Long-term Multifunctionality across Mediterranean-type ecosystems: Improving Restoration Outcomes through trait-based Modelling

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

Sebastian Fiedler

2021

This work was carried out between 2016 and 2021 in Germany under the supervision of Prof. Dr. Britta Tietjen (Freie Universität Berlin, Germany), Dr. Michael P. Perring (Universiteit Gent, Belgium) and Prof. Dr. Fernando T. Maestre (Universidad de Alicante, Spain) within the graduate program "Biodiversity, Evolution & Ecology" of the Dahlem Research School at Freie Universität Berlin.

First Reviewer: **Prof. Dr. Britta Tietjen** (Freie Universität Berlin)
Second Reviewer: **Prof. Dr. Jonathan Jeschke** (Freie Universität Berlin)
Date of disputation: 1st October 2021

This dissertation is a cumulative work of three manuscripts from my publication list, either published or to be submitted:

Fiedler S, Perring M, Tietjen B (2018). Integrating trait-based empirical and modelling research to improve ecological restoration. Ecology and Evolution. 8, 6369-6380. `https://doi.org/10.1002/ece3.4043`
Own contribution: I contributed to the research idea and the design of this study, conducted the literature review, and prepared all figures and tables after consultation with my co-authors. I wrote the first draft of the manuscript and revised it based on the co-author's and reviewers' comments.

Fiedler S, Monteiro J, Hulvey K, Standish R, Perring M, Tietjen B (2021). Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. Journal of Applied Ecology. `https://doi.org/10.1111/1365-2664.13900`
Own contribution: I contributed to the research idea and the design of this study, implemented the vegetation and hydrological model and supported the coupling to the nutrient model. I parameterized and validated the model, performed the simulation experiments, analyzed the results, and prepared all figures and tables after consultation with my co-authors. I wrote the first draft of the manuscript and I revised it based on the co-author's and reviewers' comments.

Fiedler S, Perring M, Monteiro J, Branquinho C, Buzhdygan O, Cavieres L, Cleland E, Cortina-Segarra J, Grünzweig J, Holm J, Irob K, Keenan T, Köbel M, Maestre F, Pagel J, Rodríguez Ramírez N, Ruiz-Benito P, Sheffer E, Valencia E, Tietjen B (to be submitted soon). Context-dependency of restoration towards multiple improved ecosystem functions across Mediterranean-type ecosystems.
Own contribution: I contributed to the research idea and the design of this study, supported and revised the cluster analysis, parameterized the model, performed the simulation experiments, analyzed the results, and prepared all figures and tables after consultation with my co-authors. I wrote the first draft of the manuscript and I revised it based on the co-author's comments.

I hereby declare that all parts of the work described in this thesis are done by myself. Where I used published or unpublished data by others, it is indicated in the text. The three main Chapters 2 to 4 are written as independent articles in cooperation with coauthors. The published Chapters 2 and 3 were improved based on suggestions of the reviewers and the journal editors. Chapter 4 will soon be submitted to an international scientific journal.

Curriculum Vitae

Positions & Education

07/2021 – present	**Universität Göttingen, Germany.** Research assistant in Ecological Modelling Department led by Prof Dr Kerstin Wiegand
02/2016 – 09/2021	**Freie Universität Berlin, Germany.** PhD student in Theoretical Ecology Group led by Prof Dr Britta Tietjen
03/2020 – 12/2020	**Universität Bayreuth, Germany.** Research assistant in Ecological Modelling Group led by Prof Dr Michael Hauhs
08/2014 – 12/2015	**Freie Universität Berlin, Germany.** Research assistant in Theoretical Ecology Group led by Prof Dr Britta Tietjen
01/2012 – 08/2014	**Universität Potsdam, Germany.** Research assistant in Plant Ecology & Nature Conservation Group led by Prof Dr Florian Jeltsch
10/2010 – 10/2013	**Universität Potsdam, Germany.** Master of Science "Ecology, Evolution & Nature Conservation" (very good: 1.3). *Thesis: "Adapting an Ecohydrological Dryland Model for Simulating Soil Water and Vegetation Dynamics of the Qinghai-Tibetan Plateau" supervised by Dr Geißler, Prof Dr Herzschuh, Prof Dr Jeltsch*
10/2007 – 09/2010	**Universität Potsdam, Germany.** Bachelor of Science "Biology" (good: 1.9). *Thesis: "Field Studies to Examine Preferences of Ants with Regard to the Dispersal of Diaspores" supervised by PD Dr Heinken*

Further Training (selected)

2016 – 2018	**Teaching Qualification Program** at Freie Universität Berlin (Germany)
05/2017	**Bayesian calibration, forecasting and multi-model predictions of processbased vegetation models.** PROFOUND Spring School in Rencurel (France)

08/2016	**Practical Application of Multi-Criteria Analysis in Participative Ecological Restoration.** Training course in Freising (Germany)
09/2015	**The Use of Trait Based Approaches in Community Ecology and Stress Ecology.** Training course at University of Coimbra (Portugal)

Awards & Scholarships

09/2019 – 03/2020	**Scholarship funded by German Academic Exchange Service (DAAD)** for Research Stays in Berkeley (USA) and Alicante (Spain)
07/2019 – 09/2019	**Scholarship funded by University Alliance for Sustainability** for a Junior Research Stay in Rehovot (Israel)
05/2019	**Scholarship ERASMUS+ Staff Mobility for Teaching** in Ghent (Belgium)
05/2017	**Poster award** at the 12th Annual Workshop of the Young Modellers in Ecology (YoMos) in Buchenbach (Germany)

Teaching & Supervision

Lecturer	**Geoecology: How to give a good scientific presentation?** Seminar at Universität Bayreuth for Bachelor students (90 mins/week, half a semester)
	Introduction to R. Lecuture and Practical at Universität Bayreuth for Bachelor students (90 mins/week, one semester)
	Simulation modelling with NetLogo. Lecture and Practical at Universität Bayreuth for Bachelor students (3 hours/week, one semester)
	Dryland Ecology: Mediterranean-type ecosystems. Lecture at Universität Potsdam for Master students (90 mins, three semesters)
	Introduction to Ecological Modelling with NetLogo. Lecture and Practical at Freie Universität Berlin for Master students (2 days, two semesters)
	Selected Methods in Ecological Modelling. Lecture and Practical at Freie Universität Berlin for Master students (4 hours/week, two semesters)
Master theses	Yari O.: **Behavioral changes of the Common Eider in response to predation by the Arctic Fox – A simulation approach.** Together with Florian Ruhland
	Madlen S.: **Combined effect of land use and soil textures on water fluxes in a Mediterranean-type ecosystem**

	Julia A.: **The role of plant functional diversity for water cycling in a Mediterranean-type ecosystem.** Together with José A.F. Monteiro
Master projects	Jannis W.: **Climate change impacts on grassland communities and selected ecosystem services on the Tibetan Plateau**
	Madlen S.: **Modelling the effect of soil texture on water fluxes in a Mediterranean- type ecosystem**
	Yari O.: **Modeling population dynamics of the Common Eider in Iceland** *and* **Impact of different migration scenarios on Common Eider populations in Iceland.** Together with Florian Ruhland
	Andreas M.: **Impact of the invasive American Mink on seabird populations in Iceland.** Together with Florian Ruhland

Conference Contributions (since 2016)

06/2021	**Fiedler, S.**, Monteiro, J., Hulvey, K., Standish, R., Perring, M., Tietjen, B. Restoration Ecologists might not get what they want: Global Change shifts Trade-offs among Ecosystem Functions *Oral presentation at the 9th Virtual World Conference on Ecological Restoration by the Society for Ecological Restoration.*
12/2018 and 09/2018	**Fiedler, S.**, Monteiro, J., Perring, M., Tietjen, B. What should we plant to maximise the supply of multiple ecosystem services in the long-term? *Oral presentations at the 58th Annual Meeting of the Ecological Society of Australia in Brisbane (Australia) at the Annual Meeting of the 11th European Society for Ecological Restoration in Reykjavik (Iceland).*
04/2018	**Fiedler, S.**, Monteiro, J., Perring, M., Tietjen, B. What should we plant to increase ecosystem service supply in the long-term? *Oral presentation at the Annual Havel-Spree-Kolloquium in Berlin, Germany.*
12/2017	**Fiedler, S.**, Perring, M., Tietjen, B. What is the optimal vegetation composition for restoring MTEs? - An integrated empirical and simulation modelling approach.*Oral presentation at the joint annual meeting of BES, GFÖ, NECOV, EEF in Ghent, Belgium.*
08/2016	**Fiedler, S.**, Perring, M., Tietjen, B. Resilient and Multifunctional Mediterranean- type Ecosystems: Improving restoration by trait-based simulation modelling. *Poster presentation at the 10th Annual Meeting of the European Society for Ecological Restoration in Freising, Germany.*

Peer-reviewed Publications

2021 **Fiedler, S.**, Monteiro, J., Hulvey, K., Standish, R., Perring, M., Tietjen, B. Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. *Journal of Applied Ecology.*

Wu, J., Li, M., Zhang, X., **Fiedler, S.**, Gao, Q., Zhou, Y., Cao, W., Hassan, W., Mărgărint, M. C., Tarolli, P., Tietjen, B. Disentangling climatic and anthropogenic contributions to nonlinear dynamics of alpine grassland productivity on the Qinghai-Tibetan Plateau. *Journal of Environmental Management* 281.

2020 Pietzsch, B., **Fiedler, S.**, Mertens, K.G., Richter, M., Scherer, C., Widyastuti, K., Wimmler, M.-C., Zakharova, L., Berger, U. Metamodels for Evaluating, Calibrating and Applying Agent-Based Models: A Review. *Journal of Artificial Societies and Social Simulation* 23(2) 9.

2019 Geissler, K., **Fiedler, S.**, Ni, J., Herzschuh, U., Jeltsch, F. Combined effects of grazing and climate warming drive shrub dominance on the Tibetan Plateau. *The Rangeland Journal* 41(5) 425–439.

Wu, J., Li, M., **Fiedler, S.**, Ma, W., Wang, X., Zhang, X., Tietjen, B. Impacts of grazing exclusion on productivity partitioning along regional plant diversity and climate gradients in Tibetan alpine grasslands. *Journal of Environmental Management* 231, 635–645.

2018 **Fiedler, S.**, Perring, M.P., Tietjen, B. Integrating trait-based empirical and modelling research to improve ecological restoration. *Ecology and Evolution* 8(12), 6369–6380.

Guo, T., Weise, H., **Fiedler, S.**, Lohmann, D., Tietjen, B. (2018) The role of landscape heterogeneity in regulating plant functional diversity under different precipitation and grazing regimes in semi-arid savannas. *Ecological Modelling* 379, 1–9.

Acknowledgement

I thank all the people and institutions who supported me in one way or another during my doctoral studies. In particular, I want to express my gratitude to Britta who paved the way for me in summer 2014 when she offered me to support her in a research grant application for a project that met my interests very well. I will never forget the first months and years in Britta's young research group, when I could be part of the exciting growing process of the group. Thank you, Britta, for your countless support to any aspects of my academic life. Next to Britta, Mike was the one who supported me and this project from the beginning: Without the restoration experiment in Ridgefield set up by him and colleagues in Ridgefield, this project would have never been able to be developed in the first place. Thank you, Mike, for your always very thorough and very fast feedback to my work, and for your constant Skype call offers. I was lucky to be surrounded by a very pleasant working environment at the Freie Universität Berlin, with group members with whom I shared a lot of my time and great experiences. Thanks to all current and former group members for all your scientific and mental support. In addition, I want to thank my third supervisor Fernando for his motivating supervision, all colleagues all over the world who supported this project, the HPC team of the Freie Universität Berlin for their technical support, and the Freie Universität Berlin, the Universität Bayreuth, the German Research Foundation, the German Academic Exchange Service, the University Alliance for Sustainability, the ERASMUS+ programme for their financial support, Hanna, Katja, Marcus and Selina for giving helpful feedback on the thesis, Jonathan Jeschke for agreeing to review my thesis, and last but not least my family, partners, and friends for their mental support.

Contents

1

General Introduction

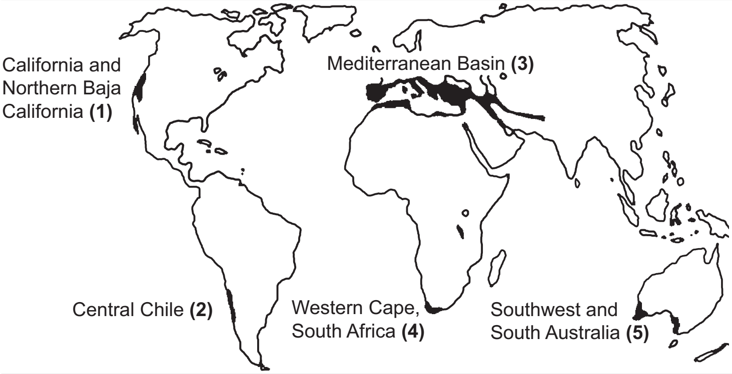
Humans have long been interacting with Earth's ecosystems and relying on them for their survival. With this, they have shaped and used their environment often not sustainably which has led to a loss in biodiversity and underlying functioning of these systems with adverse consequences for current and future human livelihoods. Therefore, anthropogenically motivated restoration of degraded ecosystems was increasingly being realised to counteract ecological degradation and to achieve long-term ecosystem multifunctionality. Successful restoration towards resilient and multifunctional ecosystems, however, still requires more knowledge about the functioning of these ecosystems, in particular on how ecosystem functions are affected by different biotic and abiotic conditions. In this thesis, I aim at filling relevant knowledge gaps to support restoration of degraded Mediterranean-type ecosystems towards long-term multifunctionality.

1.1 Characteristics of Mediterranean-type ecosystems

The Mediterranean biome is one of the global biodiversity hotspots and provides many ecosystem services to humans world-wide. At the same time, it undergoes dramatic degradation due to global change risking the livelihood of millions of people depending on these systems (Millennium Ecosystem Assessment, 2005; Myers et al., 2000; Sala, 2000). Mediterranean-type ecosystems or Mediterranean climatic regions are located between 30° and 40° northern and southern latitude with five distinct regions, which altogether belong to the Mediterranean biome, i.e., California and Northern Baja California, Central Chile, Western Cape of South Africa, Mediterranean Basin, and Southwest and South Australia (Figure 1.1). These ecosystems are part of the global drylands and characterised by mild, wet winters and hot, dry summers. Typically, 90% or more of the annual rainfall falls in and around wintertime, with mean annual precipitation ranging between 120 and 900 mm (Rundel and Cowling, 2013). The Mediterranean biome covers only about 2% of the Earth's land area but at the same time contains a high biodiversity and human population (Rick et al., 2020; Rundel and Cowling, 2013). About 20% of the global plant diversity and a high degree of endemism can be found in these ecosystems, both promoted by long human land use activities in these areas (Rundel and Cowling, 2013; Vallejo et al., 2012). Vegetation across the regions is mostly dominated by broad-leaved evergreen sclerophyllous woodlands that are called chaparral in California, matorral in Chile, fynbos and renosterveld in South Africa, matorral, maquis and garrigue in the Mediterranean Basin, as well as kwongan and mallee in Australia (Blumler, 2005; Cowling et al., 1996). Plants are primarily adapted to limited water and nutrients as well as regular fires, with exception of Chile where fires occur very rarely (Rundel and Cowling, 2013). Humans have used and depended on Mediterranean-type ecosystems for a long time. With the use of these ecosystems, humans significantly shaped the environment to its current form. History of land use has been quite different across the Mediterranean biome (Rundel, 1998). At present, these ecosystems are largely used for regional and global food, timber, and wine production as well as tourism (Blondel et al., 2010; FAO and Plan Bleu, 2013; Rick et al., 2020). Increasing unsustainable land use due to growing human population and demand has, along with other global change factors, led to severe degradation of Mediterranean-type ecosystems and their functioning with consequences for ecosystem service provision (e.g., FAO and Plan Bleu, 2018; Houerou, 2000; Vallejo et al., 2001).

1.2 Degradation of Mediterranean-type ecosystems

Ongoing and future land use changes in combination with increasing biotic invasion, nitrogen deposition, atmospheric CO_2 as well as changing climate exacerbate degradation in these systems with severe consequences for the long-term provision of ecosystem services (FAO and Plan Bleu, 2018; IPBES, 2019; Mace et al., 2012; Millennium Ecosystem Assessment, 2005;



Region	Area (10^6 km^2)	Native plant species	Endemic plant species (%)
1	0.32	4,450	48
2	0.14	2,900	50
3	2.30	25,000	50
4	0.09	8,600	68
5	0.11	80,00	75
Total (% / world)	**2.96 (2)**	**48,950 (20)**	**57**

Figure 1.1: Overview of Mediterranean-type regions on Earth. After Cowling et al. (1996); Médail and Quézel (1997).

Sala, 2000).

Land use across Mediterranean-type ecosystems has a long and diverse history and has impacted these ecosystems for centuries (Houerou, 2000; Rick et al., 2020). Deforestation, unsustainable agricultural and management practices, as well as urbanisation have been the major threats for these ecosystems across the globe which has led to increased fire hazards, decreased carbon sequestration, desertification, soil erosion, salt mobilisation and salinisation, and nutrient losses (Cowling et al., 1996; Hobbs, 1998; Vallejo et al., 2001). Sala (2000) projected that Mediterranean-type ecosystems are particularly threatened by future changes in land use with consequences for biodiversity and ecosystem functioning. For instance, increasing irrigation in agriculture might further diminish ground water availability in surrounding ecosystems, which leads to less carbon sequestration and a higher risk of salinisation (Nainggolan et al., 2013). Abandonment of agricultural fields or forest plantations might further increase biotic invasions and fire risks (Doblas-Miranda et al., 2017; Holman et al., 2017).

With increasing globalisation, *biotic invasion* has become problematic in Mediterranean-type ecosystems and might even intensify in the future (Godoy et al., 2011; Rouget et al., 2003). Invasion of alien species is one of the main drivers of biodiversity loss (Gaertner et al., 2009; IPBES, 2019; Vilà et al., 2011) with often unclear consequences for ecosystem functioning. In some studies, biotic invasion was associated with increased carbon and nitrogen fluxes as well as primary productivity (Liao et al., 2008; Rout and Callaway, 2009; Vilà et al., 2011), which might increase the risk of droughts due to higher water use.

Water-limited Mediterranean-type ecosystems might be particularly vulnerable to increasing water losses through *climate change* (Alessandri et al., 2015; Cramer et al., 2018). Climate projections for the end of the 21st century show an increase in surface temperatures by

1.5 – 2.0 °C and a reduction of average precipitation of up to 50%, which both will further increase water shortages in Mediterranean-type ecosystems (IPCC, 2014) with consequences for irrigation for food production and drinking water supply. Also, primary productivity and therefore carbon sequestration will decrease under drier conditions (Lindner et al., 2010; Murphy et al., 2010; Pereira et al., 2007), while the risk of fire and erosion will further increase (Fried et al., 2004; Inbar et al., 1998; Moriondo et al., 2006), which in turn might promote the establishment of alien species (Keeley, 2001).

Nitrogen deposition in Mediterranean-type ecosystems is expected to continue with rates of up to 15 kg nitrogen per hectare and year (Bobbink et al., 2010). The impact of nitrogen deposition is expected to be particularly severe in these nutrient limited systems (Sala, 2000). As a result of higher nitrogen availability, a shift from well adapted to more nitrophilous plant species is predicted which might reduce biodiversity (Ochoa-Hueso and Stevens, 2015; Southon et al., 2013). In addition, primary productivity may increase, leading to lower soil moisture and higher risk of droughts (Manning et al., 2006). Long-term carbon sequestration, however, is expected to be reduced (Manning et al., 2006; Ochoa-Hueso et al., 2013), which might be due to increased litter decomposition under elevated nitrogen concentrations (Valera-Burgos et al., 2013). The current *atmospheric* CO_2 level of about 400 ppm is predicted to increase to up to 450 – 1000 ppm by 2100 (IPCC, 2014) with uncertain long-term impacts on Mediterranean-type ecosystems. Primary productivity has been found to increase under elevated CO_2 due to higher water use efficiency and higher growth rates of plants (Nunes et al., 2015; Santini et al., 2014) and might therefore increase carbon sequestration. In addition, the nutrient composition of Mediterranean plants' tissue is expected to alter which may have an effect on future nutrient cycling (Körner and Miglietta, 1994). As a consequence of past, ongoing and projected global changes, the future provision of multiple ecosystem services demanded by the human population in Mediterranean-type ecosystems will continue to be threatened (Matteucci et al., 2013; Palahi et al., 2008). This necessitates strategies to restore ecosystems that are resilient to future alterations of global change factors and to improve the sustainable supply of ecosystem services (Bullock et al., 2011; Perring et al., 2012).

1.3 Restoration of Mediterranean-type ecosystems

Reverting the consequences of ecosystem degradation needs strategies to assist degraded, damaged, transformed or even destroyed ecosystems (Bullock et al., 2011). This is increasingly realised through the process of ecological restoration towards specific goals (Society for Ecological Restoration, 2004). Restoration goals have changed through time, particularly with the increasing realisation of what global environmental changes mean for attaining restoration targets (Perring et al., 2015).

Originally, restoration efforts were often motivated by the intent to recreate a reference system, either by restoring a past state of the specific ecosystem (temporal reference) or by emulating a spatially distinct ecosystem (spatial reference) with similar environmental properties (Bullock et al., 2011; Fry et al., 2014). Identifying an appropriate reference system is not always straightforward and is particularly difficult in Mediterranean-type ecosystems given their often diverse and long history of land use (Shackelford et al., 2013). Furthermore, restoration efforts from across the globe towards identified reference systems have shown that biodiversity and ecosystems services could not fully be restored with this approach (Benayas et al., 2009; Jaunatre et al., 2014). Moreover, the resilience (i.e., the ability of ecosystems to absorb changes of state variables, driving variables, and parameters, and still persist despite disturbances, Holling, 1973) of these recreated reference systems towards global change is not accounted for (Harris et al., 2006; Choi et al., 2008), and thus the restored system might be highly susceptible to current and future perturbations.

Some restoration efforts in the past focused on enhancing one ecosystem function (Bullock et al., 2011), an approach that has been termed rehabilitation as the focus is not on reinstating the pre-existing biotic integrity in terms of species composition and community structure (Society for Ecological Restoration, 2004). For instance, planting particularly fast-growing pines can reduce soil erosion and thus protect soils in abandoned landscapes in the Mediterranean Basin (Bonet, 2004), or can increase timber production and carbon sequestration in the south-eastern part of the USA (Cademus et al., 2014). Such a focus implicitly takes account of functional traits by choosing species based on their perceived ability to provide the desired service. However, focusing on single and specific ecosystem functions and services can negatively impact the provision of other functions and services (Bennett et al., 2009). Planted pine forests might for example also increase water extraction, which in turn might lead to more frequent or intense ecological droughts and reduced ground water recharge (Cademus et al., 2014) as well as increased risk of fire hazard and spread (Pausas et al., 2004). More recently, with increasing evidence that higher levels of ecosystem functioning and therefore supply of services is associated with greater species numbers (e.g., Soliveres et al., 2016), restoration has focused on increasing biodiversity (Nelson et al., 2009). However, enhanced biodiversity does not necessarily increase the simultaneous provision of multiple desired ecosystem services (Naidoo et al., 2008) and their resilience towards global change (Balvanera et al., 2006). Recently, there has been an increased focus on restoration towards multifunctional and resilient ecosystems that provide multiple ecosystem services at the same time (e.g., Eastburn et al., 2017; Lorilla et al., 2018; Perring et al., 2012; Valencia et al., 2015). In this context, the focus on certain plant characteristics, so-called plant traits, has been proven suitable as traits are linked to ecosystem functions depending on the environment. Based on these links, restorationists can select plant species based on their traits to manage desired ecosystem functions (so-called effect traits) that persist under specific environmental conditions (so-called response traits) (Funk et al., 2008; Laughlin, 2014a; Suding et al., 2008).

Although the plant functional trait concept has long been studied for different ecosystems and for various links between plant traits and ecosystem processes/functions (Funk et al., 2017; Lavorel and Garnier, 2002; Suding and Goldstein, 2008), there are still many knowledge gaps that allow successful restoration towards long-term multifunctionality across Mediterranean-type ecosystems. First, plant traits co-vary and thus restoration based on individual traits might lead to unfavourable outcomes, in particular if multiple traits affect the same functions differently (de Bello et al., 2010). Second, abiotic conditions directly and indirectly, via filtering plant species compositions and their traits, affect ecosystem functions (Funk et al., 2017). Thus, changes in abiotic conditions across space and time might lead to different ecosystem functioning which may be relevant for the long-term restoration of abiotically diverse Mediterranean-type ecosystems. Third, multiple environmental factors may interactively affect traits and functions (Xu et al., 2013), whereas the majority of studies mostly consider single factors (e.g., Cochrane et al., 2015; LeRoy et al., 2014; Prieto et al., 2015). We increasingly study and understand single links within the complex multi-layered relationship of multiple environmental factors that directly and indirectly, via multiple plant traits, affect multiple functions and services. However, studying multiple links at the same would be needed to gain applicable knowledge for restoration towards long-term and resilient multifunctionality across Mediterranean-type ecosystems. Due to the complexity of the relationships, empirical studies often cannot study multiple links at the same time as this would require much more space, time, and funding. With increasing computational technologies, simulation modelling that theoretically describe ecosystem processes with mathematical equations became a growing approach that is able to study complex full-factorial designs without the resource restrictions of an experimental study. However, to my knowledge there is no comprehensive process-based simulation model to date that is able to unravel the multi-layered relationship of environmental factors, plant traits and ecosystem functions for Mediterranean-type ecosystems in an applied restoration context. The reason for this could be the lack of sufficient empirical knowledge needed to develop and validate such ecosystem models.

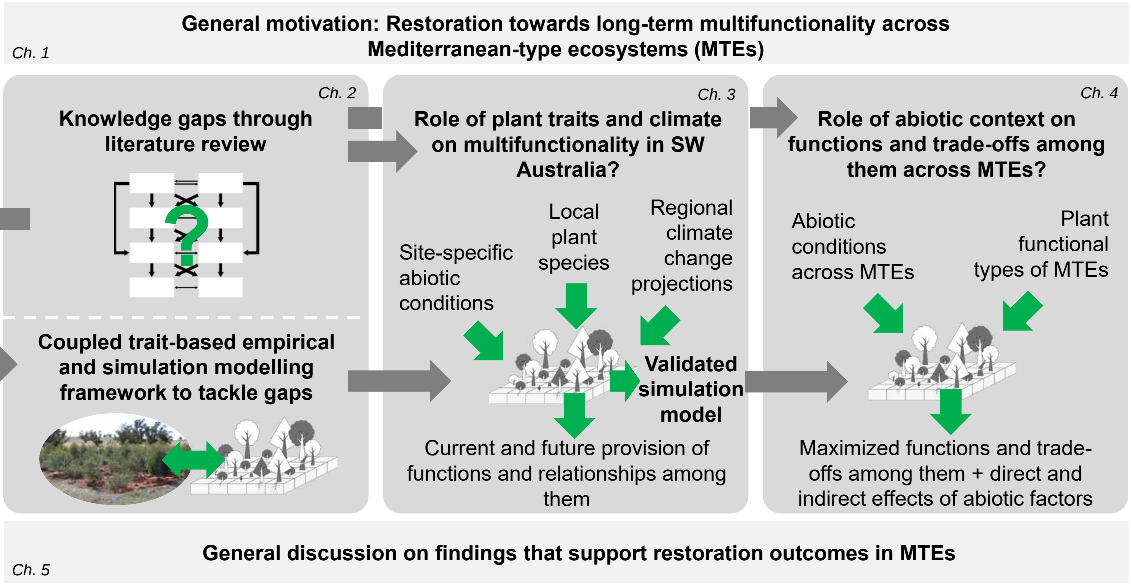


Figure 1.2: Overview of the structure of the thesis.

1.4 Objectives and structure of the thesis

With this thesis, I aim at advancing the field of restoration ecology to support restoration of degraded Mediterranean-type ecosystems towards the long-term provision of multiple ecosystem functions and services (Figure 1.2). In particular, the main objectives of this thesis are:

1. to identify current knowledge gaps in restoration ecology in order to support restoration towards the long-term provision of multiple ecosystem functions/services (Chapter 2),
2. to understand the link between plant traits, the provision of ecosystem functions/services and trade-offs among them in Mediterranean-type ecosystems (Chapter 3 and 4), and
3. to understand the impact of different environmental contexts across the Mediterranean biome as well as global environmental changes on this link (Chapter 3 and 4).

In Chapter 2 (published as Fiedler et al., 2018, in Ecology and Evolution), I reviewed the literature on trait-based and functional ecology to identify current knowledge gaps to support restoration towards a long-term provision of multiple ecosystem functions/services across Mediterranean-type ecosystems. I found that we still lack a full understanding of the interactive effects of different environmental factors on the long-term provision of multiple ecosystem functions/services, and a quantification of trade-offs and synergies among them, as well as how environmental factors either directly and/or indirectly, via changes in plant trait compositions, affect ecosystem functioning. To close this gap, I proposed a coupled trait-based empirical and modelling framework that can unravel this complex multi-layered relationship.

In Chapter 3 (published as Fiedler et al., 2021, in Journal of Applied Ecology), I applied this proposed coupled approach to a large-scale restoration experiment in SW Australia, the so-called Ridgefield experiment (Perring et al., 2012). As no small-scale trait-based simulation model exists that combines the dynamics of water, nutrients and individual plants in Mediterranean-type ecosystems, I developed the spatially explicit and individual-based simulation model ModEST (Modelling Ecosystem Functions and Services based on Traits), which combines these processes in a single model. ModEST can now be used in an applied restoration context to estimate different ecosystem functions and services over time for a given environmental setting including soil texture, climatic conditions, topography, and woody plant compositions with their traits. I successfully validated ModEST based on the data available from the Ridgefield experiment and subsequently simulated the provision of multiple ecosystem functions for various planted species composition (as means of restoration) in combination with different climate change scenarios. This went beyond the treatments done in the Ridgefield experiment and thus appended the knowledge gained from the experiment.

In Chapter 4, I synthesised the role of ecological restoration for maximised ecosystem functioning across the entire Mediterranean biome. In doing so, I applied ModEST to different environmental settings, with respect to precipitation, temperature, solar radiation and soil texture, that are characteristic for the five Mediterranean regions across the globe. By a cluster analysis, I constructed six generic plant functional types that best described the woody plant species across the Mediterranean biome based on plant trait data from the TRY database (Kattge et al., 2020). In a full factorial design of all environmental conditions that can be found across the Mediterranean biome as well as all possible plant functional type compositions available for restoration, I assessed how maximized ecosystem functions and trade-offs among them were related to planted species compositions depending on the environmental context. With this, I was able to assess how environmental factors combined, directly and indirectly (via changes in plant trait compositions) affected ecosystem functioning.

Finally, in the general discussion, I integrate the knowledge gained from Chapter 2 to 4 in particular by answering the questions (i) to what extent the link between plant traits and ecosystem functions might be useful for the restoration of degraded ecosystems, (ii) what challenges come up by focusing on ecosystem multifunctionality as a restoration goal, and (iii) how the integrated empirical and simulation modelling approach applied in this thesis supported this research and could be furtherly improved for future research endeavours.

2

Integrating trait-based empirical and modeling research to improve ecological restoration

published as **Fiedler S, Perring M, Tietjen B (2018). Integrating trait-based empirical and modelling research to improve ecological restoration. Ecology and Evolution. 8, 6369-6380.** `https://doi.org/10.1002/ece3.4043`

Abstract A global ecological restoration agenda has led to ambitious programs in environmental policy to mitigate declines in biodiversity and ecosystem services. Current restoration programs can incompletely return desired ecosystem service levels, while resilience of restored ecosystems to future threats is unknown. It is therefore essential to advance understanding and better utilize knowledge from ecological literature in restoration approaches. We identified an incomplete linkage between global change ecology, ecosystem function research, and restoration ecology. This gap impedes a full understanding of the interactive effects of changing environmental factors on the long-term provision of ecosystem functions and a

quantification of trade-offs and synergies among multiple services. Approaches that account for the effects of multiple changing factors on the composition of plant traits and their direct and indirect impact on the provision of ecosystem functions and services can close this gap. However, studies on this multilayered relationship are currently missing. We therefore propose an integrated restoration agenda complementing trait-based empirical studies with simulation modeling. We introduce an ongoing case study to demonstrate how this framework could allow systematic assessment of the impacts of interacting environmental factors on long-term service provisioning. Our proposed agenda will benefit restoration programs by suggesting plant species compositions with specific traits that maximize the supply of multiple ecosystem services in the long term. Once the suggested compositions have been implemented in actual restoration projects, these assemblages should be monitored to assess whether they are resilient as well as to improve model parameterization. Additionally, the integration of empirical and simulation modeling research can improve global outcomes by raising the awareness of which restoration goals can be achieved, due to the quantification of trade-offs and synergies among ecosystem services under a wide range of environmental conditions.

2.1 Introduction

The provision of ecosystem services that people rely on for their well-being is declining worldwide, a decline which is likely to continue in light of multiple global changes (e.g., land use, biotic invasion, and climate; Millennium Ecosystem Assessment, 2005). Improving the long-term supply of ecosystem services necessitates strategies to assist degraded, damaged, transformed, or even destroyed ecosystems (Bullock et al., 2011). Ecological restoration at regional and landscape scales is increasingly touted as being one such viable strategy, and this recognition has recently led to a global agenda to fully commit to restoration (Benayas et al., 2009; Society for Ecological Restoration, 2004; Shackelford et al., 2013; Suding et al., 2015). Here, we suggest that current and future restoration approaches might not achieve a goal of resilient (i.e., the ability of ecosystems to absorb changes of state variables, driving variables, and parameters and still persist after disturbances; Holling, 1973), multifunctional ecosystems due to a lack of knowledge about trade-offs among multiple ecosystem services (Bennett et al., 2009) as well as the effect of multiple changing environmental factors on services. We propose a framework that integrates simulation modeling and experimental approaches to address this critical knowledge gap. Arguments have been advanced that incorporating approaches focusing on plant functional traits—measurable properties of an individual plant or plant species, which can be compared across individuals and plant species, such as plant height, the specific leaf area, or specific root length (Bardgett et al., 2014; McGill et al., 2006; Violle et al., 2007)—can improve ecological restoration outcomes toward ecosystem service delivery (Funk et al., 2008; Laughlin, 2014a; Perring et al., 2015). These measurable traits have been found to be linked to ecosystem processes that drive the transfer of energy and/or materials, such as nutrients and water, over time and space—so called ecosystem functions—(Lavorel and Garnier, 2002), which provide the base for the provision of ecosystem services (Daily, 1997). Until now, most trait-based approaches have studied the effect of plant traits on only a single ecosystem function or service and thereby a priori neglected possible trade-offs among multiple functions/ services (e.g., Ruiz-Benito et al., 2014; Simpson et al., 2016, further examples in Tables A.1.1 and A.1.2). These trade-offs are potentially very important for service delivery. For instance, the plant trait "leaf area per unit ground surface area" (LAI) is positively linked to photosynthesis (Gratani et al., 2013), and species with high LAI may therefore be chosen to reach a goal of increased carbon sequestration. However, higher leaf area per unit dry mass (SLA, specific leaf area), which is positively correlated to LAI (Pierce et al., 1994), might at the same time negatively impact soil water content due to decreased water use efficiency (Medrano et al., 2009), which might result in a trade-off between carbon sequestration and water retention. In addition, individual traits may not only be linked to individual functions (Medrano et al., 2009). Instead, multiple traits can influence one function, and multiple functions can be influenced by a single trait (de Bello et al., 2010, and examples in Tables A.1.1 and A.1.2). As such, it is difficult to suggest traits that vary orthogonally, that is, that independently represent different functions. Although there is some evidence to suggest that there are orthogonal axes that determine plant strategies (e.g., the leaf-height- seed strategy scheme of Westoby, 1998), and there are thus a few traits that are a good description of plant responses to environmental change, subsequent research has shown correlations among even these axes (Garnier et al., 2004; Lavergne et al., 2003). In addition, there may also be other axes to consider (Laughlin, 2014b) and the fact that traits that respond to environmental change may have different effects on ecosystem functioning (Suding et al., 2008). As such, it will be valuable for both restoration and fundamental ecological understanding to continue to identify traits important to ecosystem service delivery, quantify covariation among traits across scales, and to assess whether there is environmental context dependency in this covariation (Funk et al., 2017; Vilà-Cabrera et al., 2015; Garnier et al., 2016). The strength and direction of the links between traits, functions, and services also need to be assessed for multiple environmental change settings, such as different combinations of land use, biotic invasion, and climate. This will enable plant trait compositions to be identified that are likely resilient to multiple factors, given traits and function maintain their association, thus, allowing continued provision of multiple ecosystem functions and services. So far, the effects of single environmental factors on plant traits and ecosystem functions are well investigated (e.g., Cochrane et al., 2015; LeRoy et al., 2014; Prieto et al., 2015), but less attention has been given to the simultaneous effects of multiple changing factors (see Table A.1.2). This is an important knowledge gap, as the overall effect of multiple factors may not be a simple sum of the individual effects (so called additive effects). Instead, the overall effect might result from the interaction of multiple changing environmental factors that cannot be predicted by the sum of the individual effects (so called nonadditive or interactive effects). For instance, nitrogen fertilization can increase the negative effect of drought on biomass production due to increased evaporative demands (Meyer-Grünefeldt et al., 2015). Accordingly, there might be nonadditive effects of nitrogen deposition and increasing aridity on carbon sequestration, emphasizing the importance of accounting for simultaneous impacts of multiple changing factors on the provision of ecosystem services. Most trait-based studies primarily focused on single environmental factors, and studies on simultaneous changes and thereby considering interacting effects of more than two changing environmental factors on ecosystem functions and services via plant traits are rare (e.g., Ashbacher and Cleland, 2015; Pérez-Camacho et al., 2012, see Table A.1.2). In addition to direct effects of changed factors, the indirect effects of these factors via changes in plant trait composition hamper the assessment of changes in ecosystem functions. For example, an increase in temperature directly impacts nutrient supply by the increased rate of litter decomposition (Rustad et al., 2001). As temperature might also impact plant species composition and thus litter quality, this could additionally indirectly impact decomposition rates and nutrient supply (LeRoy et al., 2014; Sariyildiz et al., 2005). Until now, there are in fact numerous short-term studies that particularly evaluated the direct effects of environmental factors on plant traits as well as on ecosystem functions (see Table A.1.2). However, only a few studies have taken into account the potentially important indirect effects of environmental change on ecosystem functioning via changing plant traits (e.g., Godoy et al., 2010; Valera-Burgos et al., 2013). In summary, most trait-based studies do not explicitly account for the full path from changing environmental factors via plant traits to ecosystem functions and services as given in Figure 2.1. Instead, they focus on only single links in the pathway and neglect interactions among environmental factors themselves, and between changing environments, plant traits, and functions. Thus, it is currently not clear to what extent the goal of restoring resilient multiple ecosystem services can be successfully achieved. A major reason for this knowledge gap might be that empirical studies often allow only for a limited complexity of the experimental design and short-time scales of assessment, due to restricted financial, spatial, or other resources. Therefore, a full factorial design, in which all plant trait combinations are integrated and changes in various environmental factors are evaluated to assess the long-term supply of various ecosystem functions and services, is normally not feasible. Process-based ecological simulation models that describe a simplified representation of an ecosystem, including its components such as individual plants and processes such as plant growth, and that explicitly account for plant traits could close the gap. However, such models depend on field data for model input (e.g., time series of weather conditions), parameterization (e.g., trait measurements such as specific leaf area) and validation of the model output (e.g., aboveground biomass). Here, we suggest that to fully realize the potential of trait-based approaches, empirical and simulation modeling research agendas need integrating.

