or 1) of species i at site j at occasion k; p_{ijk} are the respective detection probabilities; $\alpha.p$ is the intercept of the logit-linear predictor of detection probability, indexed by species; $\beta.r$ is the effect camera-trap effort (effort) on detection probability given by the number of days a camera-trap was working within a 10-day occasion. Species-specific detection intercepts and $\beta.r$ come from a normal distribution with community means and standard deviations.

We implemented the model in a Bayesian framework using JAGS accessed through the R package *rjags v.4.7* (Plummer, 2018). We ran three parallel Markov chains with 250,000 iterations, of which we discarded 20,000 as burn-in, and we thinned the remaining iterations by 20 to make the output more manageable. We assessed chain convergence using the Gelman-Rubin statistic where values < 1 indicated convergence (Gelman et al, 2004). We report results as posterior mean and standard deviation, and 95% and 75% Bayesian confidence intervals (95% BCI, 75% BCI, the 2.5% and 97.5%, and 12.5% and 87.5% percentiles of the posterior distribution, respectively).

Occupancy-based defaunation index

We calculated an occupancy-based defaunation index for the 15 species and species pairs by incorporating the posterior distributions of occupancy probability into the defaunation index proposed by Giacomini and Galetti (*50*). We used the distribution of occupancy estimates from Deramakot FR as our reference assemblage. We selected Deramakot FR as the reference because it is the least degraded site and is not subject to hunting pressure. We attach confidence intervals to each estimate of defaunation (D) by incorporating the uncertainty associated with the occupancy estimates (ψ). We used Monte Carlo sampling to construct the probability distribution of D. To do this we sampled random values from the posterior distributions of species-specific occupancy probabilities for all five sites for each species pair and used these values to calculate D where $N_{k,r}$ and $N_{k,f}$ are the occupancy of species k in the reference and focal assemblage, respectively. We repeated this procedure 30,000 times to generate a distribution of D values. 95% confidence intervals were calculated using the 2.5% and 97.5% percentiles of the distribution as confidence limits.

Assessing covariate effect sizes

To assess the effects of covariates on estimated ψ, we derived covariate effect sizes using regression coefficients for each species from the community occupancy models. We calculated a community average value for β values of predictor variables. We scaled all covariates before analysis, with covariates scaled independently between the hunted and degraded sites, respectively. Numbers further from 0 indicate a stronger effect of the associated covariate. A positive effect size indicates that occupancy probability increases as the associated covariate increases.

Results

Functional extinction

For the historical defaunation analysis, we defined functional extinction as species that were recorded in < 2.5% of the total camera-trap locations in a study site (see Methods for more details). Using the defaunation index (see Methods), we found that the three hunted sites have functionally lost a considerable proportion of their terrestrial mammal and bird community (D_{equal} Bach Ma NP = 0.48, D_{equal} Saola NRs = 0.48, D_{equal} Xe Sap / Palé = 0.45), whereas functional extinction rates were low in all degraded sites (D_{equal} Deramakot FR = 0.06, D_{equal} Tangkulap FR = 0.16, D_{equal} Kuamut FR = 0.09)(Figure 1). Functional extinction levels were substantially higher for threatened and larger species in the hunted sites ($D_{threatened}$ Bach Ma NP = 0.68, $D_{threatened}$ Saola NRs = 0.66, $D_{threatened}$ Xe Sap / Palé = 0.54; D_{size} Bach Ma NP = 0.96, D_{size} Saola NRs = 0.91, D_{size} Xe Sap / Palé = 0.87) but there was little difference when these species weightings were applied to the faunal community in the degraded sites ($D_{threatened}$ Deramakot FR = 0.12, $D_{threatened}$ Tangkulap FR = 0.21, $D_{threatened}$ Kuamut FR = 0.15; D_{size} Deramakot = 0.10, D_{size} Tangkulap FR = 0.12, D_{size} Kuamut FR = 0.11). The same patterns were evident when the three hunted are combined as one site and three degraded sites are combined and evaluated as one site (D_{equal} hunted = 0.38, $D_{threatened}$ hunted = 0.55, D_{size} hunted = 0.91; D_{equal} degraded = 0.06, $D_{threatened}$ degraded = 0.12, D_{size} degraded = 0.10). Defaunation levels also showed distinct patterns among the individual sites. Amongst the hunted sites, under equal species weighting, Bach Ma NP and the Saola NRs had the highest defaunation values, followed by Xe Sap / Palé. When species were weighted to reflect conservation priority and size, Bach Ma NP has the highest defaunation, followed by the Saola NRs, followed by Xe Sap / Palé. Defaunation levels in the degraded sites showed a consistent pattern, independently of the species weighting. Amongst the degraded sites, Tangkulap FR had the highest defaunation values, followed by the most degraded site (Kuamut FR), followed by the least degraded site (Deramakot FR). In the degraded landscape only four species (11.1%) were considered functionally extinct. However, in the hunted sites 25 (55.6%) species were considered functionally extinct. We found no evidence in the hunted sites of large carnivores, megaherbivores, or a substantial component of the galliform community that would have historically existed in the area.

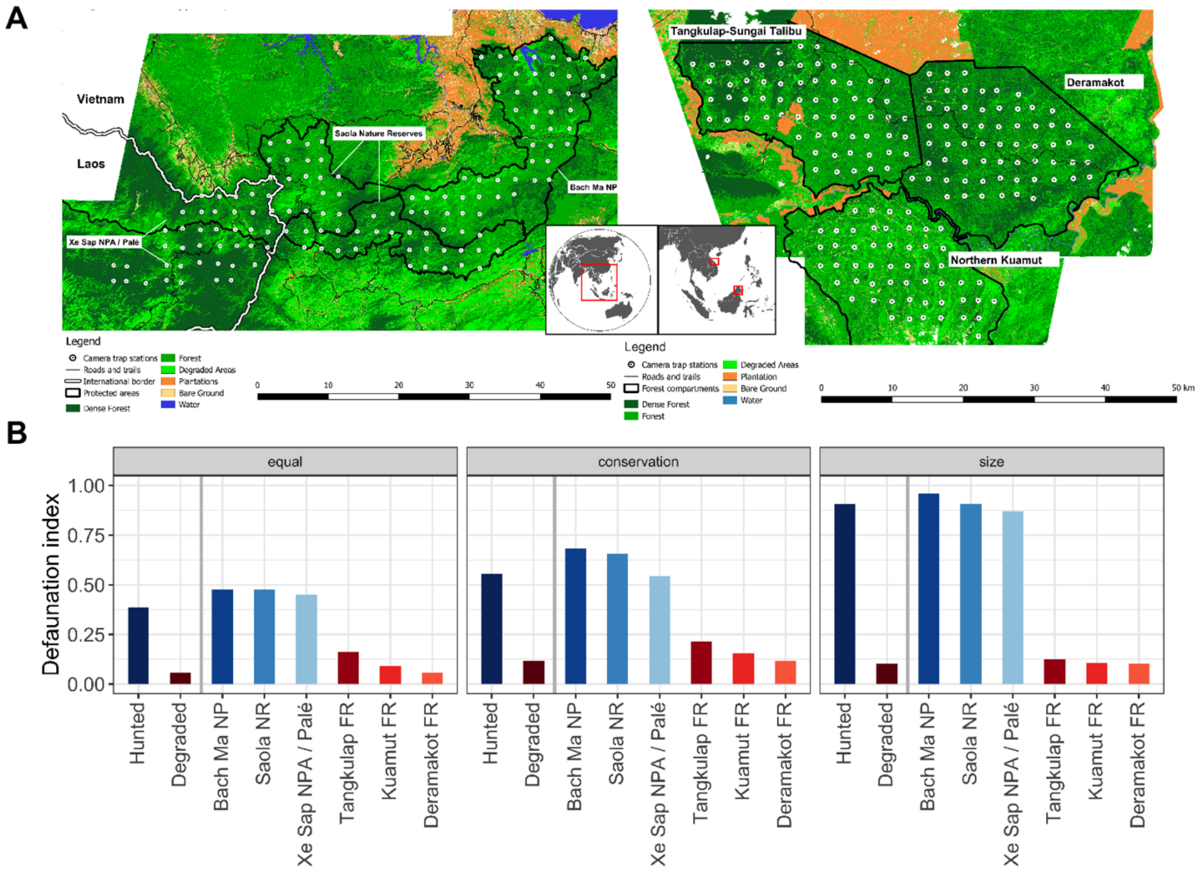

Figure 1. (a) Study sites in Vietnam / Laos (hunted) and Malaysian Borneo (degraded). **(b)** Historical Defaunation indexes for hunted and degraded sites. Defaunation values were calculated using a measure of functional extinction, defined as species recorded in <2.5% of camera trap stations per site. Larger and more threatened species have higher levels of functional extinction. Species importance is weighted in three ways: all species given equal importance (equal), based on conservation status (conservation), and based on species average body size raised to the power of ¾ (size)

Species occurrence patterns

To assess and compare the impacts of defaunation on species occurrence, we used terrestrial mammal and large galliform species or species pairs that still occurred in both landscapes. In total 15 species or species pairs were found to still occur in both landscapes and thus could be included in the analysis. Species pairs were chosen based on taxonomic and ecological similar-

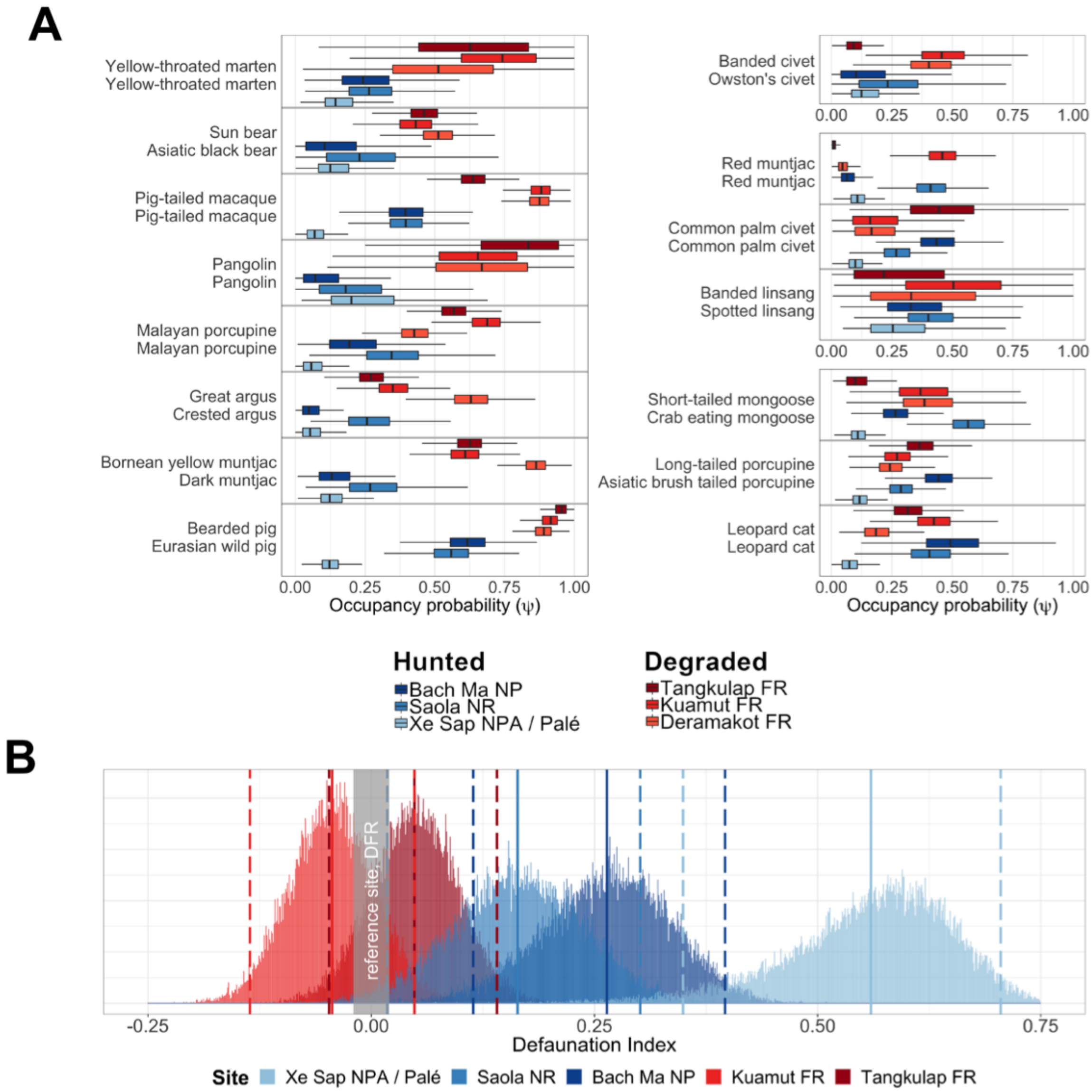

Figure 2. (a) Bayesian community occupancy estimates for 15 mammal and terrestrial bird species or species pairs for each of the six study sites. Species occupancy estimates (mean and 95% BCI) from the hunted and degraded sites. Species occupancy estimates for the hunted sites are shown in blue colors. Species occupancy estimates for the degraded sites are shown in red colors. Average occupancy was higher in the degraded sites than in the hunted sites for most species [pairs (lefthand panel). **(b)** Occupancy-based defaunation index for 15 mammal and terrestrial bird species or species pairs in two hunted and three degrades sites. The degraded but non-hunted site (Deramakot FR) is used as a reference site (zero defaunation). The occupancy-based defaunation index is higher for the hunted than the degraded sites. Solid lines represent mean values; dotted lines represent 95% Bayesian credible intervals.

ities. We used Bayesian community occupancy models to estimate and compare probabilities of occurrence between the hunted and degraded landscapes. We included two covariates in the analyses: village density ($x_{village}$) and canopy closure (x_{canopy}). We found that estimated occupancies were lower in all three hunted compared to the three degraded sites for eight of the 15 species pairs (Figure 2A), whereas there were no cases where the occupancies in all of the hunted sites are higher than the occupancies in all of the degraded sites. One species pair showed higher occupancies in two of the three degrades sites, with estimated occupancy for the third degraded site similar to the three hunted sites. Three species pairs had occupancies that were similar among the hunted and degraded sites. An additional three species pairs also showed occupancies that were similar among the hunted and degraded sites, but with one hunted site having a higher estimated occupancy than any of the degraded sites. Four of the six species with comparable occupancies among hunted and degraded sites were generalist mesocarnivores.

The effects of defaunation on species occurrence was also assessed using an occupancy-based defaunation index, calculated using the posterior occupancy estimates from the Bayesian community occupancy model for the 15 species pairs, and using the least degraded and non-hunted site (Deramakot FR) as the reference assemblage ($D_{occupancy} = 0$). Defaunation values were higher for the three hunted sites ($D_{occupancy}$ Bach Ma NP = 0.26 ± 0.07, $D_{occupancy}$ Saola NRs = 0.16 ± 0.07, $D_{occupancy}$ Xe Sap / Palé = 0.56 ± 0.09) than the two degraded sites ($D_{occupancy}$ Tangkulap FR = 0.05 ± 0.05, $D_{occupancy}$ Kuamut FR = -0.04 ± 0.05) and the reference site (Fig. 2B). Among the hunted sites, the most defaunated site was Xe Sap / Palé, and the least defaunated site were the Saola NRs. Among the degraded sites Tangkulap FR had a higher defaunation value than the reference site ($D_{occupancy}$ Tangkulap FR = 0.05 ± 0.05), as expected by the higher degradation. However, the most degraded site Kuamut FR had a lower defaunation value ($D_{occupancy}$ Kuamut FR = -0.04 ± 0.05) than the reference site. The negative defaunation value for Kuamut FR indicates that estimated occupancies are higher in the more degraded site than in the reference site for these 15 species.

Drivers of species occurrence

To assess the third hierarchical level of defaunation, we investigated how anthropogenic and habitat-based factors influence species occurrence. We evaluated covariate ($x_{village}$ and x_{canopy}) effect sizes for the 15 species pairs within the Bayesian community occupancy framework. For most species in the degraded landscape occurrence was strongly influenced by the habitat-based covariate (nine species with 95% BCI's that do not overlap zero for x_{canopy})(Figure 3a). In contrast, the environmental driver had minimal impact on species occurrence for species in the hunted landscape (no species with non-overlapping effect size 95% BCIs, two species with non-overlapping 75% BCIs for x_{canopy}). Species occurrence in the hunted landscape was strongly associated with the anthropogenic covariate (three species with non-overlapping effect size 95% BCI's, seven species with non-overlapping 75% BCIs for $x_{village}$) but had minimal effect on species occupancies in the degraded sites (no species with non-overlapping effect size 95% BCIs, three species with non-overlapping 75% BCIs for $x_{village}$). To assess if the greater response to x_{canopy} in the degraded sites was due to more variability in the canopy closure covariate in Malaysian Borneo compared to the Annamites sites, we subsetted the canopy closure sampling locations for the degraded sites so that the mean and variation was similar to the hunted sites, and ran a community occupancy model for the 15 species. Our results show a similar response for canopy closure, even with the subsetted data.

When the effect sizes for $x_{village}$ and x_{canopy} are plotted against each other, canopy closure showed a strong effect on species occurrence for the degraded sites, but weak effect in the hunted sites. Village density shows a strong effect on species occurrence for the hunted sites, with little impact on occupancies for the degraded sites (Fig. 3b). Canopy closure shows both positive and negative effects on species occurrence in the degraded sites. In contrast, village density shows a persistent negative impact on species occurrence in the hunted sites, with only one species, Northern pig-tailed macaque *Macaca leonina*, having higher estimated occupancy in areas closer to villages.