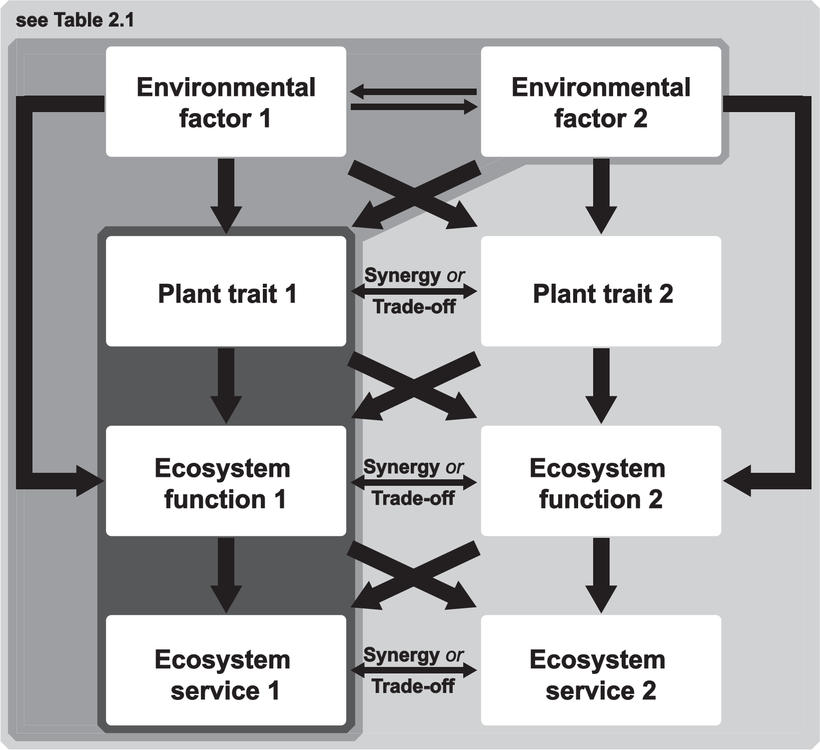


Figure 2.1: Components (boxes) and relationships (arrows) needed to assess the resilient provision of multiple ecosystem services. Based on literature for Mediterranean-type ecosystems, trait-based studies can be categorized as those that consider the effect of plant traits on (single) ecosystem functions and services (dark gray area, see Table A.1.1) and as those that consider the effects of changing environmental factors on single plant traits and/or on single ecosystem functions and services (medium gray area, see Table A.1.2). Table 2.1 (light gray area) explores the integration of simulation modeling and empirical approaches to tackle the research gaps identified by this framework.

In the following, we outline a stepwise research agenda that integrates empirical research and simulation modeling to better understand environmental change and plant trait effects on ecosystem services. We argue that implementing this agenda will aid practitioners and scientists in their aim of reinstating and maintaining ecosystem services on degraded land. Although we illustrate our research agenda with reference to Mediterranean-type ecosystems, our arguments pertain to furthering ecological restoration globally.

2.2 The way forward: Integrating trait-based empirical and simulation modelling research

Achieving a resilient supply of ecosystem services toward future environmental change requires integrative approaches that combine the knowledge gained from empirical studies with process- and trait-based simulation models. Such integrative approaches, however, have been generally missing until now. Ideally, the coupled approach should be initiated at the same time to identify synergies between empirical and modeling approaches at the earliest opportunity: for example (1) what are the joint research questions, (2) how can modeling and empirical research complement each other, (3) what components and processes of the system should be included to answer these questions, and (4) what data should be measured for model parameterization and validation. To achieve the goal of multifunctional and resilient ecosystems, we suggest the following fundamental and applied research questions need tackling (Figure 2.2):

1. Which relationships among ecosystem services result from reasonable plant trait compositions under current environmental conditions?
2. What are the indirect and direct impacts of changing environmental factors on ecosystem functioning? And which simultaneous effects of multiple changing environmental factors on ecosystem functioning and service provisioning are nonadditive and why?
3. Are there plant trait compositions that provide a resilient supply of multiple ecosystem services under global change?

Here, we briefly propose and describe three consecutive steps of a coupled agenda that describes how empirical and modeling research can be integrated to achieve the ultimate goal of multifunctional and resilient ecosystems (Table 2.1). We then elaborate these steps using an ongoing case study to illustrate the potential power of our approach.

2.2.1 Step 1: Development of trait-based simulation model

Empirical approaches can improve our understanding for mostly shorter-term ecosystem dynamics and less complex experimental designs (e.g., question 1). Models can complement this by assessing more complex designs (e.g., question 2) as well as the long-term success of

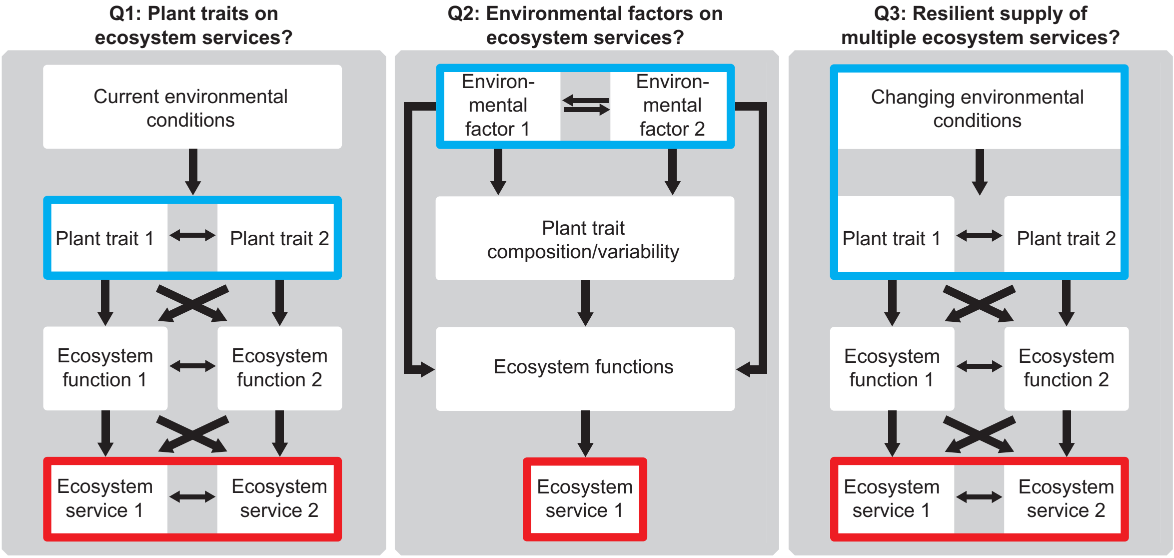


Figure 2.2: Schematic overview of potential research questions (Q1–Q3) that could be answered with the coupled approach. Boxes and arrows indicate which relationships among environmental conditions, plant traits, ecosystem functions, and services are addressed in each question. The blue boxes indicate the factor(s) that are systematically changed to answer the questions Q1–Q3, whereas the red boxes indicate the respective output(s).

restoration efforts (e.g., question 3). In order to answer more complex questions, a model should be developed that defines and simulates ecosystem stocks and fluxes that global changes influence and that underpin restoration goals in a coupled manner. Often validated models or processes already exist in the literature, and they only have to be adapted to the system studied (e.g., by including the effect of nutrient availability on plant growth) or newly linked (e.g., by coupling of vegetation, nutrient, and water processes). In answering our research questions, model components should include water, nutrient, and vegetation processes (respectively, e.g., infiltration, mineralization, and growth as a function of photosynthesis and respiration) and associated stocks (e.g., moisture at different soil depths, nutrient availability, and above-and belowground plant biomass). In addition, we need to incorporate explicitly plant traits that determine these dynamics, along with abiotic conditions. Incorporating traits in simulation models, rather than specific species, would also allow for assessing the whole variability range of a trait, both intra-and interspecifically. In addition, using plant traits with clear links to measured ecosystem functions and services is a prerequisite to better connect empirical and simulation modeling research. The specific empirical data required to feed into and assess simulations will depend upon the questions posed. We elaborate this in an example case study below and also highlight the challenges that require addressing to enable integration.

Table 2.1: Framework of a coupled trait-based empirical and simulation modeling approach to improve ecological restoration toward resilient and multifunctional ecosystems. Shown are three main consecutive steps stating the goal of each step, the actions needed in a simulation modeling approach, and the linkages to empirical approaches

Goal	**Simulation modeling approach**	**Link to empirical approach**
Step 1: Development of trait-based simulation model		
Existence of fully coupled ecosystem model that links from traits to ecosystem services	Implementation of coupled vegetation, water and nutrient processes, and their linkage to plant traits	Model parameterization based on measured plant traits, climatological data, and soil properties
	Definition of ecosystem measures to quantify ecosystem services	Additional empirical experiments proposed during model development
Step 2: Model validation and testing		
Gain confidence in modeled outputs and understand their sensitivity to parameters	Simulation experiments that resemble the empirical experiments for model validation	Model validation based on measured fluxes and states
	Sensitivity analyses of parameters	Comparison of modeled and measured ecosystem services
Step 3: Simulation experiments of scenarios and restoration options		
Improve restoration outcomes by detecting species compositions providing multiple ecosystem services resilient to environmental change	Long-term model simulations on multiple plant species compositions and changing environmental factors	Model assesses the same but also additional plant species combinations and treatments
	Evaluations of trade-offs and synergies among ecosystem services	Model suggests improved species combinations that are then planted and monitored to inform future work
	Evaluation of additive and nonadditive effects of multiple environmental factors	

2.2.2 Step 2: Model validation and testing

The step of model validation and testing is a crucial step to gain full confidence of the model developed which should always be repeated once the model has been changed or before it will be applied to another system. Local (single changed parameters) or global sensitivity analyses (multiple changed parameters at once) of model outcomes may be performed to find sensitive parameters that should be parameterized with high precision as well as less sensitive parameters for which some uncertainty can be accepted (Reuter et al., 2011; Ruget et al., 2002). However, if a sensitive parameter is uncertain, this uncertainty should be propagated through model simulations to establish a full range of potential outcomes (e.g., via an uncertainty analysis, see e.g. Hopfe and Hensen, 2011). For model validation, simulated dynamics should be compared to measured dynamics that have not been used for model parameterization (e.g., biomass dynamics that have not been used to calculate the growth rate). Process validation can require custom-made assumptions of model goodness (see e.g., Reuter et al., 2011; Sargent, 2013). If a stock cannot be validated, the description of the involved model processes might be adapted (see Step 1). Once the model is satisfactorily validated (Oreskes et al., 1994), simulation experiments for answering the research questions can be performed (see Step 3).

2.2.3 Step 3: Simulation experiments of scenarios and restoration options

Model experiments do not only resemble empirical experiments for model validation (see Step 2). Calculated simulations can additionally complement shorter-term empirical studies by evaluating a full factorial design of multiple changing environmental factors as well as plant species composition scenarios and by assessing potential long-term effects. A simulation modeling approach allows modifying environmental changes singly, or together. A major challenge is that multiple changes occur simultaneously and there are an overwhelming number of relationships; this ability of models to simulate factors in a controlled manner allows investigating likely mechanisms behind ecosystem responses. One can also consider whether environmental change factors themselves interact and assess the outcome of such relationships. More and more complex scenarios (e.g., with more environmental changes, a greater number of ecosystem functions) can be efficiently analyzed with such a modeling approach. Indeed, Figure 2.1 only hints at the complexity of the situation—environmental factor 2 could have direct effects on ecosystem function 1, while there is the potential for more than two environmental factors to be changing. The outcome of the factorial experiments allows for a systematic assessment of trade-offs and synergies among multiple ecosystem services. Direct and indirect effects, and additive and nonadditive interactions, of multiple changing environmental factors can also be evaluated. As a result, restoration scientists and practitioners can assess which trait compositions, if any, maximize the resilient supply of multiple ecosystem services in the face of simultaneous environmental changes. During this step, we can potentially generate better hypotheses of what will happen over time and across space outside of the empirically measured system, which can then be tested by additional empirical experiments. The outcome of such additional experiments can help to improve the development of the ecosystem model.

2.3 Case study — The Ridgefield Restoration Experiment

We exemplify our integrative agenda using an ongoing case study with focus on Mediterranean-type ecosystems. Although these systems cover only about 2% of the global terrestrial area, they contain about 20% of all plant species with a high degree of endemism (Cowling et al., 1996; Médail and Quézel, 1997). Long-term extensive human activity has contributed to the high biodiversity in Mediterranean-type ecosystems (Bugalho et al., 2011). However, altered and intensified anthropogenic land use during the last century combined with other factors of global change (e.g., biotic invasion, climate, nitrogen deposition, and atmospheric CO_2) led to the contemporary threatening situation for their unique biodiversity (IPCC, 2013; Sala, 2000), making them global biodiversity hotspots (Myers, 1990). Worldwide, many Mediterranean-type regions undergo a similar fate: deforestation, unsustainable agricultural and management practices, urbanization, and invasion by alien species are the major threats (Cowling et al., 1996). As a result of ecosystem degradation, ecosystem functions have altered. These changes lead to an increased fire hazard, decreased carbon sequestration, desertification, soil and water erosion, salinization, and nutrient losses (Hobbs, 1998; Vallejo et al., 2001). Ongoing and future alterations in global change factors have the potential to exacerbate degradation of Mediterranean-type ecosystems, leading to a further decrease in their provision of ecosystem services (Mace et al., 2012; Millennium Ecosystem Assessment, 2005; Sala, 2000). This requires plant communities that could be planted to restore Mediterranean-type ecosystems with respect to their ecosystem service supply as well as their resilience to future threats. To find these ideal plant communities, our approach is integrating a large-scale field experiment in an agricultural landscape in South West Australia (the Ridgefield Experiment, Perring et al., 2012) with a simulation model. The model (currently under development) is being parameterized through measurements at the site, to eventually investigate the long-term effects of functional diversity and multiple environmental factors on the supply of multiple ecosystem services, and trade-offs and synergies among them. The intention of future modeling will be to close the knowledge gaps to further the research field of restoration ecology, for example, in terms of process knowledge, suitable trait combinations and transferability of site-specific knowledge to other environmental conditions. In the following, we will describe the application of the three consecutive steps we argue are necessary to integrate simulation and empirical trait-based research. This description highlights the actions and potential links between simulation modeling and the field experiment that each step involves in order to address our research questions (Figure 2.3).

2.3.1 Step 1: Development of trait-based simulation model

In our coupled study, the Ridgefield experiment was set up in August 2010 (Perring et al., 2012), whereas the model development has started recently (Figure 2.3, Step 1). Although various trait-based simulation models of Mediterranean-type ecosystems exist and have been used, for example, to assess the impact of climate and fire on vegetation composition or performance, none of these models can currently fully assist restoration efforts toward multifunctional and resilient ecosystems. For example, several model approaches neglect soil water and nutrient

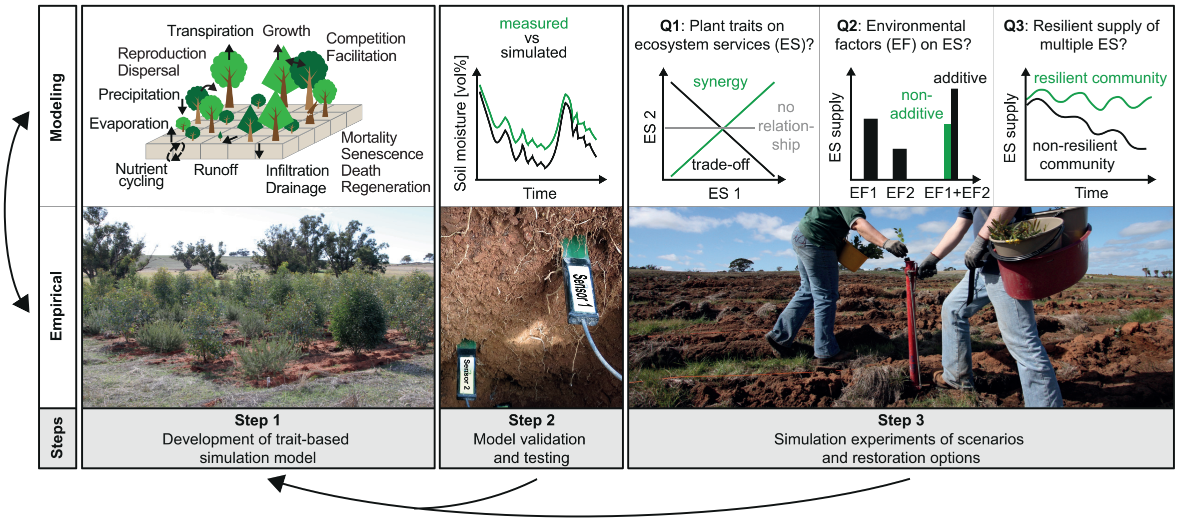


Figure 2.3: Steps of the coupled trait-based simulation modeling (first row) and empirical approach (second row) in our case study. Step 1 shows a model that simulates the fate of individual plants by calculating soil water, nutrient, and plant processes in a spatially explicit landscape divided into grid cells (first row) as well as a picture showing a plot of the large-scale restoration experiment in SW-Australia, Ridgefield (second row, © Richard J. Hobbs, 2012). Step 2 exemplifies how to validate the model by a comparison of simulated and measured soil moisture dynamics (first row) that was measured with soil sensors in different soil depths in Ridgefield (second row). Step 3 shows how to assess the research questions as shown in Figure 2.2 (first row). The first question (Q1) compares the outcome of two ecosystem services at a certain point in time and assess the relationships among them (no relationship, synergy, or trade-off). Additive and nonadditive effects of multiple environmental factors (Q2) are assessed through comparing the effects of single changes on the delivery of ecosystem services with the effects of combined changes. The third question (Q3) models initial plant trait compositions and asks which provide ecosystem services in a resilient manner over time. Those compositions can then be planted to aid restoration of degraded ecosystems (second row, © Cristina E. Ramalho, 2010). Importantly, these are monitored to assess whether supply of ecosystem services is resilient. Findings from both Step 2 and Step 3 can be used to further improve the simulation model, as indicated by the arrow returning to Step 1.

dynamics, as well as their feedbacks to vegetation dynamics (e.g., Esther et al., 2011; Moore and Noble, 1990; Pausas, 1999) and are therefore too simplified to assess the impact of global change. Other models explicitly consider water dynamics, but neglect nitrogen dynamics (e.g., Fyllas and Troumbis, 2009; Mouillot et al., 2001) and thus cannot account for the effects of nutrient deposition, for example, on invasive species or on ecosystem functions such as dissolved and particulate leaching and gaseous nutrient loss. In addition, these models are often rather conceptual and thus not thoroughly parameterized and validated against field data, which limits their suitability for applied restoration projects. Therefore, we are developing a process-based model that addresses the issues raised by linking processes for calculating water, nutrient, and vegetation dynamics.

Model overview

We divided the total modeled landscape (25 by 25 m^2, reflecting a plot in Ridgefield) into grid cells (each cell: 5 by 5 m^2) and different soil layers per cell. The size of the grid cells and the depth of the different layers depend on the site-specific soil heterogeneity. Each layer is defined by soil traits characterizing the local prevalent soil texture. Individual plants are distributed over the landscape and are characterized by plant traits. The main simulated ecosystem stocks that are necessary to measure ecosystem service supply over the landscape include above-and belowground living biomass, litter and dead biomass, plant cover, soil nutrient, and soil water content (Table 2.2 and Figure A.1.1). In order to simulate these stocks, nutrient, hydrological, and vegetation processes are calculated for each grid cell and/or soil layer driven by plant and soil traits and other internal (i.e., the outcome of other processes) as well as external drivers (e.g., weather conditions) (see Figure A.1.1). We briefly describe these inter-related processes below and provide references for readers who wish to know further details.

Table 2.2: Overview of the desired ecosystem services in the case study and how they will be measured from the simulated ecosystem and which model stocks will be considered to allow their quantification

Ecosystem service	Ecosystem measure	Model stocks
Carbon sequestration	Sum of sequestered carbon in biomass and soil	Aboveground living biomass
		Belowground living biomass
		Litter/dead biomass
		Soil carbon content
Nutrient supply	Sum of available nutrients for plants	Soil nutrient content
Erosion control	Total root fraction in the upper layer	Belowground living biomass in the upper layer
	Total vegetation cover	Plant cover
Invasion resistance	Invasive plant cover (in relation to total vegetation cover)	Invasive plant individuals
		Plant cover
Fire control	Plant functional diversity of fire strategy traits	Plant individuals with fire traits (e.g., resprouter vs. reseeder, flammability)
		Plant cover
Water retention	Total soil water content	Soil water content

Vegetation processes

Vegetation processes capture the entire life cycle of individual woody plants distributed over the landscape and include processes such as germination/establishment, growth, reproduction/dispersal, mortality, and where applicable recovery after fire (see further description in e.g., Smith et al., 2001). As we account for space, overlapping among neighboring individuals (above-as well as belowground) is explicitly modeled and thereby competition or facilitation for water, nutrients, and light is considered. All processes depend on plant-specific traits (e.g., leaf longevity, rooting depth) and are driven by soil moisture (as a result of hydrological processes), nutrients (as a result of nutrient processes), and actual weather conditions (either measured time series or time series generated from climate data). In addition to woody plants, the herbaceous understorey could also be modeled (Landuyt et al., 2018), as this may determine, for example, recruitment success of the woody plants, as well as being important for fire dynamics.

Hydrological processes

We simulate soil moisture dynamics by calculating all relevant hydrological processes (e.g., infiltration, runoff, drainage, evapotranspiration) for the different soil layers in the grid cells (see further description in e.g., Tietjen et al., 2009b). These processes depend on soil properties and topography, weather, and plant properties (from vegetation processes).

Nutrient cycling processes

Nutrient cycling processes (e.g., decomposition, denitrification, nitrification) and nutrient fluxes between the plant and soil compartment (e.g., nitrogen uptake, soil nutrient input, leaching) are calculated for each grid cell dependent on soil properties, soil moisture, plant properties (as a result of vegetation processes) (see further information on this relationship in e.g., Everard et al., 2010), actual temperature conditions, and nitrogen deposition (time series data on nitrogen deposition) (see further description in e.g., Wu et al., 2007). We are focusing on only nitrogen processes as Mediterranean-type ecosystems are primarily nitrogen-limited. However, if necessary, the model could also be extended by considering other nutrients such as phosphorus (e.g., Daroub et al., 2003). A challenge during this step is that processes can act on different temporal or spatial scales (e.g., water processes act on much smaller scales than vegetation processes). However, this challenge can be approached using a modular setting (such as used in Johnson et al., 2008; Tietjen et al., 2009a), which calculates processes in separate submodels running on different temporal and spatial resolutions. During this step, we have additional measurements of plant traits not already characterized, as well as measuring soil moisture dynamics in different soil layers, to allow for a thorough model parameterization and validation. Necessary parameters that cannot be measured due to restricted resources (e.g., specific rooting depth of plant species) will be gathered from data bases (e.g., TRY: Kattge et al., 2011) or parameterized through calibration, such that model outputs match measured stocks and processes (pattern-oriented modeling or Bayesian methods: e.g., Grimm et al., 2005; Hartig et al., 2012).

2.3.2 Step 2: Model validation and testing

For model validation, the model is parameterized and initialized based on the settings of the treatments in the Ridgefield experiment, which includes the actual spatial distribution of the individual plants, their traits and initial structure (e.g., above- and belowground biomass), the soil texture, and topography of the treatment plots across the site. The model should then be run under the same weather and nitrogen deposition time series as in the field experiments. Simulated soil moisture dynamics are compared to measured dynamics of the Ridgefield experiment (see Figure 2.3, Step 2). If there is a low root-mean- square deviation (also called RMSD) between measured and simulated soil moisture data, all model processes determining soil moisture can be seen as validated at least with respect to the outcome of the soil moisture. All main stocks that are used for quantifying the ecosystem services (Table 2.2) should be validated whether the processes have not been validated already elsewhere. As such, the simulated biomass of all species, the amount of soil carbon, and soil nitrogen could be compared to actual data.

2.3.3 Step 3: Simulation experiments of scenarios and restoration options

In the following, we demonstrate how the simulation experiments can be constructed and evaluated to answer our research questions (Figures 2.2 and 2.3, Step 3).

Which relationships among ecosystem services result from reasonable plant trait compositions under current environmental conditions?

For the Ridgefield experiment, eight woody plant species (*Eucalyptus loxophleba* ssp. *loxophleba*, *E. astringens*, *Acacia acuminata*, *A. microbotrya*, *Banksia sessilis*, *Hakea lissocarpha*, *Calothamnus quadrifidus*, and *Callistemon phoeniceus*) with different traits were planted in a complete randomized block design (in each block: similar soil type, aspect, and soil moisture) of ten plant assemblages. Plant species were selected based on their nutrient acquisition strategy, growth form and size, rooting depth, flower color, and bloom time. Plant assemblages were chosen to represent increasing functional and species richness. For all treatments, ecosystem services such as carbon sequestration, biotic resistance toward invading species, nutrient cycling, biodiversity maintenance, and pollination are regularly evaluated via different absolute as well as proxy measurements (detailed description of the field experiment in Perring et al., 2012). We complement the field experiment by simulating a full factorial design, in which more than eight plant species or plant functional types are integrated, starting from their seedling stage. In the simulation experiment, the same ecosystem services are quantified by ecosystem measures similar to those used in the field experiment (Table 2.2). Additional plant species compositions are simulated by artificially assembling reasonable trait compositions that include often found covariations (e.g., trade-offs between seed size vs. seed number) in repeated long-term simulations covering at least two life cycles of the target species and accounting for random processes such as weather events and plant dispersal. Also, to assess the effect of trait variation and covariation on selected functions/services, either single trait changes (via local sensitivity analyses) or joint trait changes (via global sensitivity analyses) could be tested (see general Step 2). We assess the supply of multiple ecosystem service supply for current environmental conditions. We evaluate trade-offs or synergies between the provision of selected ecosystem services by pairwise comparisons. As well as pairwise comparisons, the multifunctionality of the system could be assessed with various methodologies, for example, threshold approaches (Byrnes et al., 2014).

What are the indirect and direct impacts of changing environmental factors on ecosystem functioning? And which simultaneous effects of multiple changing environmental factors on ecosystem functioning and service provisioning are nonadditive and why?

To assess the indirect and the direct effects of changing environmental factors (such as nitrogen deposition, climate), the separate impact of a realistic change in each environmental factor is assessed for various species assemblages. For each environmental change, two scenarios are calculated: (1) to include only indirect effects, all direct environmental effects are kept on a constant level (e.g., the direct effect of temperature on the growth function), while community change occurs through altered leaf and/or root traits as the simulation progresses, and (2) to assess the additional impact of direct effects, the same simulations are run accounting for both direct and indirect effects. To assess whether the effects of changing environmental factors are additive or not, all changing environmental factors should be run separately and in different combinations in a full factorial design. Scenario outcomes of multiple changing factors are compared with the cumulative outcomes of the individual factors. For all analyses, the provision of ecosystem services is evaluated as described in question 1, that is, either via pairwise comparisons or indices of multifunctionality.

Are there plant trait compositions that provide a resilient supply of multiple ecosystem services under global change?

For the Ridgefield experiment, the ten plant assemblages are treated with or without nitrogen deposition and invasive plant species (via herbaceous biomass removal) in a nested split-plot design. Simulation experiments accounting for more than these two changing factors (i.e., also changes in climatic conditions) complement the field experiment. In particular, we run long-term simulations for projected changes of multiple environmental factors. Plant trait compositions are detected that optimize the current and future supply of multiple ecosystem services. Additionally, we assess whether service delivery over time is resilient (i.e., is maintained either through resisting change or recovering from change back to desired levels). Our model approach explicitly accounts for site-specific characteristics of the Ridgefield experiment such as soil type, topography, and land use legacy. Through the use of a case study such as this, we can suggest site-specific species assemblages that restore multiple ecosystem services and improve their resilient supply for degraded Mediterranean-type ecosystems in South West and South Australia with similar characteristics. Modifying site conditions, for example, soil type, while keeping other environmental factors constant, would allow us to investigate whether recommendations change for such different conditions. In addition, we will improve our theoretical understanding of the multilayered relationship consisting of multiple environmental factors influencing multiple plant traits and ecosystem functions/services. In a follow-up analysis, we can advance the knowledge about Mediterranean-type ecosystems in general, for example, by testing whether trade-offs among ecosystem services are site-specific and related to particular plant trait attribute values, or transferable to the entire Mediterranean biome. To this end, model experiments (Step 3) can be rerun for different Mediterranean sites around the world after the model has been retested and validated for the respective sites (Step 2). In addition, a systematic comparison between Mediterranean-type ecosystems can be conducted that evaluates (1) if similar trait values lead to a maximization of specific ecosystem services, and (2) if the trade-offs between services are similar for different regions with different characteristics and species pools. Future work could also consider whether there are global change factors, for example, chemical pollutants, ecosystem functions, and/or services that deserve greater attention when planning and assessing restoration.

2.4 Conclusion

To our knowledge, there are no mechanistic trait-based approaches that investigate relationships among multiple ecosystem services under the simultaneous impact of more than two changing environmental factors. We believe that our proposed integrative framework will close the gaps and thereby further the research field of restoration ecology to ultimately improve outcomes of the global restoration agenda. Our framework can contribute to trait-based research with respect to theory development and testing. Most importantly, our framework could for a given site suggest plant species compositions that could maximize the supply of multiple ecosystem services in the long term for given environmental changes. Through this endeavor, it could directly assist restoration efforts toward resilient multifunctional ecosystems. Alternatively, by not only simulating a single ecosystem but instead multiple connected ecosystems representing a landscape, it can highlight when integrating multiple restored ecosystems better provides desired, resilient, multifunctional landscapes as opposed to one single multifunctional ecosystem "type". Reaching the restoration goal of resilient supply of multiple ecosystem services in a changing environment needs integration of different research approaches. Our proposed framework provides a critical link between simulation modeling and in the ground research, to ultimately allow scientists, policy makers, and stakeholders to deliver the required improved restoration outcomes globally.

3

Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality

published as **Fiedler S, Monteiro, J, Hulvey K, Standish R, Perring M, Tietjen B (2021). Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. Journal of Applied Ecology.** `https://doi.org/10.1002/ece3.4043`

Abstract Ecological restoration increasingly aims at improving ecosystem multifunctionality and making landscapes resilient to future threats, especially in biodiversity hotspots such as Mediterranean-type ecosystems. Plants and their traits play a major role in the functioning of an ecosystem. Therefore, successful restoration towards long-term multifunctionality requires a fundamental mechanistic understanding of this link under changing climate. An integrated approach of empirical research and simulation modelling with a focus on plant traits can allow this understanding. Based on empirical data from a large-scale restoration project in a Mediterranean-type ecosystem in Western Australia, we developed and validated the spatially explicit simulation model Modelling Ecosystem Functions and Services based on Traits (ModEST), which calculates coupled dynamics of nutrients, water and individual plants characterised by functional traits. We then simulated all possible combinations of eight plant species with different levels of diversity to assess the role of plant diversity and traits on multifunctionality, the provision of six ecosystem functions that can be linked to ecosystem services, as well as trade-offs and synergies among the functions under current and future climatic conditions. Our results show that multifunctionality cannot fully be achieved because of trade-offs among functions that are attributable to sets of traits that affect functions differently. Our measure of multifunctionality was increased by higher levels of planted species richness under current, but not future climatic conditions. In contrast, single functions were differently impacted by increased plant diversity and thus the choice and weighting of these functions affected multifunctionality. In addition, we found that trade-offs and synergies among functions shifted with climate change due to different direct and indirect (mediated via community trait changes) effects of climate change on functions. With our simulation model Modelling Ecosystem Functions and Services based on Traits (ModEST), we show that restoration towards multifunctionality might be challenging not only under current conditions but also in the long-term. However, once ModEST is parameterised and validated for a specific restoration site, managers can assess which target goals can be achieved given the set of available plant species and site-specific conditions. It can also highlight which species combinations can best achieve long-term improved multifunctionality due to their trait diversity.

3.1 Introduction

Global change is contributing to a decline in biodiversity and ecosystem functions, which can underpin some of the ecosystem services that people rely on for their well-being (IPBES, 2019). Degradation associated with past change, and concern for the future supply of multiple ecosystem services is particularly apparent in Mediterranean-type ecosystems where remarkably high diversity is threatened by multiple environmental changes (Cowling et al., 1996; Sala, 2000). Reverting the consequences of ecosystem degradation may necessitate the process of ecological restoration which can target different goals such as the recovery of historic conditions or functional integrity of an ecosystem (Gann et al., 2019). In socio-ecological systems such as Mediterranean-type ecosystems, restoration may seek to achieve a long-term and simultaneous delivery of multiple ecosystem functions and services (Shackelford et al., 2013).

Managing landscapes for multiple functions or services simultaneously requires a direct comparison of their delivery (e.g., Byrnes et al., 2014; Manning et al., 2018). With increasing evidence that higher levels of ecosystem functions and services are associated with greater species numbers (e.g., Cardinale et al., 2012; Soliveres et al., 2016), the traditional focus of restoration on plant biodiversity appears justified (Perring et al., 2015). Enhanced biodiversity, however, does not necessarily increase the simultaneous and resilient provision of multiple ecosystem functions and services (Gamfeldt and Roger, 2017; Meyer et al., 2018; van der Plas et al., 2016) and the effect of global change on species and ecosystem functioning remains unclear (Giling et al., 2019).

In an attempt to further the understanding of biodiversity's role within ecosystems, restoration ecology has more recently made use of the functional trait concept allowing selection of plant species based on their response and effect traits (Laughlin, 2014a; Lavorel and Garnier, 2002). A focus on effect traits, which have been found to be linked to many ecosystem functions (Lavorel and Garnier, 2002), allows for a better comparison across individuals and plant species. Individual environmental factors affect individual functions/services via plant traits (e.g., Lavorel and Garnier, 2002; Suding et al., 2008). However, plant traits are not always linked to single functions. Instead, multiple traits can affect one function, and multiple functions can be affected by a single trait (de Bello et al., 2010), and multiple functions can influence a single ecosystem service (Fu et al., 2013). Such relationships are particularly important if traits positively affect one function while at the same time negatively impacting another one—so-called trade-offs (Bennett et al., 2009). Knowing the trade-offs as well as synergies among plant traits and functions is therefore important for selecting plant species based on their traits to simultaneously improve multiple functions/services.

In addition, multiple environmental change factors that directly, or indirectly (via altered plant trait distributions), affect ecosystem functions can have non-additive effects (e.g., Luo et al., 2008). Restoration strategies based on individually studied effects could therefore be problematic when trying to achieve a long-term supply of functions and services. Furthermore, traits within a plant community may be affected differently by environmental factors, and therefore the provision of trait-mediated ecosystem functions may be affected differently as well. Consequently, trade-offs among ecosystem functions/services observed under current environmental conditions might not be the same under future conditions.