Discussion

Our results provide insight into the differential impacts of moderate habitat degradation and intensive, indiscriminate hunting on tropical mammal and bird communities at multiple hierarchical levels of the defaunation process. At the most fundamental level habitat degradation and indiscriminate hunting drive species extinctions. We found that both defaunation drivers resulted in functional extinctions in our study sites, but that the relative impact of these drivers differed substantially. Higher defaunation in the hunted sites suggests that, within the context of species loss in tropical forests, widespread indiscriminate hunting is unsustainable and may be

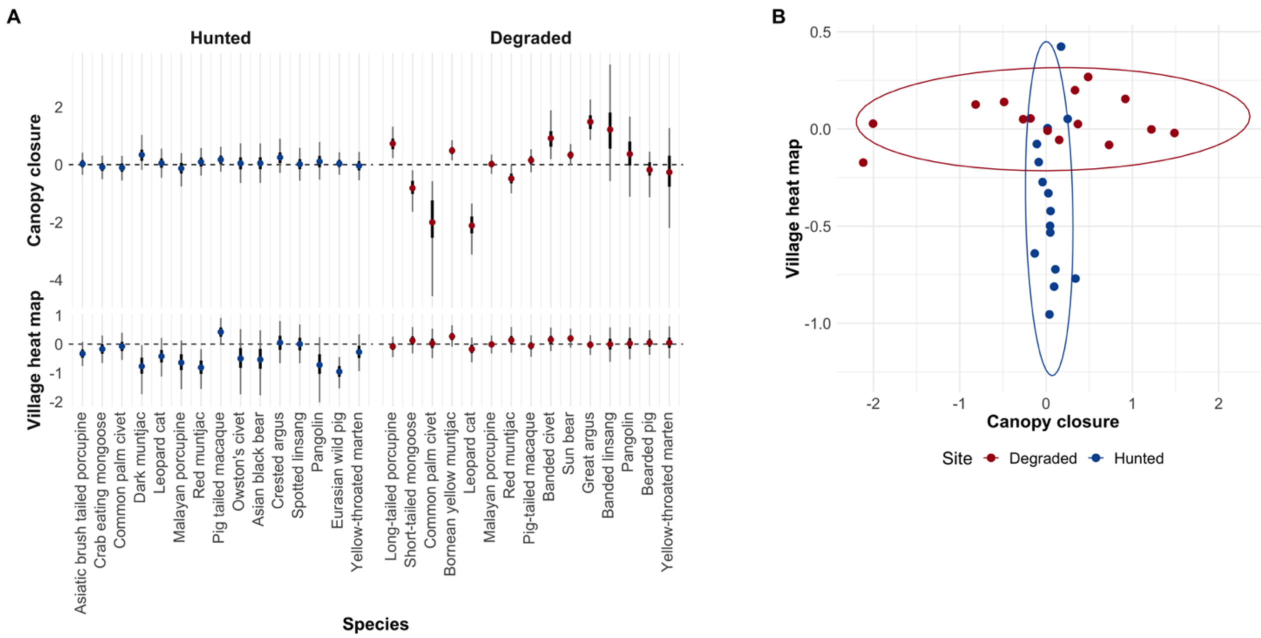

Figure 3. a Effect sizes for two covariates, canopy closure and village density, on Bayesian occupancy model results for 15 species or species pairs in the hunted and degraded sites. Canopy closure is used as a proxy for hunting pressure. 75% BCIs are shown with a thick black line, 95% BCIs are shown with a thin black line. **b** Mean covariate effect sizes for each species pair plotted against each other. The ellipses represent the 95% data ellipses.

a more severe short-term threat than the moderate levels of habitat degradation considered in this study. On first sight these results contradict conventional thinking on the consequences of these two drivers, because hunting is often considered to impact a few target species, whereas degradation is seen to impact all species within a community. However, it is important to note that, in contrast to earlier studies that predominantly assessed the effects of gun-hunting on faunal communities (*26-28*), our study investigated the consequences of indiscriminate snaring. Our findings support earlier observations that show that snaring causes declines in a wide range of ground-dwelling vertebrates (*41*). To date, large-scale conservation initiatives in tropical countries have predominantly focused on habitat conservation. Our results suggest that, to protect tropical terrestrial mammal and bird communities, a paradigm shift may be warranted, in which these initiatives focus as much on addressing unsustainable hunting as on activities that result in moderate levels of habitat degradation.

We also found that functional extinction rates were higher in the hunted sites for both threatened and larger species compared to the equal species weighting, but that there was little difference in the degraded sites. Greater susceptibility of conservation-priority and larger species further underscores the potentially greater negative impact of hunting compared to degradation. Threatened species are important from a conservation perspective, and may serve as flagships for wider conservation initiatives (Caro & O'Doherty, 1999). Larger mammals often have greater impacts on ecosystems through predation and herbivory, and their extinction can cause fundamental changes in ecosystem functions (Sinclair, 2003). We note that, because we gave all species a scaled body mass weighting, the body size bias in the size-weighted defaunation index is a function of the total body mass of the community, and should not be caused solely by the loss of the largest mammal species. However, to ensure that the loss of the largest mammalian species (elephant *Elephas maximus*, gaur *Bos gaurus*) did not disproportionally skew our results, we also tested a ranked order weighting, which gave results similar to the weighted analyses. The loss of either threatened species or larger mammals undermines conservation and sustainability-based objectives. The fact that our degraded sites experienced relatively low levels of functional extinction highlights the potential conservation value of secondary forests. This finding is consistent with previous studies that have shown that logged secondary forests can still retain substantial components of their original faunal assemblage (Clark et al, 2009; Kleinschroth & Healey, 2017). However, we note that the conservation value of degraded areas would be low if these areas have experienced heavy hunting pressure, which is a likely scenario given the fact that hunting and logging are often closely linked (Kleinschroth & Healey, 2017). It is therefore possible that the low levels of functional extinction that we documented in our degraded sites represent a best-case scenario. Nonetheless, we believe that our results provide an optimistic assessment for the potential of degraded forests to contribute to the maintenance of tropical biodiversity. In some situations, the financial revenues from sustainable logging might provide additional resources that could help protect forests from hunting.

Defaunation also decreases species abundance and distribution. We found that most species pairs that occurred in both hunted and degraded sites showed lower occupancy in the hunted sites, and that occupancy-based defaunation values for these species were several times greater in sites that were subject to hunting pressure (Figure 2). Because decreases in species occupancy often lead to local extinctions, this finding has obvious conservation implications, especially for range-restricted species. Annamite striped rabbit occupancy is already so low in Bach Ma NP that, without immediate reduction in snaring pressure, the species will soon become locally extinct in the protected area (Tilker et al, 2019). The loss of a range-restricted Annamite endemic from one of the few areas where the species has been confirmed (Tilker et al, 2019) is a poignant reminder of the link between declining occurrence and extinction. Decreases in abundance and distribution can also have less obvious, more systemic consequences. Declines in species occurrence can degrade ecological interactions, leading to fundamental changes in ecosystem processes (Valiente-Banuet et al, 2015). Previous studies, for example, have shown that ungulate declines may reduce seed dispersal, which in turn impacts vegetation communities and forest structure (Kurten, 2013). Such changes in forest structure across large areas of the tropics have numerous implications. Recently, Bello et al (2015) showed that faunal declines may fundamentally erode carbon storage capacities in tropical rainforests. Thus, increasing conservation emphasis on overhunting may not only prevent functional extinctions, but also preserve the ecological integrity of tropical forests.

We found that four of the six species with comparable occupancies among hunted and degraded sites were mesocarnivores (Figure 2). We were surprised to find that these mesocarnivore occupancies were similar between heavily defaunated and more intact sites. One explanation for this finding is that mesocarnivores embody traits that make them more resilient to hunting pressure. When compared to apex predators, mesocarnivores tend to have more flexible dietary requirements, often preying on small mammals or invertebrates that are not utilized by carnivores at higher trophic levels (Prugh et al, 2009). Furthermore, some mesocarnivores are also highly omnivorous. For example, the common palm civet *Paradoxurus hermaphroditus*, one of the most abundant mesocarnivores in our hunted sites, has been known to subsist on fruit (Nakashima et al, 2010). These generalist traits may make mesocarnivore species less susceptible to declines due to hunting. An alternative explanation is that small carnivores have increased in abundance and distribution in our hunted sites through a mesopredator release mechanism (Soulé et al, 1988; Crooks & Soulé, 1999). Historically, our hunted sites would have included a range of top carnivore species – including tiger *Panthera tigris*, leopard *Panthera pardus*, dhole *Canis alpinus*, clouded leopard *Neofelis nebulosa*, and Asian golden cat *Catopuma temminckii* – all of which are now locally extirpated or present at functionally extinct levels. Studies in other terrestrial ecosystems have shown that the decline of apex predators reduces both direct and indirect competition on mesocarnivores, often resulting in unnaturally high densities for these species (Brashares et al, 2010). Although our findings give some insight into the persistence of mesopredators in faunally impoverished systems, we note that more in-depth studies are needed to assess the extent to which defaunation drivers benefit this species group, and therefore contribute to the biotic homogenization (McKinney & Lockwood, 1999) of tropical faunal communities.

Surprisingly, we found that occupancy-based defaunation values were lower in our most degraded site (Kuamut FR) than in the least degraded reference site (Deramakot FR), indicating that overall occupancy for these 15 species increased with degradation. We believe this result can be explained by the fact that our analysis was limited to species that were recorded in both the hunted and degraded landscapes. Many of the species present in the hunted sites were highly adaptable generalist mammal species known to be resilient to anthropogenic pressures. Our comparative analysis may therefore be biased towards more generalist species that tend to be more resilient to both defaunation drivers. To test this assumption we ran occupancy models for the entire suite of mammal and bird species in the degraded sites (in total 32 species instead of the subset of 15) and the results clearly show that, while species-specific responses vary, habitat degradation negatively impacts the faunal community as a whole, and our reference site (Deramakot FR) had on average the highest species occupancies and thus the lowest defaunation value.

Defaunation drivers also impact the underlying factors that influence species distribution. We found that anthropogenic and habitat-based covariates differed in their importance in explaining species occurrence patterns in our study sites (Figure 3). Understanding the factors that influence species occurrence is important for numerous tools used in conservation science. For example, in recent years species distribution modeling has become an integral component of conservation planning (Rodriguiez et al, 2007; Guisan et al, 2013). To date, the field of species distribution modeling has largely focused on the use of ecological variables to predict distribution (Elith & Leawick, 2009), with less emphasis on the inclusion of anthropogenic covariates that reflect spatial variation in hunting pressure (but see Lippitt et al [2008]). In areas characterized by hunting-driven declines, spatial prioritizations built upon species distribution models that only use ecological variables may poorly represent actual biodiversity patterns, which can in turn lead conservation stakeholders to misallocate limited conservation resources. We acknowledge that finding proxies that accurately capture hunting pressure may be challenging, as hunting pressure itself is a complex phenomenon resulting from various socio-economic and cultural influences. However, we are optimistic that recent advances in statistical modeling and earth observation science (Bush et al, 2017) will provide new opportunities for the development of increasingly sophisticated anthropogenic covariates for use in species distribution models. In the Annamites, novel approaches are already being developed that take into account hunter accessibility across both spatial and temporal dimensions (Tilker et al, 2020). We hope that our findings encourage further developments into this field as hunting is a key driver of species occurrences and therefore should not be neglected.

Our comparative analyses provide new insights into the effects of moderate habitat degradation and indiscriminate hunting on tropical mammal and bird communities. However, we also recognize that, because these defaunation drivers are the result of complex and often locally-specific processes, further research is needed to provide a more holistic understanding of their impacts. We first acknowledge that data from additional sites is needed to obtain a more holistic picture of how different defaunation drivers impact faunal communities, especially as our three study sites in the two landscapes were adjacent to one another. Although we believe that our landscape approach, with study sites over 300-400 km^2 in size (much larger than the home range of any species included in this analysis), make our study less vulnerable to the spatial effects that could arise from surveying adjacent sites, our sites might not be spatially independent in the strictest sense of the term. Second, we recommend that future landscape-scale systematic camera-trapping include areas subject to more extreme levels of habitat degradation. Although our most degraded study sites had undergone intensive conventional logging, none of our study areas had been clear-cut. Disturbance levels in these sites are therefore at the moderate, rather than severe, end of the degradation spectrum. Although some studies have assessed faunal communities in degraded areas, most have been conducted over relatively small spatial scales (Brodie et al, 2015), failed to account for imperfect detection probabilities (Babweteera & Brown, 2009), or used meta-analyses that rely on datasets that cover large spatial extents but may not be well-suited for in-depth analyses (Burivalova et al, 2014). Additional standardized surveys using occupancy-based approaches may reveal a bleaker picture of degradation-driven declines than we found. We caution that, until such studies are conducted, our results should only be interpreted within the context of moderate levels of habitat degradation. A similar point can be made with regard to hunting pressure. Because indiscriminate snaring impacts a wide range of taxa (Gray et al, 2018), it is likely that areas subject to more selective gun-hunting will not show the same degree, or species-specific patterns, of faunal decline. Our findings are therefore most applicable to other areas where nonselective methods of wildlife exploitation predominate. We also recognize that the magnitude of snaring in our sites is exceptionally high, and that future studies in areas under less extreme snaring pressure may provide a more nuanced perspective into hunting-driven defaunation. However, here we point out that, because industrial-scale snaring is rapidly expanding across the tropics, especially in Southeast Asia (Gray et al, 2018), we believe that our findings may be directly relevant to an increasing number of tropical regions in the near future.

Given future population projections (Gerland et al, 2014) and road expansion in developing countries (Meijer et al, 2018), tropical rainforests will be subjected to ever-increasing levels of degradation and exploitation. Pantropical defaunation can only be prevented if conservation stakeholders develop effective conservation solutions to address these threats in the most efficient way. But determining how best to implement these solutions with limited conservation resources remains a challenge. Our results show that, while both defaunation drivers negatively impact tropical faunal communities, unsustainable hunting practices such as the widespread, indiscriminate hunting examined here may be the more severe short-term threat for terrestrial mammal and bird species. We suggest that conservation strategies that seek to protect tropical faunal communities may benefit by focusing on actions that mitigate against unsustainable hunting, rather than moderate levels of habitat degradation. Because unsustainable hunting is linked to such a complex range of social, economic, and cultural issues, developing strategies to address this challenge may require new ways of thinking. Ultimately, maintaining healthy tropical faunal communities is in the best interest of conservationists that want to protect biodiversity, national governments that seek to maintain ecosystem services, and local communities that rely on having access to sustainable forest resources. Bringing these diverse stakeholders together may help in the development of novel conservation approaches.

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Chapter 3

Identifying conservation priorities in a defaunated tropical biodiversity hotspot

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Conceptual design: AT, AW; data collection: AT, AN; data analysis: AT, J FA, LH, JA, RS; assisted with the field surveys: BMR, HANQ, FG, TN, ML; led the manuscript writing: AT. JFA, AW; commented and reviewed the manuscript: all authors.

Aim: Unsustainable hunting is leading to widespread defaunation across the tropics. To mitigate against this threat with limited conservation resources, stakeholders must make decisions on where to focus anti-poaching activities. Identifying priority areas in a robust way allows decision-makers to target areas of conservation importance, therefore maximizing the impact of conservation interventions.

Location: Annamite mountains, Vietnam and Laos.

Methods: We conducted systematic landscape-scale surveys across five study sites (four protected areas, one unprotected area) using camera-trapping and leech-derived environmental DNA. We analyzed detections within a Bayesian multi-species occupancy framework to evaluate species responses to environmental and anthropogenic influences. Species responses were then used to predict occurrence to unsampled regions. We used predicted species richness maps and occurrence of endemic species to identify areas of conservation importance for targeted conservation interventions.

Results: Analyses showed that habitat-based covariates were uninformative. Our final model therefore incorporated three anthropogenic covariates as well as elevation, which reflects both ecological and anthropogenic factors. Conservation-priority species tended to found in areas that are more remote now or have been less accessible in the past, and at higher elevations. Predicted species richness was low and broadly similar across the sites, but slightly higher in the more remote site. Occupancy of the three endemic species showed a similar trend.

Main conclusion: Identifying spatial patterns of biodiversity in heavily-defaunated landscapes may require novel methodological and analytical approaches. Our results indicate to build robust prediction maps it is beneficial to sample over large spatial scales, use multiple detection methods to increase detections for rare species, include anthropogenic covariates that capture different aspects of hunting pressure, and analyze data within a Bayesian multi-species framework. Our models further suggest that more remote areas should be prioritized for anti-poaching efforts to prevent the loss of rare and endemic species.

Keywords: Annamites, camera-trapping, defaunation, environmental DNA, multi-species occupancy, species richness, tropical rainforest, unsustainable hunting

Introduction

Tropical biodiversity is declining at an alarming rate as a result of intense anthropogenic pressures (Bradshaw et al, 2009). Although habitat loss and degradation are major drivers of these declines (Rosa et al, 2016), unsustainable hunting is increasingly emerging as the primary threat to wildlife in tropical biodiversity hotspots (Benítez-López et al, 2017). Large and medium-sized mammals tend to be particularly vulnerable to hunting because they often occur at lower average population densities, have lower intrinsic rates of increase, and longer generation times (Bodmer et al, 1997; Cardillo et al, 2005; Davidson et al, 2009). Indeed, the “empty forest syndrome” that Redford (1992) warned about almost three decades ago is now a commonplace phenomenon and, given the ever-increasing demand for wildlife products in the world’s tropical regions (Rosen & Smith, 2010; Ripple et al, 2016), this trend is unlikely to slow in the coming years. Without urgent and effective measures to address overexploitation, tropical wildlife populations will continue to decline, and species extinctions will follow. Confronting the pantropical defaunation crisis has become one of the most important challenges facing conservation today (Bradshaw et al, 2009).

Defaunation has been particularly severe in Southeast Asia, where high human densities, a thriving illegal wildlife trade, weak protected area governance, and rapid infrastructure development have synergistically contributed to unsustainable, industrial-scale hunting (Duckworth et al, 2012; Wilcove et al, 2013; Harrison et al, 2016). Within Southeast Asia, the Annamites ecoregion on the border of Vietnam and Laos has undergone severe defaunation as a result of widespread illegal hunting (Harrison et al, 2016; Timmins et al, 2016). Poaching in the Annamites is primarily accomplished by the setting of indiscriminate wire snares (Gray et al, 2018). Numerous mammals are regionally extinct (Walston et al, 2010; Brook et al, 2014), and even once common species now survive at low densities (Duckworth et al, 2016). High levels of unsustainable hunting pressure are particularly worrisome from a conservation perspective, because the region is home to several endemic mammal species. Mammals restricted to this ecoregion include the saola *Pseudoryx nghetinhensis*, large-antlered muntjac *Muntiacus vuquangensis*, Annamites dark muntjac species complex *Muntiacus rooseveltorum / truongsonensis*, Owston’s civet *Chrotogale owstoni*, and Annamite striped rabbit *Nesolagus timminsi* (Tordoff et al, 2003; Hurley et al, 2005; Long et al, 2005). Taken together, the high

poaching pressure and unique biodiversity in the Annamites make it one of the highest priority tropical regions in Southeast Asia for the prevention of imminent hunting-driven extinctions.
To maximize the effectiveness of conservation interventions to prevent unsustainable hunting in tropical biodiversity hotspots, it is imperative to make optimal use of limited conservation resources. In the Annamites, the magnitude of the snaring crisis (Gray et al, 2018), coupled with nascent protected area enforcement capacities and lack of sufficient resources, has overwhelmed efforts to adequately reduce this threat at the landscape level. Given these limitations, targeting snare removal efforts to specific areas within a landscape may be critical to reduce snaring to levels that would allow population recovery. To implement this approach, it is first necessary to identify priority areas. In the Annamites, areas that harbor threatened and endemic species are top priorities for targeted in situ protection measures. These species often occur at low densities, and are therefore particularly susceptible to local extirpation. To identify priority areas, it is important to apply appropriate analytical techniques. Species distribution modeling provides an ideal framework for mapping spatial patterns of biodiversity, and thus identifying conservation-priority areas (Rodríguez et al, 2007; Guisan et al, 2013).

There are, however, two fundamental challenges to the modeling of species distributions in tropical rainforest environments. First, tropical mammal species are often difficult to detect because they are rare, elusive, and occur at low densities. Second, even when these species can be detected, it may be difficult to obtain enough data to construct robust species distribution models (Cayuela et al, 2009), particularly in defaunated areas, where mammal populations are depleted.