To improve understanding and allow more informed restoration, (Fiedler et al., 2018) suggested an integrated approach that focuses on plant traits and combines the strengths of empirical and simulation modelling studies. Empirical approaches can support modelling approaches with essential data, while simulation models can extend empirical approaches by allowing assessment of the multi-layered relationship between multiple environmental factors, plant traits and ecosystem functions/services over larger temporal and spatial scales. Current trait-based simulation models provide a good basis for this approach (e.g., Esther et al., 2011; Fyllas and Troumbis, 2009; Schaphoff et al., 2018). However, to be able to support restoration towards multifunctional and resilient ecosystems, simulation models need to be combined and extended to meet the following criteria: (a) coupled processes for soil water, nutrient and plants as well as the respective feedbacks allowing to mechanistically study the impact of global change on ecosystem functioning (Fiedler et al., 2018), (b) consideration of individual interactions (e.g. facilitation and competition) as well as spatial heterogeneity relevant for applied restoration projects implemented on smaller spatial scales (DeAngelis and Grimm, 2014; Pacala and Deutschman, 1995) and (c) a thorough validation of model outcomes against field data to make simulation models applicable for restoration.

Based on existing model tools and a restoration experiment in a Mediterranean-type ecosystem in SW Australia (Perring et al., 2012), we therefore developed and validated the individual- and trait-based simulation model Modelling Ecosystem Functions and Services based on Traits (ModEST). ModEST links water, nitrogen and plant processes dependent on climatic and other environmental conditions and exhibits enough generality to transfer findings beyond this specific study site. In our model analysis, we focused on six biophysical ecosystem functions that might be important when restoring degraded Mediterranean-type ecosystems (i.e. groundwater recharge, ecosystem water use efficiency, ecosystem nitrogen use efficiency, litter quality, plant and soil carbon increments) with the goal to improve them simultaneously under current and future climatic conditions. Even though we focused on these specific functions, they can be linked to several provisioning and regulating ecosystem services, such as water supply, wood production, nutrient cycling and carbon sequestration which might be of greater interest to particular stakeholders.

In this study, we approached the following specific research questions:

1. What is the role of planted species richness under current and future conditions on multifunctionality, and the provision of the six separate ecosystem functions?
2. How will environmental changes affect trade-offs and synergies among the ecosystem functions of simulated plant communities?
3. What sets of plant traits and correlations among them in the simulated plant communities provide our focal ecosystem functions under current and future conditions?

With this approach we highlight that ModEST can be used for supporting long-term restoration if enhancement of ecosystem functions/services via planting woody plants under changing climate is the general goal. We further discuss how ModEST can be used for different environmental contexts and restoration targets.

3.2 Material and Methods

3.2.1 Model description

We developed a spatially explicit model, ModEST which simulates the coupled daily dynamics of nutrients, water and individual woody plants (Figure 3.1), from which different ecosystem functions and services can be estimated (Fiedler et al., 2020). The model landscape is subdivided into grid cells (5×5 m^2), two soil layers and individual plants characterised by coordinates within the landscape. The model runs for different environmental settings concerning soil texture, climatic conditions, topography, initial plant composition and their traits, with full descriptions given in Appendices A.2.1 and A.2.2. In the following, we briefly describe the three coupled modules of ModEST.

The nutrient module is based on processes for simulating soil nitrogen and soil carbon described in the model SWAT (Kemanian et al., 2011). Daily dynamics of soil organic matter (SOM), nitrate and ammonium in two soil layers are driven by nitrogen deposition from the atmosphere, decomposition and humification of plants' residue to SOM, immobilisation, mineralisation to ammonium, nitrification to nitrate as well as nutrient losses through volatilisation, denitrification and leaching.

We based the hydrological module on the approach of Tietjen et al. (2009b), who simulated surface water and soil moisture in two soil layers. Daily water dynamics are driven by precipitation, lateral water redistribution of surface water (affected by vegetation cover), infiltration, vertical fluxes and water losses via evaporation and transpiration. For ModEST, we adopted these processes with the exception of transpiration which we implemented after LPJ and LPJml (Schaphoff et al., 2018; Sitch et al., 2003) to better account for stomatal conductance (see description of the transpiration process in Appendix A.2.1) as well as infiltration which is now affected by the proportion of plant roots in the two soil layers. Evaporation, lateral surface water distribution and infiltration are affected by vegetation simulated in the plant module.

The plant module is mainly based on LPJ and LPJmL (Schaphoff et al., 2018; Sitch et al., 2003; Smith et al., 2014) and local processes as described for an individual-based plant model by May et al. (2009). The module simulates the life cycle of individual woody plants placed in the landscape, their dynamic below- and above-ground carbon and nitrogen pools as well as structural components (e.g. plant height, crown area) based on plant traits and abiotic conditions. We adopted—with some changes—the plant processes photosynthesis, transpiration, respiration, reproduction and allocation after Sitch et al. (2003) and Schaphoff et al. (2018), nitrogen uptake after Smith et al. (2014), as well as dispersal and establishment after May et al. (2009). We added a simple plant mortality process based on annual plant growth and a species-specific growth threshold below which the individual plant dies. Given these adaptations, we fully describe this module in Appendix A.2.1.

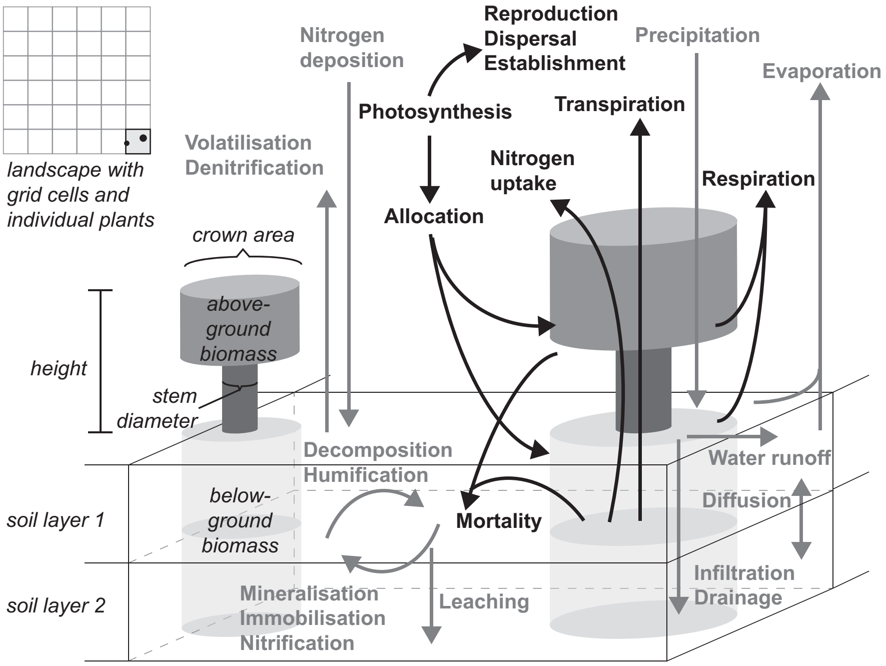


Figure 3.1: Structure (italic) and processes (bold) of Modelling Ecosystem Functions and Services based on Traits. The modelled landscape is subdivided into grid cells consisting of two soil layers as well as individual woody plants that are characterised by above- and below-ground features and are continuously distributed over the landscape. Coupled processes are calculated, that is hydrological and nutrient processes for each grid cell and soil layer (bold grey) as well as plant processes for each individual plant (bold black) depending on the resources of its covering grid cell.

3.2.2 Model parameterization and validation

We parameterised and validated ModEST based on the settings of the Ridgefield experiment, a large-scale restoration experiment situated in the wheatbelt of SW Australia on former agricultural land (Perring et al., 2012). The experiment is located in a Mediterranean-climate region (32°29’S 116°58’E, elevation 350 m a.s.l.) with mean annual rainfall of 453 mm (2013–2019) and precipitation mainly during winter. The average maximum daily temperature in January is 30.7°C and the average minimum daily temperature in August is 7.6°C.

We parameterised morphological, reproductive and physiological traits (Table A.2.2) of eight evergreen shrub and tree species (*Eucalyptus loxophleba* ssp. *loxophleba*, *E. astringens*, *Acacia acuminata*, *A. microbotrya*, *Banksia sessilis*, *Hakea lissocarpha*, *Calothamnus quadrifidus*, *Callistemon phoeniceus*). Species were selected because they had different nutrient acquisition strategies, growth forms and sizes, rooting depths, flower colours and bloom times, all properties that we expected to influence ecosystem functions, including some not modelled here, for example, pollination (Perring et al., 2012). We used the most prevalent soil type (loamy sand, Table A.2.1) in the experiment (see Appendix A.2.2 for full description of model parameterisation).

For model validation, we checked the outcome of the parameterised model against measurements from Ridgefield plots (see Appendix A.2.2 for model settings). We quantitatively compared simulated and observed dynamics using Spearman's rank correlation r and the root mean square error RMSE (Figure A.2.2). Simulated above-ground alive biomass, mean plant height and surviving individual counts agreed well with the measured data [i.e. significant ($p < 0.01$) correlations, low RMSE]. Exceptions were the biomass dynamic of *B. sessilis* and the population dynamics of *C. quadrifidus* and *C. phoeniceus*, where correlations were insignificant. However, RMSE for these cases remained low ($\text{RMSE} < 1.0$), indicating only small deviances between simulated and measured dynamics, and suggesting reasonable model behaviour.

3.2.3 Simulation experiments

We simulated a full-factorial design of plant species combinations using the eight species included in the Ridgefield study (and thus simulating plant assemblages beyond those planted at Ridgefield) to assess ecosystem functioning under current and future climatic conditions. The flat modelled landscape (50×50 m^2) contained a homogenous soil texture of loamy sand, with initial soil moisture (=0.15 m^3/m^3), ammonium (=2.35 mg/kg) and nitrate (=9.92 mg/kg) set to the mean measured values across all Ridgefield plots with soil texture loamy sand. Each scenario was repeated 10 times to account for stochasticity in the initialisation of plant individuals (see Species richness scenarios), weather input (see Climate change scenarios) and the dispersal process (see model description in Appendix A.2.1).

Species richness scenarios

All possible combinations of the eight woody plant species used in the Ridgefield experiment were simulated leading to 255 different plant species compositions. Using this design, communities covered a wide range of different plant trait combinations, and species richness varied from monocultures to eight-species mixtures with increasing functional diversity (Figure A.2.6). For each simulation, 500 one-year-old individuals with the same or a similar initial individual number of each present species were randomly positioned in the landscape with 2 m distance to neighbouring individuals. Initial plant heights were randomly drawn from a species-specific normal distribution that was obtained from height distributions of the 1-year planted individuals in the Ridgefield experiment (Figure A.2.3).

Climate change scenarios

For current climatic conditions, we used corrected daily precipitation, minimum and maximum air temperature and solar radiation data from 1990 to 2018 from the weather station in Pingelly (32°31'S 117°04'E, 297 m a.s.l.) about 12 km away from our study site (Bureau of Meterology, 2015, Appendix A.2.3). Atmospheric CO_2 was set to 400 ppm.

For assessing impacts of climate change, we obtained the anomalies for future conditions (2080–2099) compared to past conditions (1986–2005) separately for each season based on the four climate projection Representative Concentration Pathways (RCPs) for SW Australia (Hope et al., 2015). We added the median reported trend between past and future climate from different global climate model simulations to the current weather data from Pingelly to generate realistic time series of future weather data. Atmospheric CO_2 was set according to IPCC (2014).

For each model repetition, we randomly selected annual weather data from the current or future weather dataset, given the climate scenario, to get 50 years of weather time-series input data.

For better clarity, we focused on the most extreme climate projection RCP 8.5 with an increase in mean annual air temperature of 3.4 °C and a decrease in mean annual precipitation of 16% (Table A.2.3; Figure A.2.4). Across the different RCPs, ecosystem functioning exhibited qualitatively similar patterns (Figure A.2.7).

3.2.4 Evaluation of simulation outcomes

To assess the provision of, and trade-offs and synergies among, ecosystem functions, we determined the supply of six functions related to water, nitrogen and carbon (Table 3.1), that is, groundwater recharge (GWR), ecosystem water use efficiency (EWU), ecosystem nitrogen use efficiency (ENU), ecosystem litter quality (ELQ), total plant (PCI) and soil carbon increments (SCI). We selected these functions as they may be important to consider when restoring water- and nutrient-limited Mediterranean-type ecosystems (Luo et al., 2020). These functions can be linked to several provisioning and regulating ecosystem services, such as water supply, wood production, nutrient cycling and carbon sequestration. For measuring multifunctionality, we first standardised each ecosystem function value based on the maximum and minimum value found for the same function. As these extreme values varied across the climate scenarios, we assessed how the context (current vs. future climate) affected the standardisation of the functions. Therefore, we standardised each function value based on the extreme values found either within, or across, climate scenarios. We then calculated multifunctionality for a given simulation as the mean of these standardised single function values, thus giving two values per simulation, that is, within a climate scenario, or across climate scenarios. The multifunctionality measure follows the approach by van der Plas et al. (2016), however, without comparing functioning against a desired minimal threshold which significantly affects the outcome (see Figure A.2.8, left panel). In the absence of other information, we weighted all ecosystem functions equally, therefore giving them equal importance within our measure of multifunctionality. We assessed the sensitivity of our outcomes by using different measures of multifunctionality (see Figure A.2.8, right panel) or by different inclusions or weightings of our focal functions (see Figure A.2.9). We calculated the community weighted mean (CWM) for selected traits (Table 3.2) to evaluate the plant trait distribution. These traits are measurable in the field and therefore applicable for ecosystem restoration.

Table 3.1: Ecosystem functions assessed in this study, how they are measured from ModEST, and their potential linkages to ecosystem services

Ecosystem function	**Model output**	**Unit**	**Potential link to ecosystem service**
Groundwater recharge (GWR)	Annual deep (>2 m in soil depth) soil water drainage per m^2	mm/year	Water supply
Ecosystem water use efficiency (EWU)	Annual net primary productivity (NPP) per m^2/Annual precipitation per m^2	$g\ L^{-1}\ year^{-1}$	Water supply, Wood production
Ecosystem nitrogen use efficiency (ENU)	Annual NPP per m^2/Annual mean soil avail. nitrogen per m^3	$kgNPP\ m^{-2}\ kg^{-1}\ m^{-3}$	Nutrient cycling, Wood production
Ecosystem litter quality (ELQ)	Annual nitrogen per m^2/Annual carbon per m^2 from plant's residue	$gN\ year^{-1}\ kgC^{-1}\ m^2\ year^{-2}$	Nutrient cycling
Total plant carbon increment (PCI)	Annual plant carbon increment	$kg\ m^{-2}\ year^{-1}$	Carbon sequestration
Total soil carbon increment (SCI)	Annual soil carbon increment	$t\ m^{-2}\ year^{-1}$	Carbon sequestration

Table 3.2: Focal plant traits assessed in this study. Trait values for the plant species used in this study are shown in Table A.2.2

Abbreviation	**Description of plant trait**	**Unit**
SLA	Specific leaf area	m^2/kg
rootL1	Fraction of total root mass between 0 and 50 cm of the soil horizon	—
seedMass	Seed mass	mg
WP	Relative water content at wilting point for soil texture loamy sand	—
CNleaf	Carbon to nitrogen ratio in the leaves	—
LM/RM	Allometric constant describing optimal ratio of leaf to root mass	—
meanDisp	Mean dispersal distance of seeds	m
maxCA	Maximum crown area	m^2
WD	Wood density	kgC/m^3

3.3 Results

3.3.1 Planted species richness effects on ecosystem functioning

Ecosystem multifunctionality, with individual functions standardised within a given climate scenario, increased with planted and realised richness under current climate conditions, but decreased under future conditions (Figure 3.2A, left; see also Figure A.2.10). However, when considering minimum and maximum value per function across climate scenarios, current multifunctionality decreased with greater richness (Figure 3.2A, right). In addition, the relationship between multifunctionality and planted richness depended not only on the calculation of multifunctionality (Figure A.2.8) but also on the choice and weighting of ecosystem functions (Figure A.2.9).

In the latter, our measure of multifunctionality was not always enhanced by increased planted species richness since single ecosystem functions increased or decreased with planted species richness under current conditions (Figure 3.2B). Climate change strengthened this pattern and increased variability for most of the functions, except for groundwater recharge and litter quality. For communities with up to three or four planted species, groundwater recharge declined, whereas the water use efficiency of the ecosystem increased. If more than three or four species were planted, both functions remained stable. Nitrogen use was most efficient for monocultures. In contrast, litter quality increased with higher planted richness under current conditions reaching maximum quality for the most speciose community, while under future conditions litter quality declined with higher planted richness. Soil carbon increments and to a lower extent plant carbon increments were enhanced with higher planted richness, reaching their maximum at an intermediate richness, and remaining stable for higher values. Except for plant carbon increment, all ecosystem functions showed a decreasing spatial and temporal variability with increasing planted richness (Figure 3.2B; Figure A.2.11).

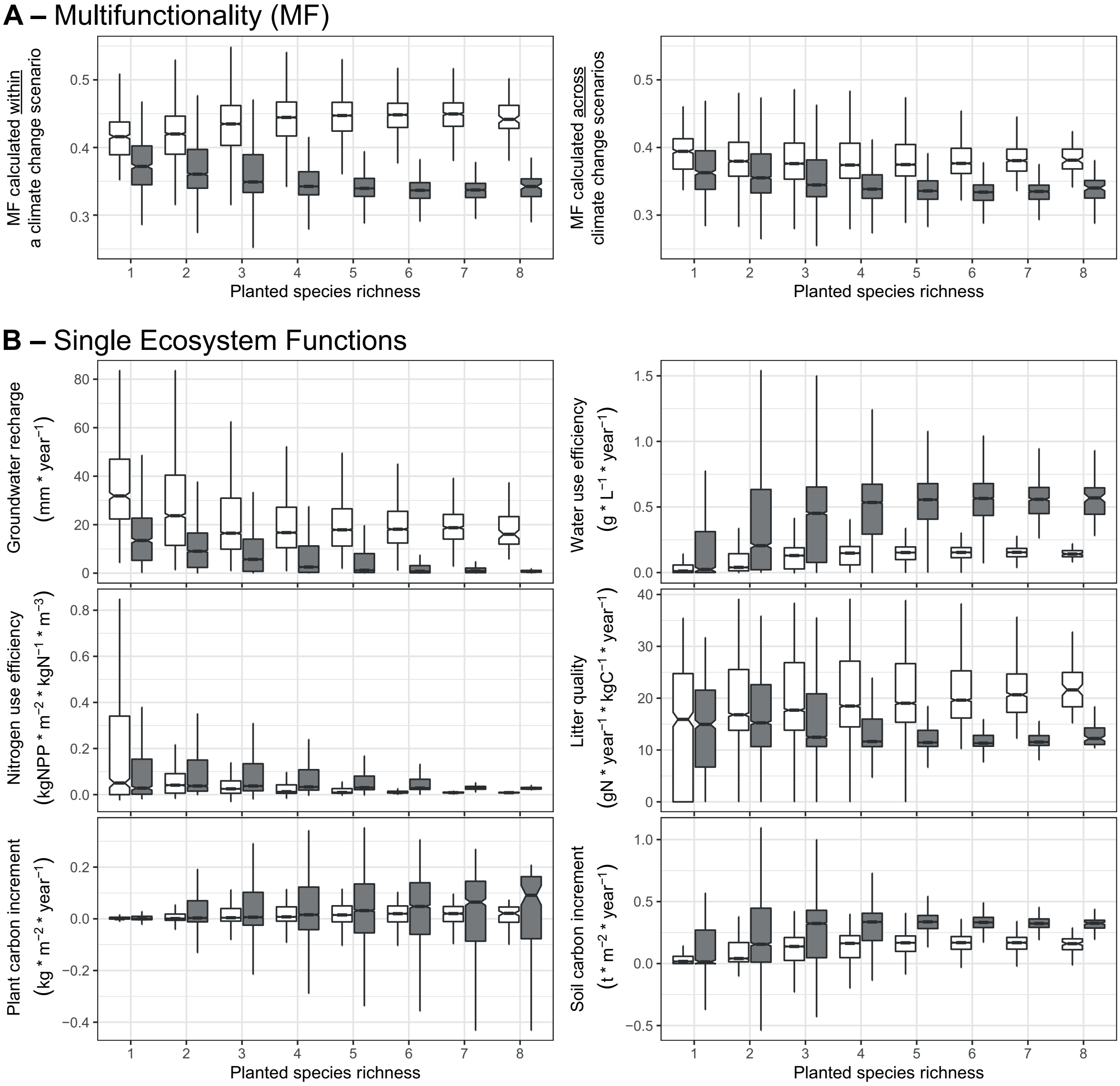


Figure 3.2: Multifunctionality (A) and single ecosystem functioning (B) for each planted species richness under current (white boxplots) and future climatic conditions (grey boxplots). Multifunctionality is either calculated within each climate scenario (A, left) or across climate scenarios (A, right). Shown is functioning for the last 10 simulated years and for 10 model repetitions as well as for 255 different plant communities which are unevenly distributed across the different planted species richness scenarios according to maximal possible combinations out of the pool of eight focal plant species. For better comparability among boxplots, single outliers are not shown.

3.3.2 Trade-offs and synergies among ecosystem functions

With the eight plant species considered in this study, ecosystem multifunctionality could not fully be achieved, in current or future conditions (MF much smaller than 1, Figure 3.2A), since there are negative correlations (trade-offs) among functions (Figure 3.3A). Multifunctionality benefited from a strong positive correlation (synergy) between soil carbon increment and water use (Figures 3.2B and 3.3A). However, stronger trade-offs between ecosystem nitrogen use and litter quality as well as between groundwater recharge and ecosystem water use or soil carbon increment constrained the enhancement of the multifunctionality.

Most relationships between nitrogen use efficiency and other functions reversed under future conditions: in contrast to current conditions, an increase in nitrogen use efficiency was now accompanied by a decline in groundwater recharge as well as a strong increase in water use and soil carbon increment in the ecosystem. In addition, ecosystem litter quality and groundwater recharge could be increased at the same time under future conditions, which was not possible under current conditions. Some trade-offs and synergies observed under current conditions strengthened under the future climate scenario: trade-offs between ecosystem litter quality and ecosystem water usage, or soil carbon increment, became more apparent, whereas ecosystem nitrogen use efficiency and plant carbon increment were increased at the same time.

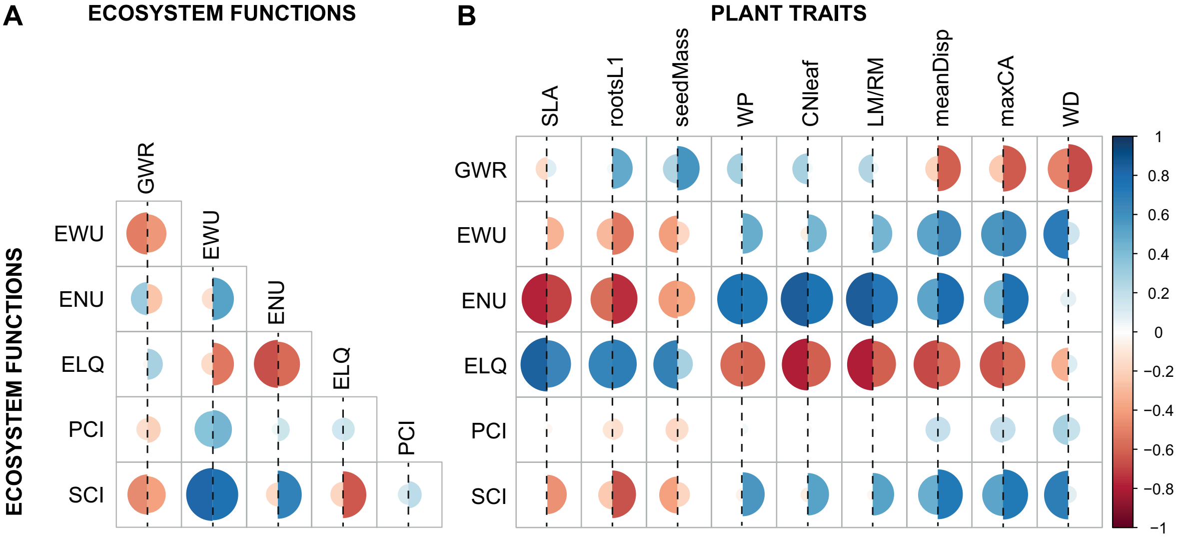


Figure 3.3: Negative (trade-off, red) and positive (synergy, blue) relationships among ecosystem functions (A) as well as between functions and community weighted mean (CWM) plant traits (B) under current (left half circle) and future climatic conditions (right half circle). Shown are significant Spearman's rank correlations ($\alpha = 0.05$) based on the last 10 simulated years and for 10 model repetitions across all 255 simulated plant communities. GWR, Groundwater recharge; EWU, Ecosystem water use efficiency; ENU, Ecosystem nitrogen use efficiency; ELQ, Ecosystem litter quality; PCI, Total plant carbon increment; SCI, Total soil carbon increment (see Table 3.1). Meaning of abbreviations for CWM plant traits can be found in Table 3.2.

3.3.3 Plant traits in the community and ecosystem functioning

Community-weighted mean plant traits could be linked to single ecosystem functions (Figure 3.3B). Particular trait combinations rather than single traits affected individual functions. Water- and nitrogen-related functions showed contrasting correlations to plant traits in the community, explaining their strong trade-offs. For example, under current conditions groundwater recharge (GWR) was enhanced by communities with a low SLA, higher investment into leaves than into roots (LM/RM), smaller crowns (maxCA), lower wood density (WD) and a higher wilting point (WP). In contrast, to achieve an improved ecosystem water use efficiency (EWU), wood density and maximum crown area should be larger in combination with a deeper rooting system (low value of rootL1). Very similar features that improved ecosystem water use efficiency also increased plant carbon increment (PCI) and soil carbon increment (SCI) in the ecosystem, supporting the synergies among the three functions.

Under future climatic conditions, correlations between functions and traits changed especially for soil carbon increment and water-related functions (Figure 3.3B). Traits associated with ecosystem nitrogen use efficiency and litter quality showed no or limited change in importance. The underlying reason for these changes as well as the changes of the relationships among functions (Figure 3.3A) is that climate change affected functions differently: that is, either directly (e.g. Figure 3.4, changes in PCI not correlated with changes in SLA), indirectly via traits (e.g. Figure 3.4, changes in ELQ strongly correlated with changes in SLA) or by a combination of both (e.g. Figure 3.4, changes in GWR not correlated with changes in SLA but appearance of clusters of species compositions). For instance, the emerging trade-off between groundwater recharge and nitrogen use efficiency under climate warming (Figure 3.3A) was due to a negative direct and indirect effect of climate change on groundwater recharge as well as a slight positive and indirect effect of climate on nitrogen use efficiency (Figure 3.4). In addition, we found that trait compositions shifted with climate change in particular for more speciose planted communities due to a loss of many species (Figures A.2.6, A.2.10 and A.2.14), that is, shifts to plants with deeper roots, higher maximal crown area and with lighter and far-dispersed seeds. These changes led to a larger reduction in groundwater recharge and ecosystem litter quality (Figures 3.2B and 3.3B), which explains the decreasing multifunctionality with increasing planted richness under climate change (Figure 3.2A).

3.4 Discussion

3.4.1 Trade-offs among functions shift with climate change

As expected, we found that trade-offs prevented the achievement of restoration goals with simultaneous enhancement of multiple functions/services when the same trait or group of traits had positive effects on one function, but negative effects on a second function (e.g., de Bello et al., 2010; Teixeira et al., 2020). Instead, bundles of functions with synergies among

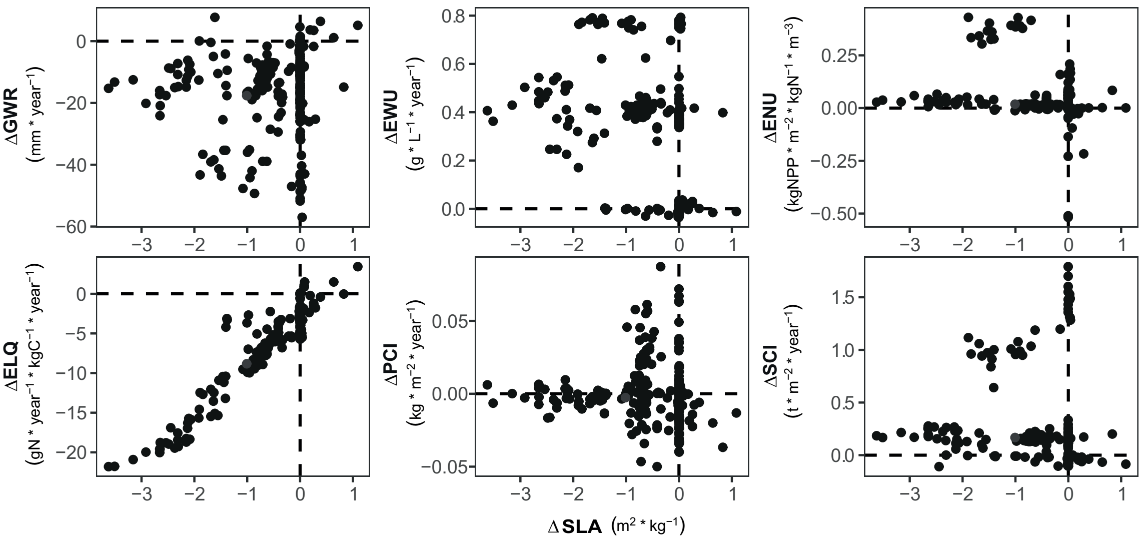


Figure 3.4: Disentangling direct and indirect effects of climate on ecosystem functioning by correlating climate change affected changes in CWM specific leaf area (ΔSLA) against changes in the six ecosystem functions. Shown are mean changes between current and future climatic conditions across the last 10 simulated years and 10 model repetitions per simulated plant community (black dots). Dashed lines separate plots into four quadrants with positive (top right) and negative (bottom left) changes in both trait and function; or trait and function differently affected (top left and bottom right). Values on dashed lines show no changes with climate change in functioning and/or trait. As we have strong trait–trait correlations that mostly remained the same under climate change (Figure A.2.12), we only show the results for changes in CWM SLA (see Figure A.2.13 for all traits). GWR, Groundwater recharge; EWU, Ecosystem water use efficiency; ENU, Ecosystem nitrogen use efficiency; ELQ, Ecosystem litter quality; PCI, Total plant carbon increment; SCI, Total soil carbon increment (see Table 3.1).

them could be increased, and thus choice of the ecosystem services to be restored might be crucial. For instance, if managers want to improve water-efficient wood production and carbon sequestration [but not groundwater supply as also found by Cademus et al. (2014)], this can be achieved by planting communities with deeper roots, greater crown area and wood density as well as small seeds with larger dispersal distances.

We additionally found that trade-offs and synergies among ecosystem functions observed under current conditions shifted under future conditions, posing a clear challenge for long-term restoration where plant compositions are planted with the aim of delivering multiple ecosystem functions and services. We observed that these shifts in the relationships among functions can be explained either by a direct change of ecosystem functioning differently affected by changing environmental conditions and/or by an indirect change through uneven shifts in underlying community plant traits and thus changes in the correlations among CWM traits (cp. Zirbel et al., 2017). In our study, simulated climate change altered species and thus trait compositions as reviewed also by Maestre et al. (2012b) for drylands as well as single trait–trait correlations as also shown by Ahrens et al. (2020). These climate change induced shifts resulted mostly through communities that for instance decreased groundwater recharge potentially via higher transpiration from the second soil layer and increased nitrogen use efficiency via less demand for nitrogen. At the same time, decrease in groundwater recharge was affected also directly by climate change via less available water for infiltration, and higher evapotranspiration due to warmer temperatures (cp. Reinecke et al., 2021). These uneven shifts mediated through different direct and indirect effects explain for instance the change from synergy to trade-off between groundwater recharge and nitrogen use efficiency. Therefore, the choice of specific plant species as well as changing environmental conditions should strongly be considered in restoration planning. Our modelling tool can facilitate this planning as it is able to simulate the short- and long-term effects of different plant species settings and environmental changes on ecosystem functioning. However, we note that we did consider only a limited pool of plant species and did not incorporate trait variation and plasticity, which might alone or in combination attenuate or enhance shifts in relationships among functions (Berzaghi et al., 2020; Liu and Ng, 2020).

3.4.2 Multifunctionality might not always be the right choice

If restoration aims to only increase ecosystem multifunctionality, we found that promoting plant diversity achieved this goal under current climatic condition, at least for our selected ecosystem functions as well as for our measure of multifunctionality. This is in line with previous findings and different measures of multifunctionality (Gross et al., 2017; Maestre et al., 2012a). However, our findings differed depending (a) on the choice of the multifunctionality measure (Figure A.2.8, see also e.g. Byrnes et al., 2014; van der Plas et al., 2016), (b) on the inclusion and weighting of certain functions (Figure A.2.9, see also e.g. Manning et al., 2018), as well as on the climatic context considered for the standardisation of the individual functions (Figure 3.2A, see also Giling et al., 2019). Therefore, if multifunctionality is the goal, these aspects should be well defined in collaboration with the stakeholders. For instance, if a certain minimum threshold of a function is desired, the level of the threshold can make a significant difference on the outcome (Figure A.2.8). If the variability of a function is important, the multifunctionality measure as suggested by Maestre et al. (2012a) might be the choice, which in contrast to our chosen measure showed no clear relationship with increased species richness under current conditions, suggesting that variability strongly affected our results.

Furthermore, even though current multifunctionality in our study was improved by greater richness, single functions were differently impacted. For instance, ecosystem nitrogen use efficiency did not benefit from higher planted richness which contrasts empirical findings that have shown complementary effects of diverse woody plant communities on nitrogen use (e.g., Schwarz et al., 2014). Even though plant structural complementarity was considered in ModEST (see Appendix A.2.1 e.g. eqn. A.29), we focused on only eight evergreen woody species with similar C:N ratios (Table A.2.2), of which only some survived (Figure A.2.10), thus complementary nitrogen use was likely not prevalent. Other functions such as litter quality increased with planted richness under current conditions. This pattern is attributed to particular surviving species characterised by a high litter quality (Figure A.2.14, low C:N in the leaves for more speciose planted combinations under current conditions).

In general, greater planted richness reduced spatial and temporal variability in ecosystem functioning (Figure A.2.11), suggesting a more consistent supply across the species combinations planted. This could be due to functional redundancy acting as stabilising effect for a resilient supply of ecosystem functions (Mori et al., 2013). Under future conditions, however, higher plant diversity did not show greater resilience to environmental changes. Instead, we observed that with climate change speciose communities experienced greater species losses, potentially through higher interspecific competition (Ruiz-Benito et al., 2013), which in turn significantly lowered functional redundancy and thus the potential higher resilience against environmental changes. Also, even though multifunctionality decreased with higher planted richness under future conditions, only single functions, that is, ecosystem litter quality, were largely affected and contributed to this decline, whereas most of the other functions increased with richness. Thus, the choice of metrics for restoration success should be considered if the goal is to improve a set of equally desired ecosystem functions and services at the same time.

3.4.3 Applicability of our results for restoration world-wide

We successfully validated the process-based simulation model ModEST for a Mediterranean site in SW Australia and simulated the long-term effect of local plant choice on multifunctionality and six separate ecosystem functions related to water, nitrogen and carbon. We found that the ultimate aim to improve restoration outcomes with respect to improving multiple ecosystem functions at the same time under current and future climatic conditions was limited by trade-offs among ecosystem functions which shifted with climate change.

Even though we focused on a specific Mediterranean site with a focus on specific ecosystem functions, we believe that our general interpretations pertain to terrestrial systems globally. Underlying mechanisms driving trade-offs among functions and shifts in the trade-offs have been fundamentally shown across different ecosystems. For example, ecosystem functions are affected by underlying plant traits (e.g., de Bello et al., 2010; Funk et al., 2017) and environmental change either directly or indirectly, via changing plant trait compositions (e.g., Deyn et al., 2008; Garnier et al., 2007). Thus, restoration ecologists across the world will face a clear challenge to achieve their targets under current conditions and in the long term.

With our validated model ModEST we were able to study the long-term coupled effects of various selected plant communities and climate change on ecosystem functioning. However, long-term functioning as well as trade-offs among functions should be further assessed by considering a wider range of inter- and intraspecific trait variability as well as further disturbances such as fire. We are aware that our findings are context dependent (e.g. dependent on local species pool, soil texture, weather and regional projected climate change) and thus differ across global ecosystems (e.g., Ding et al., 2020; Ratcliffe et al., 2017). In addition, since only bundles of services can be enhanced at the same time, different bundles could be integrated across the landscape to achieve landscape multifunctionality (Lovell and Johnston, 2009; Plas et al., 2016, 2019). These units with their abiotic and biotic characteristics could be simulated individually with ModEST but evaluated at the same time to assess how individual units should be restored to achieve landscape-scale targets. Furthermore, various ecosystems are degraded differently, and therefore restoration managers need to improve different desired functions and services.

3.4.4 Bringing ModEST into practice

With this study we applied the steps suggested by Fiedler et al. (2018) in order to improve ecological restoration and showed that models like ModEST can serve as a planning tool to better understand the suite of desired ecosystem functions and services that can be restored in any particular place based on the plant species available and the local environmental conditions. When restoration with respect to improving the long-term provision of ecosystem functions/services by planting woody plants is the goal, we suggest the following steps.