Advances in noninvasive survey methods and statistical modeling techniques provide ways to address these challenges. Two noninvasive methods have revolutionized surveys for tropical mammals: camera-traps (Tobler et al, 2008) and high-throughput sequencing of environmental DNA (eDNA) (Bohmann et al, 2013). Camera-traps are a well-established method, and have been used to gather data on even the rarest of tropical mammal species (Whitfield, 1998; Raloff, 1999; Ganas & Lindsell, 2010). The use of eDNA is relatively new but shows considerable promise. Invertebrate-derived DNA (iDNA) approaches using terrestrial hematophagous leeches, in particular, have proven adept at detecting tropical mammals (Schnell et al, 2012; Schnell et al, 2018; Weiskopf et al, 2018). Recently, Abrams et al (2019) showed that combining camera-trapping and iDNA leech data has the potential to improve detection probabilities for tropical mammal species beyond what would be provided by each method independently. The joint camera-trap and iDNA approach thus opens new possibilities for obtaining detections of elusive tropical rainforest mammals, which in turn can be used to build robust species distribution models.

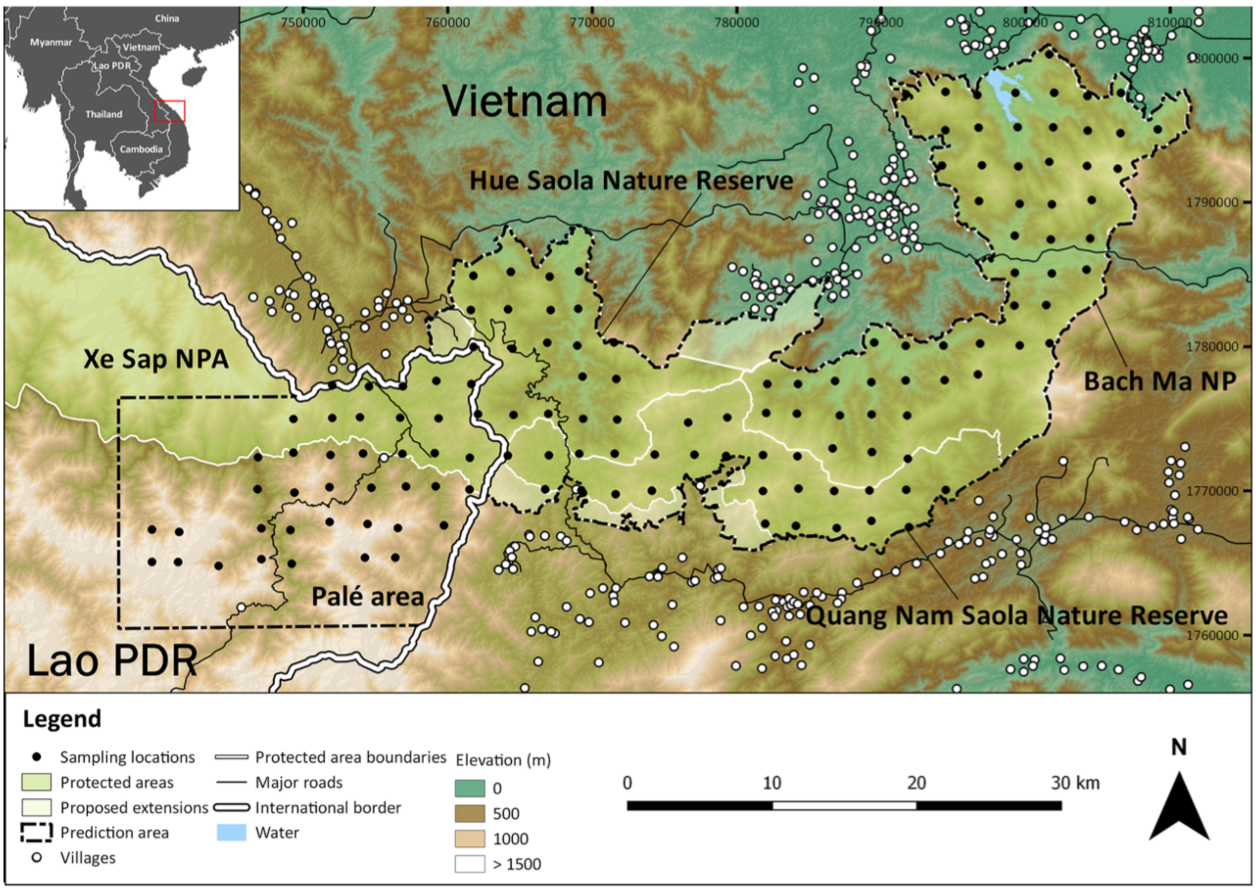

Figure 1. Map of camera traps and leech collection stations across five areas in the central Annamites landscape.

Even with improved detection methods and combined datasets, however, it may not be possible to obtain sufficient records for rare species. This shortfall represents a major issue because the rarest species are often the species of highest conservation concern. Multi-species occupancy models offer an analytical framework to address this challenge, as species with few detections borrow information from more abundant species, which improves precision of the parameter estimates for rare species (Tobler et al, 2015; Drouilly et al, 2018; Li et al, 2018). Because species-specific responses to covariates can be projected to unsampled areas, this approach can be used to generate maps of species potential occurrence (MacKenzie et al, 2017; Sollmann et al. 2017). Here, we collected a landscape-scale systematic camera-trapping and iDNA dataset across a protected area complex in the central Annamites landscape to identify priority areas for targeted conservation interventions. We used a multi-species occupancy framework and environmental and anthropogenic covariates to estimate species occurrence and predict species richness across the surveyed landscape. Our prediction maps provide insight into where to focus conservation efforts among individual study sites at the landscape scale, and more specifically can inform deployment of snare-removal teams within protected areas. We discuss our results within the context of informing targeted conservation interventions to prevent further defaunation, and species extinctions, within tropical biodiversity hotspots.

Methods

Study area

We conducted landscape-scale surveys in a large contiguous forest in the central Annamites landscape of Vietnam and Laos. The study area spans both countries and is divided into five administrative units. In Vietnam, we surveyed three sites: Bach Ma National Park (NP), the Hue Saola Nature Reserve (NR), and the Quang Nam Saola NR. In Laos, we surveyed the eastern section of Xe Sap National Protected Area (NPA) and an adjacent ungazetted forest near the village of Ban Palé (Fig. 1). Together these areas comprise approximately 900 km2 of mountainous terrain with elevations ranging between 100 – 2000 m asl. The dominant habitat type is wet evergreen tropical rainforest. Although the wider central Annamites region has experienced extensive past disturbance from defoliation and logging, habitat loss, degradation, and fragmentation within the past 20 years has been minimal within our study sites (Meyfroidt et al, 2008; Matusch, 2014). At the landscape scale, forest structure and habitat type are consistent across the study sites, characterized by mature secondary forest with a multi-tiered closed canopy. The Vietnam sites are surrounded by a densely-populated matrix consisting of human settlements, agricultural fields, and timber plantations. Human population density in the Lao sites is low and, aside from small-scale shifting cultivation, the landscape surrounding the survey areas has not been heavily modified. However, Vietnamese incursion into these areas for poaching and illegal gold mining is widespread (Tilker, 2014), and has been facilitated by the recent construction of a road connecting Vietnam and Laos that bisects the Palé area.

Poaching pressure is high across the landscape (Wilkinson 2016; WWF, 2017). Measures to mitigate illegal hunting differ in intensity and effectiveness among the five sites. Patrolling in Bach Ma NP is not intensive and has received less technical and financial support than the adjacent sites. The Hue and Quang Nam Saola NRs have benefited from WWF investment in enforcement since 2011 under the Carbon and Biodiversity (CarBi) project, maintaining active Forest Guard patrol teams to strengthen enforcement capacities in the field and provision of capacity development in patrol strategy, data collection and adaptive management for park staff. The Forest Guard teams are comprised of local community members and their primary role is to remove wire snares and destroy poacher camps (Wilkinson, 2017). Between 2011 and 2017, the patrols removed > 110,000 snares from the Hue and Quang Nam Saola NRs (WWF, 2017). The eastern section of Xe Sap NPA has also benefited from WWF-supported snare removal operations, although these efforts have not been as regular or intensive as in the Saola NRs. There are no active patrols in Palé, as it is outside of the Xe Sap NPA.

Data collection and preparation

We conducted systematic camera-trapping and leech surveys from November 2014 – December 2016. We set up a total of 140 camera-trap stations: 53 stations in Bach Ma NP, 21 in the Hue Saola NR, 25 in the Quang Nam Saola NR, 15 in eastern Xe Sap NPA, and 26 in the Palé area (Fig. 1; Table S2). Stations were spaced approximately 2.5 km apart (mean = 2.47 ± 0.233), aiming at spatial independence of sampling locations, and left in the forest for a minimum of 60 days (mean = 71.60 ± 16.39). Cameras were set 20 – 40 cm off the ground, operational 24 hour/day, and programed to take a three-photo burst with no delay between photographic events. To maximize detection probabilities, we set two camera-traps (Hyperfire Professional PC850, Reconyx®, Holmen, USA) at each station facing different directions. We treated the two cameras as a single station in our analyses. Camera-trap data was managed using the package camtrapR (Niedballa et al, 2015). We excluded arboreal species from our final species list, as these species are unlikely to be reliably detected by camera-traps placed at ground-level (Abrams et al, 2018). We also removed rodents and squirrels, given the difficulty of identifying these mammals to species-level using camera-trap images alone, and all domestic animals.

We complemented camera-trapping with the collection of terrestrial haematophagous leeches around the camera-trap stations. Leeches were collected once during camera-trap setup and again during retrieval. In Vietnam, leeches were collected in 20 x 20m sampling plots set up to assess microhabitat characteristics (see below). In Laos, we collected leeches in a grid around each camera trap station, with one camera-trap station per grid. We altered the leech collection strategy in Laos because sampling occurred during the dry season; increasing spatial coverage around the stations allowed us to collect leech numbers similar to the Vietnam sites. We separated the two types of leeches, brown and tiger, because the leeches potentially differ in their feeding behavior (Schnell et al 2015). All leeches of the same type from the same station and occasion were combined and processed as one leech bulk sample. Leeches were immediately placed in RNAlater and stored long-term at -20° C.

Leeches were processed using the laboratory procedures and bioinformatics pipeline described in Axtner et al (2019). The workflow is designed to minimize the risk of false positives that could arise from laboratory artifacts or misidentification during taxonomic assignment. To address these risks, it employs different levels of replication (i.e. extraction, PCRs), a curated reference database, and the probabilistic taxonomic assignment method PROTAX (Somervuo et al, 2017) that has been shown to be robust even when reference databases are incomplete (Rodgers et al., 2017, Richardson et al., 2017). Leech samples were digested, DNA was extracted, and then mitochondrial target DNA of host species was amplified with PCR and sequenced using Illumina high-throughput sequencing. We trained PROTAX models and weighted them toward 127 mammal and bird species expected to occur in the study area by assigning a prior probability of 90% to these species and a 10% probability to all others (Somervuo et al, 2017; see Table S2 for full weighted species list). Our protocol was slightly modified from Axtner et al (2019) in that we amplified the mitochondrial marker 16S in six PCR replicates for all samples and used genetic markers 12S and CytB only for samples where taxonomic assignment was still uncertain due to interspecific invariance or missing references (e.g. porcupines, viverrids, muntjacs). We accepted a species assignment when it was present in at least two independent PCR replicates (Axtner et al. 2019, Abrams et al. 2019). As with the camera-trapping data, we excluded arboreal species, rodents, squirrels, and domestic animals from the final species list.

Covariates

We hypothesized that mammal occurrence may be influenced by both environmental and anthropogenic factors. We measured three environmental features that characterize different aspects of microhabitat structure: canopy closure, vegetation density, and leaf litter. We used canopy closure as an indication of forest degradation, with lower values representing more disturbed habitat (Chazdon, 2003). Previous studies have shown that vegetation density may be an important microhabitat feature for some tropical mammals (Goulart et al, 2009; Martin et al, 2015; Mathai et al, 2017). Leaf litter impacts multiple aspects of vegetation community composition (Facelli & Pickett, 1991). It is also an important microhabitat for invertebrates and small vertebrates (Burghouts et al, 1992; Vitt & Caldwell, 1994), which are important food resources for insectivores and small carnivores.

To assess microhabitat features, we set up a 20 x 20 m plot around the camera-trap stations, with the centerpoint halfway between the two cameras, and oriented along the cardinal axes. To measure canopy closure we took vertical photographs at the centerpoint and at the corners of the grid. Canopy photographs were manually converted to black and white images using the GNU Image Manipulation Program (GIMP, 2017). We calculated percentage canopy closure (white pixels) for each image using R 3.4.0 (R Development Core Team, 2016). Values for each image were averaged to give a single canopy closure value for each station. To measure vegetation density we took photographs in each cardinal direction of a 1 x 1.5 m orange sheet positioned 10 m from the centerpoint. Photographs were processed using the canopy closure protocol, giving a single average vegetation density value for each station. We measured leaf litter percent cover in nine 1 x 1 m subplots located at the centerpoint, 10 m from the centerpoint in each cardinal direction, and at the plot corners. Each subplot was visually assigned a value from 0 to 4 based on the amount of leaf litter versus bare ground visible in each plot. Leaf litter values were averaged to give a single value for each station. For a detailed explanation of the microhabitat assessment see Abrams et al (2018).

In addition to the environmental covariates, we measured anthropogenic features that approximate hunting pressure. We use proxies for hunting pressure, rather than direct measures, for two reasons. First, we are not aware of any existing datasets that directly measure hunting pressure within our study sites. Second, robustly assessing poaching represents a difficult undertaking because illegal hunting is such a cryptic phenomenon. Although some studies have used presence or absence of people from camera-trapping data to represent direct measures of hunting pressure (Dias et al, 2019), such measures are not applicable in our landscape, because some local communities are allowed to legally enter the study sites to collect non-timber forest products. Further complicating the situation is the fact that these local people may engage in both legal non-timber forest product collection and illegal hunting in order to maximize potential profit. Given the difficulties in assessing hunting directly, we used measures of accessibility as proxies for hunting pressure in our study sites. Previous studies have shown accessibility and hunting to be correlated (Rao et al, 2005; Espinosa et al, 2014; Koerner et al, 2017). We used three covariates that capture different aspect of accessibility: distance from major cities, village density, and least cost path from major roads. We used city distance as a proxy for hunting pressure captured at the landscape scale. Although we measure distance to the nearest major city (Hue or Da Nang, both with population > 350,000), we also interpret this covariate as an approximation of accessibility to the densely-populated coastal areas of Vietnam. We chose to measure distance to the cities, rather than other points along the urbanized coastal areas, because Hue and Da Nang are known to be major hubs for the illegal wildlife trade (VanSong, 2003; Sandalj et al, 2016). Given the volume of bushmeat that passes through these markets (Sandalj et al, 2016), it is likely that these urban population centers create substantial natural resource demand shadows across the landscape, as has been shown in other tropical regions (Ape Alliance, 1998). We derived the city distance covariate by calculating the Euclidean distance from the camera-trap stations to the nearest major city using the package gDistance (Van Etten, 2017), then taking the lower of the two values. The city distance covariate is measured in meters, with increasing values indicating more remote areas. We then took the log of the covariate to approximate the non-linear effect that increasing distance likely has on accessibility. Village density serves as a proxy for hunting at the local scale. Local villagers often supplement their income by providing bushmeat to the bushmeat markets in regional towns and cities, and are therefore a primary driver of poaching in the central Annamites (MacMillan & Nguyen, 2014). Studies in other tropical regions have demonstrated mammal depletions surrounding local villages (Rao et al, 2005; Koerner et al, 2017; Abrahams et al, 2017). To calculate village density we first created a ground-truthed point shapefile layer documenting local villages around our study sites. We then created a heatmap in QGIS 2.18.9 (QGIS Development Team, 2016) using the village shapefile as the input point layer. To create the heatmap, we used the default quartic kernel decay function and set the radius to 15 km. The village density radius was chosen so that all individual sampling stations in our study landscape were covered in the final heatmap. Observations in the field indicate that all stations, even those in the most in the most remote areas, were subject to some level of hunting pressure. We then used the extract function in the raster package (Hijmans, 2019) to obtain heatmap values for each station. The village density covariate is unitless, with lower values indicating areas that are more remote. Finally, the least cost path covariate also serves as a proxy for hunting pressure at the local scale. However, it differs from the village density measure in two fundamental ways. First, the least cost path covariate explicitly incorporates accessibility based on terrain ruggedness characteristics, therefore providing a more accurate representation of remoteness than linear measures. Second, we calculated the least cost path covariate over three time periods (1994, 2004, and 2014) to better capture the amount of time that an area has been subjected to poaching pressure. The least cost path covariate therefore captures both spatial and temporal dimensions. To create the least cost path covariate we first used the timelapse function in Google Earth Engine (Gorelick et al, 2017) to generate a GIS layer of major roads in and around our study site for three time periods: 1994, 2004, and 2014. We converted the roads layer to points in QGIS. Next, we used the R package movecost (Alberti, 2019) to calculate travel time along least cost path routes from the stations to the nearest 50 points along the road layer, using a shuttle radar topography mission (SRTM) 30 m digital elevation model as the cost surface raster, and then selected the lowest value as the final least cost path value. We averaged the three values to give a single least cost path value for each station, which we use as an approximation of the time that an area has been accessible over the past 20 years. The roads least cost path covariate is measured in hours, with higher values indicating areas that take longer to access, and are therefore more remote.

We also included elevation as a covariate in our models. We consider elevation as both an anthropogenic and ecological covariate. Because higher elevation areas are more difficult to access, elevation serves as a measure of remoteness within our landscape. Elevation is also linked to a complex range of ecological attributes in the central Annamites, including subtle variations in forest structure and microclimate (Tordoff et al, 2003; Long, 2005).

We standardized all covariates. We tested for correlations between all possible pairs of covariates using Pearson's correlation plots. None of our covariates were highly correlated ($|r| < 0.6$.

Modeling framework

We adopted a hierarchical multi-species occupancy model to estimate species occupancy and richness (Dorazio & Royle, 2005; Dorazio et al., 2006). Occupancy models estimate the probability of species occupancy, ψ, while accounting for species detection, p, using temporally replicated detection/non-detection data collected across multiple sampling locations (MacKenzie et al., 2003). To convert camera-trapping data to an occupancy format (i.e., a detection matrix), we divided the active camera-trapping time for each station into 10-day sampling periods, yielding a minimum of six occasions for each station. For each station and sampling period, the detection matrix for a given species received an entry of "1" when the species was detected at least once during the 10-day period by at least one of the two cameras comprising the station. We chose to use a 10-day sampling period to minimize zero-inflation in the detection history matrix. We treated each leech collection event as a separate occasion for the stations. We defined z_{ij} as the true occupancy state (0 or 1) of species *i* at sampling station *j.* Occupancy state can be modeled as a Bernoulli random variable with the success probability ψ_{ij}, the occupancy probability of species *i* at site *j.* We defined *pijk* as detection probability for species *i* at station *j* during the kth sampling occasion, and y_{ijk} the observation (i.e., $y_{ijk} = 1$ if species i is observed at site *j*, occasion *k*, and 0 otherwise). Observing a species is conditional on its occurrence, so that y_{ijk} can be modeled as a Bernoulli random variable with success probability $z_{ij} \cdot p_{ijk}$.

Covariate effects on both parameters can be modeled on the logit scale. We included habitat and anthropogenic covariates on ψ_{ij} to investigate their potential effects on species occurrence. To avoid overparametizing the model, we first ran single-covariate models using each of the seven covariates that we selected a priori, and assessed covariate importance by evaluating effect sizes for each species in the community. Because the environmental covariates did not show strong effects on occupancy, with all species having 95% BCIs overlapping zero and most species showing overlapping 75% Bayesian Confidence Intervals (BCIs) (Fig. S3), these covariates were not included in the final model. Our final community model included four covariates on ψ_{ij}: city distance, village density, roads least cost path, and elevation. Following Abrams et al (2019), we used survey method (camera-trap, brown leech, or tiger leech) as a covariate on *p*. We accounted for varying survey effort by including number of days each camera-trap station was operational during each 10-day occasion (i.e., 20 days if both camera-traps at one station were operating for the 10 days) or number of leeches per sample on *p*.

We implemented the models in a Bayesian framework using JAGS (Plummer, 2003) accessed through the package rjags (Plummer, 2018). We used vague priors (e.g. normal distributions with mean zero and variance 100 for community-level occupancy and detection coefficients). We ran three parallel Markov chains with 250,000 iterations, of which we discarded 50,000 as burn-in. We assessed chain convergence using the Gelman-Rubin statistic, with values close to 1 indicating convergence (Gelman et al, 2004). We report results as posterior mean and standard deviation. We consider a coefficient to have strong support if the 95% Bayesian confidence interval (95% BCI, the 2.5% and 97.5% percentiles of the posterior distribution) does not overlap zero, and moderate support if the posterior 75% BCI does not overlap zero.

To test for spatial autocorrelation in response variables not accounted for by predictor variables, we followed an approach put forth by Moore and Swihart (2003). We calculated Moran's I using the moransI function from the R package lctools for residuals from occupancy models using a neighborhood distance of 2.5 km (average spacing of our sampling stations). We only found evidence of low to moderate spatial autocorrelation in occupancy model residuals in only 2 of the 23 species analyzed. We acknowledge that for these species we may underestimate occupancy. However, our analysis is concerned with comparisons of patterns across study sites, not among species, and for a given species, any bias should be similar across the sites.

To predict species richness across the landscape we first divided the study area into 200 x 200 m grid cells. We included proposed extensions for the Hue and Quang Nam Saola Nature Reserves in the prediction area. Next, we derived covariate values for each cell. For the city distance, village density, and roads least cost path covariates we followed the same protocols described above. Elevation values were extracted from an SRTM 30 m digital elevation model. We used estimates of the coefficients from the multi-species model linking covariates to occupancy probability to predict occupancy values for each species and grid cell and then summed the occupancy probabilities for all species per cell to produce species richness maps. To highlight areas of high richness for conservation-priority species, we produced a separate species richness map for the endemic species and those listed as Near Threatened or higher on The *IUCN Red List of Threatened Species*. To provide a further level of detail for the endemic species, we also produced single-species occupancy maps for Annamite striped rabbit, Annamite dark muntjac, and Owston's civet. We note that, although our sampling stations only covered part of the study sites, covariate values at the stations were largely representative of values across the sites. When we filtered the raster cells to remove cells that fell outside the range of our covariates at the sampling stations, we found that a small number raster cells were excluded. However, we present the full prediction maps here, both because the differences between the complete and filtered rasters were minor, and for visualization purposes.

We further used a modified Bray-Curtis index to assess compositional dissimilarity among the five study sites. The Bray-Curtis index calculates dissimilarity values by comparing composition in a reference assemblage with one or more target assemblages (Bray & Curtis, 1957). We adapted the index to compare predicted species occupancy probabilities between all possible site combinations, following the general framework proposed by Giocomini & Galetti (2013). To do this we sampled random values from the posterior distributions of species-specific occupancy probabilities for both the focal and target study sites. We repeated this procedure 30,000 times using Monte Carlo sampling to generate a distribution of values and took the mean of the posterior distribution. The final value gives an indication of how dissimilar the predicted community-level occupancies are among the sites. Dissimilarity values can range between -1 and 1. A value of 0 indicates no differences in occupancy between the focal and reference sites, a value of 1 indicates complete dissimilarity with the reference site having higher occupancies than the focal site, and a value of -1 indicates complete dissimilarity with the focal site having higher occupancies than the reference site. We calculated Bray-Curtis dissimilarities first for the entire community, and then for endemic and threatened species.

Results

We obtained data from 139 camera-trap stations totaling 17,393 trap-nights. The camera-trapping yielded 5,261 independent detections (Δ = 60 min between subsequent pictures of the same species at the same camera trap) of 27 terrestrial mammals. We identified all mammals to species, with the exception of the ferret badgers (*Melogale personata* and *M. moschata*) and pangolins (Manis pentadactyl and M. javanica), which we identified to the genus level due to the difficulty of identifying to species using camera-trap photographs, and the Annamite dark muntjac species complex *Muntiacus rooseveltorum* / *truongsonensis*, due to its unresolved taxonomic status. Our final species list resulted in 22 mammals. We obtained 193 leech samples totaling 2,043 leeches (1,888 brown, 155 tiger) from 98 stations (mean leeches / station = 21, standard deviation = 22. We were able to amplify and sequence DNA from 104 samples. PROTAX identified 25 mammals to the species level and seven to the genus level. The final species list from the leeches included 19 terrestrial mammals. Overall, the two survey methods provided similar species lists. The exceptions were pangolin, pig-tailed macaque *Macaca leonina*, spotted linsang *Prionodon pardicolor*, and yellow-bellied weasel *Mustela kathiah*, which were detected only in the camera-traps, and marbled cat *Pardofelis marmorata*, which was detected only in the leeches. The final species list used for the community occupancy analysis included 23 mammals. Four of these were threatened, three were Annamite endemics, and one species fit both categories.

Detection probabilities (p) within the mammal community varied among species and with respect to survey method. Estimates of occupancy (ψ) showed extreme heterogeneity among individual species.

Species-specific responses to the covariates were highly variable within the community (Fig. 2). Village density had the strongest negative response at the community level, with a community-level 95% BCI that did not overlap zero; at the species level, 16 species had a moderate negative and four species had a strong negative relationship with this covariate. No species responded positively to village density. There was a moderate positive relationship with elevation at the community level, with nine and four species showing moderate and strong associations with higher elevations, respectively. However, we also observed negative relationships with elevation in four species (one moderate and three strong). Due to mixed species-specific responses to distance to cities, the community response was close to zero. Specifically, six species showed a moderate positive relationship with city distance, while three species showed a moderate negative relationship, and four species showed a strong negative relationship. Responses to the road least-cost path covariate were generally weaker than the other three covariates, and the community response was close to zero. Five species had a moderate positive association with the road least cost path covariate, while four species (three moderate and one strong) showed a negative relationship with this covariate.

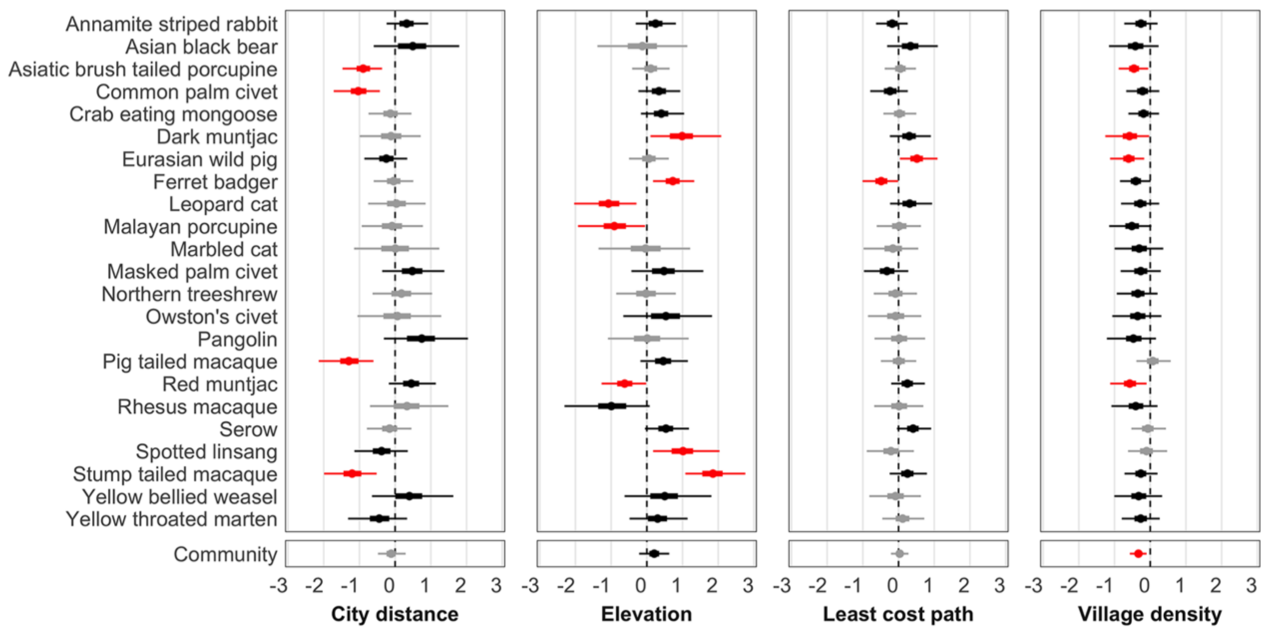

Figure 2. Standardized beta coefficients (mean, 95% BCI, 75% BCI, on the logit scale) showing covariate effects on species occupancy. Grey bars show relationships in which the 75% Bayesian credible interval (BCI) does not overlap zero, black bars indicate that the 75% interval does not overlap zero but the 95% does overlap zero, and red bars indicate that the 95% interval does not overlap zero. The community response is shown in the lower panel.

		Study site					
		Bach Ma NP	Quang Nam SNR	Hue SNR	Xe Sap NPA	Palé	All sites
Species richness	Full community	6.52 ± 1.39	6.32 ± 1.00	7.00 ± 1.24	6.89 ± 0.98	8.25 ± 1.13	7.02 ± 1.41
	Threatened and endemic species	1.79 ± 0.77	1.80 ± 0.65	1.85 ± 0.66	2.10 ± 0.70	2.97 ± 0.85	2.12 ± 0.89
Species occupancy	Annamite striped rabbit	0.15 ± 0.04	0.24 ± 0.04	0.20 ± 0.05	0.28 ± 0.03	0.36 ± 0.05	0.24 ± 0.09
	Annamite dark muntjac	0.24 ± 0.18	0.35 ± 0.15	0.30 ± 0.18	0.41 ± 0.17	0.66 ± 0.19	0.39 ± 0.24
	Owston's civet	0.05 ± 0.02	0.06 ± 0.02	0.05 ± 0.02	0.08 ± 0.02	0.13 ± 0.05	0.07 ± 0.05

Table 1. Table 1: Predicted species richness and species occupancies (mean ± SD) for five study sites in the central Annamites landscape, from multi-species community occupancy model fit to 23 mammal species. Full community indicates richness for all 23 species. Threatened and endemic species indicates richness for 10 species that are endemic and / or listed as Near Threatened or higher on The IUCN Red List of Threatened Species. Species occupancy shows predicted occupancies for each of the three Annamite endemic mammals. Occupancy values range from 0 to 1.

Figure 3. Predicted species richness across five study sites in the central Annamites landscape. Histogram showing proportion of cells in each area for predicted species numbers (left panel) and prediction map (right panel) based on community occupancy model. Predicted richness for: (**a**) all species, and **(b)** threatened and endemic species.

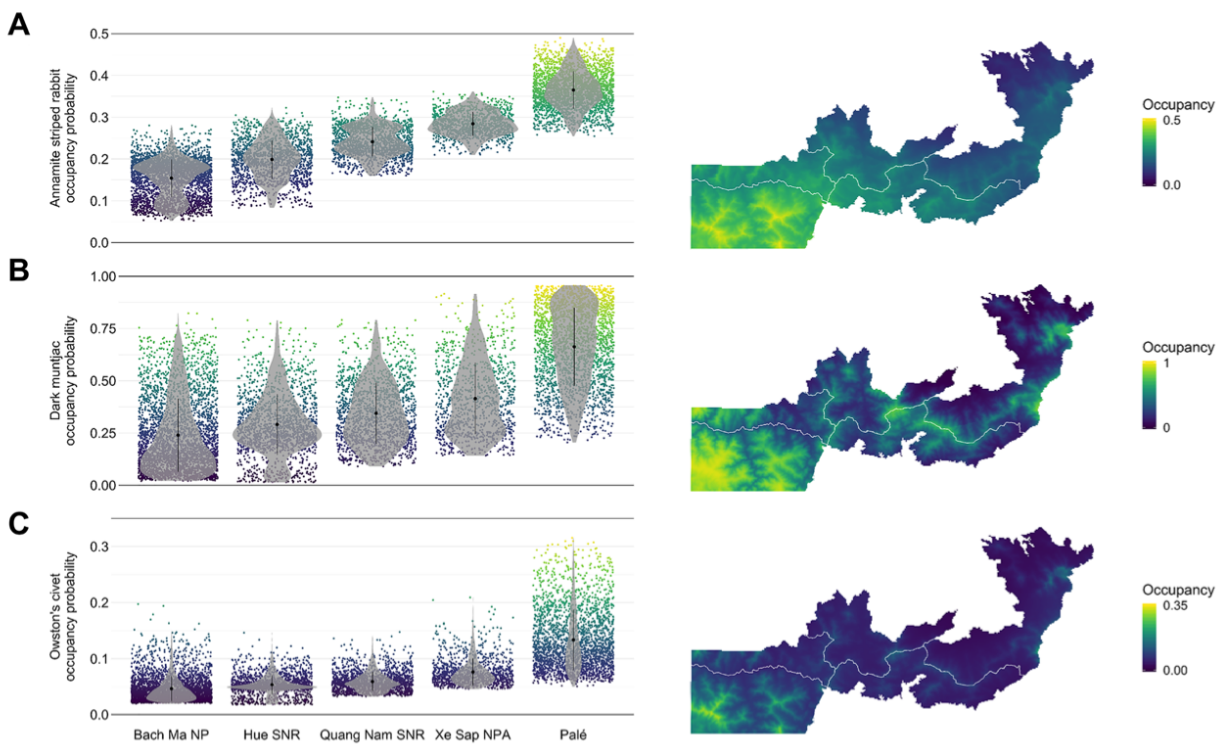

Figure 4. Predicted occupancies for three Annamite endemic species with violin plot showing predicted occupancy for each of the five study sites (left panel) and prediction map (right panel) based on community occupancy model. Predicted occupancies for **(a)** Annamite striped rabbit, **(b)** Annamite dark muntjac, and **(c)** Owston's civet.

Average predicted species richness for the full community was substantially lower than the total number of species detected in the study, and was similar among the study sites (Table 1, Fig. 3A). The Palé area had slightly higher predicted species richness than the other four areas. Richness of threatened and endemic species followed a similar pattern, with all sites showing low richness relative to the total number of conservation-priority species detected, and the highest richness in the Palé area (Table 1, Fig. 3B). Predicted occupancies for the three Annamite endemic mammals showed heterogeneity among species and sites (Table 1, Fig. 4). Annamite dark muntjac had the highest predicted occupancy, followed by Annamite striped rabbit, followed by Owston's civet. All three endemics had highest predicted occupancies in the Palé area, followed by Xe Sap NPA, Quang Nam Saola NR, Hue Saola NR, and finally Bach Ma NP.

The Bray-Curtis dissimilarity index values showed similar values for full community occupancies among Bach Ma NP, the Hue and Quang Nam Saola NRs, and Xe Sap NPA (Table 2). However, the Palé area had negative and high defaunation index values when compared to every other site, indicating that occupancies for the full suite of species are higher for this area. Dissimilarity values for endemic and threatened species showed a similar pattern. The fact that Palé area showed negative and higher dissimilarity values for both the full community and for conservation-priority species suggests that, within the context of species occurrence, the site has undergone less severe defaunation than the other sites.

Discussion

Our study highlights the landscape-scale effects of unsustainable hunting on the occurrence and distribution of terrestrial mammals within a tropical biodiversity hotspot. For a structurally-intact tropical rainforest habitat, average predicted species richness (7.02) was low (Table 1; Fig. 3A & B). For comparison, Deere et al (2018) found a predicted species richness of 14.12 in logged forests in Malaysian Borneo, and a richness of 4.54 in adjacent oil palm plantations. Given the largely homogenous landscape-scale forest structure and habitat in our study sites, the low predicted species richness is likely indicative of a community that has undergone severe hunting-driven defaunation. The extent of faunal impoverishment is further supported by the fact that we failed to record almost half of the mammal community would be expected to occur in these sites based on historical distribution maps (Tilker & Abrams, 2019).

	Bach Ma NP	Quang Nam SNR	Hue SNR	Xe Sap NPA	Palé
Bach Ma NP	0	-0.0006 ± 0.0205 0.0431 ± 0.0205	0.0406 ± 0.0119 0.0049 ± 0.0119	0.0350 ± 0.0233 0.0841 ± 0.0233	0.1338 ± 0.0315 0.2547 ± 0.0315
Quang Nam SNR	0.0006 ± 0.0205 -0.0431 ± 0.0205	0	0.0412 ± 0.0206 -0.0382 ± 0.0205	0.0357 ± 0.0061 0.04127 ± 0.006	0.1346 ± 0.0193 0.2150 ± 0.0193
Hue SNR	-0.0406 ± 0.0119 -0.0049 ± 0.0119	-0.0412 ± 0.0205 0.0382 ± 0.0206	0	-0.0055 ± 0.0206 0.0793 ± 0.0206	0.0938 ± 0.0297 0.2503 ± 0.0297
Xe Sap NPA	-0.0350 ± 0.0233 -0.0840 ± 0.0233	-0.0357 ± 0.0061 -0.0413 ± 0.006	0.0055 ± 0.0206 -0.0792 ± 0.0206	0	0.0995 ± 0.0174 0.1754 ± 0.0174
Palé	-0.1338 ± 0.0315 -0.2547 ± 0.0315	-0.1346 ± 0.0193 -0.2149 ± 0.0192	-0.0938 ± 0.0297 -0.2502 ± 0.0297	-0.0995 ± 0.0174 -0.1754 ± 0.0174	0

Table 2. Bray-Curtis dissimilarity values (mean ± SE) calculated using predicted occupancy values per site for all mammal species (top value) and for threatened and endemic species (bottom value). Values range from 0 to 1, with 0 indicating complete similarity in species occupancies between the sites, and 1 indicating complete dissimilarity.