First, define desired ecosystem functions/services, their weightings and the environmental context of interest (e.g. ecosystem under current, future or both climatic conditions) for the standardisation of the individual ecosystem functions. If threshold multifunctionality approach is of interest define the minimum desired threshold of functioning. Next, choose the potential plant species pool for the restoration of the site. Even though we focused on only biophysical ecosystem functions, they can be directly linked to several ecosystem services (see Table 3.1), which might be of greater applicability for particular restoration projects. Other ecosystem services that are not directly modelled can be indirectly estimated from additional plant characteristics of the simulated communities via known relationships between these characteristics and services. For instance, pollination is not modelled in ModEST but could be estimated from flower traits that are known for the species simulated. Species selection and the specific restoration goals and how they are measured from the model should be determined in collaboration with stakeholders.

Second, parameterise ModEST for the environmental conditions of the restoration site as well as for the selected plant species. The individual-based ecosystem model ModEST links ubiquitous processes related to hydrology, nitrogen and carbon cycling to local abiotic and biotic conditions, and therefore allows for applying the model to various terrestrial ecosystems on Earth. If enough data are available, validate the model for the site and the chosen species. Subsequently, run ModEST scenarios with all potential or selected plant combinations in a full-factorial design with climate change scenarios.

Last, analyse model outcomes and recommend plant compositions that meet restoration goals best under current and/or future conditions.

4

Context-dependency of restoration towards multiple improved ecosystem functions across Mediterranean-type ecosystems

to be submitted as **Fiedler S, Perring M, Monteiro J, Branquinho C, Buzhdygan O, Cavieres L, Cleland E, Cortina-Segarra J, Grünzweig J, Holm J, Irob K, Keenan T, Köbel M, Maestre F, Pagel J, Rodríguez Ramírez N, Ruiz-Benito P, Sheffer E, Valencia E, Tietjen B. Context-dependency of restoration towards multiple improved ecosystem functions across Mediterranean-type ecosystems.**

Abstract Global biodiversity hotspots such as the Mediterranean biome provide many ecosystem services that people depend on. At the same time, they are highly threatened by multiple global change factors with consequences for biodiversity, ecosystem service provisioning, and thus long-term human livelihoods. Anthropogenic intervention can counteract these consequences through restoration towards ecosystem multifunctionality that underpin many ecosystem services. Restorationists can select plant species based on known links between plant characteristics, so called plant traits, and ecosystem functioning to achieve their goals. However, achieving multifunctionality in different Mediterranean-type ecosystems requires knowledge on how abiotic factors such as climate and soil affect multiple functions directly and indirectly, via changes in plant species compositions, as well as trade-offs and synergies among them. We used a processed-based ecosystem model (ModEST) that connects abiotic processes of water and nutrient with the performance of individual plants characterised by traits. This allows to determine links between traits, functions, as well as relationships among functions in different environmental settings. We parameterized ModEST for different combinations of woody plant functional types that we identified as the major ones across Mediterranean-type ecosystems. We ran the model for various environmental settings (i.e., different climatic conditions and soil textures) found in Mediterranean-type ecosystems. By using a full-factorial design of plant functional type combinations and environmental factors, we assessed whether the link of plant traits to the provision of three ecosystem functions and their trade-offs are context-dependent and whether the change of functions in response to environmental conditions is a result of direct effects or of indirect effects, via changes in plant trait compositions. We found that restoration towards maximized individual functions as well as trade-offs among them was dependent on the abiotic context. This was a result of different direct and indirect effects of mean annual temperature, precipitation, and soil texture on ecosystem water use efficiency, nitrogen use efficiency and carbon increment. Direct effects were more important than indirect effects. In addition, abiotic factors mostly interactively affected our focal functions. With this study, we showed that knowledge from single sites cannot simply be transferred to sites with different abiotic conditions even though the same species for restoration are available. Instead, ecological restoration towards multifunctionality needs to account for the combined effects of different abiotic factors on single functions as well as trade-offs among them.

4.1 Introduction

Worldwide, ecosystems are degrading due to multiple global change factors such as land use and climate change, and consequently provided ecosystem services for our well-being are declining (IPBES, 2019). Therefore, restoration of degraded ecosystems towards a continued provision of ecosystem services is of growing interest (Bullock et al., 2011; Gann et al., 2019).

Anthropocentric defined ecosystem services are underpinned by ecosystem functions (or processes) which are regulated by the systems' abiotic and biotic properties (Chapin et al., 2000; Diaz et al., 2007; Lavorel and Garnier, 2002). Restoration practitioners can make use of this link by managing these properties towards enhancing single or multiple functions and services. Biotic restoration is primarily achieved by introducing plant species selected based on known links between certain plant characteristics, so called plant traits, and desired ecosystem functions and services (Carlucci et al., 2020; Funk et al., 2008; Laughlin, 2014a). For instance, particularly fast-growing pine species were planted in the past to increase timber production or carbon sequestration (Cademus et al., 2014; Pausas et al., 2004). Restoration towards improved ecosystem functions and services can also be achieved by modifications of abiotic conditions such as through mulching with the goal to decrease soil erosion and water losses due to reduced evaporation (Vallejo et al., 2012).

However, abiotic and biotic properties cannot be considered independently, as abiotic factors affect the functioning of the ecosystems not only directly but also indirectly via modulating plant trait compositions (Funk et al., 2017). For instance, temperature directly alters nutrient supply, as it affects the litter decomposition rate (Rustad et al., 2001), but also indirectly through changes in plant species composition and thus litter quality (LeRoy et al., 2014; Sariyildiz et al., 2005). Until now, most studies focus on only one of these two effects (Fiedler et al., 2018; van der Plas et al., 2020). In addition, if changes in two or more abiotic factors occur simultaneously, this can lead to interactive effects on ecosystem functioning (Xu et al., 2013). For example, an increased soil nitrogen content can increase the evaporative demand of a plant community, potentially intensifying the negative effects of drought on plant biomass production (Meyer-Grünefeldt et al., 2015).

Furthermore, if the goal of a restoration effort is the enhancement of multiple functions (so-called ecosystem multifunctionality), trade-offs and synergies among functions must be accounted for (Bennett et al., 2009). An understanding on how trade-offs and synergies among functions emerge, however, is still not fully realized. These relationships may be a result of multiple co-varying traits in a community and multiple abiotic properties affecting ecosystem functions differently (Cebrián-Piqueras et al., 2021; de Bello et al., 2010; Lavorel and Grigulis, 2012).

Even though, we have a good understanding of single relationships, the combined effects of multiple abiotic properties on multiple plant traits and functions and the relationships among them are not fully understood (Fiedler et al., 2018). Therefore, it is questionable whether knowledge on the link between plant traits and functions as well as trade-offs among them gained from single sites with specific environmental conditions (e.g., Fiedler et al., 2018; Perring et al., 2012) is transferable to different abiotic settings (Cardinale et al., 2000)). For example, ecosystem water use efficiency might be more important in more arid climates, leading to a stronger trade-off among functions related to water and carbon compared to more humid areas.

Here, we aim at unravelling this complex multi-layered relationship for the Mediterranean biome as one of the global biodiversity hotpots on Earth (Myers et al., 2000). Mediterranean-type ecosystems cover only about 2% of the global terrestrial area but contain about 20% of the global total plant diversity (Cowling et al., 1996; Médail and Quézel, 1997) and provide many ecosystem services such as wood production (FAO and Plan Bleu, 2013). Although these ecosystems are distributed across all continents except Antarctica and thus encompass a wide range of environmental gradients, they share similar plant life forms. Also, the environmental threats are similar, such as increased fire hazards, decreased carbon sequestration, desertification, erosion, salinization, and nutrient losses (Hobbs, 1998; Vallejo et al., 2001). Therefore, these systems serve as a good study region for applied restoration with respect to assess generalizability of the link between plant functional traits and the supply of ecosystems functions as well as trade-offs among them across different environmental settings. In particular, we focus on functions related to water, nitrogen, and carbon that have been of interest when restoring water- and nutrient limited Mediterranean-type ecosystems (Luo et al., 2020). We used a processed-based ecosystem model that connects abiotic processes of water and nutrient with the performance of individual plants characterised by traits. This allows to determine links between traits, processes and functions, as well as trade-offs and synergies among functions in different environmental settings found across Mediterranean-type ecosystems. In particular, we ask the following questions:

1. Given the total available pool of woody plant functional types, what is the highest achievable provision of a certain ecosystem function for different environmental settings found across Mediterranean-type ecosystems (in terms of mean annual temperature, mean annual precipitation, solar radiation, and soil texture)?
2. Will there be differences in the synergies and trade-offs among the three ecosystem functions water use efficiency, nitrogen use efficiency and carbon increment across the different environmental settings?
3. If so, how are these differences shaped by different direct and indirect effects of the multiple combined environmental factors on the provision of the ecosystem functions?

By answering these questions, we synthesize the role of woody plant functional traits on the supply of ecosystem functions and potential trade-offs among them across multiple environmental settings found in the Mediterranean biome. This will support restoration of degraded ecosystems towards ecosystem multifunctionality in the Mediterranean biome if not worldwide.

4.2 Material and Methods

We used a small-scale simulation model to determine the context-dependency of the links between plant traits and ecosystem functions, and the trade-offs among functions. We parameterized the model for different combinations of woody plant functional types (PFTs) that we identified as the major ones across Mediterranean-type ecosystems. We ran the model for various environmental settings (i.e., different climatic conditions and soil textures) found in Mediterranean-type ecosystems. By using a full-factorial design of PFT combinations and environmental factors, we assessed whether the link of plant traits to the provision of three ecosystem functions and their trade-offs are context-dependent and whether the change of functions in response to environmental conditions is a result of direct effects or of indirect effects, via changes in plant trait compositions.

4.2.1 Model description

We used the spatially explicit and trait-based simulation model ModEST (Modelling Ecosystem Services based on Traits, Fiedler et al., 2021) that simulates daily coupled dynamics of soil water, soil nitrogen and carbon, as well as biomass of individual competing woody plants (see Figure 3.1). ModEST has been developed and successfully validated for a Mediterranean site in SW Australia (Fiedler et al., 2021) but can be run for various environmental settings (i.e., different soil textures and climatic conditions) and for different woody plant species or PFTs.

The modelled landscape in ModEST is subdivided into grid cells (5 m by 5 m) and two soil layers with individual positioned plants across the landscape. For each individual plant, daily dynamics of alive below- and aboveground carbon and nitrogen pools as well as structural components (e.g., plant height, crown area) are simulated based on the following processes: CO_2 uptake with simultaneous water losses by transpiration, nitrogen uptake, gross primary production through photosynthesis, carbon losses during respiration, allocation of carbon and nitrogen to above- and belowground vegetative and reproductive pools, followed by dispersal, establishment, and mortality. The processes are driven by species-specific plant traits (Tables 4.1 and A.3.3) and abiotic conditions (i.e., air and soil temperature, photosynthetic active radiation, plant available soil water and nitrogen) found at the grid cells covered by the individual plant. For each grid cell and soil layer, daily dynamics of soil water, soil organic matter, nitrate, and ammonium are calculated. Soil water is driven by precipitation, lateral water redistribution of surface water affected by the grid cells' plant cover, infiltration affected by the proportion of plant roots in the two soil layers, vertical fluxes, and water losses through evaporation, affected by radiation and shading, and transpiration. Most of the processes are driven by soil-texture-specific parameters (Table A.3.2). Dynamics of soil organic matter, nitrate, and ammonium are mainly driven by nitrogen inputs from atmospheric nitrogen deposition as well as from the plants' residue. The plant residue is decomposed and humified to soil organic matter, which is subsequently immobilized, mineralized to ammonium, and nitrified to nitrate. Nitrate and ammonium are then either uptaken by plants or being lost through volatilization, denitrification, as well as leaching driven by vertical soil water flows. Modelled nutrient processes in their entirety are affected by soil temperature, soil water, soil texture, and the C:N ratio of the plants' residue. A full model description can be found in Fiedler et al. (2021) or publications cited therein.

4.2.2 Identification of plant functional types

For assessing the link between Mediterranean plant traits and ecosystem functions, we determined major woody PFTs that represent the woody plant species occurring across Mediterranean-type ecosystems best. The focus on PFTs instead of plant species allows us to draw general conclusions on the link between plant traits and ecosystem functions for plant communities of the Mediterranean biome. For deriving PFTs, we first acquired data of ten plant traits for all shrubs and tree taxa observations from the TRY database (Kattge et al., 2020) within the Mediterranean climate region (Csa and Csb; Köppen, 1900; Kottek et al., 2006; Peel et al., 2007). Some resulting species that were clearly not typical Mediterranean species were removed. We focused especially on those plant traits that are required to represent the spectrum of Mediterranean plant species regarding their effects on water, nutrient and carbon cycling and at the same time had a good data coverage in TRY: i.e., leaf dry mass, leaf nitrogen, leaf area, photosynthesis, plant height, stomatal conductance, specific leaf area, wood density, leaf phenology, and Nitrogen fixation (Table A.3.1). As the nomenclature in TRY is not always consistent, we merged very similar plant traits. For instance, the trait 'leaf area' included data on the entries 'leaf area', 'leaf area (in case of compound leaves undefined if leaf or leaflet, undefined if petiole and rachis are in- or excluded)', 'leaf area (in case of compound leaves: leaf, petiole included)', and 'leaf area (in case of compound leaves: leaf, undefined if petiole in- or excluded)'. Repetitions in trait measurements for the same species and region were averaged for numerical traits or the mode was taken for categorical traits. We then generated our representative PFTs with the help of a cluster analysis, which clustered all selected woody species (515 in total) based on their trait similarities. First, numeric

Table 4.1: Plant parameters. See full list of parameters and their sources in Table A.3.3. Plant traits indicated with an asterix (*) were focal traits in the analysis of the simulation outcomes.

Parameter (Unit)	**Description**	**PFT 1**	**PFT 2**	**PFT 3**	**PFT 4**	**PFT 5**	**PFT 6**	**Source**
Structural plant traits								
Phenology (-)	Evergreen (E) or raingreen (R) phenology	E	E	E	R	E	E	Cluster results
*SLA (m^2 kg^{-1})	Specific leaf area	12.421	4.7766	8.082	14.704	5.6	2.612	Cluster results
*WD (kgC m^{-3})	Wood density	624.2	597.8	606.7	637.4	623.3	668.3	Cluster results
a_1 (-)	Parameter in allometric equation that transfers stem diameter to crown area	22.65	29.16	21.05	21.21	32.15	30.16	Kattge et al. (2020)
a_2 (-)	Parameter in allometric equation that transfers stem diameter to plant height	28.36	2.29	6.7	11.26	8.68	3.59	Kattge et al. (2020)
r_{rp} (-)	Parameter in allometric equation that transfers stem diameter to crown area	0.51	0.72	0.53	0.46	0.46	0.5	Kattge et al. (2020)
*maxCA (m^2)	Maximum possible crown area	36	39	29	30	82	40	Kattge et al. (2020)
*$root_{L2}$ (-)	Fraction of roots between 50 and 150 cm of the soil horizon	0.31	0.13	0.35	0.23	0.36	0.55	Kattge et al. (2020)
Physiological plant traits								
g_{min} (mm s^{-1})	Minimum canopy conductance that occurs due to processes other than photosynthesis	0.5	0.3	0.3	0.5	0.3	0.3	Sitch et al. (2000) based on grouped leaf area from cluster results
*CN_{leaf} (-)	Carbon to nitrogen (C:N) ratio of the leaves	44.0	94.01	51.87	44.68	97.62	161.87	Kattge et al. (2020)
$CN_{leaf,min}$ (-)	Minimum bound of C:N ratio in the leaves	29.1	46.8	13.9	19.8	40.5	34.5	Kattge et al. (2020)
$CN_{leaf,max}$ (-)	Maximum bound of C:N ratio in the leaves	34.7	58.6	20.9	21	61.4	38.9	Kattge et al. (2020)
*k_{store} (-)	Constant for maximum N storage	0.05	0.05	0.05	0.15	0.05	0.05	Smith et al. (2014) based on leaf phenology from cluster results
Reproductive plant traits								
seedMass (mg)	Seed mass	34.35	20.11	13.42	37.77	25.24	40.6	Kattge et al. (2020)
meanDisp (m)	Mean dispersal distance	48.01	2.76	9.25	17.18	31.26	4.83	Thomson et al. (2011) based on median plant height from cluster results
p_{germ} (-)	Germination probability	0.84	0.89	0.88	0.81	0.82	0.86	Kattge et al. (2020)

variables were standardized by subtracting the average and dividing by the standard deviation (Stekhoven and Buhlmann, 2012). As a cluster analysis does not allow for incomplete data, we filled data gaps via additional resources (Table A.3.1) and a nonparametric imputation based on Random Forest (package 'missForest' in R allowing imputation of datasets containing continuous and/or categorical variables including complex interactions and nonlinear relations; Stekhoven and Buhlmann, 2012). For the cluster analysis, we first calculated a Gower distance matrix computing all pairwise dissimilarities between observations (function 'daisy' of package 'cluster' in R; Maechler et al., 2021, first described by (Kaufman and Rousseeuw, 1990)). We then fitted the observations based on their distances and thus similarities into different cluster numbers using the function 'pam' of the R package 'cluster' (Maechler et al., 2021). With the help of the R package 'NBclust' (Charrad et al., 2014), which suggests the best number of clusters based on 30 indices that apply different distance measures and clustering methods, we decided for a clustering into six PFTs (Figure A.3.1). We found that the woody plant species were classified into five evergreen PFTs and one deciduous PFT (PFT 4) (Figures 4.1 and A.3.2). The five evergreen PFTs were separated into PFT 1 with a high SLA and leaf nitrogen, PFT 2 with very small and light leaves as well as a low SLA, PFT 3 as a nitrogen fixer, PFT 5 with low stomatal conductance and photosynthetic activity, and PFT 6 with a low SLA but with broader, heavier and nitrogen-rich leaves. The resulting six PFTs were then parameterised for ModEST, which requires fixed parameter values for structural, physiological, and reproductive plant traits (Tables 4.1 and A.3.3). As these parameters were not fully covered by the traits used in the cluster analysis, we parametrised them based on additional data resources from TRY and further literature for the plant species that were clustered into the respective PFT (see Table 4.1). Across the species within the PFT, we used either the median value for numerical traits or the mode for categorical traits.

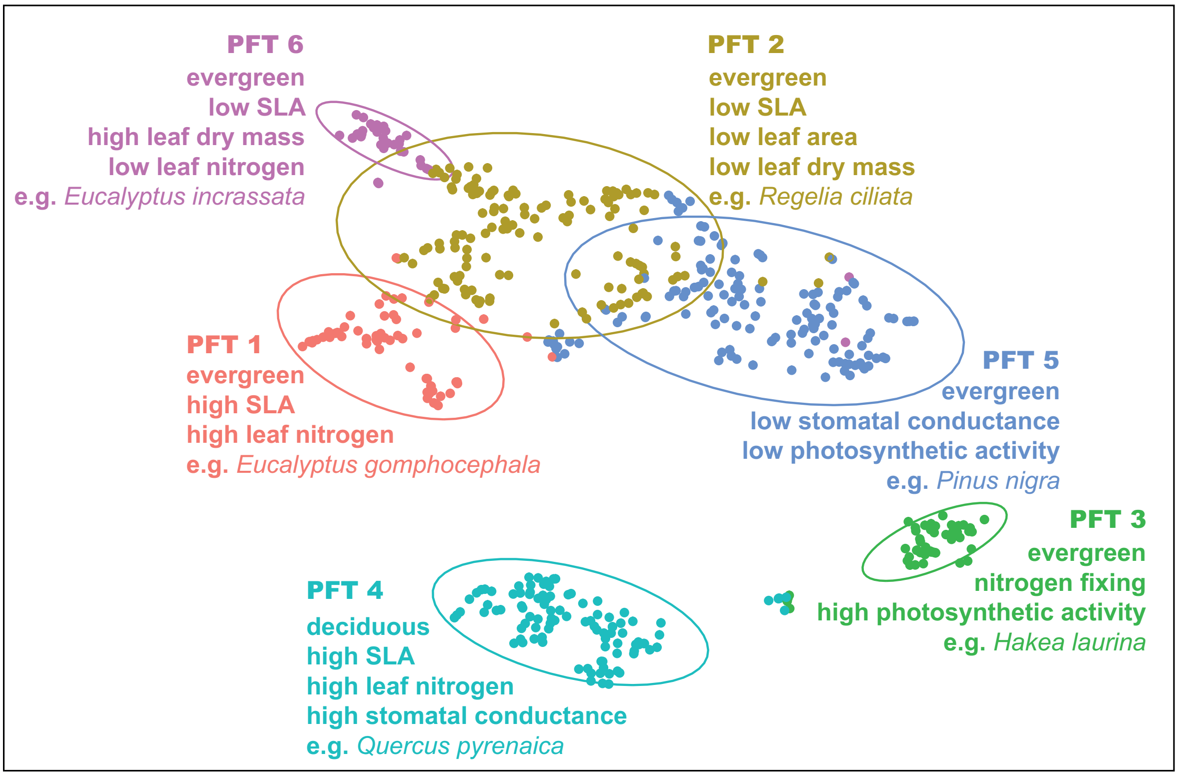


Figure 4.1: Classifications of the six plant functional types (PFTs) as a result of the cluster analysis.

4.2.3 Simulation experiments

As the aim of this study was to understand the context-dependency of trade-offs among ecosystem functions, we systematically ran the model for a broad set of potential environmental conditions. For this, we simulated a full-factorial design of all possible PFT communities (see PFT scenarios) and different environmental conditions that can be found across the Mediterranean biome including a range of mean annual temperatures, precipitations, and solar radiations (see Climate scenarios) as well as different soil textures (see Soil texture scenarios) (Figure A.3.3). Each scenario was run on a landscape of 50 m by 50 m for 100 years, to achieve a stable state, and was repeated ten times to account for stochasticity in the spatial initialization of plant individuals, weather input (see Climate scenarios), and the plant dispersal process of ModEST (see model description in Fiedler et al., 2021).

PFT scenarios

For each environmental setting, we simulated all possible combinations of the six PFTs, ranging from monocultures to the full PFT pool (63 combinations in total). For each simulation, 300 individuals evenly chosen from the selected combination of PFTs were randomly positioned in the landscape (50 m by 50 m) with 2 m distance to neighbouring individuals and a plant height of 50 cm.

Climate scenarios

For the climate scenarios, we determined the ranges of mean annual precipitation (MAP) and temperature (MAT) for each Mediterranean region (Kottek et al., 2006) from monthly modelled climate data with a spatial resolution of 0.5° x 0.5° (1901 – 2019, Harris et al., 2020). We took the 25 and 75 percentiles of MAP (200 to 1200 mm) and MAT (8 to 17 °C) across all regions to define our scenario ranges for MAP and MAT. Mediterranean ecosystems are found in latitudes between 30 and 50 degrees north and south, impacting solar radiation and thus potential evapotranspiration. We therefore set the latitude to 30°, 40°, or 50° and calculated corresponding values for solar radiation based on Tietjen et al. (2009b). For each climate scenario and model repetition, we generated 100 years of daily precipitation after Köchy (2006) as well as daily mean, minimum and maximum temperature after Tietjen et al. (2009b). For the generation of daily rainfall, we first calculated probability curves for each mean annual precipitation scenario (calculated from monthly 0.5° by 0.5° gridded data from 1901 – 2019, Harris et al., 2020) as well as daily rainfall probability and exponential fits of daily rainfall and maximum daily rainfall for each month and each mean annual precipitation (calculated from daily 0.5° by 0.5° gridded data from 1991 – 2020, NOAA, 2020b). For the generation of daily temperature, we first calculated the yearly temperature difference and daily temperature difference per month (calculated from daily 0.5° by 0.5° gridded minimum and maximum temperature from 1991 – 2020, NOAA, 2020a) for each mean annual temperature scenario. We compared these statistics across the different regions and found that they are are very similar (Figures A.3.4 to A.3.10).

Soil texture scenarios

We ran the model for the four most common soil textures across the Mediterranean biome, i.e., clay loam, loam, sandy clay loam, and sandy loam (soil parameters in Table A.3.2) that we obtained from intersecting 0.5 x 0.5° maps of climatic regions (Csa and Csb, Kottek et al., 2006) and soil textures (Koirala, 2012).

4.2.4 Evaluation of simulation outcomes

We evaluated for each combination of environmental conditions and PFT assemblage the mean results of 10 simulation replicates for the years 90 to 100 (hereafter referred to as mean simulated data). For the mean simulated data, we determined the community weighted mean (CWM) of six selected plant traits (Table 4.1) and the provision of our three ecosystem functions: i.e., 'total ecosystem carbon increment' (ECI, unit: t ha^{-1} $year^{-1}$) as the sum of the annual plant and soil carbon increment, 'ecosystem water use efficiency' (EWU, unit: g L^{-1} $year^{-1}$) as the ratio between annual net primary productivity (NPP) and annual precipitation per m^2, and 'ecosystem nitrogen use efficiency' (ENU, unit: kgNPP m^{-2} gN^{-1} m^{-3}) as the ratio between annual NPP per m^2 and annual mean soil available nitrogen per m^3. We considered the plant traits k_{Store}, maxCA, WD, $root_{L2}$, SLA, and CN_{leaf} (Table 4.1) which were not correlated (greater than Spearman's rank correlation of 0.8, Table A.3.11) and expected to be linked to the ecosystem functions of interest. All analyses were performed in R version 4.0.3 (R Core Team, 2021).

Link between plant traits and optimal functioning and trade-offs among functions

We determined the highest achievable provision of each ecosystem function expressed by its upper 10th percentile in a given environment as well as the underlying plant trait combination that led to this high provision for our mean simulated data. For this, we calculated for each environmental setting and each ecosystem function the upper 10th percentile of the functioning across the 63 simulated PFT combinations (Figure A.3.12). For the resulting plant communities leading to the maximised provision of the target function (i.e., for the upper 10th percentile), we evaluated (i) the mean provided value of this function, (ii) the mean value of the CWM traits to assess the link between traits and this function, and (iii) the mean provision of the other two functions. The latter was related to the maximum achievable provision of the other two functions in a given environment to quantify trade-offs in other functions when maximizing the target function.

Direct and indirect effects of environmental factors on functions

We wanted to understand, how different environmental factors affect the provision of ecosystem functions, directly, by altered process rates under different environmental settings and indirectly, via resulting differences in CWM plant traits and their effects on functions. To determine links between environmental factors, traits and functions, we used structural equation modelling (SEM) with the R packages 'lavaan' for testing our hypothetical SEM (Rosseel, 2012) and 'tidySEM' for plotting the final SEM (van Lissa, 2021). First, we constructed three separate hypothetical SEMs including direct and indirect effects, via CWM traits, of mean annual precipitation, mean annual temperature, and soil texture, in interaction and individually, on each ecosystem function (see Table A.3.4). The categorical variable 'soil texture' was translated into a numerical variable by taking the mean sand content for the respective soil texture as given in the USDA triangle (USDA, 2020). We then tested our hypothetical model with our mean simulated data. Ecosystem functions and plant traits were previously Ordered Quantile (ORQ) normalized (by using R package 'bestNormalize' by Peterson and Cavanaugh, 2020) to meet the assumptions of normal distribution and homoscedasticity. To assess the validity of the SEM models, we checked for several measures for goodness of fits. Usually, a Chi-Square (χ^2) is used for SEM assessment, where statistically significant results indicate that the SEM should be rejected. However, this method is not reliable for very large datasets (such as ours with more than 80.000 data points), as there is a high tendency for statistically significant results. Therefore, we solely focused our decision whether to accept or reject the SEM on measures that are more robust to larger datasets, i.e., Root Mean Square Error of Approximation (RMSEA), Comparative Fit Index (CFI), Standardized Root Mean Square Residual (SRMR), (Adjusted) Goodness of Fit ([A]GFI). We first omitted solar radiation from the SEMs as the SEMs did not converge with solar radiation included. We then started removing the least significant effects in order to get acceptable SEMs. The individual links were evaluated for significance (with p-value lower than $\alpha = 0.05$), and standardized SEM regression coefficients were used as a measure of the strength of these links.

4.3 Results

4.3.1 Context-dependency of maximized functions and trade-offs

We simulated 63 different plant functional type (PFT) compositions for each environmental setting and determined the highest achievable provision of three ecosystem functions in a given environment across PFT compositions. We found that maximized ecosystem functions were highly related to precipitation, temperature, and soil texture (Figure 4.2A, see also Figures A.3.13 to A.3.15). Solar radiation only minimally affected maximised functions (Figures A.3.13 to A.3.15). Maximum values for ecosystem carbon increment (ECI) and ecosystem nitrogen use efficiency (ENU) were provided in warmer and wetter environments and were lower in sandier soils than in clayey loamy soils. Interestingly, the positive effect of higher mean annual precipitation on ECI was only apparent above 11°C in mean annual temperature. In contrast to ECI and ENU, highest values for maximized ecosystem water use efficiency (EWU) were reached for dry conditions and for sandy loamy soils. Here, we saw a slight positive effect of temperature.

When individual ecosystem functions were maximized, the other functions showed quite contrasting results (Figure 4.2B). In most cases, we observed trade-offs among functions (indicated by a darker red color in Figure 4.2B). Strongest trade-offs were found with ENU on sandy soils: When ENU was maximized, EWU greatly decreased independent of MAP and MAT, and ECI were generally decreased except for cooler and drier climates. Under clayey soils, these strong trade-offs diminished. When ECI was maximized on sandy soils, EWU was particularly decreased under drier and cooler or under wetter and warmer conditions. However, if ENU or EWU was maximized on clayey soils, we found a strong synergy among the two functions except for cooler and wetter conditions where the maximum of the respective functions was only slightly decreased.

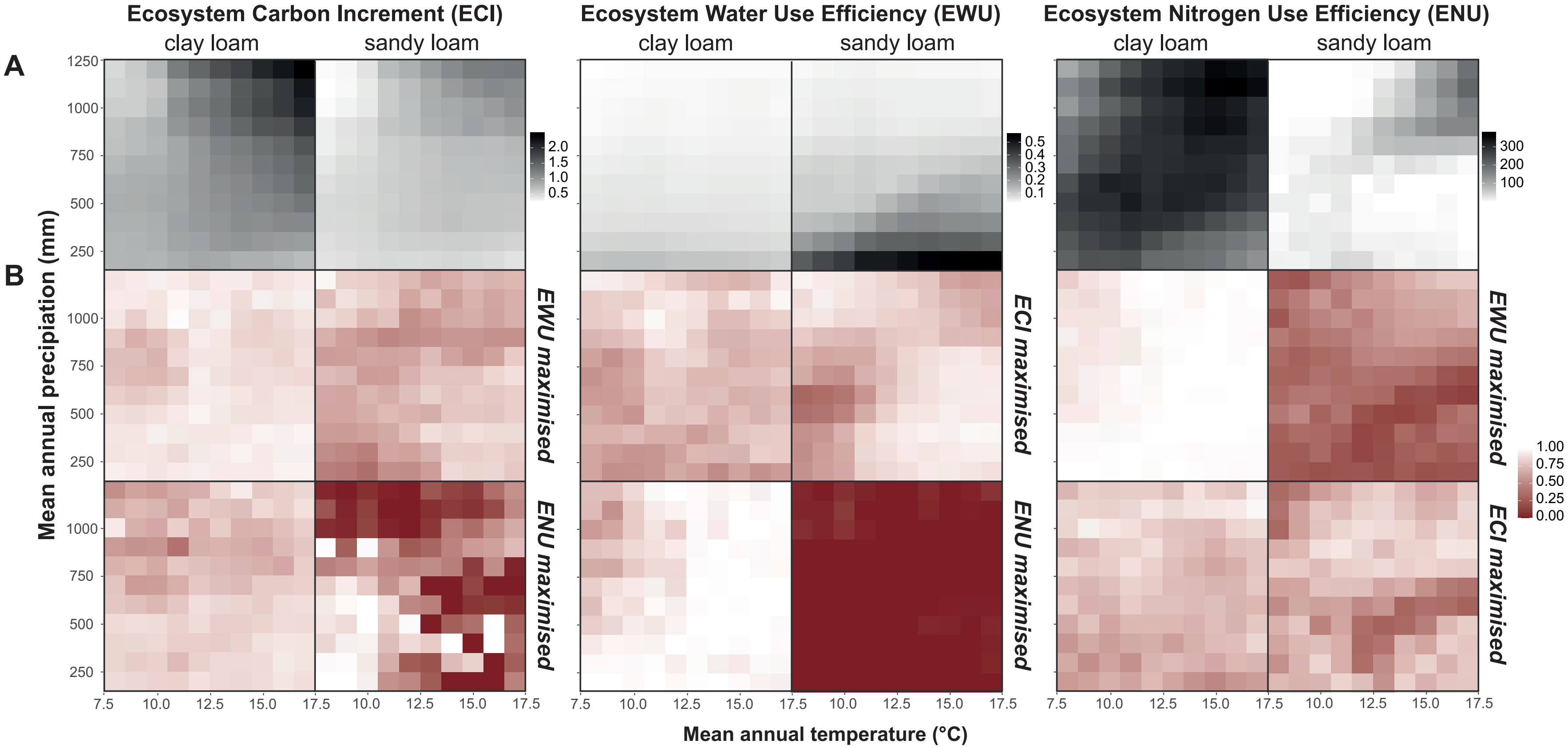


Figure 4.2: Maximised provision of each ecosystem function and their trade-offs dependent on different environmental settings. Environmental settings comprises different conditions of mean annual precipiation (y axis) and mean annual temperature (x axis), two selected soil textures (columns), and solar radiation at 40° latitude (see results for all simulated environmental conditions in Figures A.3.13 to A.3.15). (A) Absolute provision of maximised ecosystem carbon increment (left, unit: t ha^{-1} year^{-1}), ecosystem water use efficiency (center, unit: g L^{-1} year^{-1}), and ecosystem nitrogen use efficiency (right, unit: kgNPP m^{-2} gN^{-1} m^{-3}). Maximised provision of each function is calculated by the mean over the upper 10th percentile of the function across all PFT combinations for each environmental setting (see Figure A.3.12). (B) Proportion of the target function if one of the other two function is maxmised for the same environmental setting. The intensity of red represents the proportion of the maximum possible value, i.e. the redder the color the more the provision deviates from the maximum possible value.

4.3.2 Context-dependency of optimal trait compositions

Plant communities that provided maximized individual functions generally differed in their community weighted mean (CWM) traits depending on the environmental setting (Figure 4.3). Except for maximized ENU on the soil texture ‘sandy loam’, all maximized functions showed a similar pattern of best CWM traits with changes in environmental conditions: Below a threshold of about 500 mm in mean annual precipitation, optimal plant communities were almost consistently characterized by a low C:N ratio in the leaves (CNleaf) and a low maximum crown area (maxCA), intermediate values for wood density (WD) and rooting depth (rootsL2), as well as a high specific leaf area (SLA). Above this threshold, we found a less consistent pattern of CWM traits leading to a high provision of the functions with exception of ECI. Under warmer and wetter conditions on sandy soils, maximized ECI were characterized by communities with higher C:N ratio in the leaves, larger crown area, lower SLA, and shallower roots. In contrast, under wetter and cooler conditions as well as across soil textures, wood density and rooting depth were increased with intermediate levels of SLA.

Communities for highest provision of ENU on sandy loam showed completely different patterns in CWM traits across different environmental conditions. For instance, under driest and warmest conditions, communities that provided maximized ENU were characterized by a low C:N ratio in the leaves and a high SLA. Across environments and functions communities were mostly dominated by evergreen plants (kStore = 0.05) with the exception of ENU under cooler and wetter conditions on sandy loam, where also deciduous plants were present (only one deciduous PFT with kStore = 0.15 out of six PFTs, still leading to low CWM kStore).

4.3.3 Direct and indirect effects of abiotic factors on functions

In general, we found that environmental factors alone or in interaction affected our focal ecosystem functions directly and indirectly, via changes in plant trait compositions (Figure 4.4 and Table A.3.5). We found a strong positive and interactive effect of mean annual precipitation and temperature on all three functions. Mean annual precipitation and soil texture (i.e., increasing sand content) interactively affected EWU and ENU directly but with contrasting directions: For EWU, the sand content had a weaker effect for higher mean annual precipitation compared to lower values of mean annual precipitation (negative interactive effect). For ENU, this effect was vice versa and weaker. ECI was directly and interactively affected by mean annual temperature and soil texture: The sand content had a weaker effect for higher mean annual temperature. The interactive and direct effect of precipitation, temperature and soil texture on ECI and ENU was negative.