At the landscape level predicted richness was broadly similar among the five study sites, although the more remote Palé area showed the highest richness values, especially for the endemic and threatened species (Fig. 3). The Bray-Curtis dissimilarity values show a similar geographic pattern, with the Palé area having higher dissimilarity values compared to the other four areas, indicating less defaunation (Table 2). For the three endemic species, Bach Ma NP showing the lowest predicted occupancy, followed by the Hue Saola NR, Quang Nam Saola NR, Xe Sap NPA, and Palé. These findings indicate a strong landscape-scale defaunation gradient for the three endemic species (Fig. 4). Our covariate responses suggest that this gradient reflects an increasing level of remoteness (Fig. 2). Bach Ma NP lies near densely-populated coastal areas of Vietnam, has lower average elevations, and has been accessible for decades by a well-established road network. In the westernmost section is the Palé area, which is far from major cities, has few villages, higher elevations, and has only recently been accessible by road. The Saola NRs and Xe Sap NPA fall between these two extremes. Furthermore, these areas have had some level of active enforcement in the last few years, which may have slowed the decline of mammal populations.

Our results provide information that is directly applicable to conservation planning in this landscape. From a biogeographic perspective, protecting the Palé area is a top priority for the conservation of threatened and endemic species. Indeed, it may be the only place in our survey sites to harbor Owston's civet, Asian black bear *Ursus thibetanus*, and marbled cat (Fig. S7). Our predictive maps offer a robust scientific framework to support ongoing initiatives to grant Palé formal protected area status as a first step to implementing active protection measures. Our maps also provide information to guide targeted snare-removal efforts within protected areas. This information is especially useful for the Hue and Quang Nam Saola NRs, where WWF and local partners are operating snare-removal teams, but have not yet been able to significantly reduce snaring pressure across the wider protected area complex (Wilkinson, 2016). We suggest that, to maximize the impact of snare-removal efforts on conservation-priority species, the teams should focus on the more remote areas along the border of the two reserves, and in the border area of the Quang Nam Saola NR and Bach Ma NP. It is possible that these areas have maintained higher occupancies of conservation-priority species because they are more difficult to access and, as a result, have cumulatively experienced less snaring pressure. However, remoteness will not protect these areas for long. An increase in road development in recent years has created a situation where even the most remote locations in the Saola NRs can now be reached within a single day from the nearest access point, meaning that no area is inaccessible for a motivated hunter. Given the likely relationship between accessibility and increased hunting pressure, it seems inevitable that, in the absence of scaled-up enforcement efforts, snaring pressure will continue to increase in the more remote areas, especially as other parts of the protected areas become increasingly empty and poachers are forced to travel further distances to maintain comparable levels of offtake (Kümpel et al, 2010). Although threatened and endemic species appear to be absent from much of Bach Ma NP, there are isolated high-elevation areas that should be considered for intensive anti-poaching efforts. Our models indicate that the border areas of eastern Xe Sap NPA Area have undergone moderate to severe defaunation. Given that this area appears to be heavily hunted by Vietnamese poachers (Tilker, 2014), such a finding is not unexpected. The eastern section of the protected area is nonetheless a top priority for continued protection efforts, both because it may be a stronghold for the endemic Annamite striped rabbit , and more generally because effective enforcement can serve as a buffer from further cross-border incursions into the Palé area. In a best-case scenario, reducing snaring pressure in core areas within this landscape could not only prevent the local extirpation of conservation-priority species, but also allow their populations to rebound (see Steinmetz et al, 2010 for a case study on large mammal population recovery following mitigation of unsustainable hunting pressure).

In many ways, our study landscape exemplifies classical "empty forest syndrome" (Redford, 1992). All large and medium-sized predators (with the exception of Asiatic black bear), as well as all megaherbivores, appear to be locally extirpated (Tilker & Abrams et al, 2019). Large ungulates have been hunted out from most of the landscape. Yet our findings show that even in this empty forest, conservation-priority species still persist, albeit at extremely low occupancies. Based on these results, we suggest that the conservation potential of defaunated landscapes should not automatically be dismissed in the absence of comprehensive surveys. It is important that such surveys use sufficient sampling effort and be conducted over a large spatial extent for two reasons. First, species often show extreme spatial heterogeneity in defaunated landscapes because local extinctions necessarily result in reduced, often patchy, distributions. Surveys over wider areas are more likely to detect remnant populations. Second, working over larger spatial scales may better capture the underlying factors influencing species distribution, which can be especially important in landscapes characterized by complex anthropogenic pressures operating at multiple spatial scales. In our study, it was only by sampling the wider forest complex that we were able to adequately characterize the full spectrum of anthropogenic factors that appear to impact species occurrence patterns. Large-scale surveys require substantial resources. We acknowledge that, with multiple competing conservation objectives and finite resources, landscape-scale surveys may not always be possible. However, we note that because this approach can enhance the efficiency of targeted interventions, it is possible that limited conservation resources may be saved in the long term.

To overcome the challenge of detecting rare and elusive tropical mammal species, we used two complimentary survey methods: camera-trapping and leech collection. Although camera-trapping detected more species overall, leeches provided our sole detection for marbled cat, and doubled the number of records for two rare species, Owston's civet and Asian black bear. Moreover, while camera-trapping detection probabilities were higher for most species in our analysis, leeches had higher average detection rates for both Asian black bear and the endemic dark muntjac. Our results are consistent with the findings of Abrams et al (2019) that demonstrate the advantages of using both camera-trapping and eDNA to increase detection probabilities for tropical mammals. We further suggest that because utilizing multiple methods may increase detections of rare species, this approach could be especially important when surveying faunally impoverished systems. Future surveys using joint detection methods need not rely only on leeches but could use other sources of eDNA, such as water (Ushio et al, 2017) or ticks (Gariepy et al, 2012), or incorporate other noninvasive sampling techniques, such as acoustic monitoring devices (Kalan et al, 2015). The Bayesian modeling approach that we used, adapted from Abrams et al (2019), is flexible with regard to the underlying detection method used to generate spatial or temporal replicates.

We found that species occurrence in our study area appears to be primarily driven by anthropogenic factors, with no strong influence from the habitat covariates that we assessed in our models (Fig. S3). This finding was unexpected, given the importance of vegetation structure in explaining mammal occurrence patterns in other tropical rainforests (Goulart et al, 2009; Mathai et al, 2017; Sollmann et al, 2017). One possible explanation is that, as anthropogenic pressures in a landscape increase, ecological relationships weaken. Several hypothetical scenarios could give rise to this situation. Spatially nonrandom hunting pressure could, for example, differentially impact areas of preferred habitat, leaving higher occupancies in less suitable areas. Alternatively, intensive hunting across a landscape could drive stochastic local extinctions, leaving remnant populations that are distributed randomly with respect to habitat. Regardless of the underlying process, the failure of habitat-based indices to reflect faunal biodiversity, thus the “environmental decoupling” of species-habitat relationships, has broad implications. Biodiversity assessments that rely solely on remote-sensed habitat-based measures may provide information that is inaccurate because they do not accurately capture species occurrence patterns. Recently, a growing number of scientists have called for the development of standardized remote-sensing parameters, often referred to as Satellite Remote-Sensing Essential Biodiversity Variables (SRS-EBVs), to monitor biodiversity at the global scale (O'Connor et al, 2015; Skidmore et al, 2015; Pettorelli et al, 2016). While we acknowledge the value of earth observation data to provide insight into biodiversity patterns and processes at large scales (Bush et al, 2017), our results indicate that remote-sensed habitat-based measures may provide little information on the status or distribution of wildlife in defaunated landscapes. In tropical rainforests subject to hunting pressure, there is likely no substitute for large-scale in situ surveys to collect primary biodiversity data.

Our results underscore the importance of incorporating anthropogenic factors in studies that seek to explain or predict species occurrence in landscapes characterized by high human pressure. Furthermore, our findings suggest that to build robust distribution models it may be beneficial to incorporate a diverse suite of anthropogenic covariates that capture different aspects of this pressure. We used measures of village density and city distance as proxies for accessibility at the local and landscape scales, respectively. Previous studies have shown the impact of similar accessibility measures on wildlife communities at different spatial scales (Schuette et al, 2013; Koerner et al, 2017; Torres et al, 2018). Our least cost path covariate adds an additional dimension to these accessibility measures, both because it takes into account the ruggedness of the terrain in our landscape, and because it is calculated over a 20-year window. Finally, we use elevation as a proxy for both local accessibility and a complex set of ecological attributes. The relative contribution of anthropogenic and environmental traits to species occurrence along elevational gradients in the Annamites represents an intriguing question. Future studies in the region that measure a wider range of microhabitat characteristics, and ideally are conducted in areas under less severe hunting pressure, may provide insight into this issue.

Given the current magnitude of hunting across the world's tropical rainforests (Harrison, 2011; Ripple et al, 2016; Benítez-López et al, 2017), and future projections for population growth (Gerland et al, 2014) and road expansion in developing countries (Lawrence et al, 2014), it is likely that defaunation will become increasingly prevalent in tropical regions. Confronting the pantropical defaunation crisis will require a well-resourced, multi-faceted approach from conservation stakeholders worldwide. Because specific threats and potential solutions necessarily depend on local context, effective strategies to prevent unsustainable hunting must be site-specific. One constant that is applicable to conservation initiatives in all tropical hotspots, however, is that resources are limited. We show that, within this context, understanding spatial patterns of defaunation can help stakeholders prioritize areas for conservation activities, and therefore more effectively use finite conservation resources.

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Chapter 4

A little-known endemic caught in the Southeast Asian extinction crisis: the Annamite striped rabbit *Nesolagus timminsi*

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Author contributions

Study design: AT, RS, AW; fieldwork for systematic camera trap survey: AT, AN; design of non-systematic camera trap survey: TVN, ATN; analysis of camera trap data: AT, JFA; analysis of remote sensing data: TB, JN; led the manuscript writing: AT. JFA, AW; commented and reviewed the manuscript: all authors.

Abstract

The Annamite mountains of Viet Nam and the Lao People's Democratic Republic (Lao PDR) are an area of exceptional mammalian endemism but intensive poaching has defaunated much of the region, creating an extinction crisis for the endemic species. To make efficient use of limited conservation resources, it is imperative that conservation stakeholders obtain basic information about poorly known and threatened endemics. We present the first comprehensive information on the ecology, distribution and status of the little-known endemic Annamite striped rabbit *Nesolagus timminsi*. We used a systematic camera-trapping design to study the species in five areas in Viet Nam and Lao. In 29,180 camera-trap-nights we recorded 152 independent events at 36 of 266 stations. We obtained an additional 143 independent detections across 12 stations from a supplementary non-systematic survey. We analyzed activity patterns and social behavior. We also used single-species occupancy models to assess factors that influence occupancy at the landscape scale. We used N-mixture models to obtain local abundance estimates in one target area. The Annamite striped rabbit was found to be nocturnal and primarily solitary. Species occupancy was best explained by a proxy for past hunting pressure, with no significant relationships to current anthropogenic or environmental factors. Local abundance was 0.57 individuals per camera-trap station for one of our sites, and estimated to be zero at the other site where hunting appears to have been more intense. Our results provide information on priority areas for targeted anti-poaching efforts and give the first conservation baseline for the species.

Keywords

Annamite striped rabbit, Annamite mountains, *Nesolagus timminsi*, N-mixture, occupancy, snaring, South-east Asia, tropical rainforest

Introduction

South-east Asia is a global biodiversity hotspot with exceptionally high levels of mammalian richness and endemism (Schipper et al., 2008). Rapid rates of deforestation and widespread poaching have caused precipitous declines in mammals across the region (Duckworth et al., 2012), driving regional extinctions of several conservation-priority species (Brook et al., 2012) and threatening others with global extinction (Tilker et al., 2017). However, even in this biodiversity hotspot, diversity and threat levels are not uniformly distributed. Sub-regional centres of endemism are of particular concern from a conservation perspective because small global geographical range is a strong predictor of extinction risk (Cardillo et al., 2008). To design effective mitigation mechanisms for range-restricted species in endemism hotspots it is imperative that conservation scientists obtain basic information on status and distribution, as well as an understanding of the effect of anthropogenic pressures. This information is especially critical for little-known endemic species that occur in areas that are known to be under threat.
The Annamite Range, a mountain chain straddling the border of Vietnam and Lao People's Democratic Republic (Lao PDR), has one of the highest concentrations of endemic mammal species in continental South-east Asia (Baltzer, 2001; Tordoff et al., 2003). Several of these species are new to science, highlighting how little is known about the biodiversity of this ecoregion (Sterling & Hurley, 2005). All Annamite endemic mammals are facing an extinction crisis. Although habitat loss has been a factor in their decline, the primary threat is extensive poaching through the use of wire snares (Gray et al., 2017, 2018) to supply the thriving wildlife trade in Indochina (Sodhi et al., 2004; Harrison et al., 2016). Although snaring is prohibited by law in both Viet Nam and Lao, enforcement is weak and most protected areas are so-called paper parks that offer little or no protection to conservation-priority species (Brook et al., 2012). As a result of high demand for wildlife products and lax enforcement, industrial-level commercial snaring is pervasive and has caused widespread empty forest syndrome (Redford, 1992) across the entire Indochina region.

The Annamite striped rabbit *Nesolagus timminsi* is among the most understudied of the endemic mammals of this region and is currently categorized as Data Deficient on the *IUCN Red List of Threatened Species* (Abramov et al., 2008). The species was first discovered by science in 1996 from specimens found in a local market in central Lao PDR (Surridge et al., 1999; Averianov et al., 2000) and shortly thereafter was confirmed to occur in neighboring Vietnam (Dang et al., 2001). With a dark dorsal stripe, rust-colored rump, and short tail and ears, it is unlike any other lagomorph in mainland South-east Asia. The little information that biologists have indicates that the species is restricted to wet evergreen forest with little or no dry season and has no clear elevational preference (Abramov et al., 2008). The species' known range extends from the northern to central Annamites (Dang et al., 2001; Abramov et al., 2008). Like all terrestrial mammals in the Annamites it is threatened by snaring (Dang et al., 2001; Abramov et al., 2008; Tilker et al., 2017).

Standardized surveys are needed to obtain the basic information necessary to make informed conservation management decisions for the Annamite striped rabbit. However, obtaining robust data on the species has proven challenging, both because of the dense tropical rainforest and rugged terrain where it lives and the fact that all mammal densities are severely depressed across the Annamites. Automatic camera traps provide an effective way to gather data on the species. We conducted systematic camera trapping across five areas in Vietnam and Lao PDR with the objective of gathering information on the ecology, distribution and status of the Annamite striped rabbit. Here we present data on the species' activity patterns and sociality; analyse its distribution and the factors influencing its occurrence, using an occupancy model framework; and use an N-mixture framework to estimate local abundance. We discuss the implications of our results for the conservation of this little-known endemic species.

Study area

We conducted camera-trap surveys in a large contiguous forest block in the central Annamites landscape spanning both Vietnam and Lao PDR. The forest is divided into five administrative areas. In Viet Nam, surveys were conducted in three protected areas: Bach Ma National Park and the Thua Thien Hue and Quang Nam Saola Nature Reserves. In Lao, surveys were conducted in the eastern section of Xe Sap National Protected Area and an adjacent ungazetted forest block to the south near the village of Ban Palé (Fig. 1). Together these areas cover c. 900 km2. The study area has a tropical monsoon climate and is characterized by rugged terrain, with elevations of 100–2,000 m. The dominant habitat type is closed-canopy wet evergreen forest. Montane forest occurs at the highest elevations (above c. 1,300 m). Forests in this area have an extensive history of past disturbance, including chemical defoliation during the America—Vietnm war (Stellman et al., 2003), state-enterprise logging during the 1970s and 1980s (Yen et al., 2005), and ongoing illegal timber extraction. Bach Ma National Park and the Saola Nature Reserves are surrounded by a densely populated human-modified landscape. By contrast, population density in the Lao sites is low and they do not contain extensive human-modified areas. However, the Lao sites are heavily utilized by Vietnamese poachers, and mining and illegal logging operations (Tilker, 2014). A road bisecting the eastern section of Xe Sap National Protected Area and the Palé area facilitates access from neighboring Viet Nam. Despite this accessibility, the Palé area (c. 150 km2) is one of the most under-surveyed areas in the Annamites. The lack of past survey effort could be because of its particularly difficult terrain: elevations are 500–2,000 m (mean = 1,109 ± SD 307), with 59% of the area above 1,000 m, and a mean slope of 25.89 ± SD 10.47°.

Levels of active protection are generally low but vary in intensity across the landscape. Since 2011, WWF has provided support to the local government counterparts in protected area management in both Viet Nam and Lao. As part of this initiative, snare-removal teams have been active in the Saola Nature Reserves and eastern Xe Sap National Protected Area. In a 5-year timespan the teams removed >75,000 snares from the Saola Nature Reserves (Gray et al., 2018). There is no evidence of active patrolling efforts in Bach Ma National Park and Palé. Historically, these sites supported a representative suite of Annamite endemic and near-endemic species, including the saola *Pseudoryx nghetinhensis*, Owston's civet *Chrotogale owstoni*, the large-antlered muntjac *Muntiacus vuquangensis* and Edwards's pheasant *Lophura edwardsi* (Tordoff et al., 2003; Sterling & Hurley, 2005). However, intensive snaring has wiped out many terrestrial mammal and bird species (Harrison et al., 2016; Gray et al., 2017, 2018; Tilker et al., 2017).