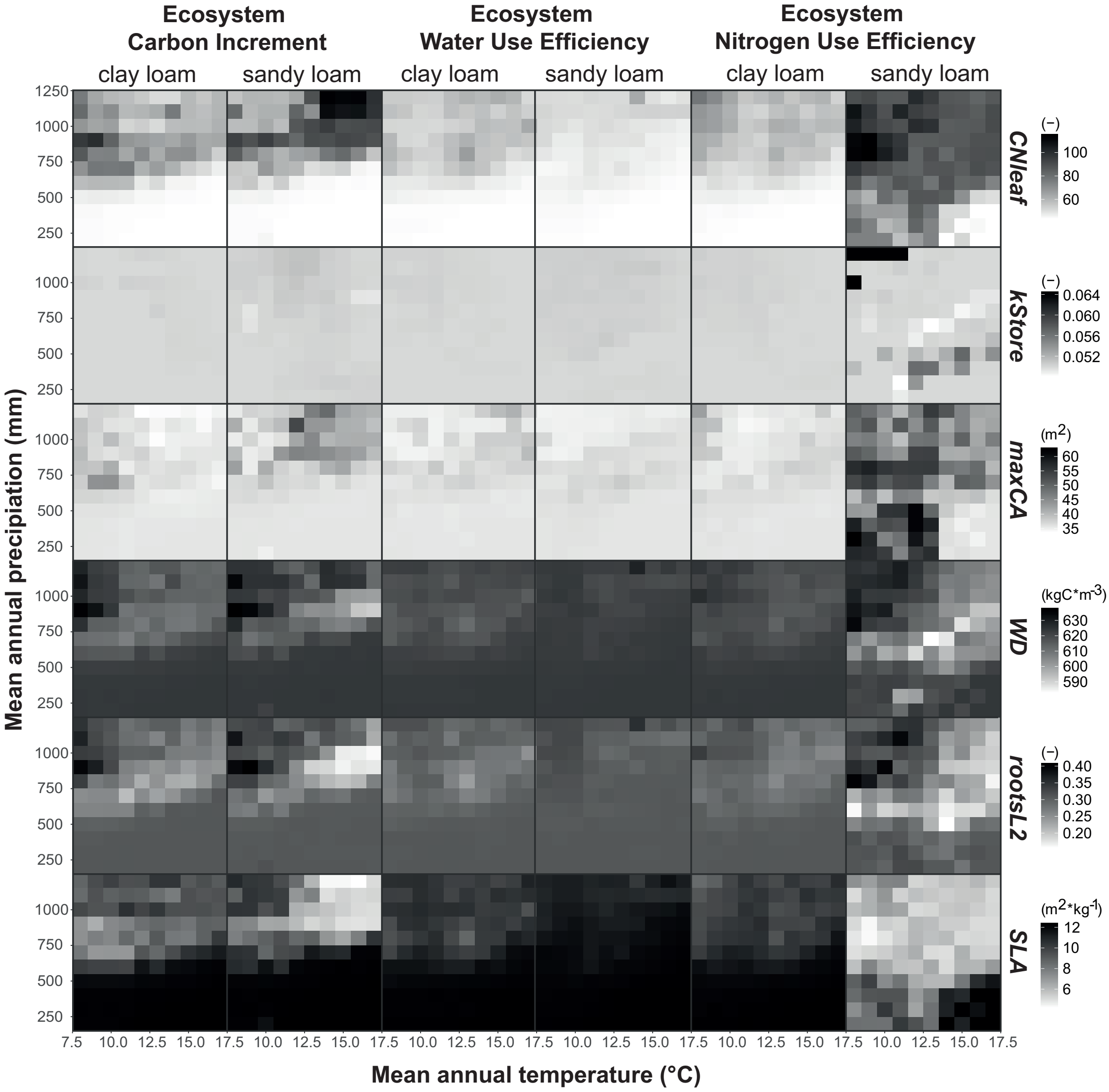


Figure 4.3: Community weighted mean (CWM) plant traits of plant communities that provide maximised ecosystem functioning for different environmental settings. CWM traits (rows) for each ecosystem function (three main columns) for different mean annual precipiations (y axis), mean annual temperatures (x axis), two selected soil textures (two sub-columns), and for solar radiation at 40° latitude.

In addition to the direct effects, we found several indirect effects of environmental conditions on the ecosystem functions via changes in community weighted mean plant traits. These effects were much less prominent than the direct effects. Due to the many existing links, we report only the interactive and indirect effects with at least 30% of the magnitude of the direct effect of the same environmental factor(s) or with a prominent indirect effect without a direct effect present (see Table A.3.5). The chosen level of 30% is arbitrarily set but we believe that an effect size lower than a third of the comparable direct effect is potentially not relevant enough in particular for restoration. ECI, EWU and ENU were strongly negatively affected via changes in SLA or leaf C:N ratio, both mediated by all three environmental factors in interaction. For ECI, this effect was much stronger than the comparable direct effect of the same three-way-interaction, whereas for EWU and ENU this direct effect was either not present or much less pronounced. For ECI, the same factors in interaction positively affected the function via plant phenology (kStore). Changes in SLA mediated by mean annual precipitation and soil texture in interaction positively affected ECI and EWU . The same two factors positively affected ENU directly and indirectly via changes in leaf C:N ratio. Mean annual temperature and soil texture in interaction negatively affected ECI via changes in the phenology (kStore) whilst it was positively affected by changes in SLA. The same factors only indirectly increased EWU mostly via SLA.

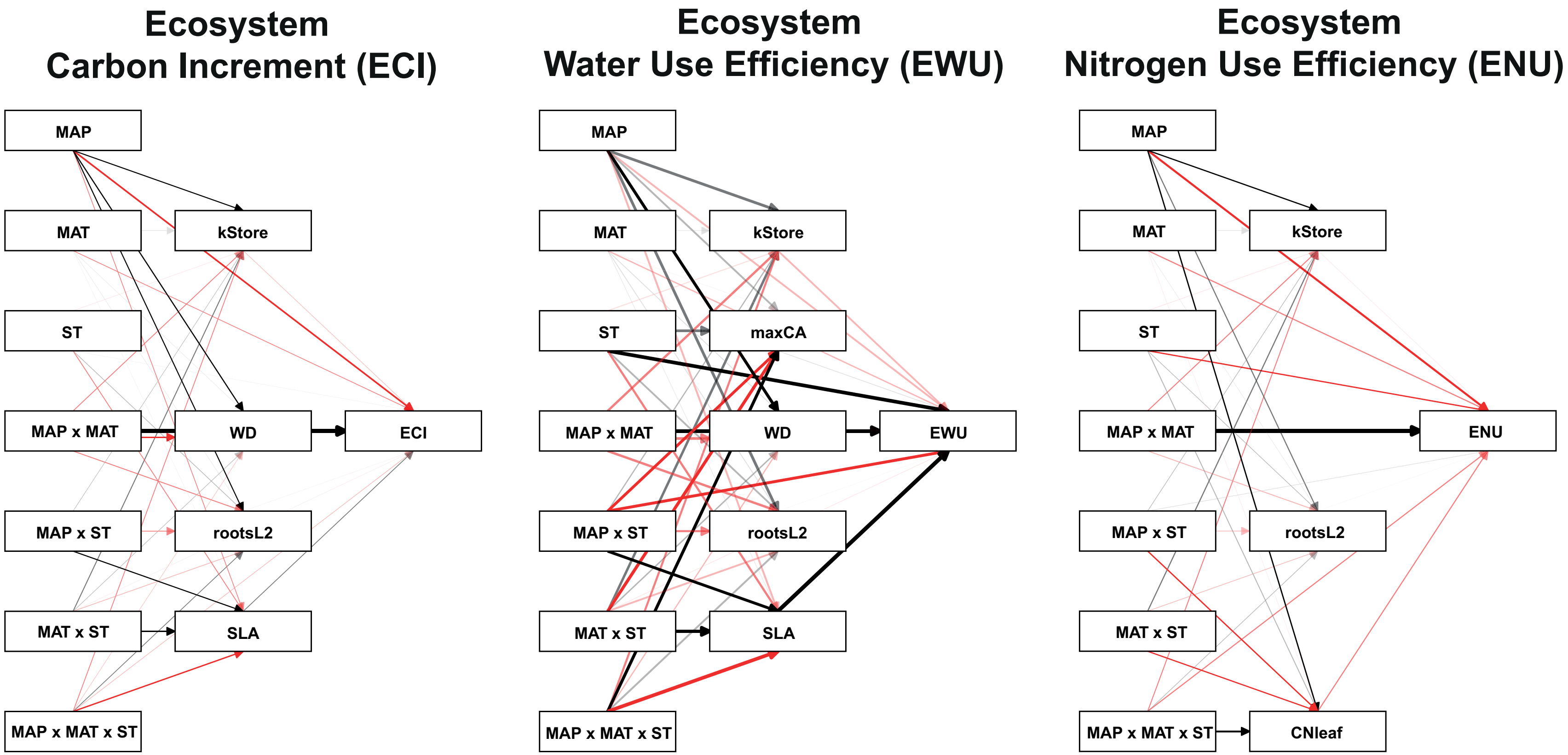


Figure 4.4: Direct and indirect effects (via community weighted mean plant traits) of multiple environmental factors on each ecosystem function. Red and black lines represent significant (i.e., $p \leq 0.05$) negative and positive path coefficients of the structural equation modelling results, respectively. Thickness of lines represent the magnitude of the standardized path coefficient of the respective link. Four different transparencies of the lines were based on the four quantiles based on the standardized path coefficients within each SEM (above 75th percentile: no transparency, between 50th and 75th percentile: light transprency, between 25th and 50th percentile: medium transparency, below 25th percentile: strong transparency). Models were well supported by our data (ECI/EWU/ENU: $\chi^2 = 5.932/15.2/5.862$, df = 3/4/2, Pchisq = 0.115/0.004/0.053, RMSEA = 0.006/0.01/0.008, PRMSEA = 1.0/1.0/1.0; CFI = 1.0/1.0/1.0; SRMR = 0.0/0.0/0.0, GFI = 1.0/1.0/1.0, AGFI = 0.998/0.996/0.997, PGFI = 0.038/0.044/0.03). RMSEA: Root Mean Square Error of Approximation; CFI, Comparative Fit Index; SRMR: Standardized Root Mean Square Residual; (A)GFI: (Adjusted) Goodness of Fit. Effect sizes of the links are given in Table A.3.5.

4.4 Discussion

Ecological restoration increasingly aims at improving ecosystem functioning by reintroducing plant species based on their traits (Funk et al., 2008; Giannini et al., 2017; Laughlin, 2014a; Padilla et al., 2009; Wang et al., 2020). Here, we used a modelling approach to determine the link between plant traits and the provision of three selected functions, the optimal plant community to achieve the highest possible provision of a specific function, resulting trade-offs for the provision of other functions, and the context-dependency of these relationships.

4.4.1 Optimal plant traits in different environments

Across the virtually planted PFT combinations, we assessed for each environmental setting those plant communities that provided the maximized provision of one of three ecosystem functions. We found that community weighted mean plant traits of these optimal PFT combinations differed across different abiotic settings, but less so across maximized functions. This suggests that PFT combinations mostly differed as result of different abiotic conditions. This is in general agreement with what has been found in numerous other studies which has been explained by a result of community assembly through biotic and abiotic filtering (Bernard-Verdier et al., 2012; Cornwell and Ackerly, 2009; Pescador et al., 2015). Mean annual precipitation seems to be the most important factor in shaping community plant traits. de la Riva et al. (2018) also found aridity to be a key abiotic factor in shaping the trait structure of Mediterranean woody communities. We found that optimal plant traits that provided maximized functioning showed similar patterns with changing environmental conditions, indicating co-variations among these traits. For instance, both optimal specific leaf area (SLA) and wood density (WD) were generally higher under drier conditions, whereas at the same time optimal C:N ratio in the leaves was lower. This suggests a positive correlation between SLA and WD, but a negative correlation of these two traits with leaf C:N ratio which is in conjunction with findings from Mediterranean-type ecosystems (e.g., Costa-Saura et al., 2016) but also with the global spectrum of plant form (Díaz et al., 2016). However, there seems to be a mismatch of trait distributions that maximizes ecosystem functions for a given environment compared to trait distributions that can be found in nature. For instance, in contrast to our results, SLA is usually decreased under drier conditions in real ecosystems (de la Riva et al., 2016a). Further investigations are needed to understand this contrasting finding. As stated above, the optimal trait distributions were mostly very similar across the maximized functions. However, for nitrogen use efficiency on sandy soils, optimal traits were completely different across different rainfall and temperature conditions compared to the traits prevalent for the other maximized functions. This indicates an either completely different link between traits and nitrogen use efficiency or a large effect of sandy soils on the function (see discussion on direct and indirect effects of abiotic factors).

4.4.2 Provision of ecosystem functions in different environments

Similar to optimal plant trait composition, we found that maximized individual functions across Mediterranean-type ecosystems through re-assembling plant species combinations was also dependent on the abiotic context. The role of abiotic context for ecosystem functioning has already been studied in the past (Cregger et al., 2014; Sun and Du, 2017). In particular, I could show that maximized ecosystem carbon increment was generally increased under higher rainfalls as also found by (Pereira et al., 2007). This indicates a high importance of water availability for accumulation of plant and soil carbon stocks in particular for water-limited Mediterranean-type ecosystems. Increasing sand content generally decreased maximized carbon increment in our study most likely due to diminished water holding capacity of sandier soils and thus less available water for carbon cycling. A negative effect of increased sand content has also been found on soil carbon contents (Augustin and Cihacek, 2016; McLauchlan, 2006). In contrast to carbon sequestration, optimal provided ecosystem water use efficiency, the amount of annual net primary production per unit rainfall (also called rain-use efficiency), increased under drier conditions. This effect has also been found across biomes in particular when water was the most limiting resource (Huxman et al., 2004). In addition, we found that multiple abiotic factors in interaction affected ecosystem functions. For instance, warmer and sandier conditions increased the positive effect of reduced annual precipitation on water use efficiency. This suggests a more efficient use of rainfall by plant communities under drier soil conditions as a result of lower rainfall, lower water holding capacity of sandier soil, and higher evapotranspiration losses due to warmer conditions. Optimal nitrogen use efficiency, the amount of annual net primary production per unit plant available soil nitrogen, was increased under wetter and warmer conditions, as well as on more clayey soils. This might be simply due to less water limitation for plant growth, and thus higher primary productivity for the same amount of nitrogen. For conditions below 11°C in mean annual temperature, maximum carbon sequestration was slightly decreasing under wetter conditions. This might be due to too moist soil conditions for organic matter decomposition by soil microorganisms and thus limited plant growth because of limited release of nitrogen into the soil. The positive effect of rainfall above 11°C on carbon sequestration was further enhanced by increased temperatures. Such a positive interactive effect of rainfall and temperature has also been found on net primary production as one important contributing aspect for carbon sequestration (Luo et al., 2008).

4.4.3 Trade-offs and synergies among ecosystem functions

Comparing the plant communities that maximized individual functions, we found that the same communities did not maximize all focal functions at the same time, thus trade-offs and synergies among the ecosystem functions exist. The existence of such trade-offs and synergies among functions are already known but the mechanisms in shaping these relationships are still not fully understood (Bennett et al., 2009). Usually trade-offs are attributed to different traits that affect functions differently. However, we found that trade-offs and synergies among functions changed depending on the abiotic setting. This has recently been shown also by Zwetsloot et al. (2021). Here, we could show with a structural equation modelling approach across all possible plant compositions and environmental settings that differences in the relationships among functions can additionally be explained by different direct and indirect effects of abiotic conditions on the functions. For instance, a strong trade-off between water use efficiency and nitrogen use efficiency was found for sandy soils independent of rainfall and temperature. In contrast, for clayey soils we observed a strong synergy between the same two functions except for warmer and wetter conditions. Soil texture has contrasting effects on both functions. Higher sand contents negatively affected water use efficiency through changes in specific leaf areas, and nitrogen use efficiency through changes in C:N ratios in the leaves. Both traits showed an intrinsic negative correlation across all planted compositions. At the same time, we found strong direct effects: Whereas increasing sand content generally increased water use efficiency, nitrogen use efficiency was strongly decreased by higher sand contents. Therefore, optimal plant trait compositions alone are not responsible for the differences in the trade-offs and synergies observed. Instead, we found that direct abiotic effects on functions seem to be even more important than indirect effects. This is supported by a study of van der Plas et al. (2020), where plants and their traits alone are found to be poor predictors of ecosystem functions. They therefore concluded that the environmental context is potentially of large importance in understanding functioning of ecosystems.

4.4.4 Restoration towards multifunctional landscapes

Here, we showed that restoration towards multiple improved functions in different Mediterranean-type ecosystems characterized by different abiotic conditions might be challenging. Environmental context significantly affected trade-offs and synergies among functions due to different direct and indirect effects of abiotic conditions on ecosystem functions. Therefore, restoration towards improved functioning just based on species selection without considering abiotic conditions might not be feasible. Here, we advanced our understanding on what maximal provision of single ecosystem functions at a certain environmental setting can be achieved by the available pool of Mediterranean woody plant species. If multifunctionality is the restoration goal, further assessments are needed what combinations of plant traits minimizes trade-offs among functions the most. Alternatively, multifunctionality across landscapes could be achieved by integrating different landscape units that individually improve single ecosystem functions given the optimal trait combination for the conditions found in this unit. We believe that our general findings are also relevant to ecosystems outside the Mediterranean biome. However, further research on the multi-layered relationship between different environmental factors, plant traits and functions is needed if different plant traits as well as other desired functions/services are relevant or of interest.

5

General Discussion

With this thesis, I advanced the understanding of the link between plant traits and multiple ecosystem functions as well as trade-offs and synergies among them to support ecological restoration of degraded Mediterranean-type ecosystems towards long-term multifunctionality. I demonstrated that restoration ecology already provides knowledge on how single changing environmental factors influence single ecosystem functions directly or indirectly via individual plant traits (Chapter 2). With a coupled trait-based empirical and simulation modelling approach, I advanced this knowledge by assessing the combined effects of multiple environmental factors and multiple plant traits on the individual and the simultaneous provision of various ecosystem functions. I found that multiple desirable ecosystem functions related to carbon, nitrogen and water were linked to plant traits of woody Mediterranean plant species and plant functional types (Chapter 3 and 4). Specifically, I showed that with increasing planted trait diversity not all of the focal functions were improved at the same time (Chapter 3). Instead, I found that trade-offs and synergies among functions were present and shifted with changing climatic conditions. In addition, I was able demonstrate that maximised functioning as well as trade-offs and synergies among them differed depending on the abiotic conditions found across Mediterranean-type ecosystems (Chapter 4). This was a result of multiple combined abiotic factors that affected functions differently. Based on my major findings, I will discuss (i) to what extent the link between plant traits and ecosystem functions might be useful for the restoration of degraded ecosystems, (ii) what challenges come up by focusing on ecosystem multifunctionality as a restoration goal, and (iii) how the integrated empirical and simulation modelling approach applied in this thesis supported this research and could be furtherly improved for future research endeavours.

5.1 Plant trait selection for restoring ecosystem functions

A quantifiable link between plant traits and ecosystem functions or processes has been shown in the past (Chapin et al., 2000; Funk et al., 2017; Grime, 1997; Tilman et al., 1997) and it has been argued that restoration can make use of this link to restore desirable ecosystem functions (Funk et al., 2008; Muler et al., 2018). However, I found that knowledge about the link between individual traits and ecosystem functions is not enough for applied restoration for three main reasons:

First, as shown in the Chapters 2 to 4, multiple plant traits were found to be simultaneously linked to the same ecosystem function. As plant traits often act dependently on functions due to co-variations among plant traits (de la Riva et al., 2016b; Díaz et al., 2016), plant species selection based on single traits might be challenging. In Chapter 4, for instance, I showed that specific leaf area and plant phenology had contrasting effects on carbon sequestration. At the same time both traits were maximal for a Mediterranean deciduous plant functional type indicating the difficulties of plant species selection for improving carbon sequestration just based on these traits. Therefore, decisions on what plant species to select should be made based on multiple co-varying traits at the species level. In Chapter 3, for instance, I focused on trait characteristics of plant species available for restoration at a specific site. However, the focus on species might only be relevant for local restoration and does not allow drawing general conclusions across different ecosystems. In Chapter 4, I aimed at assessing the role of the abiotic context for the link between plant traits and ecosystem functions, and trade-offs among functions, across Mediterranean-type ecosystems. In doing so, I grouped woody Mediterranean species into so-called plant functional types based on empirical knowledge on trait values and co-variations among traits which have been found to be consistent across the globe (Thomas et al., 2020; Wright et al., 2004). By simulating all possible combinations of the constructed plant functional types in a full-factorial design with different abiotic factors, I was able to assess the general link between plant traits and functions across different abiotic conditions. For the support of local restoration, however, the grouping into functional types might not be the best as species exist with unique trait characteristics with many of them varying independently from one another (Eviner and III, 2003; Messier et al., 2017; Wright and Sutton-Grier, 2012). These unique characteristics might have unique effects on functioning, and thus general findings of Chapter 4 might not be applicable to locally available species pools. In addition, plant trait plasticity to environmental change as well as trait variability within species and plant functional types were not accounted for but might have strong effects on ecosystem functioning especially under global change (Berzaghi et al., 2020; Butler et al., 2017; Henn et al., 2018; Mastrotheodoros et al., 2017). For instance, it has been shown that trait variability promotes species coexistence by allowing species to buffer against abiotic and biotic variations (Crawford et al., 2019; Jung et al., 2010).

Second, plant traits that were present in the overall community played a role for ecosystem functioning. As shown in the past, this link cannot simply be inferred from the link between plant traits at the individual plant level and ecosystem functioning (Bruelheide et al., 2018; Tavares et al., 2020). In Chapter 3 and 4, I virtually planted different species compositions and calculated the community weighted mean of the plant traits in the modelled landscape based on the relative contribution of the plant species' biomass. By doing so, I could show that community level plant traits were linked to the mean provision of ecosystem functions in the simulated landscape. The use of community weighted mean traits goes back to the biomass ratio hypothesis as suggested by Grime (1998) which states that the characteristics of dominant species in the community drive ecosystem properties. This has been supported by various studies across different ecosystems (Ali et al., 2016; Cortez et al., 2007; Vries and Bardgett, 2016; Jing et al., 2019). The focus on community weighted mean traits, however, might be of limited application for restoration as plant selection based on community weighted mean traits might be challenging. In addition, trait variability within a community might additionally play a role for some functions, in particular if complementary effects are dominant (Cadotte, 2017; Luo et al., 2019; Wen et al., 2019). In this thesis, the general link between mean community traits and functions was a result of two major aspects considered in the simulation model: (i) the mechanistic description of the link between traits and ecosystem processes such as the effect of plants' specific leaf area on photosynthesis (Sitch et al., 2000) and (ii) plant community assembly shaped by the abiotic and biotic environment such as through competition between individual plants for water affected by several traits. As a result of the latter, I showed that planted species and thus community weighted mean traits shifted over time in Chapter 3 or across abiotic settings in Chapter 4 with effects on ecosystem functioning.

Third, in addition to the indirect effects of abiotic conditions on ecosystem functions via changes in plant trait compositions, I found in Chapter 4 that ecosystem functions were also directly affected by abiotic conditions. Such direct and indirect effects have already been found in the past (Lavorel et al., 2011). These effects, however, differed depending on the functions as they have also been shown by Zirbel et al. (2017). Compared to the indirect effect, abiotic factors seem to have larger direct effects on functioning indicating once more that the focus on plant species alone for restoration may not be sufficient. The high importance of the abiotic context has been supported by van der Plas et al. (2020) who found that plant traits alone are poor predictors for long-term ecosystem functioning. Zirbel et al. (2019) also showed that ecosystem functions were more correlated with environmental variables than with diversity. In addition, I could show in Chapter 4 that multiple environmental factors interactively affected ecosystem functions, meaning that the combined effects of multiple factors on functions is not the simple sum of the individual effects (also called non-additive effects). This is particularly important as findings from studies that focus only on single environmental factors might not be applicable to restoration sites where multiple abiotic factors combined affect ecosystem dynamics.

5.2 Restoration towards long-term multifunctionality

Restoration increasingly aims at improving not only single functions but also multiple ones at the same time (Cruz-Alonso et al., 2019; Gaines et al., 2020; Resch et al., 2021). This has been also manifested in studying ecosystem multifunctionality as measure of multiple provided functions or services in the ecosystem (Byrnes et al., 2014; Maestre et al., 2012a; Manning et al., 2018; van der Plas et al., 2016). In this thesis, I showed that trade-offs among functions exit that hamper restoration toward ecosystem multifunctionality. Given the existence of the trade-offs, I showed that a focus on multifunctionality indices limits the understanding on how individual functions are provided. Individual levels of functions might be of additional importance for restoration. Therefore, Bennett et al. (2009) suggested to increase the understanding of the relations among ecosystem functions and services to be able to manage them with the goal to increase multifunctionality as well as ecosystem resilience by avoiding shifts in the provision of functions and services. Trade-offs in this thesis were a result of co-varying traits that were differently linked to functions as well different direct and indirect effects of abiotic factors on functions. In Chapter 3, I could demonstrate that ecosystem functions were attributed to different plant traits that showed positive and negative co-variations at the community level. In the Chapters 3 and 4, changing abiotic conditions across space and time changed trade-offs and synergies among functions as a result of different direct and indirect effects, via changes in plant species compositions. Differences in the trade-offs and synergies across different climates and land-use types has been also found by Zwetsloot et al. (2021). Due to the link between traits and functions, reintroduction of plant species can be used to manage relationships among functions (see also Hanisch et al., 2020), however only to a certain degree as abiotic conditions affect these relationships. In this thesis, I did not assess how individual functions and trade-offs among them changed over time after planting which might be of great importance to understand resilience of multiple functions to global change. For instance, I did not assess the role of fires that are particularly important in Mediterranean-type ecosystems with potentially significant effects on functioning such as carbon sequestration. If only multifunctionality is the goal, I could show in Chapter 3 that higher planted functional richness supported multifunctionality. This conforms with findings in many other studies with focus on the relationships between plant diversity and multifunctionality (Gross et al., 2017; Isbell et al., 2011; Lefcheck et al., 2015; Maestre et al., 2012a). However, this positive relationship disappeared under future climatic conditions due to species losses, indicating the further need for accounting global change. As I only focused on locally available plant species and climate warming in Chapter 3, the negative overserved effect of global change on multifunctionality might be different in other regions and for other global change factors. For example, Allan et al. (2015) found that land use change led to species loss with different effects on multifunctionality depending on the region.

5.3 Lessons learned from an integrated trait-based empirical and simulation modelling approach

I showed that the abiotic site conditions strongly modulate the link between plant traits and ecosystem functioning through changes in community compositions and direct abiotic effects on ecosystem functions. Our current understanding of the link between traits and functioning is of limited applicability for the restoration of abiotically diverse ecosystems. With the integrated trait-based empirical and simulation modelling approach used in this thesis, I began to unravel the multi-layered relationship of multiple combined environmental factors that directly and indirectly, via changes in plant traits, affect multiple ecosystem functions and relationships among them. With this, it can also serve as a decision-making tool on what plant species to consider when the goal is to improve multiple desired ecosystem functions for a given environmental setting.

In this thesis, I successfully developed the individual- and trait-based simulation model ModEST based on the settings of a large-scale restoration experiment in a woodland in SW Australia (Perring et al., 2012). Process descriptions were reimplemented from existing model tools that in turn based their formulas on empirical or theoretical knowledge on how ecosystem processes and community assembly are affected by abiotic and biotic conditions (Kemanian et al., 2011; May et al., 2009; Schaphoff et al., 2018; Sitch et al., 2000, 2003; Tietjen et al., 2009b). I modelled the fate of woody plant species or functional types as I focused on Mediterranean woodlands where woody plants play a dominant role in the functioning of the ecosystem and restoration through reintroduction of woody species is a common approach (Pausas et al., 2004; Vallejo et al., 2012). ModEST simulates individual representations of these plants characterised by traits allowing for individual interactions to the biotic and abiotic environment. The high resolution of the vegetation has the advantage of being directly applicable to local restoration attempts where individual plants are planted based on their characteristics and locally desired goals in ecosystem functioning. The benefit of using individual- and traits-based simulation models in functional and restoration ecology has been also argued elsewhere (Laughlin, 2014a; Zakharova et al., 2019). For reasons of simplicity, I neglected biocrusts that widely occur in drylands as well as herbaceous plants which both can still significantly impact ecosystem dynamics. For instance, herbaceous vegetation can directly affect carbon cycling (Pereira et al., 2007) but also the woody vegetation with consequences for ecosystem functioning (Benayas et al., 2007; Vilà and Sardans, 1999). Biocrusts are known to substantially affect carbon and water cycling in drylands (Chamizo et al., 2016; Morillas et al., 2017). Therefore, further assessments are needed on how herbaceous vegetation and biocrusts might change trade-offs and synergies among functions provided by woody plant species. ModEST could be extended by integrating dynamics of herbaceous plants and biocrusts based on descriptions from other simulation models (Porada et al., 2013; Schaphoff et al., 2018).

With increasing model complexity, however, further data is needed for model parameterisation and validation. During the development of ModEST, I was confronted with a mismatch between model parameters and what is actually being measured as well as a general lack of trait data such as for constructing plant functional types (Pillar, 1999; Wullschleger et al., 2014). In Chapter 4, for instance, I needed to apply imputation methods to fill data gaps in measured trait values with potential imputation errors. Other model parameters that are not usually measured were taken from original model publications for similar systems without any information on this parameter for Mediterranean-type ecosystems. In Chapter 3, I calibrated model parameters by comparing observed fluxes and simulated ones using a Bayesian approach.

This approach allows to estimate probability curves of the parameter values given the errors in the data observations and in the model predictions. These errors, reflected in the probability curves of the fitted parameters, could be propagated to the simulation experiments, and thus it could be tested if the findings in this thesis remain similar given the uncertainty in the parameters (Benke et al., 2018; Oijen et al., 2005). In Chapter 3, I could successfully validate ModEST with independent temporal data on plant biomass, height and survival. However, it remains questionable whether modelled relationships pertain under changing environmental conditions in space and time (Achat et al., 2016). For instance, it has been shown that higher temperatures and elevated CO_2 levels may have less effects in the long-term due to acclimation of the plants to these conditions (Smith and Dukes, 2013). Such acclimation processes are not included in ModEST, thus global change effects as presented in Chapter 3 might be less prominent. For instance, a stronger coupling of model development and so-called FACE (free-air CO_2 enrichment) experiments could improve the mechanistic understanding of elevated CO_2 levels on ecosystem functioning (Medlyn et al., 2015; Norby, 2011; Norby et al., 2016; Walker et al., 2019).

I showed that trait-based simulation models such as ModEST can simulate complex full-factorial designs involving much less resources compared to field experiments, and hence are able to complement empirical experiments. In Chapter 3, I complemented the large-scale restoration experiment in Ridgefield, SW Australia (Perring et al., 2012) by focusing on additional plant combination treatments (255 different combinations compared to 9 combinates in the experiment) as well as by assessing the long-term effects of these plant combinations on ecosystem functioning including the effects of global change. In this thesis, I focused on biophysical ecosystem functions related to carbon, water and nitrogen that might be particularly important for the restoration of water- and nutrient-limited Mediterranean-type ecosystems susceptible to climate change. However, stakeholders in Mediterranean-type ecosystems might be more interested in the quantification of ecosystem services such as food production, water availability for irrigation, carbon sequestration to decrease atmospheric CO_2 levels, and biodiversity for recreation (e.g., Blondel et al., 2010; FAO and Plan Bleu, 2013; Rick et al., 2020). Carbon sequestration can be directly translated from the function 'ecosystem carbon increment' measured in this thesis. Food production, however, cannot directly be estimated from ModEST as it does not simulate crop dynamics. Instead, ground water availability for irrigation of the crops as a relevant factor for food production could be estimated from functions such as ground water recharge as measured in Chapter 3. Plant diversity can be directly estimated as also done in Chapter 3. For a better applicability of the coupled approach for restoration of ecosystem services, I suggest to involve different stakeholders to define specific target goals.

5.4 Conclusion

With this thesis, I demonstrated that there are substantial challenges in restoration ecology in order to support restoration toward the long-term provision of multiple ecosystem functions and services. In particular, I found that a focus on plant traits alone is not enough as the effect of abiotic conditions on the provision of single and multiple ecosystem functions and services is still underestimated. Therefore, restoration still faces multiple challenges when selecting plant species to achieve ecosystem multifunctionality across space and time. I showed that a coupled trait-based empirical and simulation model approach has a great potential to fill knowledge gaps and serve as a decision-making tool. However, applying such coupled approaches necessitates the incorporation of stakeholders for the definition of target goals as well as further testing on how ecosystem functions are affected by changing abiotic and biotic environments, in particular for model parameterisation and validation.

6

Summary

6.1 English Summary

Mediterranean-type ecosystems (MTEs) are among the global biodiversity hotspots most vulnerable to multiple factors of global change, such as climate warming and elevated atmospheric CO_2. Global change is likely to exacerbate current ecosystem degradation in MTEs, with severe consequences for the long-term provision of multiple ecosystem services on which people depend, such as carbon sequestration, water and nutrient supply. Ecological restoration is increasingly aimed at counteracting the decline and improving the long-term provision of multiple ecosystem services. For successful restoration, however, ecologists require a fundamental understanding of the link between vegetation composition, related functions and services, and influencing environmental factors. Measurable traits of plant species such as specific leaf area have been recognized as a quantifiable link between vegetation composition and ecosystem functions underlying ecosystem services. Given this link, restoration can select plant species based on their traits in order to improve desired ecosystem functions. In this thesis, I aimed at assessing the linkage between plant traits and the provision of multiple ecosystem functions, as well as trade-offs among these functions under the influence of multiple changing environmental factors, to support the restoration of degraded MTEs towards multifunctionality world-wide. Through a literature review, I found that current trait-based research lacks a complete understanding of the combined effects of multiple environmental factors on the long-term provision of multiple ecosystem functions and a quantification of the trade-offs and synergies among these factors. To address this gap, I proposed a theoretical framework that complements trait-based empirical research with process-based simulation modelling. Based on this framework, I successfully developed the individual- and trait-based simulation model ModEST (*Modelling Ecosystem Services and Functions based on Traits*) that calculates the coupled dynamics of soil water, soil nutrients, and individual woody plants characterized by traits. ModEST allows quantification of ecosystem functions for a given planted trait composition over time under varying environmental conditions. As a first step, I supplemented a large-scale restoration project in Western Australia (called the Ridgefield Experiment) by evaluating all possible combinations of plant species locally available for restoration under both current and future climatic conditions using ModEST. The simulation results revealed that multifunctionality was increased by higher levels of planted species richness under current, but not under future climatic conditions. In general, multifunctionality could not be fully achieved because of trade-offs among functions that were attributable to sets of traits that affected the functions differently. Trade-offs and synergies among functions shifted with climate change as a result of differential direct and indirect impacts of environmental factors on functions. To understand how the link between plant traits and functions found in Ridgefield, as well as trade-offs and synergies among functions, can be applied to other Mediterranean-type ecosystems, I applied ModEST to several abiotic and biotic conditions found in Mediterranean-type ecosystems across the globe. Specifically, I simulated a full-factorial design of all possible combinations of six plant functional types, constructed from trait values of woody Mediterranean plant species, and various abiotic settings (i.e. mean annual precipitation, mean annual temperature, solar radiation, and soil texture) characteristic of the Mediterranean biome. I found that the maximization of multiple functions achieved by particular plant trait compositions as well as trade-offs among the maximized functions were dependent on the abiotic context. I could show that plant traits alone affected by the environment were not fully responsible for the differences in the functioning but that additionally abiotic conditions in interaction directly shaped ecosystem functioning. With this work, I have shown that there is a clear linkage between multiple environmental factors that directly and indirectly, via changes in plant traits, affect multiple ecosystem functions in MTEs, as well as trade-offs and synergies among them. My findings imply that restoration ecologists face a significant challenge in achieving their long-term multifunctionality goals in degraded MTEs across the world. I demonstrated that an integrated trait-based empirical and simulation modelling approach can unravel the complex multi-layered relationship of multiple plants traits on ecosystem functioning affected by the abiotic environment to support restoration towards multifunctionality in MTEs if not globally.