Methods

Data collection and preparation

Systematic camera trapping was conducted during November 2014–December 2016 in two phases: (1) a coarse-grid phase, in which camera-trap stations were spaced c. 2.5 km apart across the study site, and (2) a fine-grid phase, during which intensive camera trapping was conducted over a smaller area using a clustered design (Fig. 1). Camera traps were stationed along animal trails, ridgelines and water sources to maximize mammal detections. All cameras were placed on trees, 20–40 cm above the ground, were operational 24 hours per day, and were left in the field for a minimum of 60 days. At each station two independent white-flash camera traps (Reconyx

Hyperfire Professional PC850; Reconyx, Holmen, USA) were set. The coarse-grid phase was

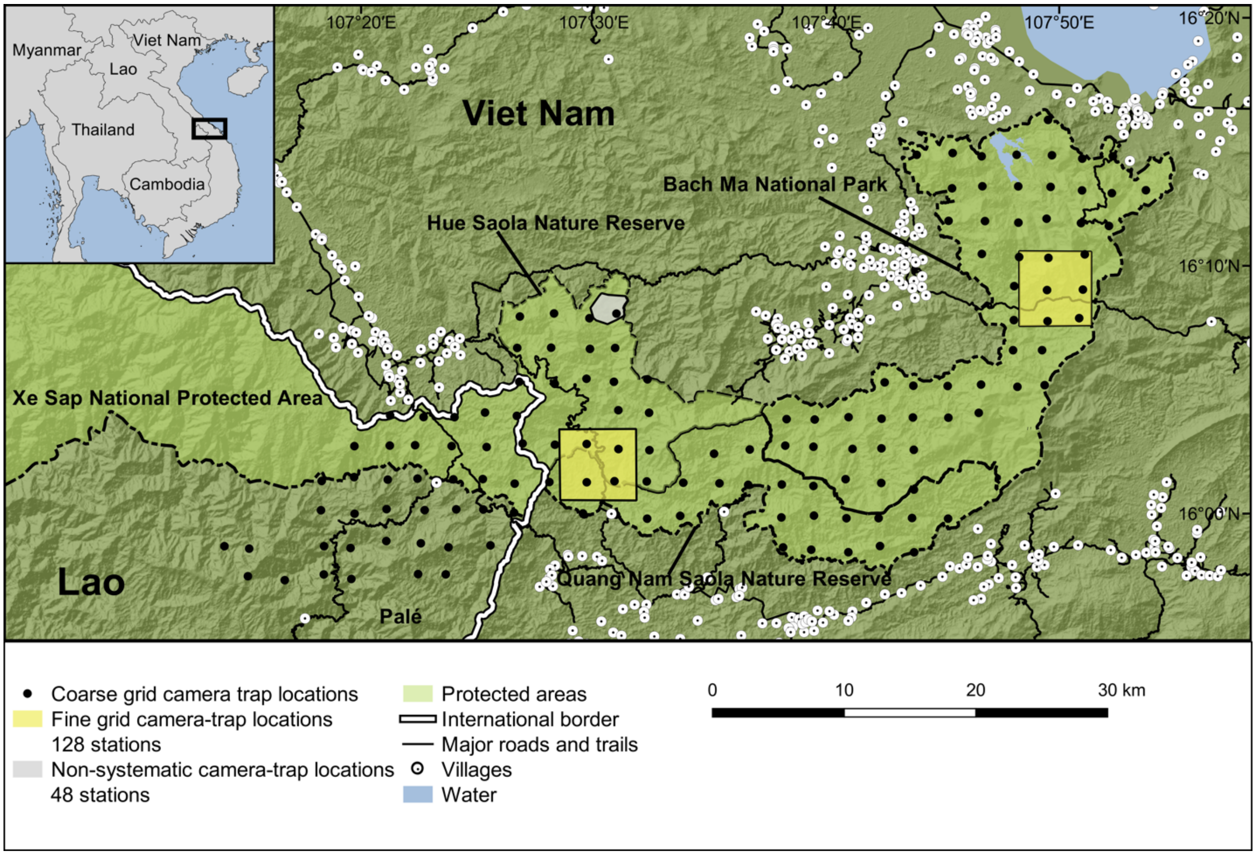

Figure 1. Camera trap locations across all study sites in the central Annamites landscape of Vietnam and Lao PDR.

designed to provide data that could be analyzed in an occupancy framework. A total of 139 coarse-grid stations were set up across the five sites: 53 stations in Bach Ma National Park, 46 in the Saola Nature Reserves, and 40 in the Xe Sap National Protected Area and Palé area. In this phase, the two cameras at each location were set facing in different directions. For analysis, we treat the two cameras as a single station. We conducted the coarse-grid camera trapping over three consecutive time periods (Table 1).

The fine-grid survey was conducted in core areas of Bach Ma National Park and the Saola Nature Reserves, where a total of 128 individual stations were set up (64 at each location). The stations were arranged in 16 clusters, spaced c. 1.5 km apart. Each cluster consisted of four camera-trap stations, spaced c. 500 m apart and arranged in a square. At each station a pair of cameras was positioned facing each other to photograph both sides of a passing animal. The fine-grid phase was designed to provide data that could be used to estimate density or abundance for species that have individually recognizable markings. Exact fine-grid survey locations within the larger protected areas were chosen to cover areas that appeared to support higher-than-average mammal densities based on information from the coarse-grid dataset.

In addition to the systematic survey, we use data from an opportunistic camera-trap survey (Bushnell Trophy Cam; Overland Park, USA) conducted in the Hue Saola Nature Reserve during November 2015–January 2017, to provide additional information on activity patterns and sociality of the Annamite striped rabbit.

To examine factors that influence Annamite striped rabbit occupancy across our study site we assessed habitat-related and anthropogenic features at both micro- and macro-scales (Table 2). In the field we established a 20 x 20 m grid around the center point of our coarse-grid stations to demarcate the area for which we collected microhabitat data. We took canopy photographs at the center point and the corners of the grid to characterize the microhabitat vegetation. To assess vegetation density, we took photographs in each cardinal direction of a 1 x 1.5 m orange sheet positioned 10 m from the center point. Other in situ habitat features that we measured include the number of bamboo stands, number of dead fallen trees, and number of water sources within the grid. To assess human activity at the camera-trap locations, we recorded human signs. Landscape-level features were evaluated using remote imagery and available geographical information system (GIS) layers. We used 5-m resolution 3A level RapidEye imagery for remote sensing. We used the Random Forest model from the randomForest package in R 3.4.0 (R Core Team, 2016) to group imagery into five categories: forest, plantations, degraded areas, bare ground, and water. To evaluate habitat quality we used a weighted mean to calculate forest score, with weights given as follows: plantations, roads and bare areas = 0, degraded areas = 1, and forest = 2. In this classification scheme a higher score corresponds to higher habitat quality. Forest score was calculated within a 50 m radius of each station (following Niedballa et al., 2015). Terrain ruggedness was measured within a 270 m neighborhood around each station using a shuttle radar topography mission (SRTM) 30 m digital elevation model. We also used the digital elevation model to further enhance water class by creating a hydrology layer using the r.terraflow function in QGIS 2.18.9 (QGIS Development Team, 2016), then calculated Euclidean distance from major streams with package gDistance in R. Euclidean distance to villages and roads was also calculated with gDistance.

Site	Survey	Dates	Stations	Camera trapping nights	Annamite striped rabbit detections*	Mammal and large galliform detections*
Bach Ma NP	Coarse grid	November 2014 - January 2015 July 2015 - October 2015	53	6,742	8	612
	Fine grid	March 2015 - May 2015	64	4,146	0	906
Hue and Quang Nam SNRs	Coarse grid	August 2015 - December 2015	46	6,480	48	978
	Fine grid	December 2015 - March 2016	64	4,347	54	1082
	Nonsystematic	November 2015 - January 2017	48	17,190	142	N/A
Xe Sap NPA / Pale region	Coarse grid	July 2016 - December 2016	39	7,465	44	552

Table 1. Details of camera trap surveys conducted in a large forest b lock in the central Annamites landscape of Vietnam and Lao PDR, with survey site, phase, date, number of stations, number of camera trapping nights, number of detections of Annamite striped rabbit, and number of detections of mammal and large galiform species.

Two other anthropogenic factors that could influence Annamite striped rabbit occupancy are current protection levels and past hunting pressure. To evaluate current protection we assigned each study area a binary score: 1 indicates presence of active snare-removal teams and 0 indicates no known patrolling. To approximate past hunting levels we used the number of detections of snaring-sensitive species, defined as all mammals and galliforms with body mass > 500 g, scaled by the number of days the camera trap was active. However, we recognize the possibility that other ecological or sampling-based factors, such as camera-trap placement, may influence detection rates (Sollmann et al., 2013). To mitigate this, we derived the detection rate for species not likely to be caught in snares, defined as all mammals and galliforms with body mass < 500 g, and included this as a covariate in our occupancy analyses. If detection rates are driven by camera-trap placement or movement behavior we would expect a correlation between detections of large and small vertebrates, and between these detection rates and the detection rate of Annamite striped rabbits. However, using a Pearson correlation test we found no strong correlations between any of our detection rates ($r < 0.4$). Therefore, we conclude that neither camera-trap placement nor similar movement patterns of Annamite striped rabbits and other mammals strongly influenced detectability. As a result we expect that, if detection rates for large vertebrates are reflective of past hunting pressure, only this detection rate would influence Annamite striped rabbit occupancy.

All continuous covariates in the occupancy analyses were standardized to have mean = 0 and SD = 1. We tested for collinearity between all possible pairs of continuous covariates, using Pearson's correlation plots; no covariates were highly correlated ($r < 0.7$; Supplementary Fig. 2).

Data analysis

All analyses were conducted in R. We used the camtrapR package (Niedballa et al., 2016) to prepare camera-trapping data. To assess Annamite striped rabbit activity patterns we compiled all independent detections ($\Delta = 60$ minutes) and then used the R package overlap to plot a kernel density estimation of daily activity. Sociality was assessed by recording the number of individuals in photographic sequences.

Covariate	Scale (macro / micro)	Type (anthropogenic / environmental)	Description
Bamboo	Micro	Environmental	Number of bamboo stands within 20 x 20 m plot around the camera trap station.
Canopy closure	Micro	Environmental	Average proportion of visible sky averaged across five locations around the camera trap station.
Dead fallen trees	Micro	Environmental	Number of dead fallen trees within 20 x 20 m plot around the camera trap station.
Distance to roads	Macro	Anthropogenic	Distance from nearest roads, paths, and trails (km).
Distance to villages	Macro	Anthropogenic	Distance from nearest villages (km).
Distance to water	Macro	Environmental	Distance from major streams and rivers as calculated from a DEM-derived hydrology layer (km).
Elevation	Micro	Environmental	GPS elevation recorded at the camera trap station (m a. s. l.).
Forest score	Macro	Environmental	Measure of habitat quality derived from high-resolution satellite imagery within 50 m of the camera trap station.
Human activities	Micro	Anthropogenic	Number of types of human activities within 20 x 20 m plot around the camera trap station.
Mammals and galliforms > 500g	Micro	Anthropogenic	Average number of detections per station per day for mammals and galliformes greater than 500g.
Mammals and galliforms < 500g	Micro	Anthropogenic	Average number of detections per station per day for mammals and galliformes less than 500g.
Protection status	Macro	Anthropogenic	Level of current anti-poaching patrol activity for an area (0 or 1).
Terrain ruggedness	Macro	Anthropogenic	Topographic position index within 270 m neighborhood around the camera trap station; derived from SRTM 30 m DEM.
Vegetation density	Micro	Environmental	Average proportion of vegetation sheet visible at four locations around the camera trap station.
Water microhabitat	Micro	Environmental	Number of water sources (streams, ponds) within 20 x 20 m plot around the camera trap station.

Table 2. Covariates used in occupancy analysis for Annamite striped rabbit. Micr-scale covariates were assessed *in-situ* around each camera trap location; macro-scale covariates were calculated in R using satellite imagery, digital elevation models, and available GIS datasets. Anthropogenic covariates are features that may influence hunting pressure directly or indirectly; environmental covariates are features related to habitat.

We fitted occupancy models to Annamite striped rabbit detections from the coarse grid. We consider our 60-day trapping period to meet the assumption of temporal independence; spatial independence was confirmed during data analysis (see below). We pooled camera-trap data into 15-day occasions, resulting in at least four sampling occasions for all stations. To determine effort at each station we combined total camera-trap nights for each camera. Detection–non-detection matrices were produced for all stations, with data from the two camera traps at each station combined and analyzed as a single station. Single-covariate models were run in the unmarked package (Fiske & Chandler, 2011). We first constructed a null model that did not include any covariates and then ran single-covariate models. Because little is known about the species, we were unable to develop a priori hypotheses regarding which factors could influence species occupancy. Therefore, we decided to test each covariate individually to first assess its importance in explaining species occupancy, and only later combine significant covariates into combination models. We included camera-trapping effort as a covariate on detection probability (p). Akaike's information criterion (AIC) was used to rank candidate models (Burnham & Anderson, 2003). We considered any model within two ΔAIC units of the top model to be significant. We evaluated the strength of each covariate using P-values.

To estimate local abundance of the Annamite striped rabbit at our fine-grid locations we identified individual rabbits based on their unique striping patterns. We were thus able to avoid double-counting within a sampling occasion. We pooled camera-trap data into 15-day occasions, then determined the number of individuals detected for each occasion. We used N-mixture models, which estimate site-level abundance using spatially and temporally replicated counts (Royle, 2004), to estimate the number of individual rabbits at each camera-trap station. Because no individual rabbit was photographed at two stations, we consider our stations for the fine-grid survey to be spatially independent. As with the occupancy model, we consider our trapping period to approximate temporal population closure. N-mixture models cannot account for heterogeneity in detection among individuals, and therefore resulting abundance estimates may not accurately reflect true abundance (Barker et al., 2018). Nonetheless, the estimates we provide present a meaningful baseline against which to assess future population change (see Discussion). N-mixture analyses were run in unmarked (Fiske & Chandler, 2011). Models were run with an underlying Poisson distribution. Although the zero-inflated Poisson and negative binomial may be used when count data are overdispersed, we did not find this to be the case with our dataset.

Results

We obtained data from 138 coarse-grid stations (20,776 camera-trap–nights in total) and 128 fine-grid stations (8,404 camera-trap nights in total). We obtained 100 independent detections across 22 stations from the coarse grid, and 54 independent detections across 14 stations from the fine grid. All fine-grid detections occurred in the Saola Nature Reserves, with no photographs from Bach Ma National Park. We identified a total of 27 individuals from the fine-grid data. From 17,190 camera-trap-nights in the non-systematic survey in the Hue Saola Nature Reserve we obtained an additional 142 independent detections across 12 stations (Table 1).

The Annamite striped rabbit was primarily solitary. Only two of 296 (< 1%) independent detections showed two individuals in the same photographic sequence. For one of these records, a third individual followed the first two individuals 22 minutes later. All records occurred during 18.00–04.00, with a peak in activity during 01.00–03.00. (Fig. 2), indicating that the species is nocturnal. We recorded the species at elevations of 198–1,304 m (mean = 637 ± SD 290; Fig. 3). Naïve occupancy for the Annamite striped rabbit was 0.13 across all sites, and predicted occupancy probability (ψ) for the top-ranked model was 0.18 ± SD 0.04). The probability of detection was 0.36 ± SD 0.05). The top model contained only one covariate, detection rate of mammals and galliforms > 500 g (Table 3). All other models had a ΔAIC > 7 from the top-ranked model. Annamite striped rabbit occupancy was strongly and positively correlated with the number of detections of other hunting-sensitive species (Fig. 4), and all other predictors, including habitat-based covariates, were uninformative in explaining occurrence (Fig. 5).

The N-mixture model estimated a mean local abundance (λ) of 0.57 ± SE 0.20 individuals per station in the Saola Nature Reserves. Detection probability (P) was estimated to be 0.19 ± SE 0.07). With no detections in the Bach Ma National Park fine-grid site, we could not estimate local abundance with N-mixture models. As survey effort in this site was high, we interpret this result as indicating that true local abundance at this site is zero or close to zero.

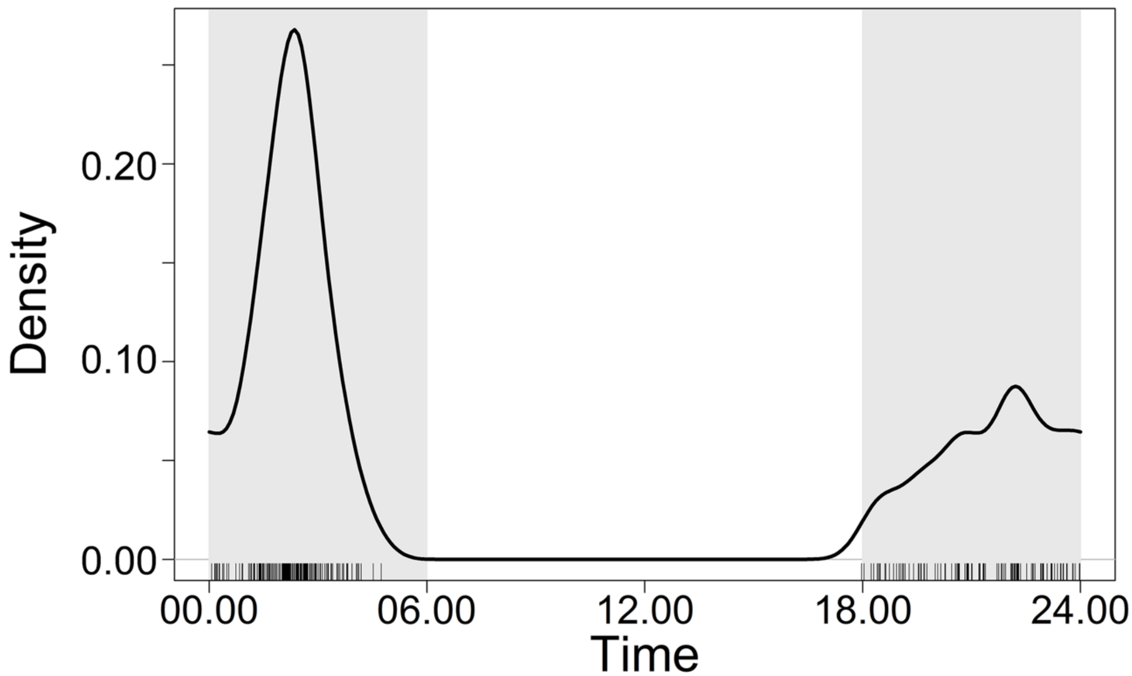

Figure 2. Kernel density estimate of daily activity patterns for the Annamite striped rabbit based on camera trap data. The vertical lines on the x-axis indicate times of individual independent detections (Δ = 60, n = 296), and the grey shading represents night time.

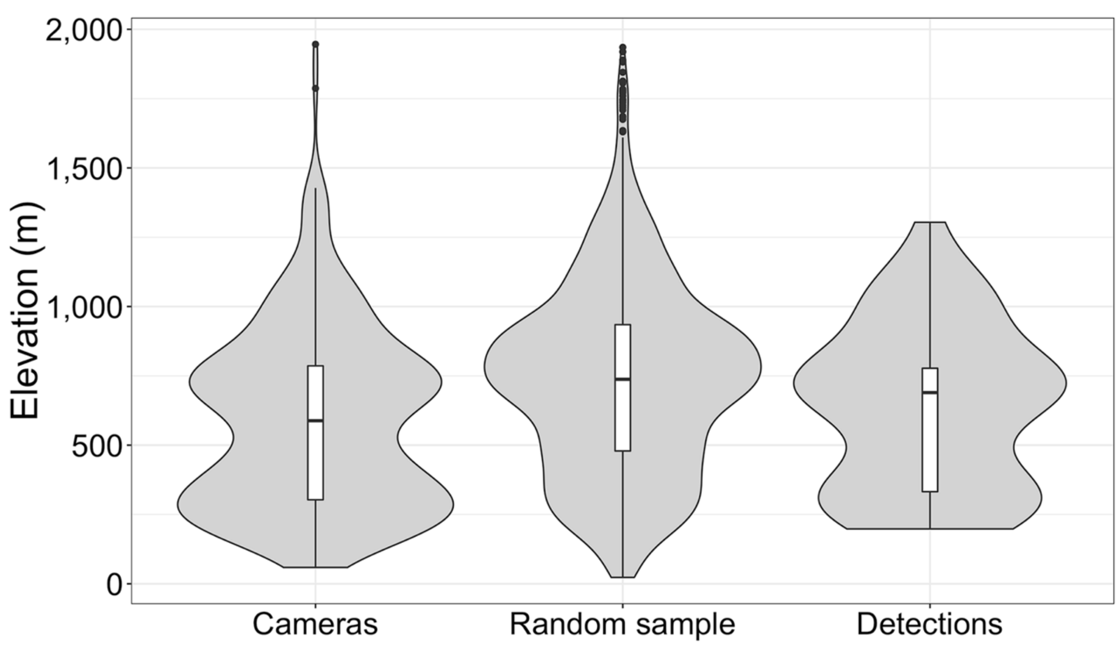

Figure 3. Distribution of all camera traps, random sample points (n = 2,000) across all the study areas, and detections of the Annamite striped rabbit by elevation.

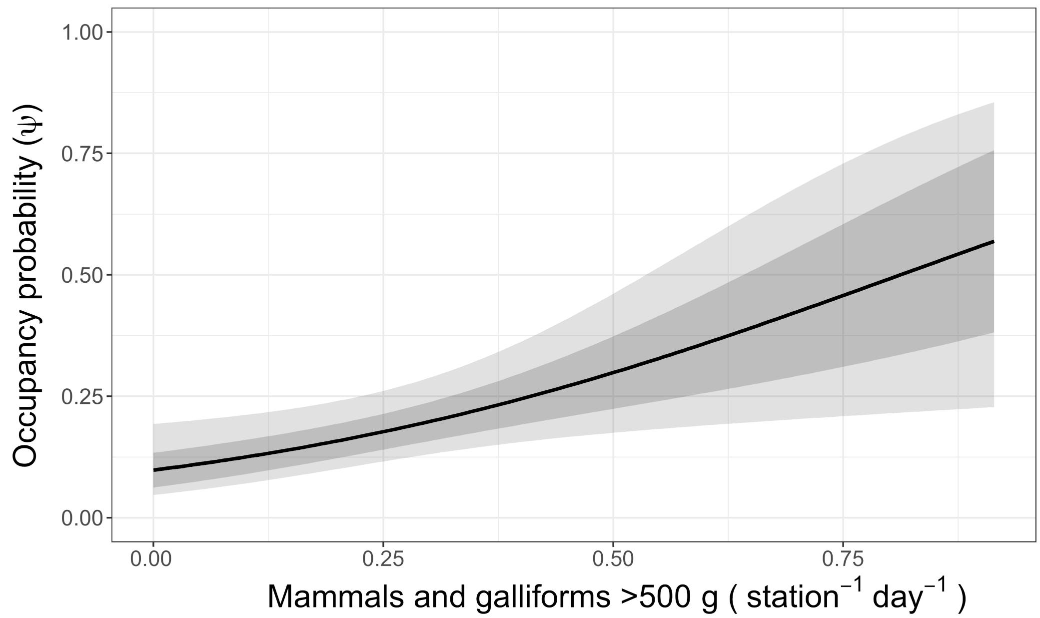

Figure 4. Response curve showing change in modelled occupancy (ψ) with detection rates for mammals and galliforms > 500g.

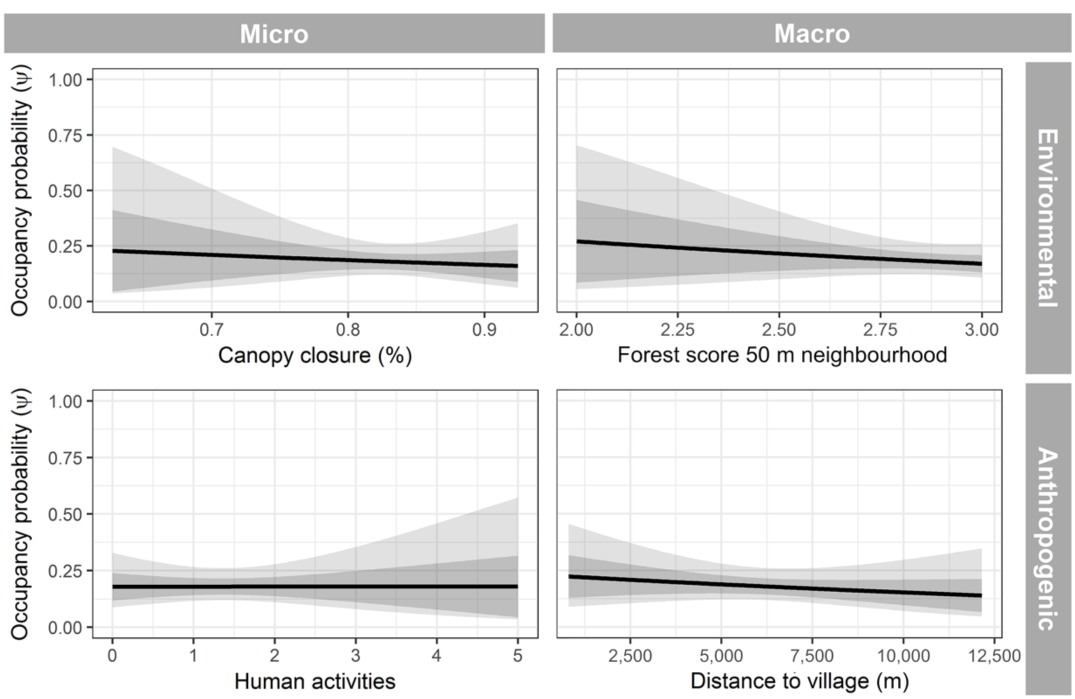

Figure 5. Annamite striped rabbit occupancy response curves, showing example non-significant results for each representative covariate class.

Discussion

As with many other lagomorphs, the Annamite striped rabbit is nocturnal. Nocturnal activity is often explained by predator avoidance, as many natural predators hunt primarily by sight. The species' solitary behavior is also consistent with most leporids (Cowan & Bell, 1986). The two observed Annamite striped rabbit pairs may indicate behavior related to breeding. In both sequences, the first rabbit moves through the frame, followed immediately by a second rabbit on a direct path to the first. All individuals were approximately the same size and are unlikely to be parent and offspring. However, because we have so few records of paired individuals and were unable to determine sex from the photographs, it is not possible to draw conclusions related to reproduction behavior from our data.

Our analysis indicates that the species shows no strong elevational preferences (Fig. 3), which is consistent with the limited information available. Dang et al. (2001) reported an individual found in a snare at 200 m elevation but also noted that hunters report the species at higher elevations. Although Abramov et al. (2008) suggested that the species can probably utilize areas as low as sea level, we did not record the species at extremely low elevations, possibly because lowland areas are readily accessible and have higher levels of past hunting pressure. The fact that we did not record the species above 1,304 m could indicate that the species does not occur in forest with montane characteristics, although our survey effort at high elevations was limited and therefore additional work is needed to investigate this.

Numerous studies have demonstrated that species occurrence is driven by multiple factors operating at various spatial scales (Gerber et al., 2012; Koerner et al., 2017). We hypothesized that occurrence of the Annamite striped rabbit would be influenced by a combination of current habitat and anthropogenic factors. Our results show that detections of other snaring-sensitive species, which we interpret as an indication of past hunting pressure, is the best predictor of occurrence of the Annamite striped rabbit in our study sites. The failure of other predictors to explain occupancy was unexpected. We believe that this finding is explained by the fact that past hunting pressure has overwhelmed environmental relationships. In this scenario, the Annamite striped rabbit would, in the absence of excessive hunting pressure, be more widely distributed and abundant in the landscape. As a result of the overwhelming snaring pressure in the Annamites (Gray et al., 2017, 2018), several endemic mammal species, including the saola, have distributions determined almost exclusively by hunting pressure (Timmins et al., 2016b). We postulate that the Annamite striped rabbit follows a similar distribution pattern within our study site. Given the range of environmental covariates we measured, and the fact that occupancy is strongly correlated to presence of other hunting-sensitive species, we suggest that the Annamite striped rabbit exhibits characteristics of a refugee species whose distribution is driven by anthropogenic pressures rather than habitat preferences (Kerley et al., 2012). Further studies are needed to investigate whether the Annamite striped rabbit also utilizes suboptimal but safer habitats, a pattern that has been observed for other refugee species (Bocherens et al., 2015).

Local abundance patterns from our fine-grid data indicate that the Annamite striped rabbit is extirpated locally in the central part of Bach Ma National Park, and present at low to moderate densities in the Saola Nature Reserves. This finding is generally consistent with our coarse-grid findings, which indicated the species was present but rare across the National Park, but not uncommon in the Saola Nature Reserves. Although intensive defaunation has occurred across all parts of this landscape, Bach Ma National Park appears to be emptier than the neighboring Saola Nature Reserves, based on detections of other hunting-sensitive species (Table 1). In addition, the Saola Nature Reserves have some level of active anti-poaching protection, whereas enforcement efforts in Bach Ma are extremely low. We suggest that more intensive snaring in Bach Ma, exacerbated by the lack of enforcement efforts, has led to the probable extirpation of the species from large parts of the protected area. The difference in local abundances between two areas with similar habitat offers additional evidence for occurrence patterns driven by hunting.

As this is the first study to estimate local abundance (λ) for the species, we cannot compare our estimates for the Saola Nature Reserves to past studies. However, because the Saola Nature Reserves have experienced heavy hunting pressure, we believe that the local abundance is well below what would exist under undisturbed conditions. Although no area in the Annamites landscape is unaffected by snaring, there are sites within the species' range that, on the basis of expert assessments and limited camera trapping, have not been as heavily affected as our sites. We recommend additional camera trapping at these sites, to obtain comparable local abundance estimates for the Annamite striped rabbit. It is likely that only surveys in less hunted areas, where the impact of hunting on distribution is weaker, will be able to offer insight into the ecology of the species.

Our results provide information that is directly applicable to Annamite striped rabbit conservation. The camera trapping provides spatially explicit data that can be used for targeted anti-poaching work. With the complete or functional extinction of numerous flagship mammal species from the Annamites, including regionally important species such as the Javan rhinoceros *Rhinocerous sondaicus* (Brook et al., 2012) and tiger *Panthera tigris* (Walston et al., 2010), and endemics such as the saola (Tilker et al., 2017), the Annamite striped rabbit may be the highest priority terrestrial mammal species with sizeable populations remaining at our study sites. We therefore recommend that current anti-poaching patrols concentrate snare-removal efforts in locations where the species was recorded. Our data further support an ongoing initiative by conservation stakeholders to gazette the Palé area as a protected area. The occurrence of the Annamite striped rabbit in multiple locations within this area, along with other conservation-priority species such as Owston's civet and the Asiatic black bear *Ursus thibetanus* (Tilker, Nguyen & Wilting, unpublished data), underscores the importance of this area for conservation. Ultimately, conservation stakeholders need to embed species conservation programmed into a holistic, adaptive management framework (Keith et al., 2011). Assessing population trends over time is a key component of adaptive management and requires a baseline for assessment of future changes. Here we establish two baselines for the Annamite striped rabbit: at the landscape scale and at a local scale within the Saola Nature Reserves. For long-term adaptive management of the species in this landscape we recommend repeating the systematic camera trapping in the near future to assess possible changes in the population within these areas in response to continued snare-removal efforts.

Several Annamite endemic species are facing imminent extinction as a result of intensive snaring. The saola is so rare that conservation breeding is now believed to be the last hope to save the species (Tilker et al., 2017). The large-antlered muntjac and Edwards's pheasant are both Critically Endangered (BirdLife International, 2016; Timmins et al., 2016a), and the latter may already be extinct in the wild (Grainger et al., 2017). The status of the Annamite striped rabbit is not as severe but the lack of records from Bach Ma National Park is cause for concern. The status and population trend of the Annamite striped rabbit in this protected area, although better than for other endemic species that have probably become extirpated there in recent years (including the saola and large-antlered muntjac), appears to be following the trajectory of these hunting-sensitive species (R. Timmins, personal communication, 2018). Without immediate and effective anti-poaching efforts, the Annamite striped rabbit may become as rare as the saola.

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Chapter 5

Discussion

The main purpose of this dissertation was to improve our understanding of how defaunation impacts tropical ground-dwelling mammal and bird communities in Southeast Asia, with a specific focus on the Annamites ecoregion of Vietnam and Lao PDR. Because the Annamites is a major center for defaunation, it represents an ideal place to study the defaunation process, and the findings from this region have broader implications for tropical biodiversity hotspots around the world. To assess how defaunation holistically impacts tropical mammal and bird communities, several methodological challenges were addressed. The findings from this research provide novel conceptual insights into the defaunation process that can be used to develop more effective on-the-ground conservation strategies.

Methodological advances to assessing defaunation

There are several challenges to rigorously assessing defaunation in tropical forests. One of the most fundamental challenges involves collecting robust data at large spatial scales. Failure to work at these scales may give an incomplete picture of community-level biological processes, or inadequately capture variation in underlying defaunation drivers. We addressed this challenge by conducting systematic surveys at landscape scales. Using sampling stations spaced approximately 2.5 km apart, we covered four protected areas and one unprotected forest block in the Annamites, and three logging concessions in Malaysian Borneo. In total, our landscape-scale approach resulted in more than 1,000 km^2 of area surveyed in each landscape. Accomplishing this survey effort required the teams to overcome numerous logistical issues. In the Annamites, for example, it was necessary to assemble and train four simultaneously operating field teams, which often spent weeks at a time in the field, and sometimes had to travel days to reach single sampling locations. Although these landscape-scale surveys were resource and time intensive, our macroscale approach allowed us to more holistically assess the impacts of defaunation on faunal communities.

Because tropical mammal and bird species often occur at low densities in defaunated communities, it is often a challenge to detect these species. We addressed this issue by employing two different survey methods at our sampling locations: camera-trapping and the identification of invertebrate-derived DNA (iDNA) from terrestrial hematophagous leeches. Camera-trapping is a well-established technique for surveying tropical mammal and bird species (Ahumada et al, 2013). The use of iDNA, on the other hand, is a relatively new development, but shows considerable promise for detecting tropical mammal and bird species (Schnell et al, 2012). By utilizing both techniques, we were able to develop a data collection procedure that optimized our ability to study terrestrial faunal communities, and increased our ability to detect rare and elusive species (Chapter 3). Several conservation-priority species were detected by only one approach. For example, pangolin *Manis* spp., one of the most threatened mammals in Southeast Asia (Heinrich et al, 2016), was only detected by camera-trapping, while the elusive marbled cat *Pardofelis marmorata*, a species that has rarely been recorded in the Annamites (Wilcox et al, 2014), was detected only from the leeches. Our findings further highlight the value of using utilizing multiple, complementary survey methods when studying defaunated tropical faunal communities.

Even when surveys successfully detect rare species in faunally impoverished systems, the data may be insufficient for most standard modelling approaches. For example, when using maximum likelihood-based occupancy analyses, a species generally has to have been detected at multiple stations for model convergence. For extremely rare species, this is unlikely to be the case. Because many rare species are often the species of most conservation concern, obtaining reliable parameter estimates is important. We addressed this challenge by using Bayesian multi-species occupancy analyses (Dorazio & Royle, 2005; Dorazio et al., 2006) (Chapters 3 and 4). Because these models use community-level hyperparameters, data-poor species can 'borrow' information from species with more detections, therefore providing robust parameter estimates for even very rare species (Tobler et al, 2015; Drouilly et al, 2018; Li et al, 2018). In the central Annamites, we were able to obtain occupancy and detection probability estimates for several rare and threatened species that were only detected at one or two sampling stations (Owston's civet *Chrotogale owstoni*, Asian black bear *Ursus thibetanus*). It should be noted that care must be taken when interpreting results from Bayesian multi-species occupancy analyses, because parameter estimates for data-poor species will inevitably be pulled towards the overall community mean (Pacifici et al, 2014). Nonetheless, this approach provides an innovative way to obtain information on rare species in defaunated landscapes.

Understanding spatial patterns of biodiversity is often a key component to designing effective conservation strategies. In the central Annamites, where unsustainable hunting has created vast areas of empty forest, conservation-priority species often have highly localized, patchy distributions. Identifying these where these species occur is a critical first step to protecting them, for example through the deployment of snare-removal teams. Species distribution models present an ideal analytical framework to identify priority areas for targeted protection measures. However, a major challenge to constructing accurate species distribution models for the Annamites is the need to incorporate covariates that capture complex patterns of hunting behavior. We addressed this challenge by utilizing four covariates (distance from major city, village density, least cost path from roads, and elevation) that characterize landscape accessibility. Our results support earlier studies that indicate the usefulness of accessibility as a proxy for hunting pressure (Muchaal & Ngandjui, 1999). However, in contrast to earlier research that used simple linear distance-based measures of accessibility (Rao et al, 2005; Peres & Nascimento, 2006; Koerner et al, 2017), we found it necessary to construct more complex covariates that represent different aspects of accessibility (Chapter 3). For example, the least cost path from road covariate incorporated terrain ruggedness, and was also measured over three successive time periods, therefore capturing both spatial and temporal dimensions of accessibility.

Unsustainable hunting in Southeast Asia

Among the major defaunation drivers that threaten biodiversity in the tropics, habitat alteration has received the most publicity, financial support, and high-level stakeholder attention from governments and major non-governmental organizations. Given the drastic habitat loss and degradation in the world's tropical rainforests (Hansen et al, 2013), this focus is understandable. Complete habitat loss is a primary threat to tropical biodiversity: Numerous studies have shown that clear-cutting results in drastic declines in tropical bird and mammal richness (Brooks et al, 2002; Brook et al, 2003; Sodhi et al, 2010). Within this context, preventing habitat loss is, and should remain, a principle objective for the conservation of tropical biodiversity. However, our findings from Malaysian Borneo and the Annamites indicate that, with regard to habitat degradation and unsustainable hunting, the situation may be more nuanced. In Chapter 2, we found that structurally intact but heavily-hunted sites have substantially higher levels of defaunation than moderately degraded but unhunted sites. Our results suggest that unsustainable hunting may be a more immediate threat than habitat degradation for tropical faunal communities. We recommend that, to protect bird and mammal species in the Southeast Asian biodiversity hotspot, conservation stakeholders should place as much emphasis on the prevention of overhunting as on habitat preservation.

Unsustainable hunting can lead to fundamental changes in tropical faunal communities. Our findings from the central Annamites are consistent with previous studies indicating that large mammals are particularly susceptible to hunting (Peres, 2000; Benítez-López et al, 2017). Several intrinsic biological traits could make larger species more sensitive to hunting, including lower reproductive rates and population densities (Purvis et al, 2000; Cardillo et al, 2005). Because large mammal and bird species often have disproportionate impacts on ecosystems, the downsizing of faunal communities is likely to have significant implications for tropical rainforests. For example, because large ungulates act as major seed dispersers, their extirpation can alter the composition and spatial dynamics of tropical vegetation communities (Wright et al, 2007). To date, no studies have been conducted examining how defaunation has impacted plant communities in the central Annamites, and this topic requires further investigation. The extirpation of large apex predators can lead to an increase in smaller, more generalist carnivore species (Soulé et al, 1988; Crooks & Soulé, 1999). We recorded higher than expected occupancies for several mesocarnivores, which may indicate that this “mesopredator release” mechanism (Soulé et al, 1988) has already occurred in our central Annamites study sites. The possibility raises a number of intriguing questions. Mesopredator release in other ecosystems has been linked to trophic cascades that impact a wide range of taxa (Prugh et al, 2009). Several studies have indicated that an increase in generalist mesopredators is associated with an increase in nest predation of songbirds, which over time may lead to avifaunal declines (Rogers & Caro, 1998; Crooks & Soulé, 1999; Schmidt, 2003). Could a rise in mesopredators in the central Annamites study sites represent an as yet unrecognized threat to the endemic songbirds in the region? Additional research is needed to answer this and other questions related to potential mesopredator-initiated trophic cascades.