6.2 Deutsche Zusammenfassung

Mediterrane Ökosysteme (MTEs) gehören zu den globalen Biodiversitäts-Hotspots, die am anfälligsten für verschiedene Faktoren des globalen Wandels sind, wie z. B. Durch Klimaerwärmung und erhöhter CO_2-Gehalt in der Atmosphäre. Der globale Wandel wird die derzeitige Degradation der Ökosysteme in den MTEs wahrscheinlich verschärfen, mit schwerwiegenden Folgen für die langfristige Bereitstellung zahlreicher Ökosystemdienstleistungen, von denen die Menschen abhängen, wie z. B. Kohlenstofffixierung, Wasser- und Nährstoffversorgung. Die ökologische Renaturierung zielt zunehmend darauf ab, diesen Rückgang entgegenzuwirken und die langfristige Bereitstellung mehrerer Ökosystemdienstleistungen zu verbessern. Für eine erfolgreiche Renaturierung benötigen Ökologen jedoch ein grundlegendes Verständnis des Zusammenhangs zwischen der Zusammensetzung der Vegetation, den damit verbundenen Funktionen und Leistungen sowie den beeinflussenden Umweltfaktoren. Messbare Merkmale von Pflanzenarten (so genannte *Plant Traits*) wie die spezifische Blattfläche wurden als quantifizierbares Bindeglied zwischen der Vegetationszusammensetzung und den Ökosystemfunktionen, die den Ökosystemdienstleistungen zugrunde liegen, erkannt. Mit Hilfe dieses Bindeglieds können Pflanzenarten aufgrund ihrer Eigenschaften ausgewählt werden, um die gewünschten Ökosystemfunktionen zu verbessern. In dieser Arbeit hatte ich zum Ziel, den Zusammenhang zwischen Pflanzenmerkmalen und der Bereitstellung mehrerer Ökosystemfunktionen sowie die Trade-Offs zwischen diesen Funktionen unter dem Einfluss mehrerer sich verändernder Umweltfaktoren zu untersuchen, um die Renaturierung degradierter MTEs in Richtung Ökosystemmultifunktionalität weltweit zu unterstützen. Durch eine Literaturrecherche habe ich herausgefunden, dass die derzeitige trait-basierte Forschung ein vollständiges Verständnis der kombinierten Effekte mehrerer Umweltfaktoren auf die langfristige Bereitstellung mehrerer Ökosystemfunktionen und eine Quantifizierung der Trade-Offs und Synergien zwischen diesen Faktoren fehlt. Um diese Lücke zu schließen, schlug ich ein theoretisches Framework vor, das die trait-basierte empirische Forschung mit prozessbasierter Simulationsmodellierung ergänzt. Basierend auf diesem Framework habe ich erfolgreich das Individuen- und trait-basierte Simulationsmodell ModEST (*Modelling Ecosystem Services and Functions based on Traits*) entwickelt, das die gekoppelte Dynamik von Bodenwasser, Bodennährstoffen und einzelnen, durch Traits charakterisierten Gehölzen berechnet. ModEST ermöglicht die Quantifizierung von Ökosystemfunktionen für eine gegebene pflanzliche Zusammensetzung über die Zeit unter variierenden Umweltbedingungen. In einem ersten Schritt ergänzte ich ein groß angelegtes Renaturierungsprojekt in Westaustralien (das sogenannte Ridgefield-Experiment), indem ich alle möglichen Kombinationen von Pflanzenarten, die lokal für die Renaturierung zur Verfügung stehen, sowohl unter aktuellen als auch unter zukünftigen Klimabedingungen mit ModEST evaluierte. Die Simulationsergebnisse zeigten, dass die Ökosystemmultifunktionalität unter den aktuellen, nicht aber unter den zukünftigen Klimabedingungen durch eine höhere gepflanzte Diversität erhöht wurde. Im Allgemeinen konnte die Ökosystemmultifunktionalität nicht vollständig erreicht werden, da es zu Trade-Offs zwischen den Funktionen kam, die auf Gruppen von Pflanzenmerkmalen zurückzuführen waren, die die Funktionen unterschiedlich beeinflussten. Trade-Offs und Synergien zwischen den Funktionen verschoben sich mit dem Klimawandel als Ergebnis der unterschiedlichen direkten und indirekten Auswirkungen von Umweltfaktoren auf die Funktionen. Um zu verstehen, wie das in Ridgefield gefundene Bindeglied zwischen Pflanzenmerkmalen und Funktionen sowie die Trade-Offs und Synergien zwischen den Funktionen auf andere mediterrane Ökosysteme übertragen werden können, habe ich ModEST auf verschiedene abiotische und biotische Bedingungen angewandt, die in mediterranen Ökosystemen auf der ganzen Welt zu finden sind. Insbesondere simulierte ich ein vollfaktorielles Design mit allen möglichen Kombinationen von sechs Pflanzenfunktionstypen, basierend aus Merkmalen von holzigen mediterranen Pflanzenarten, sowie verschiedenen abiotischen Bedingungen (d.h. mittlerer Jahresniederschlag, mittlere Jahrestemperatur, Sonneneinstrahlung und Bodentextur), die für das mediterrane Biom charakteristisch sind. Ich fand heraus, dass die Maximierung mehrerer Funktionen, die durch bestimmte Zusammensetzungen von Pflanzenmerkmalen erreicht werden, sowie die Trade-Offs zwischen den maximierten Funktionen vom abiotischen Kontext abhängen. Ich konnte zeigen, dass die von der Umwelt beeinflussten Pflanzeneigenschaften allein nicht vollständig für die Unterschiede in den Ökosystemfunktionen verantwortlich sind, sondern dass zusätzlich abiotische Bedingungen in Interaktion direkt die Funktionsweise des Ökosystems prägten. Mit dieser Arbeit habe ich gezeigt, dass es eine klare Verbindung zwischen mehreren Umweltfaktoren gibt, die direkt und indirekt, über Veränderungen der Pflanzeneigenschaften, mehrere Ökosystemfunktionen in MTEs beeinflussen, sowie Trade-Offs und Synergien zwischen ihnen. Meine Ergebnisse implizieren, dass Restaurierungsökologen vor einer großen Herausforderung stehen, wenn sie ihre langfristigen Ökosystemmultifunktionsziele in degradierten MTEs auf der ganzen

Welt erreichen wollen. Ich habe gezeigt, dass ein integrierter trait-basierter empirischer und simulationsbasierter Modellierungsansatz die komplexen, vielschichtigen Beziehungen mehrerer Pflanzeneigenschaften auf die Ökosystemfunktionen, die von der abiotischen Umwelt beeinflusst werden, entschlüsseln kann, um die Renaturierung in Richtung Ökosystemmultifunktionalität in MTEs, wenn nicht sogar global, zu unterstützen.

A

Appendix

A.1 Appendix to "Trait-based modeling to improve ecological restoration"

Assessing the state of knowledge, we performed a literature search of papers published between 2009 and 2016 in the database “Web of Science”. First, we assessed the knowledge on the effect of plant traits on ecosystem functions and ecosystem services and trade-offs among them. To this end, we searched for publications on the key words “Mediterranean”, “plant trait”, “ecosystem function” or “ecosystem service” and/or “trade-off”. From this search examples are summarised in Table A.1.1. Secondly, we assessed the knowledge on effects of environmental change factors on ecosystem functioning and service provisioning. Therefore, we searched for publications on the key words “Mediterranean”, “plant trait” and on the following environmental change factors: “land use”, “invasion”, “climate warming”, “drought”, “nitrogen deposition” or “carbon dioxide”. If the resulting studies assessed the effect of one of the factors on ecosystem functions/properties and/or plant traits, the studies were sorted according to the environmental change factors studied. Affected plant traits and functions, and whether the study assessed a direct or indirect effect of environmental change were recorded and relevant papers were summarised in Table A.1.2. Inspection of these papers showed us that there was a gap in knowledge regarding the multi-layered relationship among environmental change, plant traits and the delivery of ecosystem services, which we briefly introduce in the paper. The main text then focuses on how this knowledge gap can be addressed through a coupled simulation model – empirical research agenda.

Table A.1.1: Examples of trait-based approaches (since 2009) contributing to the assessment of ecosystem services in Mediterranean-type ecosystems. For several ecosystem services (italicised bold text) we have put the class of plant traits linked to specific affected functions, and the proxy measures that trait-based studies used. The study marked with a * directly measured the ecosystem service and not a function.

Plant trait	**Affected ecosystem function**	**Affected ecosystem measure**	**References**
Carbon sequestration			
Leaf traits	Photosynthesis	Photosynthetic leaf surface area	Gratani et al. (2013)
Root traits	-*	Biomass, Total soil organic carbon	Butterfield and Suding (2013)
Diversity of plant traits	Carbon storage	Biomass, Species-specific carbon content	Ruiz-Benito et al. (2014)
Nutrient supply			
Root traits	Decomposition	Decomposition rate	Birouste et al. (2012)
Erosion control			
Stem, leaf, plant morphological traits	Soil retention	Mass of sediment trapped per unit volume	Burylo et al. (2012)
Invasion resistance			
Diversity of plant traits	Establishment and reproduction of invaders	Number of established individuals, Number of flower heads and seeds, Total stem length	Hooper and Dukes (2010)
Fire control			
Leaf traits	Flammability	Time to ignition, Predicted rate of fire spread, Flaming time, Combustion rate	Simpson et al. (2016)
Water retention			
Leaf traits	Transpiration	Assimilation rate, Stomatal conductance, Transpiration rate	Medrano et al. (2009); Yates et al. (2010)

Table A.1.2: Examples of trait-based approaches studying the effect of global environmental change factors (italicised bold text) on plant traits and ecosystem functions/services in Mediterranean-type ecosystems (as defined in Figure 2.1). Studied effects of global change are distinguished (third column) between studies that assess (i) the effect of global change on traits but not on ecosystem functioning (-), (ii) the direct effect of global change on traits and on functioning separately (without accounting for the link from plant traits to ecosystem functioning), and (iii) the effects of global change on ecosystem functions via plant traits (indirect effects). Highlighted references focus on two changing environmental factors

Affected plant trait	**Studied ecosystem function/property**	**Studied effect**	**References**
Land use			
Leaf (litter) traits	None	-	Castro et al. (2010a); Targetti et al. (2013); Batriu et al. (2015)
	Decomposition	Indirect	Cortez et al. (2007); Castro et al. (2010a)
	Decomposition, growth	Indirect	Kazakou et al. (2006)
Root traits	None	-	Prieto et al. (2015)
Other morph. traits	None	-	Lavorel et al. (1999); Castro et al. (2010b); Pérez-Camacho et al. (2012) ; Gutiérrez-Girón and Gavilán (2013)
	Soil moisture, compaction, nutrients	Direct	Dobarro et al. (2013)
Reproductive traits	None	-	Lavorel et al. (1999); Castro et al. (2010b)
	Soil moisture, compaction, nutrients	Direct	Dobarro et al. (2013)
Biotic invasion			
Leaf (litter) traits	None	-	Lloret et al. (2005); Acosta et al. (2006); Grotkopp and Rejmanek (2007); Stanisci et al. (2010)
	Decomposition	Indirect	Godoy et al. (2010)
	Decomposition	Direct and indirect	LeRoy et al. (2014)
	Nitrogen supply and carbon storage	Direct	Wolkovich et al. (2010)
	Photosynthesis	Direct	Garcia-Serrano et al. (2009)
	Growth	Direct	Domènech and Vilà (2008)
Root traits	None	-	Stanisci et al. (2010)
	Nitrogen use, biomass	Direct	Werner et al. (2010)
	None	-	Lloret et al. (2005); Acosta et al. (2006)

Table A.1.2 continued from previous page

Affected plant trait	Studied ecosystem function/property	Studied effect	References
Other morph. traits	Growth	Direct	Domènech and Vilà (2008)
	Competition, nitrogen use, biomass	Direct	Werner et al. (2010)
Reproductive traits	None	-	Lloret et al. (2005); Acosta et al. (2006); Godoy et al. (2009b,a); Stanisci et al. (2010); Castro-Díez et al. (2014)
	Germination, emergence, establishment, growth, reproduction	Direct	Sans et al. (2004)
Physiological traits	Growth	Direct	Ashbacher and Cleland (2015)
Climate			
Leaf (litter) traits	None	-	Crescente et al. (2002); Martin-StPaul et al. (2013)
	Biomass	Direct	Cochrane et al. (2015)
	Growth, biomass	Indirect	Cochrane et al. (2015)
	Growth	Direct	Domènech and Vilà (2008)
	Competition, nitrogen use, biomass	Direct	Werner et al. (2010)
Root traits	Photosynthesis	Direct	Garcia-Serrano et al. (2009)
	Competition, nitrogen use, biomass	Direct	Werner et al. (2010)
	None	-	Pérez-Camacho et al. (2012) ; Lázaro-Nogal et al. (2013)
Other morph. traits	Growth	Direct	Domènech and Vilà (2008)
	Nitrogen use, biomass	Direct	Werner et al. (2010)
Reproductive traits	None	-	del Cacho et al. (2013); Lázaro-Nogal et al. (2013); Hänel and Tielbörger (2015)
Physiological traits	None	-	Martin-StPaul et al. (2013); Lázaro-Nogal et al. (2013)
	Growth	Direct	Ashbacher and Cleland (2015)
Fire strategy traits	Germination	Direct	Paula and Pausas (2008)
Nitrogen deposition			
	Organic matter and inorganic nitrogen content, nitrogen and carbon fluxes	Direct	Dias et al. (2013)
	Productivity, nitrogen and carbon fluxes	Direct	Vourlitis et al. (2009)

Table A.1.2 continued from previous page

Affected plant trait Leaf (litter) traits	**Studied ecosystem function/property**	**Studied effect**	**References**
	Decomposition	Indirect	Kazakou et al. (2009); Valera-Burgos et al. (2013)
Atmospheric CO_2			
Leaf (litter) traits	Decomposition	Direct and indirect	Gahrooee (1998)
Reproductive traits	Emergence success, biomass	Direct	Grünzweig and Dumbur (2012)

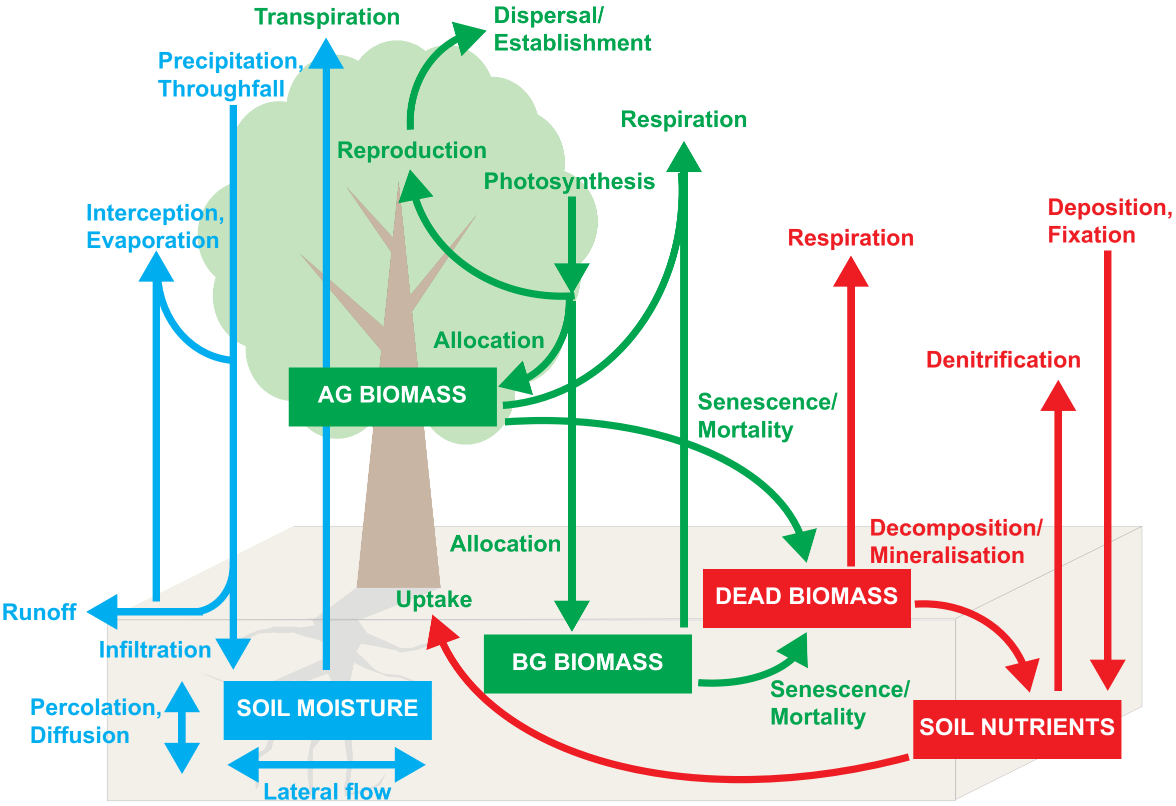


Figure A.1.1: Overview of the stocks (boxes) and processes (arrows) of the developed model in the case study presented in the main text. Blue colours refer to the hydrological module, green colours to the vegetation module and red colours to the nitrogen module.

A.2 Appendix to "Global change shifts trade-offs among functions"

A.2.1 Description of the plant module of ModEST

As described in the main text, the plant module is mainly based on LPJ and LPJmL (Schaphoff et al., 2018; Sitch et al., 2003; Smith et al., 2014) and local processes as described for an individual-based plant model by May et al. (2009). The plant module simulates the life cycle of individual woody plants placed in the landscape, their dynamic below- and aboveground carbon and nitrogen pools as well as structural components based on plant traits (see Table A.2.2) and abiotic conditions. As this module is a combination of several literature sources, a few adaptations or corrections to the processes described therein and a new mortality process, we decided to fully describe the plant module in the following. This module is fully coupled to a spatially explicit hydrological and nutrient module (see description of both modules in the main text), meaning that soil water and nutrient fluxes are influenced by individual plants, and vice versa. If not stated otherwise, all plant processes are calculated on a daily basis for each individual plant in a random order to avoid advantages to first individuals if order was maintained. This module has closed boundary conditions affecting dispersal, resource acquisition and litter accumulation. Interaction with soil resources in grid cells are proportional to the individual's intersected crown area which we assume to be their zone of influence. The processes are executed in the order we describe them.

Phenology

In this study, woody plants were evergreen. In this module, however, woody plants could potentially be distinguished between evergreen, winter deciduous, and drought deciduous phenology types as described in Sitch et al. (2003). Phenology $phen$ (ranging between 0 and 1) varies between fully shed and fully covered with leaves and affects photosynthesis, transpiration and respiration. Evergreen plants retain a constant full leaf coverage over the year. Phenology of drought deciduous depends on a threshold of water supply and water demand (see transpiration for $wlim$), whereas phenology of winter deciduous is a daily updated fraction of current growing degree days based on a species-specific temperature level (GDD) and the maximum GDD for full leaf cover ($fullGDD$). In the case of senescence, 50% of the optimal leaf nitrogen content will be allocated to the plant's nitrogen storage but only up to its maximum nitrogen storage capacity (Smith et al., 2014). The shed leaves will be added to the aboveground litter pool (proportionally to covered grid cells).

	Phenology status	*Senescence*
Evergreen	$phen = 1.0$	–
Winter deciduous	$phen_t \; = \; min \left\{ 1.0, \; \frac{GDD_t}{full_{GDD}} \right\}$	The first time if temperature drops below 5.0°C in autumn.
Drought deciduous	$phen_t = \begin{cases} 1.0, & w_{lim} \geq 0.35 \\ 0, & w_{lim} < 0.35 \end{cases}$	$w_{lim} < 0.35$

Photosynthesis

Photosynthesis is based on Sitch et al. (2003); Smith et al. (2014); Schaphoff et al. (2018) and calculates gross primary production GPP [kgC day^{-1}] based on light-limited J_E [kgC hour^{-1}] and Rubisco-limited photosynthesis J_C [kgC hour^{-1}]:

$$GPP \; = \; \frac{J_E \; + \; J_C \; - \sqrt{(J_E \; + \; J_C\;)^2 \; - \; 4 \times \theta \times J_E \times J_C}}{2 \times \theta} \; \times \; daylength \tag{A.1}$$

with daylength as daylight hours [hours] and $\theta \; = \; 0.7$, a shape parameter that describes the co-limitation of light and Rubisco activity [dimensionless].

Daylength is simulated as:

$$daylength = \frac{24}{\pi} \; \times \; \arccos \left(- \frac{\sin\left(\varphi \; \times \; \frac{\pi}{180}\right) \times \; \sin\delta}{\cos\left(\varphi \; \times \; \frac{\pi}{180}\right) \times \; \cos\delta} \right) \tag{A.2}$$

with φ giving the latitude of the site [rad] and δ the solar declination [rad]:

$$\delta \; = \; 0.4093 \; \times \; \sin \left(\frac{2\pi}{365} \times day - 1.405 \right) \tag{A.3}$$

with day as day number of the year.

J_E depends on absorbed photosynthetically active radiation APAR, daylength, and air temperature.

$$J_E = c_1 \times \frac{APAR}{daylength} \tag{A.4}$$

$$c_1 = \alpha_{C3} \times T_{Stress} \times \left(\frac{p_i - \Gamma_*}{p_i + 2\Gamma_*}\right) \tag{A.5}$$

with $\alpha_{C3} = 0.08$ as the intrinsic quantum efficiency for CO_2 uptake in C_3 plants [dimensionless], T_{Stress} as a species-specific temperature inhibition function [dimensionless] (Schaphoff et al., 2018), p_i as leaf internal partial pressure of CO_2 [Pa], and Γ_* as the photorespiratory CO_2 compensation point [Pa].

$$\begin{aligned} T_{Stress} &= \frac{1.0}{1 + e^{k_1(k_2 - T_{air})}} \times \left(1.0 - 0.01 \times e^{k_3 \times (T_{air} - T_3)}\right) \\ k_1 &= 2.0 \times \frac{\ln\left(\frac{1.0}{0.99} - 1.0\right)}{T_1 - T_2} \\ k_2 &= 0.5 \times (T_1 + T_2) \\ k_3 &= \frac{\ln \frac{0.99}{0.01}}{T_4 - T_3} \end{aligned} \tag{A.6}$$

with $T_1$to T_4 as species-specific temperature limits [°C], T_{air} as air temperature [°C].

$$p_i = \lambda \times p_a \tag{A.7}$$

with p_a as ambient pressure of CO_2 [Pa], λ as parameter describing the ratio of the intercellular to the ambient CO_2 concentration [dimensionless].

$$\Gamma_* = \frac{[O_2]}{2\tau} \tag{A.8}$$

with $[O_2] = 20900$ as partial pressure of O_2 [Pa], τ as specificity factor that reflects the ability of Rubisco to discriminate between CO_2 and O_2 [dimensionless].

$$\tau = \tau_{25} \times Q_{10_\tau}^{(T_{air} - 25) \times 0.1} \tag{A.9}$$

with $\tau_{25} = 2600$ as τ at 25°C [dimensionless], $Q_{10_\tau} = 0.57$ as temperature sensitivity factor [dimensionless], T_{air} as mean daily air temperature [°C].

APAR $[\frac{kgC}{day}]$ is the fraction of incoming net photosynthetically active radiation PAR $[\frac{kgC}{m^2 day}]$ that is absorbed by the unshaded plant fractional coverage $FPC_{unshaded}$ [m^2] given the daily phenological status [dimensionless].

$$\begin{aligned} PAR \;&=\; PAR \;\times\; FPC_{unshaded} \;\times\; phen \\ PAR =&\; 0.5 \;\times c_q \times\; c_{mass} \times R_a \end{aligned} \tag{A.10}$$

with $c_q \;=\; 4.6 \;\times\; 10^{-6}$ $[\frac{J}{mol}]$ conversion factor from J to mol for solar radiation at 550 nm, $c_{mass} \;=\; 12.0107 \;\times\; 10^{-3}$ $[\frac{kg}{mol}]$ as atomic mass of carbon, and R_a as extraterrestrial radiation $[\frac{J}{m^2 \;\times\; day}]$. $FPC_{unshaded}$ of an individual is calculated from the leaf area index LAI [dimensionless] and the individual unshaded crown area $CA_{unshaded}$ [m^2] which is the crown area that is not overlapped by the crowns of larger surrounding individuals.

$$\begin{aligned} FPC_{unshaded} \;&=\; \left(1 -\; e^{-0.5 \;\times\; LAI}\right) \;\times CA_{unshaded} \\ LAI \;&=\; \frac{C_{leaf} \;\times\; SLA}{CA} \end{aligned} \tag{A.11}$$

with C_{leaf} as dynamic carbon mass in the leaves [kg], and SLA as species-specific leaf area $[\frac{m^2}{kg}]$. J_C is calculated as a function of maximum Rubisco capacity V_m $[\frac{kgC}{day}]$.

$$J_C = \frac{c_2 \;\times\; V_m}{24} \tag{A.12}$$

$$c_2 = \frac{p_i \;-\; \Gamma_*}{p_i \;+\; K_c \;\times\; \left(1.0 \;+\; \frac{[O_2]}{K_o}\right)} \tag{A.13}$$

with $K_c \;=\; 30$ and $K_o = 30000$ as Michaelis-Menten constants at 25°C [Pa] and other symbols as defined previously.

$$V_m = \frac{1}{b} \;\times\; \frac{c_1}{c_2} \;\times\; [(2 \times \theta \;-\; 1) \;\times\; s \;-\; (2 \times \theta \times s \;-\; c_2) \;\times\; \sigma] \;\times\; APAR \;\times\; n_{lim} \tag{A.14}$$

with $b \;=\; 0.015$ as leaf respiration as fraction of V_m for C$_3$ plants, n_{lim} as nitrogen limitation factor (see description of Nitrogen uptake) which is a simplification of nitrogen limited Rubisco activity as described in Smith et al. (2014).

$$s \; = \; \frac{24}{daylength} \; \times \; b \tag{A.15}$$

$$\sigma \; = \; \sqrt{1.0 \; - \; \frac{c_2 \; - \; s}{c_2 \; - \; \theta \times s}} \tag{A.16}$$

Stomatal conductance g_c [mm s^{-1}] is calculated as:

$$g_c = \; \frac{1.6 \; \times \; NPP_{mm/s}}{c_a \times (1.0 - \lambda)} \; + \; g_{min} \tag{A.17}$$

with as net daytime primary production $NPP_{mm/s}$ [mm s^{-1}], c_a as ambient mole fraction of CO$_2$, and g_{min} as species-specific minimum canopy conductance [mm s^{-1}] that occurs due to processes other than photosynthesis.

$$c_a = \frac{p_a}{p} \tag{A.18}$$

with $p = \; 1 \; \times 10^5$ [Pa] as atmospheric pressure, and p_a as defined previously. $NPP_{mm/s}$ is calculated using the ideal gas equation:

$$NPP_{mm/s} \; = \; \frac{NPP}{conv_{DtoS}} \; \times \; \frac{1}{c_{mass}} \; \times \; \bar{R} \; \times \; \frac{T_{air} \; + \; 273.15}{p} \; \times \; 1000 \tag{A.19}$$

with $conv_{DtoS} \; = \; 3600 \; s \times$ hour$^{-1}\times$ daylength as conversion factor from daylight hours to seconds, $\bar{R} \; = \; 8.314$ [m^3 Pa K^{-1} mol^{-1}] as ideal gas constant. Net primary productivity NPP [kgC day^{-1}] results from GPP (see eqn. A.1) after leaf respiration R_{leaf} [kgC day$^-$1]:

$$NPP = \; GPP \; - \; R_{leaf} \tag{A.20}$$

$$R_{leaf} \; = \frac{daylength}{24} \; \times \; b \; \times \; V_{m} \tag{A.21}$$

As described in Sitch et al. (2003), under non-water-stressed conditions $\lambda \; = \; 0.8$ for C$_3$ plants, and therefore the resulting g_c is the potential stomatal conductance which will be used in the Transpiration process to assess the potential water demand. If the water demand cannot be fulfilled by the water supply W_{sup} (see Transpiration), equations involving water demand W_{dem} (see Transpiration), g_c, and NPP will to be solved again but this time simultaneously to obtain values for g_c and λ that meet W_{sup}. This ultimately leads into a down-regulation of the photosynthesis and thus a decreased GPP.

Nitrogen uptake

Nitrogen uptake is simplified after the description of Smith et al. (2014). An individual's potential nitrogen demand $N_{pot,dem}$ [kgN] is the sum of the nitrogen demand for the leaves $N_{leaf,dem}$, sapwood $N_{sap,dem}$ and roots $N_{root,dem}$ as well as demand for the storage of labile nitrogen $N_{store,dem}$.

$$N_{pot,dem} = N_{leaf,dem} + N_{sap,dem} + N_{root,dem} + N_{store,dem} \tag{A.22}$$

Demand for each tissue $N_{tissue,dem}$ is based on the optimal carbon to nitrogen ratio CN_{tissue} and the current carbon mass of the tissue C_{tissue} [kgC].

$$N_{tissue,dem} = \frac{C_{tissue}}{CN_{tissue}} \tag{A.23}$$

Demand for nitrogen storage pool $N_{store,dem}$ is the difference between current storage N_{store} and the maximum nitrogen storage capacity $N_{store,max}$.

$$N_{store,dem} = N_{store,max} - N_{store} \tag{A.24}$$

$N_{store,max}$ is related to the current sapwood carbon C_{sap}, leaf nitrogen N_{leaf} and carbon C_{leaf}, as well as k_{store} a constant which is set to 0.05 for evergreen woody and 0.15 for deciduous woody plants.

$$N_{store,max} = k_{store} \times C_{sap} \times \frac{N_{leaf}}{C_{leaf}} \tag{A.25}$$

Actual nitrogen demand $N_{act,dem}$ is limited by maximal possible N uptake N_{max}. If the potential demand cannot be fulfilled by N_{max}, tissue demand will be adjusted accordingly.

$$N_{act,dem} = \begin{cases} N_{pot,dem}, & N_{pot,dem} < N_{max} \\ N_{max}, & N_{pot,dem} \geq N_{max} \end{cases} \tag{A.26}$$

N_{max} depends on the plant available soil nitrogen f_{avN}, soil temperature $f_{T,soil}$, current N:C status of the plant f_{NC}, and root carbon mass C_{root}.

$$N_{max} = \ 2.0 \ \times \ up_{N,root} \ \times \ f_{avN} \ \times \ f_{T,soil} \ \times \ f_{NC} \ \times \ C_{root} \tag{A.27}$$

with $up_{N,root} \ = \ 2.8 \times 10^{-3} \ \frac{kgN}{kgC \ day}$ for woody plant species.

$$f_{avN} = 0.05 \ + \ \frac{N_{soil}}{N_{soil} \ + \ k_{max} \ \times \ fc \ \times \ z_{soil} \ \times \ CA} \tag{A.28}$$

with N_{soil} as the nitrate NO_3 [kg] and ammonium NH_4 [kg] content in the zone of influence of the individual plant (output from nutrient module); $k_{max} \ = \ 1.48 \ \times 10^{-3} \ \frac{kgN}{m^3}$ as the half-saturation concentration for N uptake for woody plant species; fc as field capacity of the soil $[\frac{m^3}{m^3}]$, z_{soil} soil depth in which the plant is rooting [m]; and crown area CA [m^2] .

$$N_{soil} \ = \sum_{C}^{nC's} \sum_{L}^{nL's} (NO_{3,L} \ + \ NH_{4,L}) \times \ root_L \ \times relCA_C \tag{A.29}$$

with $relCA_C$ being the relative plant's crown area intersected for each grid cell C, and $root_L$ being the relative fraction of root mass per soil layer L.

$$f_{T,soil} = \ 0.0326 \ + \ 0.00351 \ \times \ T_{av,soil}{}^{1.652} \ - \ \left(\frac{T_{av,soil}}{41.748}\right)^{7.19} \tag{A.30}$$

As soil temperature T_{soil} [°C] (from nutrient module, see Kemanian et al. (2011)) is different across soil layers L and grid cells C, an average soil temperature $T_{av,soil}$ per plant individual is calculated based on the fraction of roots per soil layer $root_L$ [–] and the relative intersected crown area per grid cell $relCA_C$ [–].

$$T_{av,soil} \ = \sum_{C}^{nC's} \sum_{L}^{nL's} T_{soil,L} \times \ root_L \ \times relCA_C \tag{A.31}$$

$$
\begin{aligned}
f_{NC} &= \frac{x_1}{x_2} \\
x_1 &= \frac{N_{leaf} + N_{root}}{C_{leaf} + C_{root}} - \frac{1}{CN_{leaf,min}} \\
x_2 &= \frac{2.0}{CN_{leaf,max} + CN_{leaf,min}} - \frac{1.0}{CN_{leaf,min}}
\end{aligned}
\tag{A.32}
$$

with $CN_{leaf,max}$ and $CN_{leaf,min}$ as the maximum and minimum bounds for leaf C:N, respectively. Nitrogen is taken up according to the actual N demand of root, sapwood and leaf tissue and the storage pool. If there is only enough available N to meet the demand of the tissue, demand for the storage will not be fulfilled. If there is not enough to meet tissue N demand, N from the storage pool will be used. If there still is not enough available N to meet the tissue's demand, photosynthesis will be re-calculated with limiting term n_{lim} (see Photosynthesis).

$$
n_{lim} = min\left\{ 1.0,\ \frac{N_{av,soil} + N_{store}}{N_{leaf,dem} + N_{sap,dem} + N_{root,dem}} \right\} \tag{A.33}
$$

Transpiration

Transpiration E_T is based on the approach by Sitch et al. (2003); Schaphoff et al. (2018) and is assumed to be the minimum between water demand W_{dem} and water supply W_{sup}.

$$
E_T = min\{W_{dem} \ , \ W_{sup}\} \tag{A.34}
$$

If W_{sup} cannot meet W_{dem}, water limitation wlim will be calculated and considered in the allocation (see Allocation), as well as stomatal conductance g_c will be re-calculated given W_{sup} (see Photosynthesis). The amount of water transpired is calculated proportional to the covered grid cells and the root fraction in the different soil layers.

$$
w_{lim} = min\left\{1.0 \ , \ \frac{W_{sup}}{W_{dem}}\right\} \tag{A.35}
$$

W_{dem} [mm] is calculated based on potential evapotranspiration E_{pot} (from hydrological module, Tietjen et al., 2009b) and fractional plant cover FPC (see $FPC_{unshaded}$ in Photosynthesis but with full crown area CA) and stomatal conductance g_c (see Photosynthesis).

$$W_{dem} = E_{pot} \times FPC \times \frac{\alpha_m}{1 + \frac{g_m}{g_c}} \tag{A.36}$$

with maximum Priestley-Taylor coefficient $\alpha_m = 1.1$ (Monteith, 1995) and conductance scaling factor $g_m = 5.0$ (Sitch et al., 2003). W_{sup} [mm] is calculated based on a species-specific maximum water transport capacity e_{max} [mm day^{-1}], fractional plant cover FPC, relative water content available for the plant W_{av}, phenology phen, and a scaling term based on the current root to leaf mass ratio allowing more or less water supply with deviating species-specific leaf mass to root mass ratio LM/RM.

$$W_{sup} = e_{max} \times FPC \times W_{av} \times phen \times \frac{C_{root} \times LM/RM}{C_{leaf}} \tag{A.37}$$

Relative water content available for the plant W_{av} is the difference between the current relative water content W (output from hydrological module) and water content at which plant starts to wilt WP as a fraction of field capacity fc of the soil.

$$W_{av} = \sum_{C}^{nC's} \sum_{L}^{nL's} \left(\frac{W_L - WP}{fc} \right) \times root_L \times relCA_C \tag{A.38}$$

with $relCA_C$ being the relative plant's crown area intersected for each grid cell C, and $root_L$ being the relative fraction of root mass per soil layer L.

Respiration

Respiration is modelled as described in Sitch et al. (2003) and updates described in Schaphoff et al. (2018). An individual's total respiration R [kgC] is a sum of maintenance leaf R_{leaf} (see photosynthesis), sapwood R_{sap} [kgC] and root respiration R_{root} [kgC] as well as growth respiration R_{growth} [kgC].

$$R = R_{leaf} + R_{sap} + R_{root} + R_{growth} \tag{A.39}$$

Maintenance respiration depends on tissue-specific carbon to nitrogen ratio CN_{tissue}, air or soil temperature T_x for sapwood or root respiration, respectively, tissue's biomass C_{tissue} and phenology $phen$ for root respiration.

$$R_{sap} = \ r_{coef} \ \times \ k \ \times \ \frac{C_{sap}}{CN_{sap}} \ \times \ A_x \tag{A.40}$$

$$R_{root} = \ r_{coef} \ \times \ k \ \times \ \frac{C_{root}}{CN_{root}} \ \times \ A_x \times \ phen \tag{A.41}$$

with r_{coef} as species-specific respiration coefficient [kgC kgN−1 day−1], $k \ = \ 0.095218$ and Arrhenius temperature-respiration function.

$$A_x = \ e^{308.56 \ - \ \left(\frac{1}{56.02} \ - \ \frac{1}{Tx \ + \ 46.02}\right)} \tag{A.42}$$

with x as air or average soil temperature ($T_{av,soil}$, see Nitrogen Uptake) for sapwood or roots, respectively. Growth respiration is a fixed proportion of 25% of the remaining GPP after subtracting maintenance respiration.

$$R_{growth} = r_{gr} \times (GPP - R_{leaf} - R_{sap} - R_{root}) \tag{A.43}$$

with $r_{gr} \ = \ 0.25$. As a result, net primary production $NPP \ = \ GPP \ - R$ will be calculated.

Reproduction

Reproduction is modelled as described in Sitch et al. (2003). 10% of daily NPP goes into reproductive carbon mass $m_{rep,d}$ and will be summed up over one year $m_{rep,y}$ [kgC]. The remaining net primary productivity NPP_{rem} [kgC day^{-1}] will be calculated as follows:

$$NPP_{rem} \ = \ NPP \ - m_{rep,d} \tag{A.44}$$

Allocation

Allocation is based on Sitch et al. (2003) and updates as described in Smith et al. (2014). Accordingly, GPP after respiration and reproduction, NPP_{rem}, will be allocated to above- and below-ground carbon pools, i.e. leaves, fine roots and sapwood by satisfying four allometric relationships (eqns. A.47 to A.50).

$$NPP_{rem} = \Delta C_{leaf} + \Delta C_{root} + \Delta C_{sap} \tag{A.45}$$

$$\begin{aligned} LA &= LtS \ \times \ SA \\ SA &= \frac{C_{sapwood}}{WD \ \times \ H} \end{aligned} \tag{A.46}$$

with LA as average individual leaf area [m^2], SA as sapwood cross sectional area [m^2], LtS as a species-specific ratio between leaf area to sapwood area, WD as species-specific wood density [kgC m^{-3}], and H as plant height [m].

$$\Delta C_{leaf} = LtR_{scal} \times \Delta C_{root} \tag{A.47}$$

with LtR_{scal} as leaf mass to root mass constant depending on species-specific LtR as well as water or nutrient limitation leading to greater allocation to the roots driven by the most limiting resource.

$$CA = \begin{cases} LtR, & NPP \leq 0 \\ LtR \ \times \ min\left\{w_{lim} \ , \ n_{lim}\right\}, & NPP > 0 \end{cases} \tag{A.48}$$

$$H \ = \ a_2 \times \ D^{a_3} D \ = \ \left(\frac{4 \times (C_{heartwood} + C_{sapwood})}{\pi \times WD \ \times \ a_2}\right)^{\frac{1}{a_3+2}} \tag{A.49}$$

with D as stem diameter [m] as well as a_2 and a_3 as species-specific allometric parameters.

$$CA = \begin{cases} a1 \times D^{k_{rp}}, & CA < CA_{max} \\ CA_{max}, & CA \geq a1 \times D^{k_{rp}} \end{cases} \tag{A.50}$$

with CA as crown area constrained by a species-specific maximum crown area CA_{max} and species-specific allometric parameter a_1 as well as $k_{rp} \ = \ 1.6$. If there is negative NPP, this results in negative ΔC_{leaf}, ΔC_{root} and potentially negative ΔC_{sap}. In this case, leaf and root carbon will be lost to the aboveground or belowground litter pool, and sapwood carbon will be transformed to heartwood carbon mass. Total nitrogen in the lost tissue $N_{turnover}$, which is calculated from ΔC_{leaf}, ΔC_{root} and ΔC_{sap} and the species- and tissue-specific CN_{tissue}, is moved to the plant's labile nitrogen storage which is constrained by the maximum possible nitrogen storage $N_{store,max}$. Excess nitrogen will be equally added to the above- and belowground nitrogen litter pools.

$$N_{turnover} = \sum_{tissue}^{n} \frac{|\Delta C_{tissue}|}{CN_{tissue}}, \Delta C_{tissue} < 0 \tag{A.51}$$

$$N_{storet} = min \{N_{storet-1} + N_{turnover}, N_{store,max} \} \tag{A.52}$$

Dispersal & Establishment

The dispersal routine is based on May et al. (2009) and is executed once a year on July 1st or for leap years on July 2nd (for southern hemisphere). Number of seeds will be determined by the individual's reproductive carbon mass allocated over the year $m_{rep,y}$ divided by the species-specific mass of one seed $seedMass$ [kg]. Distance [m] is drawn from a log normal distribution with species-specific mean meanDisp and standard deviation sdDisp of dispersal distance which resembles the species-specific dispersal kernel. Dispersal direction [deg] for each seed is drawn from a uniform distribution.

The saplings establish as an individual plant at the determined location with a height of 10 cm and a species-specific initial leaf area index LAI_{sap} (to obtain initial leaf carbon, eqn. A.12) (i) with a species-specific germination probability p_{germ}, (ii) if the target position is not covered by another individual assuming too limited light resources (May et al., 2009, after), and (iii) with a species-specific establishment probability p_{estab} which equals mseed taking into account increased probability of establishment with higher endosperm resources (Hallett et al., 2011). Seeds that do not establish will be transferred to the aboveground carbon litter pool.

Mortality

Mortality events due to resource limitations take place the last day of the year for individuals older than one year. As plant growth depends on resource availability, individual plants die if the ratio between current and previous year's total plant biomass exceeds a species-specific mortality threshold t_{mort}. Except for the heartwood pool, which remains as standing biomass, all other individual's above- and belowground carbon and nitrogen pools will be transferred to the respective litter pools of those grid cells and soil layers the individual's crown area intersect with – proportional to the covered crown area per grid cell and the fraction of roots per soil layer frootLx.

A.2.2 Model parameterisation and validation

Whenever possible, the model parameters of ModEST were parameterized according to values from measurements in Ridgefield, literature, or databases (see Tables A.2.2 and A.2.1). Parameters with unknown values were calibrated. For E. astringens additional known parameters through measurements (i.e. LM/RM, a_2, a_3) were included in the calibration process, as they proved important for a successful calibration.

For the actual calibration, ModEST was initialised for conditions found in Ridgefield in 2011. We used the same plot size, the coordinates of individual plants, and their measured heights. Soil conditions of these plots were mimicked in terms of the measured nitrate and ammonium content in the soil, bulk density, and clay content (Perring et al., 2012). We run simulations from 2011 to 2016 using weather time series dataset from Ridgefield where available (2013 – 2016) and filled the gap in the first years with the nearby weather station in Pingelly (Bureau of Meteorology, 2019, 2011 – 2012). The modelled landscape was flat with 50 and 150 cm in depth for the first and the second soil layer, respectively. Since monoculture data was only available for *E. loxophleba*, we calibrated the parameters of each plant species consecutively. We first used a monoculture plot for *E. loxophleba* (for which soil parameters were calibrated at the same time), followed by a two-species mixture plot for *E. astringens*, and then four-species mixtures plots for *A. acuminata*, *A. microbotrya*, *B. sessilis*, *H. lissocarpha*, *C. quadrifidus*, *C. phoeniceus* (see Perring et al., 2012 for information on the mixtures). For each plant species, we compared yearly simulated mean aboveground alive biomass, mean plant height and individual counts with measured data from the plots. We compared estimates for August, since this is when these variables were measured in the experiment, on an annual basis from 2011 until 2014 (for individual counts until 2016). Soil moisture time series data were only available for the

E. loxophleba plot, therefore we calibrated soil parameters for this plot using daily time series data of the first soil layer (Fig. A.2.1). Calibrated parameters were obtained by a Bayesian approach implemented in the R package BayesianTools (Hartig et al., 2019) using 100,000 iterations, 3 chains, and the DEzs sampler. Input parameter ranges (priors) can be found in Tables A.2.2 and A.2.1. Optimisation across the abovementioned four output variables was measured by a root sum square error between measured m and simulated data s at each time of the measurement i normalized by the standard deviation σ_m of the measured data (nRSSE):

$$nRSSE = \frac{\sqrt{\sum_i (m_i - s_i)^2}}{\sigma_m} \tag{A.53}$$

For each parameter, we used the maximum probable value of its calibrated posterior distribution.

For model validation (see also in the main text *Model parameterization and validation*, Fig. A.2.2), we used the same settings as described for model calibration. Soil water and nutrient dynamics could not be validated due to a lack of empirical data.

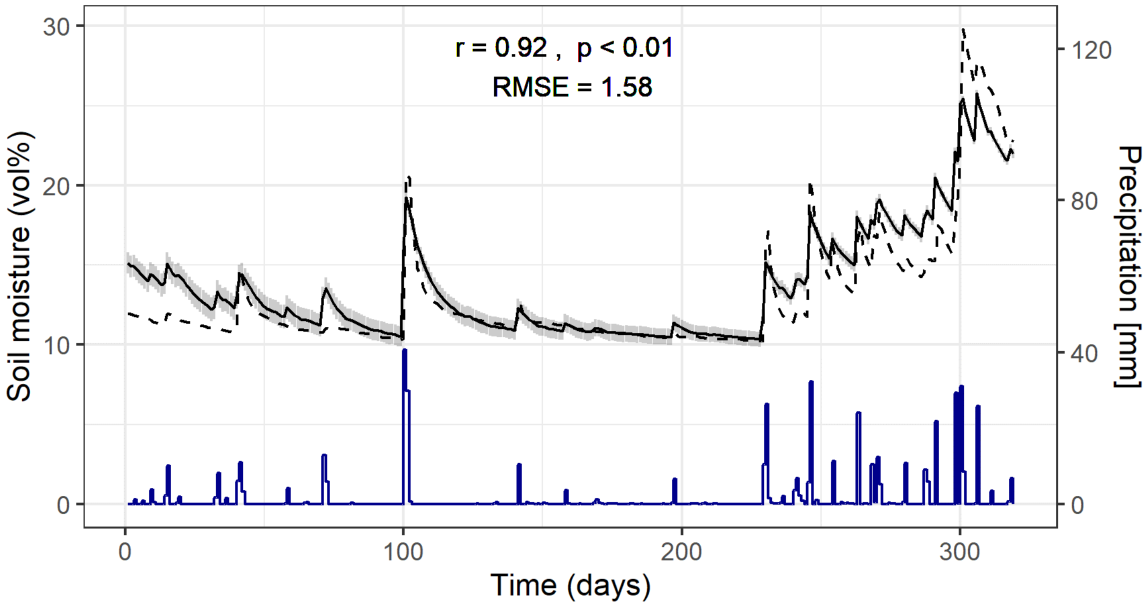


Figure A.2.1: Calibration results. Shown are measured (dashed line), mean simulated moisture of the first soil layer (solid line) and forcing rainfall (blue line). Measured dynamics show measurement for an annual cycle of a *E. loxophleba* monoculture with loamy sand. Standard deviation shown for simulated results represent 10 model repetitions accounting for random plant height initialisation of neighboring individuals. Shown are Spearman's rank correlation coefficient r, corresponding p-value as well as the root mean square error RMSE.

Table A.2.1: Hydrological and nutrient parameters. Parameter shown for the soil texture loamy sand. Parameters used in plant module (PM, Appendix A.2.1), hydrological module (HM) by Tietjen et al. (2009b), and nutrient module (NM) by Kemanian et al. (2011).

Parameter	**Abb.**	**Reference to submodules**	**Unit**	**Value**	**Source**
Effective suction	Sf	HM: eqn. 4	mm	61.3	Rawls et al. (1992)
Saturated hydraulic conductivity	K_s	HM: eqns. 4, 9	mm h^{-1}	62.2	Rawls et al. (1998)
Field capacity	fc	HM PM: eqn. A.28	m^3 m^{-3}	0.332	calibrated between 0.019 and 0.432 (default = 0.3) based on Rawls et al. (1992)
Evaporation factor	a_{ET}	HM: eqn. 13	-	0.203	calibrated between 0.01 and 1.0 (default = 1.0)
Residual Water Content	r_w	HM: eqn. 13	m^3 m^{-3}	0.08	calibrated between 0.003 and 0.12 (default = 0.1)
Infiltration rate into layer 2	$FL_{2,frac}$	HM: eqn. 2	-	0.242	calibrated between 0.01 and 1.0 (default = 0.1)
Bare soil infiltration rate into layer 2	$FL_{2,bare}$	HM: eqn. 3	-	0.8	estimated depending on K
Maximum total infiltration into layer 2	$FL_{2,max}$	HM	mm h^{-1}	1.5	Rawls et al. (1992)
Constant for diffusion coefficient	d	HM: eqn. 9	-	0.253	calibrated between 0.01 and 1.0 (default = 0.01)
Bulk density	BD	NM: eqn. 4	g cm^{-3}	variable	For calibration and validation depending on measured value of the Ridgefield plot (Perring et al., 2012)
				1.265750857	For scenarios based on mean across all treatments with soil texture loamy sand (Perring et al., 2012)
Clay content	c_{clay}	NM: eqns. 3c, 4, 8	m^3 m^{-3}	variable	For calibration and validation depending on measured value of the Ridgefield plot (Perring et al., 2012)
				0.06	For scenarios based on mean across all treatments with soil texture loamy sand (Perring et al., 2012)
Daily nitrogen deposition	ndep	NM	g ha^{-1} year^{-1}	4.93	Dentener et al. (2006)

A.2.3 Simulation experiments

Processing of weather data from Pingelly

The weather data from Pingelly (Bureau of Meteorology, 2019, see main text *Climate Change Scenarios*) had to be corrected by filling data gaps and removing leap days. Data gaps of up to two subsequent days were filled by the mean of the previous and the next day. For more than two missing days, we filled the gaps by taking the mean of the same days from the previous

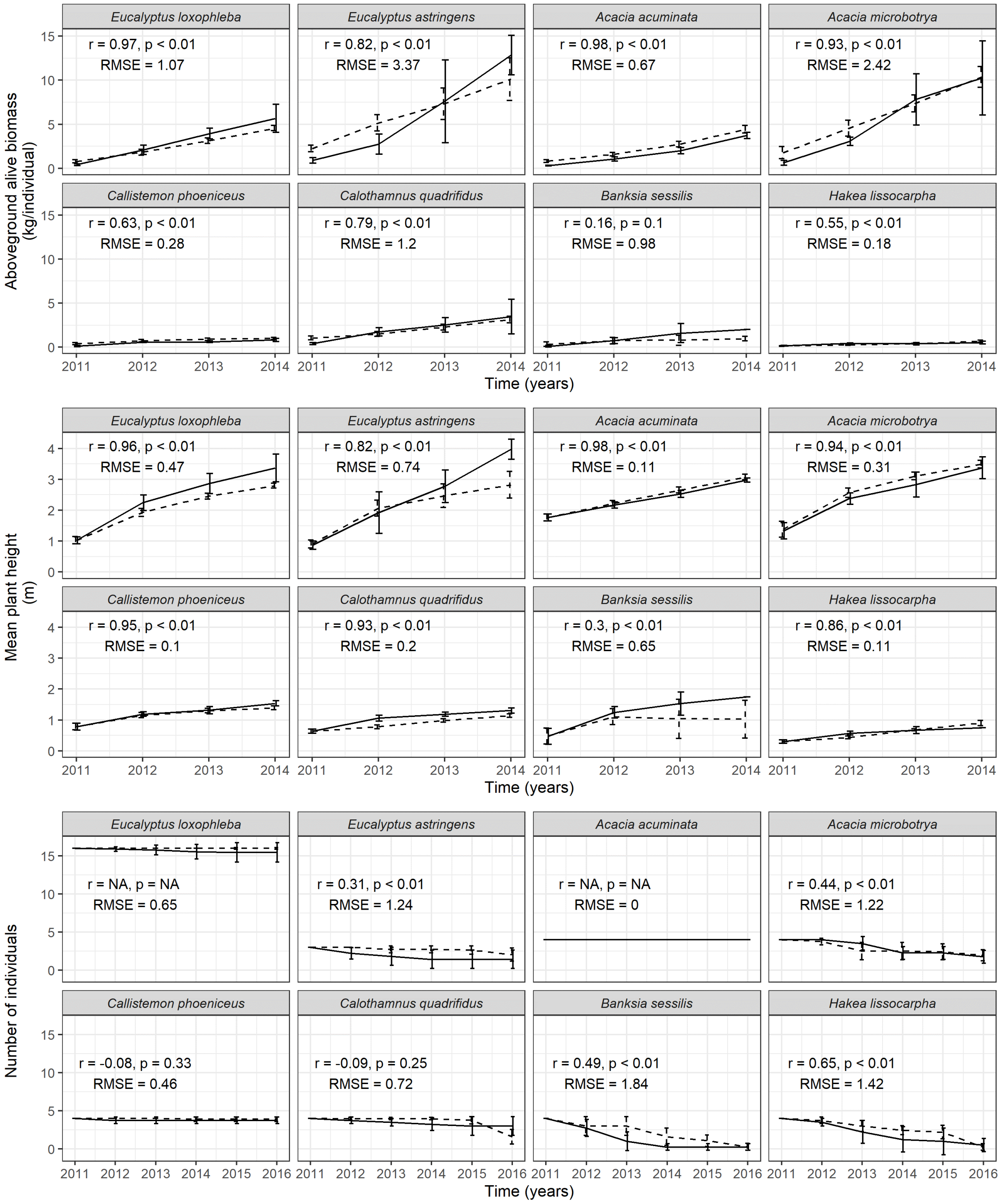


Figure A.2.2: Validation results. Shown are mean measured (dashed line, Perring et al., 2012, and unpublished data) and mean simulated data (solid line) for aboveground alive biomass, plant height and population size over time and for the eight plant species planted in Ridgefield. Error bars show standard deviation over all repetitions for the assemblages plus in case for the simulation results over 10 model repetitions accounting for random plant height initialisation of neighbouring individuals to account for edge effects. Shown are Spearman's rank correlation coefficient r, corresponding p-value as well as the root mean square error RMSE. NAs for the correlation between measured and simulated number of individuals resulted when individual numbers over time were constant.

Table A.2.2: Plant parameters. For meaning of the parameters see plant module description in section A.2.1. Highlighted parameters in grey were focal traits in this study (Table 3.2 in main text). EL: *Eucalyptus loxophleba* ssp. *loxophleba*, EA: *E. astringens*, AA: *Acacia acuminata*, AM: *A. microbotrya*, BS: *Banksia sessilis*, HL: *Hakea lissocarpha*, CQ: *Calothamnus quadrifidus*, CP: *Callistemon phoeniceus.*

Parameter	**Unit**	**Equation**	**Value for each woody evergreen plant species**								**Source**
			EL	**EA**	**AA**	**AM**	**CP**	**CQ**	**BS**	**HL**	
T_1	°C	eqn. A.6	-4								Sitch et al. (2000), temperate needle/broad-leaved evergreen species
T_2	°C		20								
T_3	°C		30								
T_4	°C		42								
SLA	$m^2\ kg^{-1}$	eqn. A.11	4.14	3.3	6.4	6.17	3.18	3.35	5.42	4.07	Fiedler et al., (unpublished)
g_{min}	$mm\ s^{-1}$	eqn. A.17	0.64	0.991	0.992	0.999	0.301	0.957	0.302	0.326	calibrated between 0.3 and 1.0 (default = 0.5) based on Schaphoff et al. (2018)
CN_{leaf}	-	eqn. A.23	32.4	53.4	16.9	20.4	48.7	36.7	53	72.4	Fiedler et al., (unpublished)
CN_{sap}	-	eqns. A.23,A.40	100	172.6	41.9	50.8	81.9	86.3	112	92.9	Fiedler et al., (unpublished)
CN_{root}	-	eqns. A.23,A.41	84.6	123.18	34.6	44.6	100.6	49.9	73.6	54.75	Perring et al., (unpublished)
k_{store}	-	eqn. A.25	0.05								Smith et al. (2014)
$root_{L1}$	-	eqns. A.29,A.31 (also used in hydrological module)	0.023^{*1}	0.012^{*1}	0.48^{*1}	0.027^{*1}	0.999^{*2}	0.201^{*2}	0.387^{*2}	0.011^{*2}	*1: calibrated between 0 and 0.5 (default = 0.5) for trees *2: calibrated between 0 and 1.0 (default = 0.5) for shrubs
$CN_{leaf,min}$	-	eqn. A.32	29.1	46.8	13.9	19.8	40.5	34.5	38.3	66.2	Fiedler et al., (unpublished)
$CN_{leaf,max}$	-	eqn. A.32	34.7	58.6	20.9	21	61.4	38.9	71.1	83.7	Fiedler et al., (unpublished)
e_{max}	$mm\ day^{-1}$	eqn. A.37	12.953	7.527	5.092	5.544	5.02	5.17	13.328	12.169	calibrated between 5 and 15 (default = 5) based on Sitch et al. (2003)

Table A.2.2 continued from previous page

Parameter	**Unit**	**Equation**	**Value for each woody evergreen plant species**								**Source**
			EL	**EA**	**AA**	**AM**	**CP**	**CQ**	**BS**	**HL**	
LM/RM	-	eqn. A.37	0.92^{*1}	3.933^{*2}	0.43^{*1}	0.47^{*1}	0.96^{*1}	1.73^{*1}	0.8^{*1}	1.54^{*1}	*1: Perring et al., (unpublished) *2: calibrated between 0.9 and 4.26 (default = 2.06) based on Perring et al., (unpublished)
WP	-	eqn. A.38	0.102	0.148	0.085	0.148	0.066	0.1	0.143	0.093	calibrated between 0.05 and 0.15 (default = 0.1) based on Rawls et al. (1992) for loamy sand
r_{coef}	kgC kgN^{-1} day^{-1}	eqns. A.40,A.41	0.057	0.015	0.069	0.05	0.759	0.467	0.407	1.192	calibrated between 0.01 and 1.2 (default = 0,2) based on Schaphoff et al. (2018)
LtS	-	eqn. A.46	8000								Sitch et al. (2003)
WD	kgC m^{-3}	eqns. A.46,A.49	973.791^{*1}	824.946^{*1}	951.424^{*1}	815.68^{*1}	846.363^{*1}	971.899^{*2}	771.1^{*1}	832.5135^{*1}	*1: Kattge et al. (2011) *2: calibrated between 600 and 1000 (default = 800)

Table A.2.2 continued from previous page

Parameter	Unit	Equation	Value for each woody evergreen plant species								Source
			EL	EA	AA	AM	CP	CQ	BS	HL	
a_2	-	eqn. A.49	34.9^{*1}	40.48^{*2}	43.075^{*1}	33.235^{*1}	63.614^{*2}	30.328^{*2}	141.98^{*1}	61.959^{*2}	*1: Perring et al., (unpublished) *2: calibrated: EA between 21.7 and 56.6 (default = 39.15) based on Perring et al., (unpublished), CP between 1 and 100 (default = 100), CQ between 10 and 200 (default = 100), HL between 1 and 100 (default = 10) based on pre-tests
a_3	-	eqn. A.49	0.79^{*1}	0.97^{*2}	0.825^{*1}	0.825^{*1}	1.002^{*2}	1.113^{*2}	1.33^{*1}	1.171^{*2}	*1: Perring et al., (unpublished) *2: calibrated: EA between 0.56 and 1.08 (default = 0.82) based on Perring et al., (unpublished) CP between 1 and 2 (default = 1.5), CQ between 0.5 and 2 (default = 1), HL between 0.8 and 1.2 (default = 1) based on pre-tests
a_1	-	eqn. A.50	585.485	565.529	589.553	596.315	597.588	145.158	592.695	210.474	calibrated between 50 and 600 (default = 500) based on Schaphoff et al. (2018)

Table A.2.2 continued from previous page

Parameter	Unit	Equation	Value for each woody evergreen plant species								Source
			EL	**EA**	**AA**	**AM**	**CP**	**CQ**	**BS**	**HL**	
maxCA	m^2	eqn. A.50	100	100	50	50	15	15	40	10	estimated from maximum height (Perring et al., 2012, see): maxCA = 6.7 * maximum height
seedMass	mg	Dispersal & Establishment	0.87	7.95	15.64	28.67	0.0462	0.91	36.67	23.9	Kattge et al. (2011)
meanDisp	m	Dispersal & Establishment	13.815	13.815	1.708	1.708	1.604	4.01	4.812	1.203	Relationship between plant height (Perring et al., 2012) and dispersal distance (Thomson et al., 2011) and dispersal mode (Harris and Standish, 2008)
sdDisp	m	Dispersal & Establishment	2								assumed
p_{germ}	-	Dispersal & Establishment	0.97	0.92	1	1	1	0.9	0.88	0.96	Kattge et al. (2011)
LAI_{ini}	-	Dispersal & Establishment	5.042	5.786	1.072	5.997	1.675	2.932	1.755	2.621	calibrated between 1 and 6 (default = 3)

Table A.2.2 continued from previous page

Parameter	Unit	Equation	Value for each woody evergreen plant species								Source
			EL	**EA**	**AA**	**AM**	**CP**	**CQ**	**BS**	**HL**	
t*mort*	-	Mortality	1.021^{*1}	1.255^{*1}	1^{*2}	1.186^{*1}	1^{*2}	1.134^{*1}	1.446^{*1}	1.542^{*1}	*1: calibrated between 0.5 and 2.0 (default = 0.9) *2: assumed

and the following year. If there was missing data in the previous or the following year, data gaps were only filled by the value of the year that has data available. Leap days were deleted in order to allow for random weather year selection. In this case, precipitation events occurring on the leap day were added the next day. Precipitation events on the 28th of February were moved to the previous day to avoid doubling of these events when re-adding a leap day in the final weather input data set.

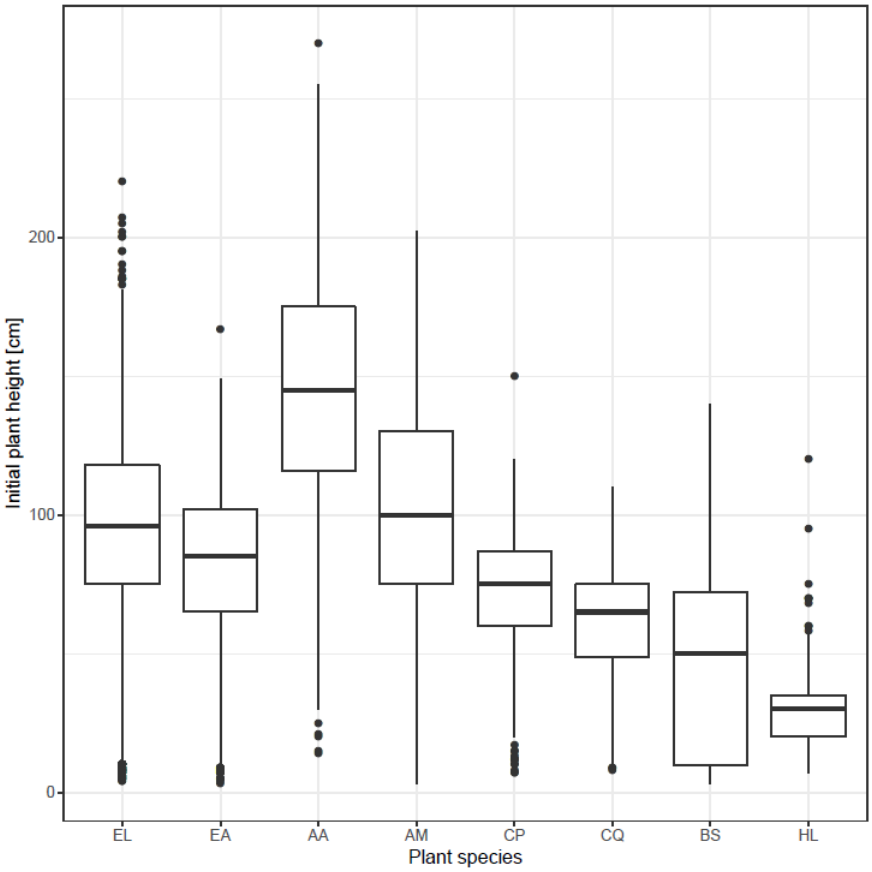


Figure A.2.3: Plant heights of the one-year old eight species in the Ridgefield experiment. Data derived from Perring et al. (2012). EL: *Eucalyptus loxophleba*, EA: *E. astringens*, AA: *Acacia acuminata*, AM: *A. microbotrya*, CP: *Callistemon phoeniceus*, CQ: *Calothamnus quadrifidus*, BS: *Banksia sessilis*, HL: *Hakea lissocarpha*.

Table A.2.3: Median annual and seasonal climate trends. Simulated data derived from Hope et al. (2015). Values provide the difference between 1995 (1986 – 2005) and 2090 (2080 – 2099) for SW Australia and RCP 8.5. Assumed atmospheric CO_2 of RCP 8.5 is derived from IPCC (2014).

	Annual	**Winter (Jun to Aug)**	**Spring (Sep to Nov)**	**Summer (Dec to Feb)**	**Autumn (Mar to May)**
Mean air temperature [°C]	+3.36	+3.02	+3.50	+3.54	+3.39
Minimum air temperature [°C]	+3.19	+2.72	+3.23	+3.50	+3.31
Maximum air temperature [°C]	+3.64	+3.46	+4.02	+3.63	+3.45
Precipitation [%]	-16.00	-25.82	-31.70	-4.22	-2.29
Solar radiation [%]	+1.90	+5.95	+2.17	-0.30	-0.22
Atmospheric CO_2 [ppm]	+450	-	-	-	-

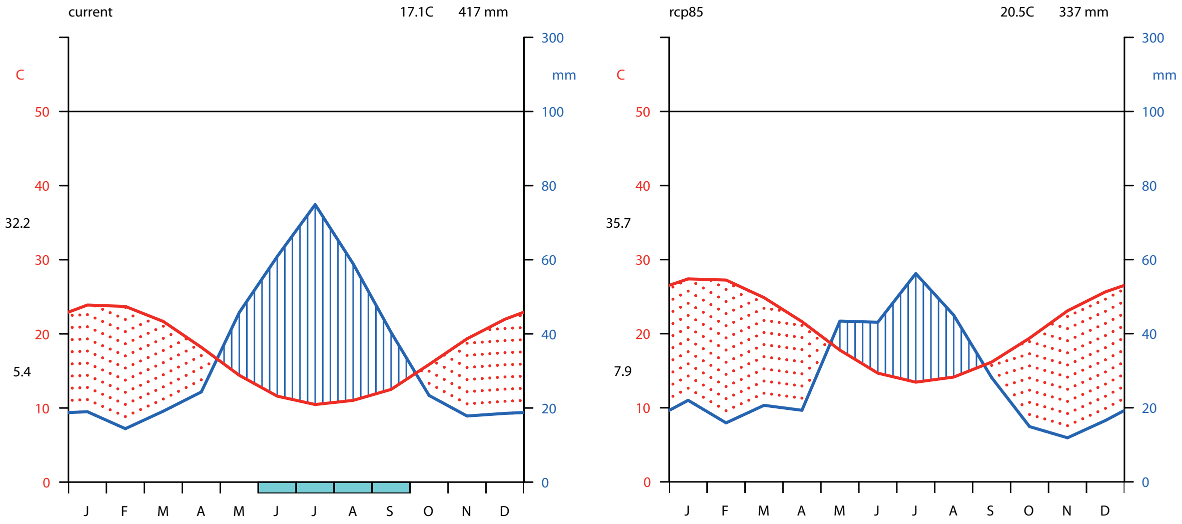


Figure A.2.4: Current (left) and future (right) climate diagrams for Pingelly. Climate diagrams following the standard by Walter and Lieth (1967) created with R package by Guijarro (2019). Current climate (left) refers to the period 1990 and 2018 with mean annual precipitation of 417 mm as well mean annual temperature of 17.1°C, future climate (right) refers to the same period but with projections of RCP 8.5 (see main text *Climate change scenarios*) with mean annual precipitation of 337 mm as well mean annual temperature of 20.5°C . In each diagram monthly rainfall (blue) and temperature (red) is shown.

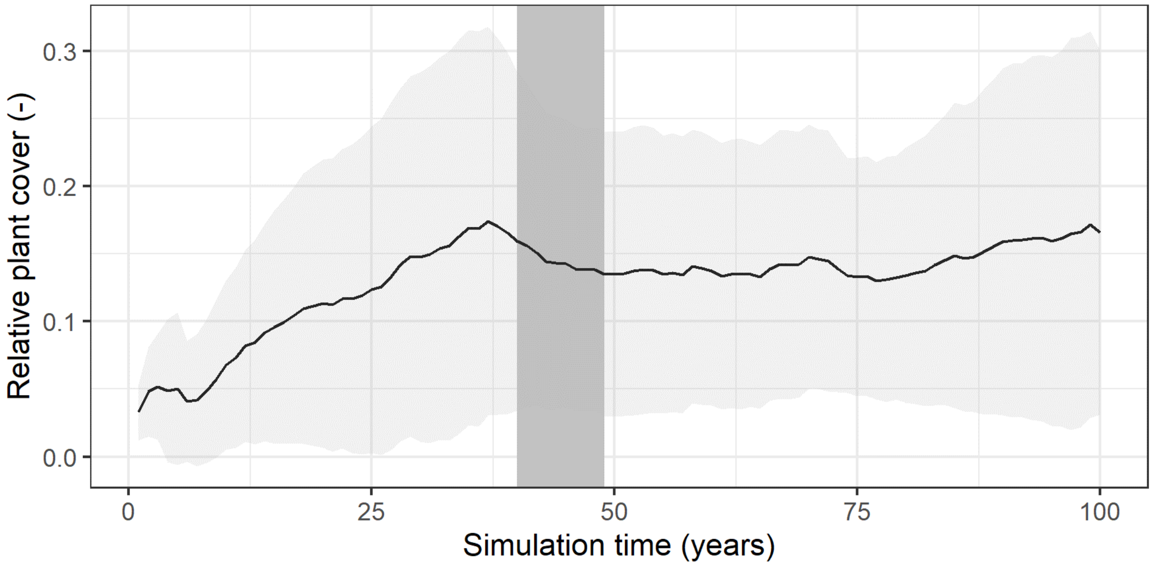


Figure A.2.5: Relative plant cover over time for the 8-species mixture under current climatic conditions. Shown is mean and standard deviation over 10 model repetition. Rectangle between 40 and 49 simulation years highlights the time period during which simulation outcomes in this study where evaluated.

A.2.4 Supporting results

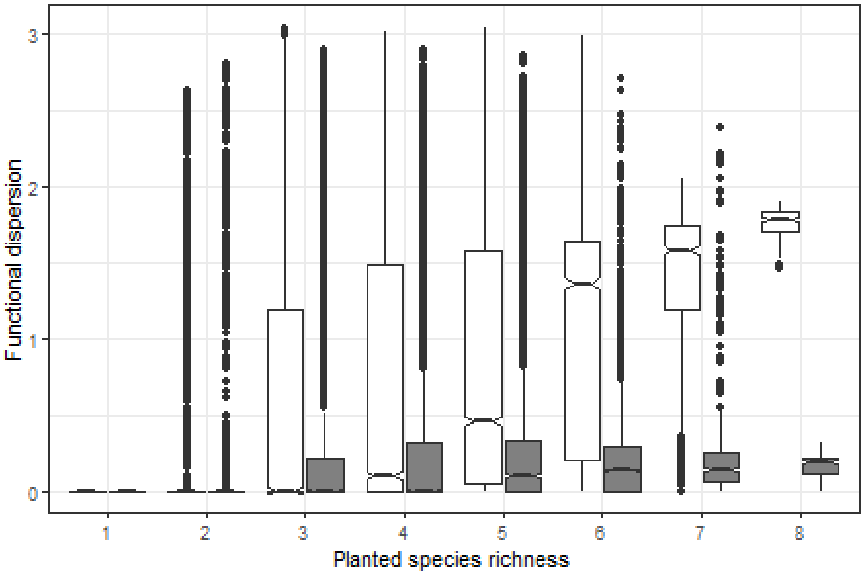


Figure A.2.6: Functional dispersion for each planted richness under current (white) and future conditions (grey). Shown is functional dispersion for the last 10 simulated years, 10 model repetitions, and 255 different plant communities. Functional dispersion, a measure for functional diversity, was calculated based on the focal plant traits of this study (see Table 3.2 or highlighted traits in Table A.2.2) after Laliberte and Legendre (2010) using the R package FD by Laliberté et al. (2014).

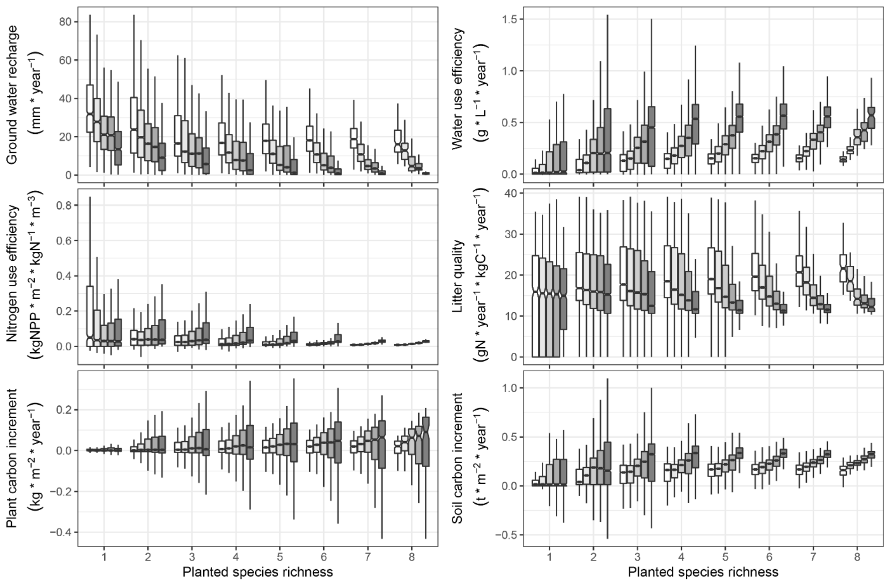


Figure A.2.7: Ecosystem functioning for each planted species richness under current (white boxplots) and different future climatic conditions (boxplots in different shades of grey in the order: RCP 26, 45, 60, and 85). Shown is functioning for the last 10 simulated years and for 10 model repetitions as well as for 255 different plant communities which are unevenly distributed across the different planted species richness scenarios according to maximal possible combinations out of the pool of eight focal plant species. For better comparability among boxplots, single outliers are not shown.