Snaring is especially destructive to tropical terrestrial mammal and bird communities. Unlike gun-hunting, snaring is indiscriminate, impacting a wide range of species (Gray et al, 2018). Our findings from the central Annamites are characteristic of community-wide faunal declines caused by intensive snaring. In Chapters 2 and 3, we show that mammal and ground-dwelling bird communities in our study sites represent a fraction of the original species composition that would be expected to occur there, were broadly similar across the landscape, and largely comprised of generalist species believed to be highly resilient to hunting-pressure. Overall, these findings suggest that these sites have undergone severe biotic homogenization (McKinney & Lockwood, 1999), with faunal communities shifting towards species that are able to tolerate high levels of snaring pressure. Because species that are particularly susceptible to anthropogenic pressures tend to be the species of most conservation concern, biotic homogenization in tropical biodiversity hotspots is likely to disproportionately impact rare and threatened species. The homogenization of tropical ecosystems could also have fundamental consequences that impact human well-being: Several studies have linked diversity in tropical rainforests to ecosystem services and overall stability (Naeem et al, 1994; Tilman et al, 2014; Hautier et al, 2015). While all forms of hunting have negative consequences for tropical biodiversity, our findings suggest that snaring is particularly detrimental, and may ultimately contribute to the erosion of ecosystem-level processes.

Addressing unsustainable hunting in Southeast Asia will take a large-scale, well-funded, collaborative effort from conservation stakeholders. Major international organizations such as such the United States Agency for International Development (USAID) could play key parts in such an endeavor. These stakeholders have the financial resources and political influence to pursue strategies that could lead to in high-level systemic change within governments. But change does not need to only come from the top. The role of local stakeholders is equally important, because without these organizations it is difficult to enact effective conservation measures at the site level. Southeast Asia has a rich variety of local non-government organizations, many of whom fill a critical role in the implementation of activities that address unsustainable hunting in protected areas. Together, the combination of international and local-scale organizations offers a promising model to address unsustainable hunting in Southeast Asia.

The central Annamites: empty forests, worth protecting

Our landscape-scale surveys across five central Annamites study sites revealed that these forests display archetypal "empty forest syndrome" (Redford, 1992): more than half of the ground-dwelling mammal and bird species that would be expected to occur based on historical distribution records were not recorded in our surveys, and the species that do persist tend to be common species that are highly resilient to anthropogenic pressures. A particularly worrisome finding, though not surprising given the level of defaunation in these sites, was our failure to detect three Critically Endangered and endemic species: the saola *Pseudoryx nghetinhensis* (Timmins et al, 2016a), large-antlered muntjac *Muntiacus vuquangensis* (Timmins et al, 2016b), Edwards's pheasant *Lophura edwardsi* (BirdLife International, 2018). It is likely that these species have been lost from our survey sites.

However, even in this empty forest, conservation-priority species still persist. We recorded four endemic mammals and pheasant species (Annamite dark muntjac species complex *Muntiacus rooseveltorum / truongsonensis*, Annamite striped rabbit *Nesolagus timminsi*, Owston's civet, crested argus *Rheinardia ocellata*) and two non-endemic but threatened mammals (Asiatic black bear, pangolin). Furthermore, we obtained a single record of marbled cat, a species which, although not globally threatened (Ross et al, 2016), appears to be extremely rare within the central Annamites (Wilcox et al, 2014). Our results therefore indicate that, even though this protected area complex has undergone severe defaunation, it is nonetheless important for species conservation initiatives. The sites may be a particularly important stronghold for Annamite striped rabbit. Although a lack of comprehensive and systematic camera-trapping across the region prevents direct comparisons between Annamite striped rabbit populations in our study sites and other areas, information collated for the reassessment of the *IUCN Red List of Threatened Species* account (Tilker et al, 2019) suggests that populations in these sites may be healthier than in other areas within the species' range. The Hue and Quang Nam SNRs could play a central role in the future conservation of this species, as snare-removal efforts in these areas are higher than other sites in the central Annamites.

There are other reasons to protect these sites in addition to the presence of rare and threatened species. The landscape is important culturally for the Katu people, an indigenous group found only in the central Annamites that formerly led a forest-dependent and semi-nomadic existence (Århem, 2015). Traditional ways of life have deteriorated significantly over preceding decades among the Katu, largely as a result of modernization and forced resettlement programs (Thang et al, 2010), and protecting the central Annamites forests and their biodiversity is a key step to preventing further cultural erosion. These sites also provide valuable ecosystem services to surrounding communities, particularly as an important source of clean water for villages adjacent to the protected areas (Long, 2005). Given the considerable overlap between cultural, socio-economic, and biodiversity-related elements in this area, it is clear that there are numerous potential synergies that could be developed to the benefit of all three. One project in the area, the WWF Carbon and Biodiversity (CarBi) project, was active from 2012 to 2017, and developed this type of holistic approach that pursued biological and cultural conservation objectives within the context of sustainable socio-economic development. The project will be active for a second phase starting in 2019.

Conservation implications

Snare removal patrols currently represent the most widely-used on-the-ground conservation response to protecting rare and endemic species in the central Annamites (Wilkinson, 2016). Although these patrols have removed large volumes of snares (Wilkinson, 2016; Gray et al, 2018), patrol strategies do not currently take into account spatial patterns of biodiversity, simply because these patterns have not been identified in a scientifically robust way. In Chapter 3, we predicted the occurrence of endemic and threatened species across the protected area complex with the goal of providing spatial-explicit information to guide future snare-removal strategies. We found that among the five study sites predicted occupancies for conservation-priority species generally increased from east to west, with low values in Bach Ma NP, medium values in the Hue and Quang Nam SNRs and eastern Xe Sap NPA, and the highest values in the Palé area (Chapter 3, Fig. 3). Our results suggest that, from a biogeographic perspective, protecting the Palé area is a top priority because of its diversity of endemic and threatened species. It is imperative to gazette the Palé area and implement effective anti-poaching activities there as soon as possible.

Several remote areas on the border of the Hue and Quang Nam SNRs also have high predicted occupancies for endemic and threatened species, and should be targeted for snare-removal. Bach Ma NP is unlikely to support significant populations of conservation-priority species, though high elevation areas near the summit and the eastern border of the protected area may retain populations of Annamite striped rabbit and dark muntjac.

Our findings also provide information that can also be used to develop species-specific conservation strategies for a little-known endemic mammal, the Annamite striped rabbit (Chapter 4). We established the first conservation baselines for the species: one at the landscape scale across all study sites, using an occupancy framework, and one at the local scale within the SNRs, using N-mixture models that provide local abundance estimates. These baselines can be used to assess Annamite striped rabbit population trends over time, thus enabling conservation stakeholders to assess the impact of conservation actions for the species. The fact that other protected areas within the species range (Pu Mat NP, Phong Dien NR, Song Thanh NR) have recently used the same camera-trap design to establish conservation baselines is a promising development for the monitoring of Annamite striped rabbit populations in other parts of its range. Finally, findings from this study also contributed to the development of more holistic conservation plans for the species. In 2002 and 2008, the Annamite striped rabbit was listed as Data Deficient on *The IUCN Red List for Threatened Species* (Smith, 2002; Abramov et al, 2008). Data from the current study provided critical information for an updated Red List assessment that ultimately listed the species as Endangered (Tilker et al, 2019). The updated assessment highlights, in a more formal way, the urgency of immediate conservation actions to protect the Annamite striped rabbit, and has already led to discussions among key stakeholders about the possibility of establishing an insurance population in the near future.

The empty forests of the central Annamites can be seen as a cautionary lesson highlighting the disastrous effects of intensive snaring pressure on tropical mammal and bird communities. Industrial-scale snaring has caused almost complete faunal collapse in our central Annamites sites: More than 55% of terrestrial mammal and bird species are extirpated or present at functionally-extinct levels, including megaherbivores and all medium- and large-sized carnivores (Chapter 2). Even species considered to be common in other parts of Southeast Asia, such as the Eurasian wild pig *Sus scrofa* and red muntjac *Muntiacus vaginalis*, persist at low occupancies. Fortunately, most parts of Southeast Asia have not been subjected to this level of snaring, but there is mounting evidence from across the region suggesting that snaring is on the rise (Risdianto et al, 2016; Gray et al, 2017; Rostro-García et al, 2018). If this trend continues, it is only a matter of time before other areas experience levels of "empty forest syndrome" (Redford, 1992) similar to the central Annamites. Protected areas that have not yet been subjected to industrial-scale snaring are unlikely to be prepared for it when it comes. It is therefore imperative that conservation stakeholders act now to proactively prepare for snaring in other parts of Southeast Asia.

Ultimately, to protect tropical faunal communities in the central Annamites and other parts of Southeast Asia from snaring, it will be necessary to do more than simply remove snares that have already been set in protected areas. Between 2011 and 2016, for example, tens of thousands of snares were collected every year in the SNRs, with no significant reduction in overall snaring levels (Wilkinson, 2016; Gray et al, 2018). The snare collection data from the SNRs shows that, in the absence of real disincentives, the benefits of setting snares far outweigh the costs. A dozen wire snares can be purchased for pennies in almost any market in rural Vietnam, and yet a single pangolin can be sold for more than 500 USD (MacMillan & Nguyen, 2014). To stop snaring in the short term, conservation stakeholders must arrest and prosecute people engaged in snaring. A critical component of successfully prosecuting snare-setters will be the strengthening of legislation that penalizes the possession of snares. Ideally, the wire material used to make snares would also be regulated. In the long run, demand reduction programs, combined with education and outreach activities, will be needed to shift cultural attitudes that condone purchasing of wildlife products. For species like the saola *Pseudoryx nghetinhensis*, these possible solutions have come too late: urgent captive breeding is now believed to be the only way to save the species (Tilker et al, 2017), and it is possible that even this conservation strategy has come too late. Other species are not in such a dire situation, but if snaring continues to increase and spread to other areas, their populations could quickly decline to critical levels. Although the challenges to reducing snaring are substantial, with adequate support from local governments, reinforced with further support and financial backing from international stakeholders, the snaring crisis can be addressed.

Conclusion

The central Annamites landscape of Vietnam and Lao PDR is unique both because of its exceptional biodiversity and the magnitude of threat that its wildlife faces from intensive, indiscriminate hunting. Without immediate and effective conservation solutions to address the Annamite's snaring crisis, the region's endemic species face imminent extinction. Unfortunately, the story of the central Annamites may not be a unique one for very long. Given future population projections (Gerland et al, 2014) and the infrastructure development plans (Laurence et al, 2014) in the world's tropical regions, it is likely that pantropical defaunation will continue into the foreseeable future. In the absence of effective solutions to address drivers of defaunation, the empty forests of the central Annamites may be a portent of things to come. To prevent the further loss of mammal and birds in tropical hotspots, it is important to study the defaunation process, and use this information to develop more effectual conservation strategies.

In this dissertation we assessed multiple aspects of defaunation and its consequences for tropical mammal and bird communities in Southeast Asia, with a focus on the central Annamites. This process, in itself, required the development of new methodological and analytical approaches. We show that intensive, indiscriminate hunting may be a more immediate threat to tropical faunal communities than moderate levels of habitat degradation, and urge conservation stakeholders to prioritize actions to address the snaring crisis (Chapter 2). We identified spatial patterns of biodiversity in a heavily-defaunated landscape in the central Annamites, providing the first robust information on how defaunation has emptied these sites, but more importantly, where endemic and threatened species are likely to still occur (Chapter 3). Finally, we assessed how defaunation has impacted a little-known endemic species, the Annamite striped rabbit, and provide specific recommendations for its conservation (Chapter 4). Although these findings provide new insights into defaunation, it is our hope that, outside of the world of academia, they can be used to further on-the-ground conservation efforts to prevent biodiversity loss in tropical rainforests.

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Acknowledgements

First, I wish to express my deepest gratitude for my supervisor, Dr. Andreas Wilting, for giving me the opportunity to pursue a PhD. Your guidance, support, and encouragement over the years have made it possible for me to realize this accomplishment. From the fieldwork to the analysis to the writing – you have taught me so much. There are many supervisors, but relatively few, I dare say, can be considered true mentors. And you have been the best mentor that I could ever have hoped for. Your mentorship has allowed me to grow both professionally and personally in ways that I never could have imagined, and will leave a lasting impact on me.

Thank you also for Prof. Heribert Hofer for accepting me as a doctoral student, and your mentorship over the course of my PhD career. I consider myself lucky to have been part of an institution with a director who shows such a deep personal interest in its students, and who is so genuinely invested in helping them reach their full potential.

I wish to respectfully thank Dr. Prof. Heribert Hofer and Dr. Carsten Niemitz for evaluating this dissertation.

Thank you also to my colleagues at the Leibniz Institute for Zoo and Wildlife Research, especially An Nguyen, Azlan Mohamed, Dr. Jesse F. Abrams, Dr. Jan Axtner, Jürgen Niedballa, Roshan Guharajan, Badru Mugerwa, and Thanh Nguyen. This dissertation is very much the product of a combined group effort – which includes help with coding and analyses and writing, but also warm and lively lunch discussions at the Tierpark. Thank you! I also wish to thank the entire Department of Ecological Dynamics, especially Dr. Stephanie Kramer-Schadt, for additional support. Being part of this group gave me the strong foundation needed to finish my PhD.

I wish to extend a special thanks to Dr. Jesse F. Abrams for his enormous support over the years. Without your statistical and modelling expertise, I simply could not have published these chapters. Equally important was your constant encouragement and friendship, which were invaluable during hard times. I am so fortunate to have had the opportunity to have worked with you. And it was fun too!

The data that contributed to this dissertation was collected over several years of intense fieldwork in the rainforests of central Vietnam and Lao PDR. An Nguyen deserves immense credit for essentially running this complex field operation. An, thank you for your support and friendship. I could not have asked for a better field partner. I am deeply indebted to my colleagues working with CarBi Project under WWF for their support, in particular, Dr. Van Ngoc Thinh, Dr. Benjamin M. Rawson, Fanie Bekker, Hoa Anh Quang Nguyen, Hung Luong Viet, Francois Guegan, Amphone Phommachak, and Soukaseum, Malychansy. Thank you also to the administrative staff at both the WWF Hue and WWF Pakse offices for their support with logistics. I also wish to thank the staff of the protected areas where we worked, and all of our field assistants and team leaders, especially Đặng Công Viên and Võ Văn Sáng.

Thank you to Stephanie Vollberg for your kindness and generosity over the years. My stay in Germany got off to a good start in part because you and your family took me in and helped me get settled. And I cannot tell you how much it has meant to me to have a person to go to with allof the general living-in-Germany question that came up.

I am grateful to the Leibniz Institute for Zoo and Wildlife Research administrative team. I cannot imagine how much time and effort it took to process our extensive travel documents.

Finally, my deepest heartfelt thanks and love goes out to my entire family, especially my parents, Kris and Paula. Without your support and guidance, I would not have been able to finish this part of my journey – and more importantly, appreciate all of the experiences along the way. Thank you for your unwavering encouragement to follow my path wherever it led, even when that path took me to parts unknown. Your belief in me has been the most important factor in getting where I am today. And I also wish to thank my 'second set of parents', Ben and Patt Wallace, for their support as well. By introducing me to the natural world at a young age, and fostering that love over the years, you set me on this path. Without all the years of hunting and fishing – I would not have pursued this dream. Thank you.

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Professional

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- Primary role to develop and oversee conservation projects for highly-threatened Asian species October 2019-present
- Responsibilities include:
  - Identifying and developing strategic partnerships with both national and international
  - conservation stakeholders
  - Maintaining and expanding existing species programs
  - Identifying opportunities for expansion of protected areas in key biodiversity hotspots
  - Developing population monitoring systems to be used for adaptive management in protected areas
  - Mentoring young conservation scientists under the Associate Conservation Scientist program

Education

Leibniz Institute for Zoo and Wildlife Research
Doctoral student Berlin, Germany

- Junior Research Group for Southeast Asian Biodiversity and Biogeography July 2014-present
- Research emphasis: ecology and conservation of endangered and endemic mammals in Vietnam and Laos

University of Texas at Austin Austin, TX
Masters, Department of Ecology, Evolution, and Behavior September 2014

- GPA: 3.67/4.00
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Midwestern State University Wichita Falls, TX *B.S. in*
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- Overall GPA: 3.95/4.00
- National Dean's List (4 years)

Research Experience

Leibniz Institute for Zoo and Wildlife Research, *project leader* central Vietnam / southern Laos

- Leader for all field work in the IZW Species Resilience to Global Change June 2014-2017 (ScreenForBio) project
- Goals: To conduct the first-ever landscape-scale mammalian biodiversity surveys across Bach Ma National Park (Vietnam), the Hue and Quang Nam Saola Nature Reserves (Vietnam), and Xe Sap National Protected Area (Laos) using camera trapping and leech collection
- Responsibilities: Implementing all aspects of the data collection and analysis
- Project involves intensive collaboration with PA anti-poaching staff and WWF Forest Guards

US Fulbright Exchange Program, *recipient*

- Awarded a Fulbright fellowship for the 2014-2015 through Vinh University to conduct an independent research project in Vietnam — Vietnam, August 2014-May 2015
- Research is focused on ecology and conservation of threatened mammals
- Strong focus on mentoring young and aspiring Vietnamese conservation biologists through Vinh University

World Wildlife Fund—Vietnam, *biodiversity consultant* — Hue and Quang Nam Provinces, Vietnam

- Led surveys into Hue and Quang Nam Saola Nature Reserves and Bach Ma National Park with the World Wildlife Fund—Vietnam — July 2013-January 2014
- Goals: To use leech collection and camera trapping to survey for Annamite mammals, particularly endemic ungulate species
- Responsibilities: Planned all aspects of biodiversity surveys, processing of data, reporting back to NGO and government counterparts

Affiliations

IUCN Large-antlered Muntjac Working Group / Deer Specialist Group, *coordinator* — 2017-Present

- Focus: ecology and conservation of the Large-antlered muntjac (*Muntiacus vuquangensis*)
- Leader of the Working Group, contributing to projects in both Laos and Vietnam focused on protecting this little-known Critically Endangered species

IUCN Saola Working Group / Asian Wild Cattle Specialist Group, *member* — 2013-Present

- Focus: ecology and conservation of Saola (*Pseudoryx nghetinhensis*) populations in Central Vietnam and Laos
- Involvement in saola conservation initiatives in both Vietnam and Laos for more than seven years, working with a variety of local counterparts

IUCN Lagomorph Specialist Group, *co-coordinator* — 2013-Present

- Focus: ecology and conservation of the Annamite striped rabbit (*Nesolagus timminsi*)
- Extensive research on the species and leader of IUCN Red List assessment

Selected publications

Tilker, A., Abrams, J.F., Nguyen, A., Hörig, L., Axtner, J., Louvrier, J., Rawson, B.M., Quang, H.A.N., Guegan, F., Van Nguyen, T. & Le, M. (2019). Identifying conservation priorities in a defaunated tropical biodiversity hotspot. *Diversity & Distributions.* 26(4), 426-440.

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Selbständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Doktorarbeit eigenständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Berlin, 13.05.2020

Andrew Tilker