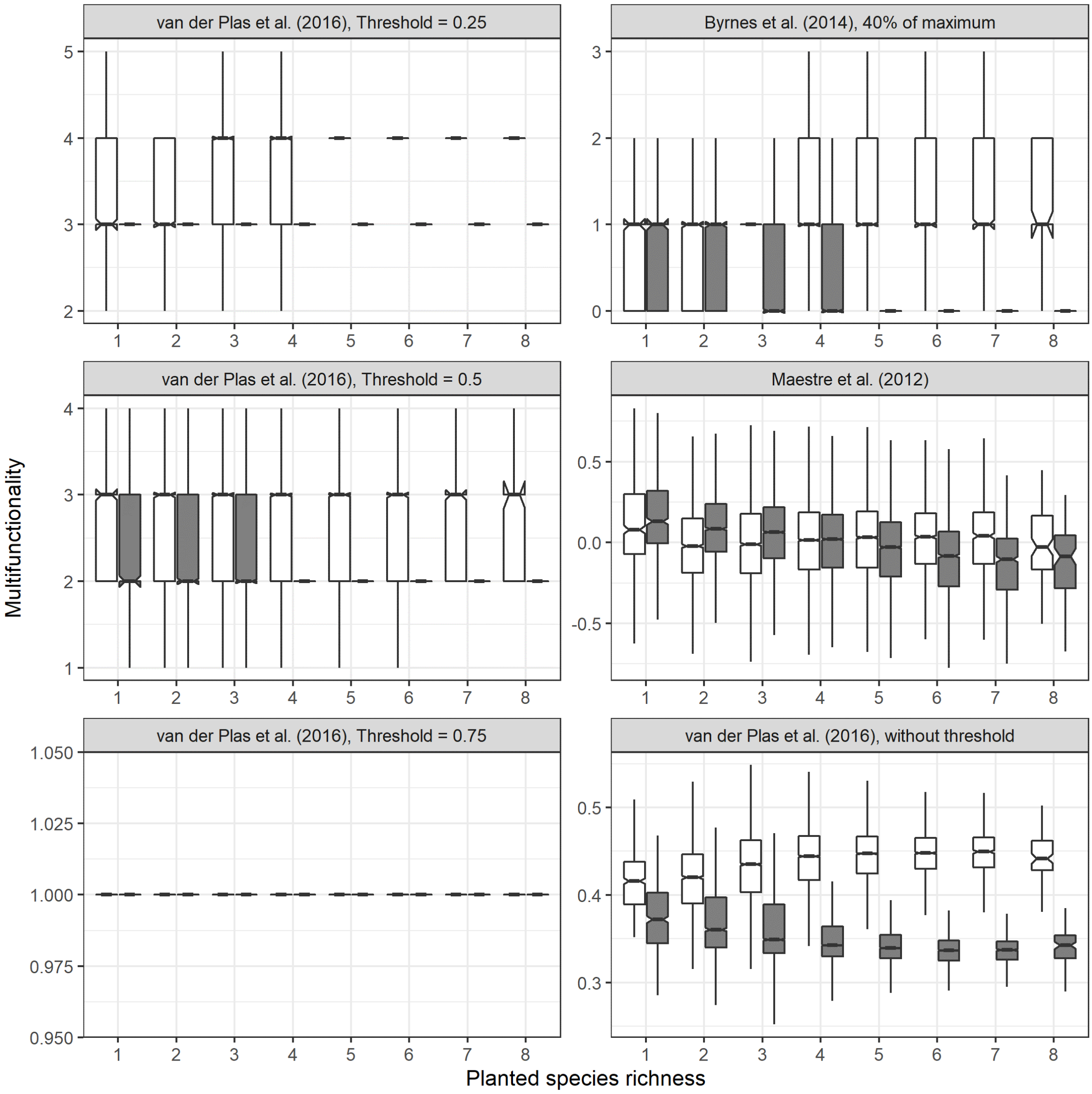


Figure A.2.8: Comparison of different multifunctionality indices across the different species richness and climate change scenarios (white: current, grey: future). Left: Number of previously standardised functions between 0 and 1 based on the minimum and maximum value as suggested by van der Plas et al. (2016) above three potentially desired thresholds: i.e. individual functions were only counted if they provided more than 0.25 (top), 0.5 (centre), or 0.75 (bottom) of its standardized value in a given climate scenario. Comparison shows that the choice of the threshold strongly affects the outcome. Top right: Threshold approach by Byrnes et al. (2014) counting functions with at least 40% of its maximum functioning. Centre right: Average over Z scores of the functions in a given climate scenario as suggested by Maestre et al. (2012a), which accounts for the distance of each functioning to the mean of the same function. Bottom right (used in this study): Mean over previously standardised functions between 0 and 1 based on the minimum and maximum value in a given climate scenario changed after van der Plas et al. (2016). Comparison shows the approach by Byrnes et al. (2014) showed quantitatively similar trends as shown for van der van der Plas et al. (2016) without a threshold or a 0.25- or 0.5-threshold. In contrast, multifunctionality calculated after Maestre et al. (2012a) decreased with greater planted richness under current conditions.

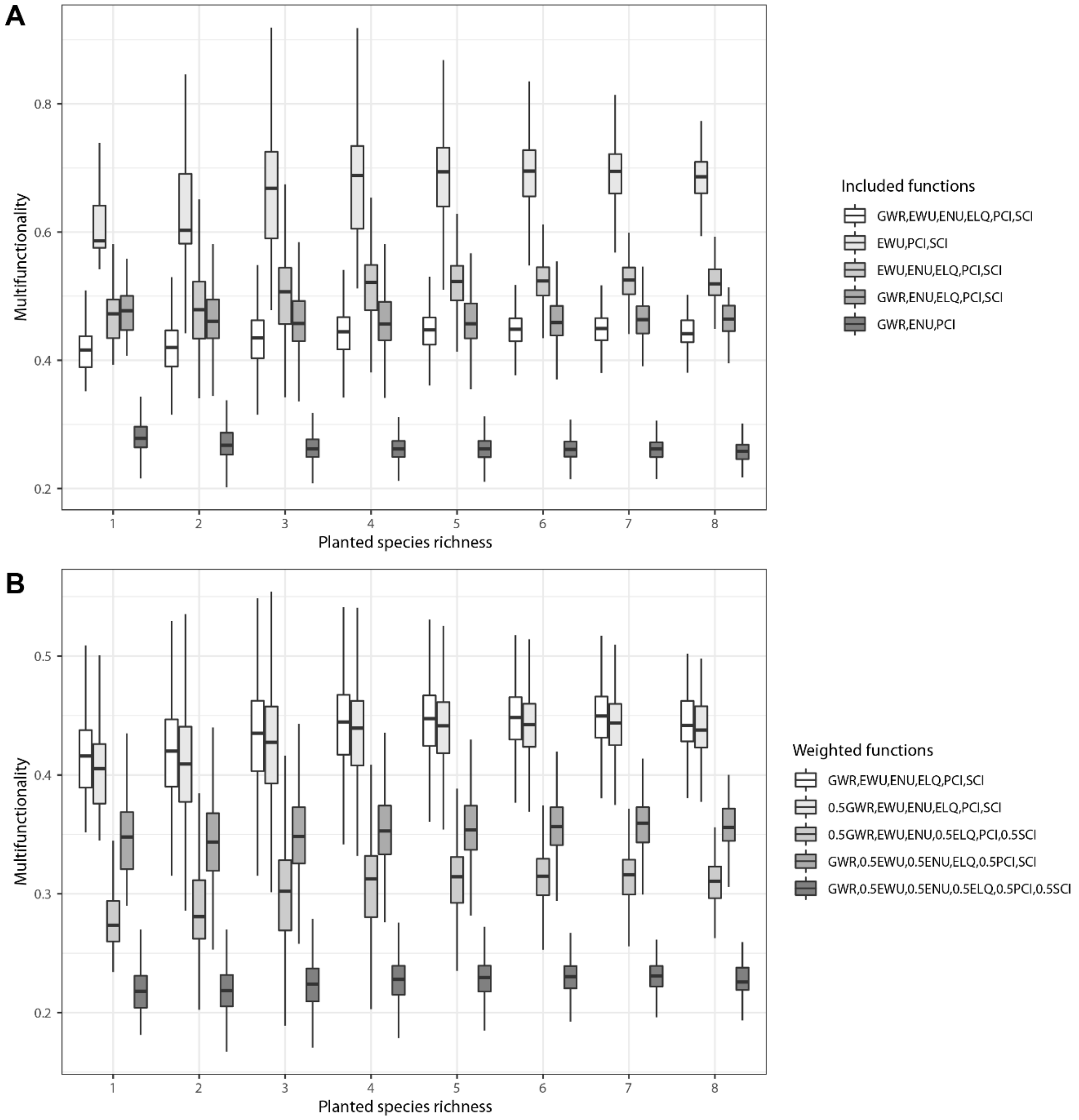


Figure A.2.9: Multifunctionality for each planted species richness under current climatic conditions with different functions included (A) and differently weighted (B) compared to all included and equally weighted functions as presented in the main text (white boxplots). We calculated all possible combinations of inclusions (A) as well as weightings by 0.5 (B) and only show the combinations that resulted to most extreme changes in multifunctionality with increased richness compared to what we found when we included all six function equally weighted (white boxplot, as also shown in Fig. 3.2A, left). B: Some ecosystem functions were considered only half as important as others and therefore multiplied by 0.5 as indicated in the legend. Shown is functioning for the last 10 simulated years and for 10 model repetitions as well as for 255 different plant communities which are unevenly distributed across the different planted species richness scenarios according to maximal possible combinations out of the pool of eight focal plant species. For better comparability among boxplots, single outliers are not shown.

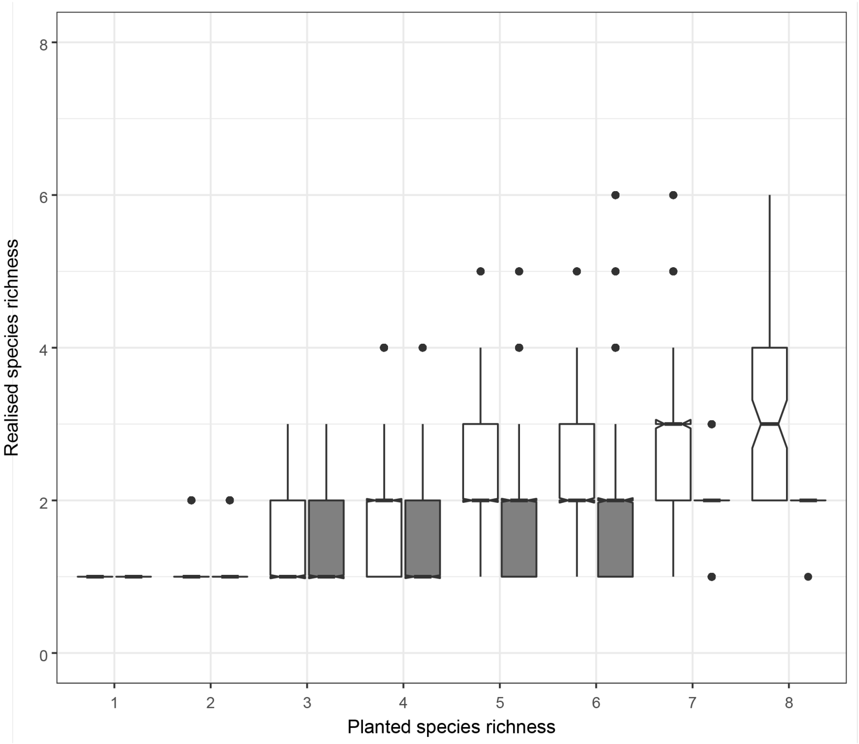


Figure A.2.10: Realised richness for each planted richness for current (white) and future conditions (grey). Shown is realised richness over the last 10 simulated years and over 10 model repetitions.

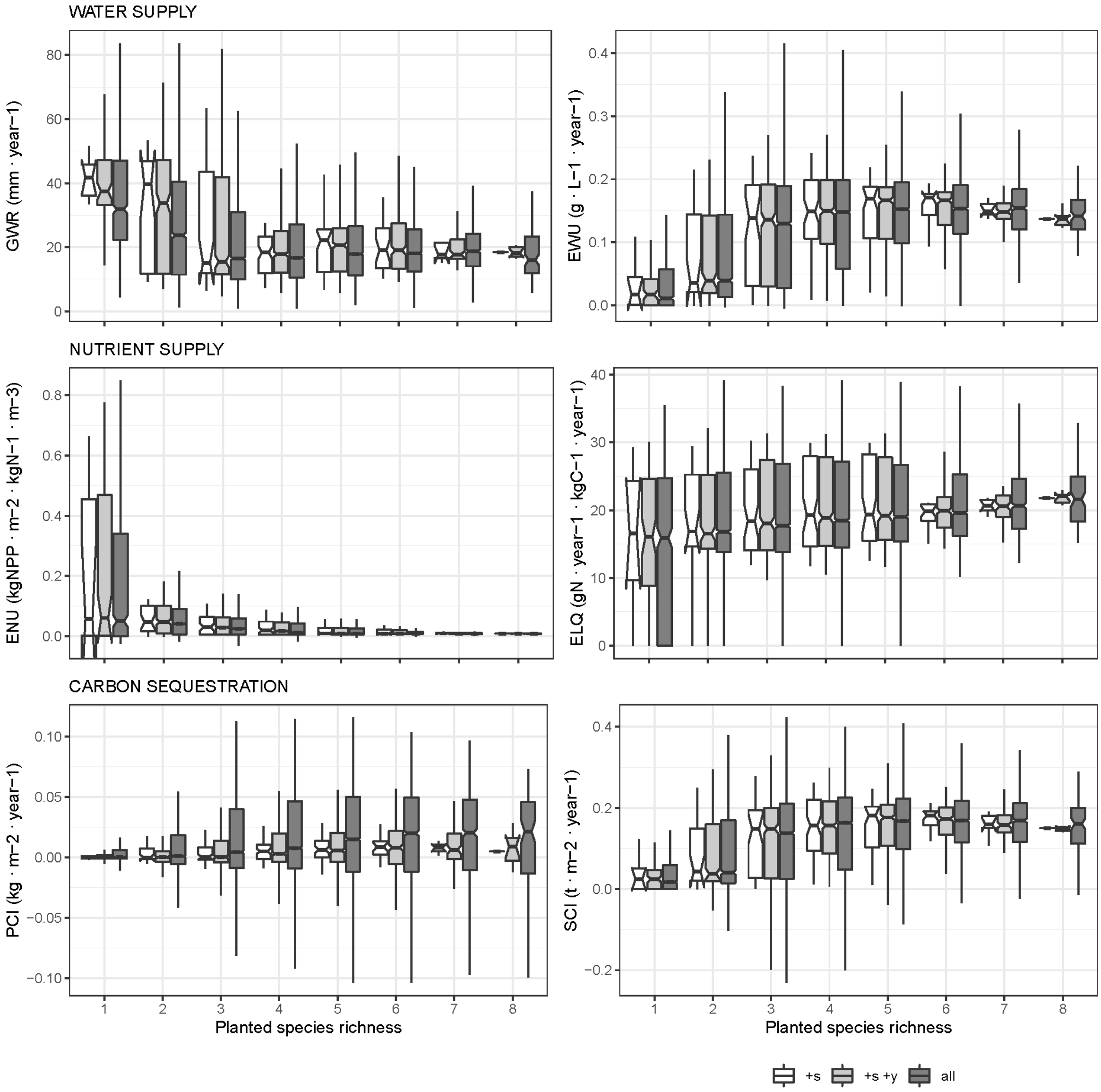


Figure A.2.11: Variability of ecosystem functioning under current conditions. +s: mean functioning across years and model repetitions and thus represent variability of species compositions, +s +y: mean functioning over model repetitions and thus represent variability of species compositions across simulated years, all: functioning across species compositions, years and model repetitions (as shown in Fig. 3.2B in main text).

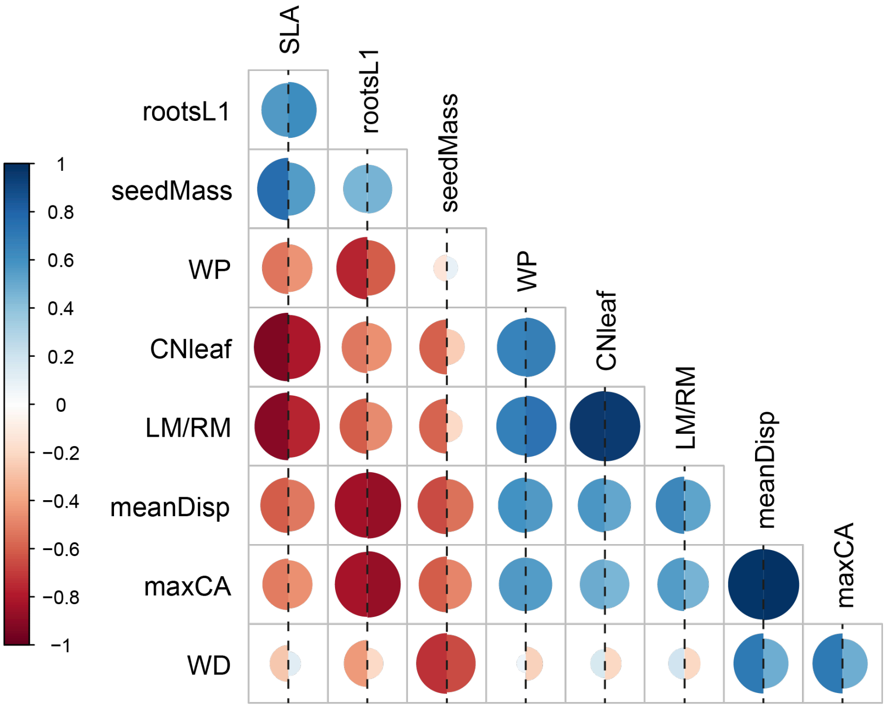


Figure A.2.12: Intrinsic community trait correlations under current (left half circle) and future climatic conditions (right half circle). Shown are significant ($\alpha = 0.05$) Spearman's rank correlation among CWM plant traits based on the last 10 simulated years and for 10 model repetitions across all 255 simulated plant communities. Meaning of abbreviations can be found in Table 3.2.

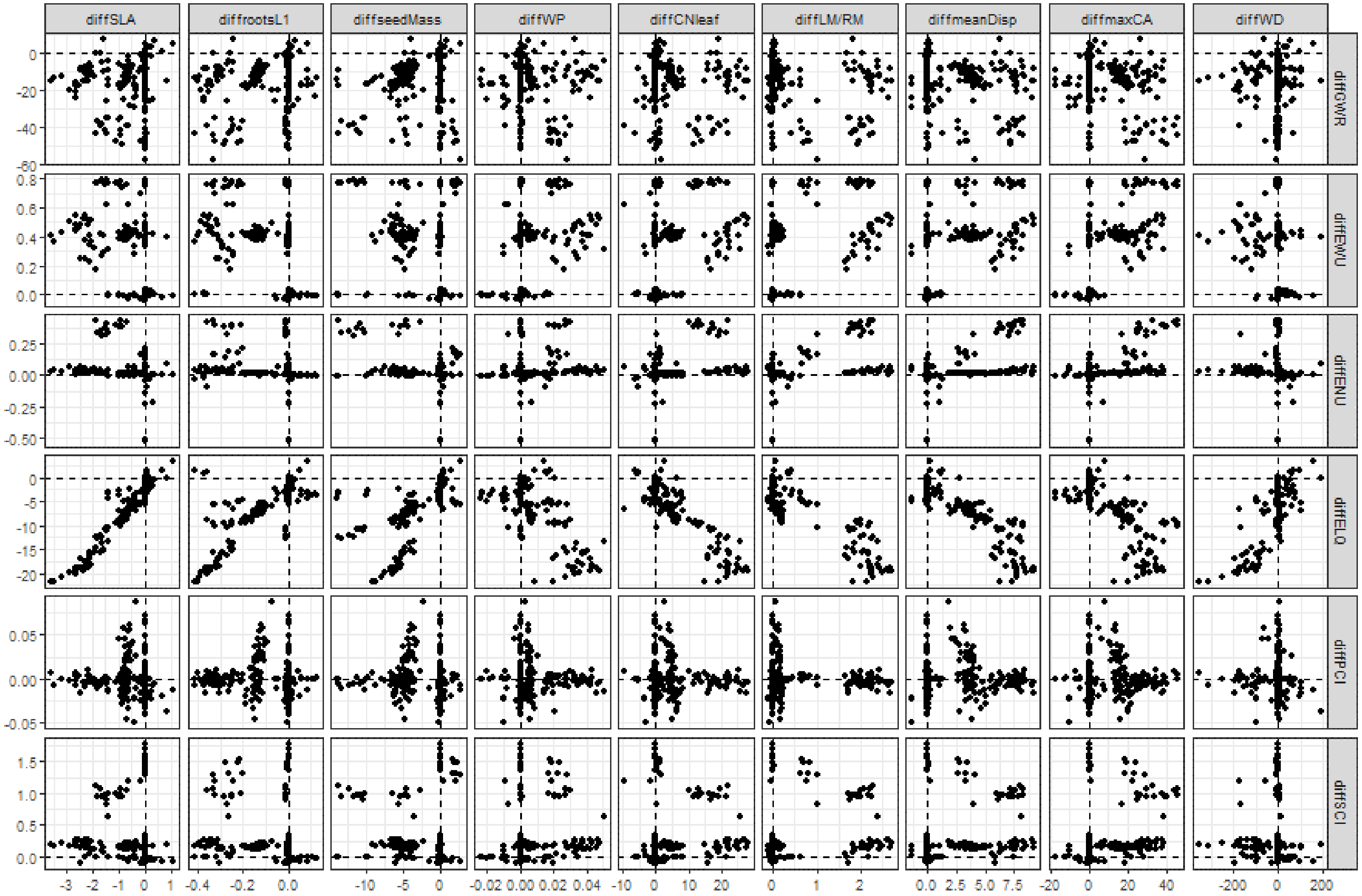


Figure A.2.13: Disentangling direct and indirect effects of climate on ecosystem functioning by correlating climate change affected changes in our nine focal CWM plant traits (columns) against changes in the six ecosystem functions (rows). Shown are mean changes between current and future climatic conditions across the last 10 simulated years and 10 model repetitions per simulated plant community (black dots). Dashed lines separate plots into four quadrants with positive (top right) and negative (bottom left) changes in both trait and function; or trait and function differently affected (top left and bottom right). Values on dashed lines show no changes with climate change in functioning and/or trait. As we have strong trait-trait correlations that mostly remained the same under climate change (Fig. A.2.12), we only show the results for changes in SLA in the main text (see Fig. 3.4). Meaning of abbreviations and units can be found in Tables 3.1 and 3.2.

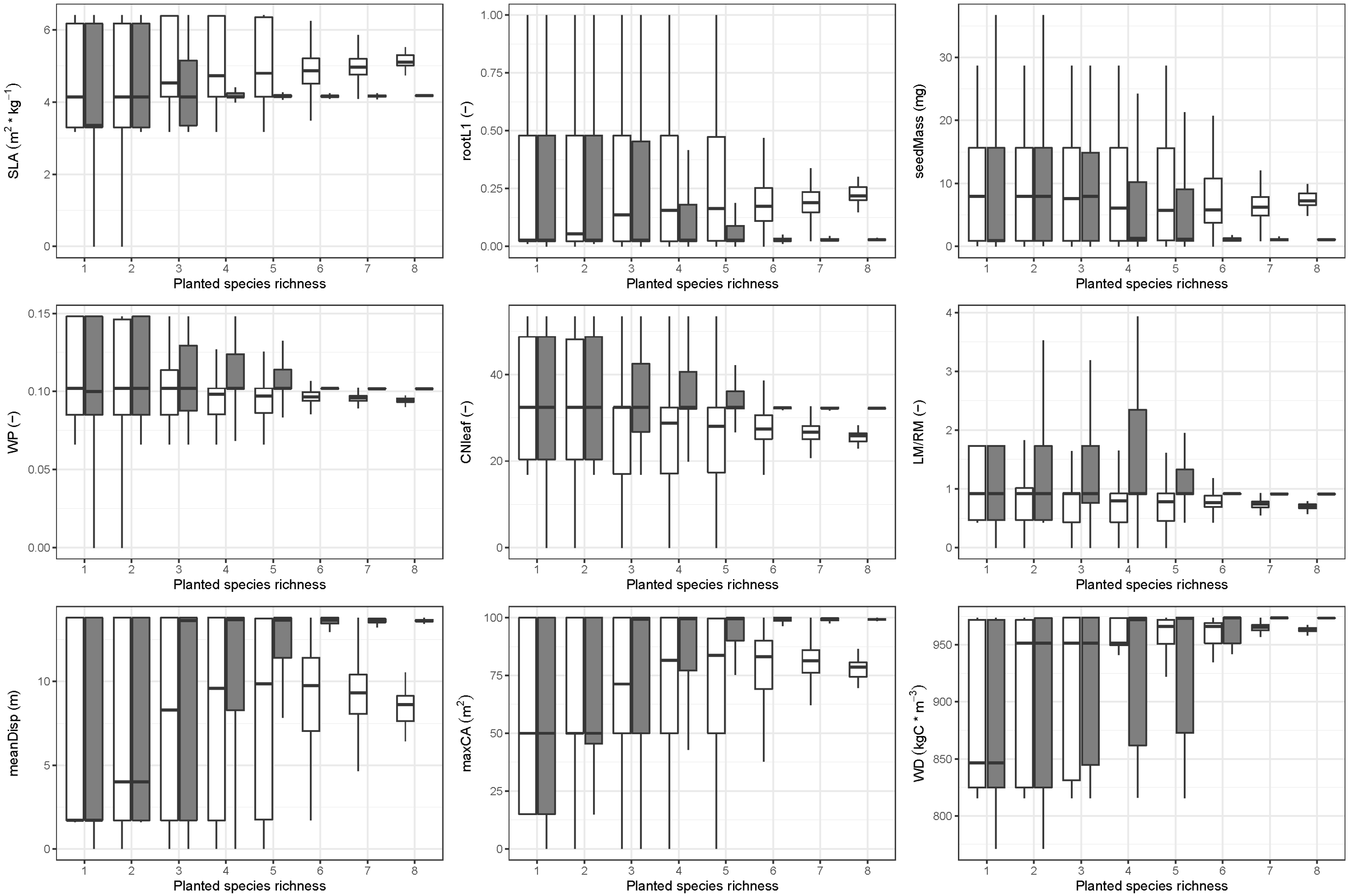


Figure A.2.14: CWM trait values for each planted richness for current (white) and future conditions (grey). Shown is CWM over the last 10 simulated years and over 10 model repetitions. Meaning of abbreviations can be found in Table 3.2 in the main text.

A.3 Appendix to "Context-dependency of restoration"

A.3.1 PFT construction

Table A.3.1: Focal traits for PFT classification, their abbreviations, units, sources, and data coverage per trait for all selected 515 plant species.

Plant trait	**Abbr.**	**Unit/Level**	**Data Source**	**Data coverage (%)**
Leaf dry mass	Ldm	mg	Kattge et al. (2020)	36.9
Leaf nitrogen	LNdm	mg g^{-1}	Kattge et al. (2020)	67.6
Leaf area	La	mm^2	Kattge et al. (2020)	62.3
Photosynthesis	Photo	$\mu mol*m^{-2}*s^{-1}$	Kattge et al. (2020)	32.0
Plant height	Ph	m	Kattge et al. (2020), SA National Biodiversity Institute (http://pza.sanbi.org), Melanie Kölbel (unpublished data)	40.2
Stomatal conductance	Stom	$mmol*m^{-2}*s^{-1}$	Kattge et al. (2020)	29.5
Specific leaf area	SLA	mm^2*mg^{-1}	Kattge et al. (2020)	71.5
Wood density	Wd	$mg*mm^{-3}$	Kattge et al. (2020)	24.7
Leaf phenology	LPhen	Evergreen vs Deciduous	Kattge et al. (2020),Expert knowledge, California Native Plant Society (https://calscape.org/)	88.7
N fixation	Nfix	Yes vs No	Kattge et al. (2020), Expert knowledge, California Native Plant Society (https://calscape.org/)	49.5

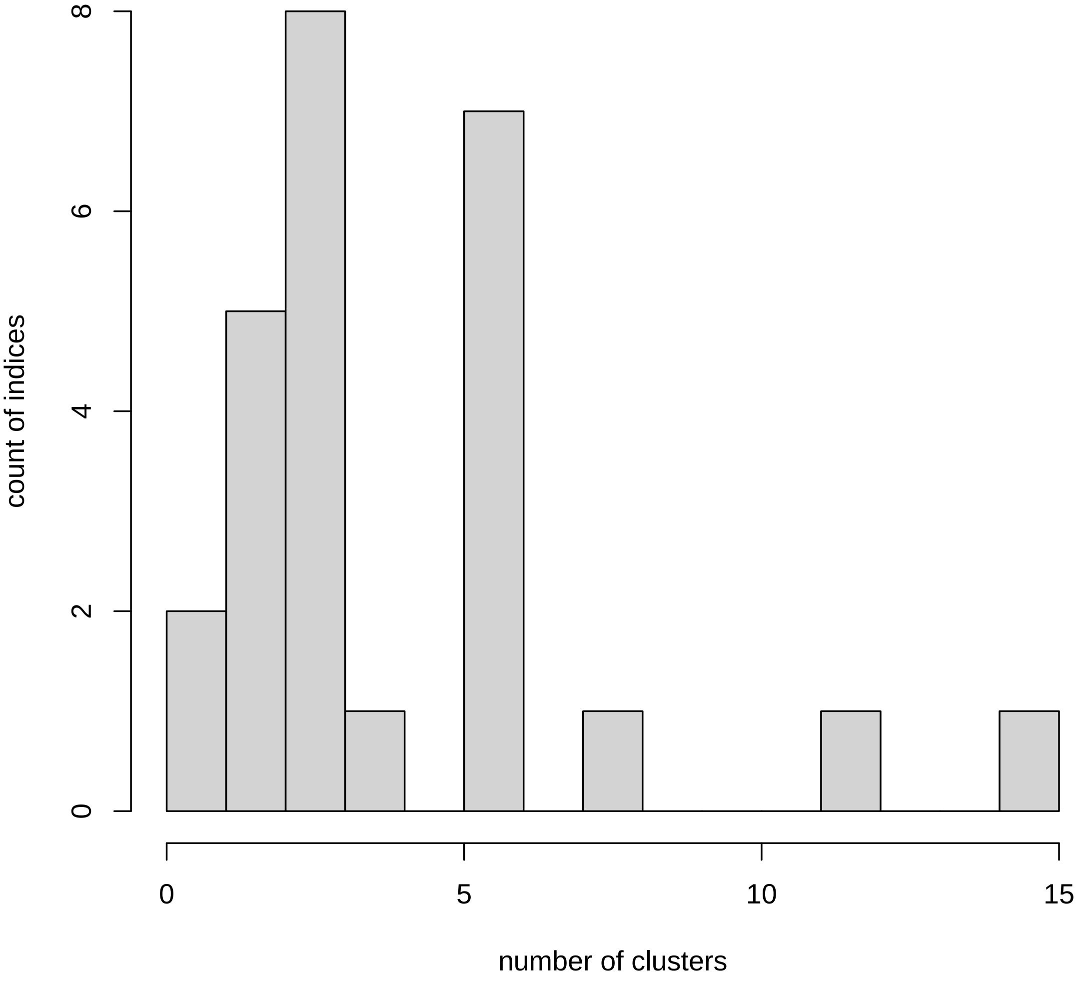


Figure A.3.1: Number of indices per cluster analysis that decided for this particular number of clusters.

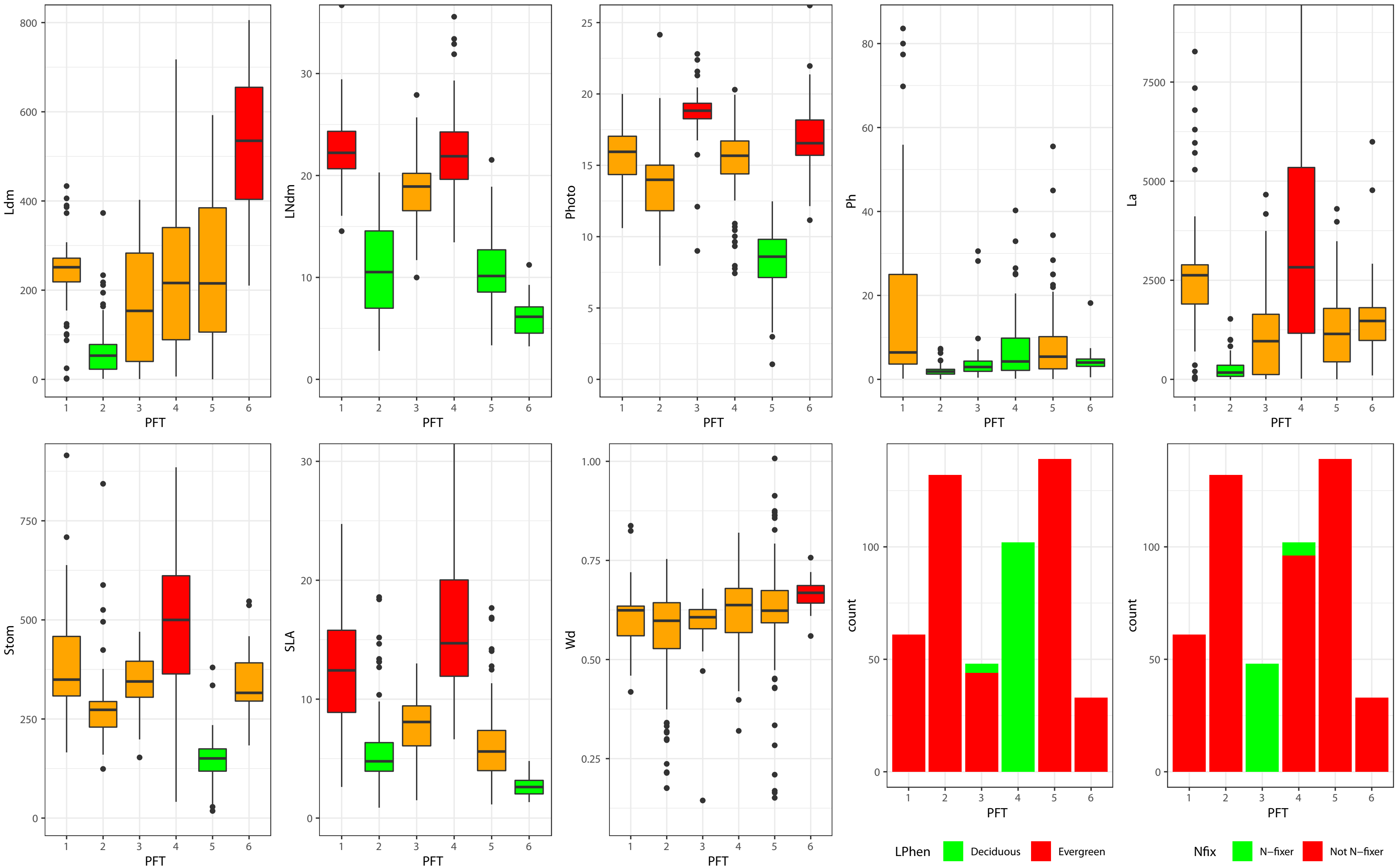


Figure A.3.2: Distributions for each trait (for abbreviations and units see Table A.3.1) and for each of the six PFTs and for the three levels per trait (derived from another cluster analysis per trait to separate each trait into reasonable levels (green: low, orange: medium, red: high).

A.3.2 Model parameterisation

Table A.3.2: Soil parameters.

Parameter	**Unit**	**Description**	**Clay loam**	**Loam**	**Sandy clay loam**	**Sandy loam**	**Source**
Sf	mm	Effective suction	208.8	88.9	218.5	110.1	Rawls et al. (1992)
K_s	mm h^{-1}	Saturated hydraulic conductivity	4.2	3.9	2.8	55.8	Rawls et al. (1998)
fc	m^3 m^{-3}	Field capacity	0.371	0.303	0.305	0.27	Rawls et al. (1992)
r_w	m^3 m^{-3}	Residual Water Content	0.075	0.027	0.068	0.041	Rawls et al. (1992)
$F_{L2,frac}$	-	Infiltration rate into layer 2	0.1	0.1	0.1	0.1	Tietjen et al. (2009b)
$F_{L2,max}$	mm h^{-1}	Maximum total infiltration into layer 2	1.5	1.5	1.5	1.5	Rawls et al. (1992)
d	-	Constant for diffusion coefficient	0.01	0.01	0.01	0.01	Tietjen et al. (2009b)
BD	g cm^{-3}	Bulk density	1.425	1.425	1.625	1.45	Rawls et al. (1992)
c_{clay}	m^3 m^{-3}	Clay content	0.35	0.2	0.3	0.1	USDA (2020)
n_{dep}	g ha^{-1} $year^{-1}$	Daily nitrogen deposition	4.93	4.93	4.93	4.93	Dentener et al. (2006)

Table A.3.3: Plant parameters

Parameter	**Unit**	**Description**	**PFT 1**	**PFT 2**	**PFT 3**	**PFT 4**	**PFT 5**	**PFT 6**	**Source**
Phenology	-	Evergreen (E) or raingreen (R) phenology	E	E	E	R	E	E	Kattge et al. (2020)
T_1	°C	Lowest temperature limit for photosynthesis	-4	-4	-4	-4	-4	-4	Sitch et al. (2000), temperate needle/broad-leaved evergreen species
T_2	°C	Lower temperature limit for optimal photosynthesis	20	20	20	20	20	20	Sitch et al. (2000), temperate needle/broad-leaved evergreen species
T_3	°C	Higher temperature limit for optimal photosynthesis	30	30	30	30	30	30	Sitch et al. (2000), temperate needle/broad-leaved evergreen species
T_4	°C	Highest temperature limit for photosynthesis	42	42	42	42	42	42	Sitch et al. (2000), temperate needle/broad-leaved evergreen species
SLA	$m^2\ kg^{-1}$	Specific leaf area	12.421	4.7766	8.082	14.704	5.6	2.612	Kattge et al. (2020)
g_{min}	$mm\ s^{-1}$	Minimum canopy conductance that occurs due to processes other than photosynthesis	0.5	0.3	0.3	0.5	0.3	0.3	Kattge et al. (2020) for leaf area clustered into two groups (needle versus broad leaved) and parameter value from Sitch et al. (2000) for broad-leaved (0.5) and needle-leaved (0.3) plants
CN_{leaf}	-	Carbon to nitrogen ratio of the leaves	44.0	94.01	51.87	44.68	97.62	161.87	Kattge et al. (2020)
CN_{sap}	-	Carbon to nitrogen ratio of the sapwood	100.76	142.43	109.79	101.6	144.49	172.25	Correlation with C:N in leaves from Kattge et al. (2020) and equations from measured data in Perring et al. (2012) and Fiedler et al., (unpublished)

Table A.3.3 continued from previous page

CN_{root}	-	Carbon to nitrogen ratio of the roots	75.94	101.61	81.5	76.46	102.88	119.98	Correlation with C:N in leaves from Kattge et al. (2020) and equations from measured data in Perring et al. (2012) and Fiedler et al., (unpublished)
k_{store}	-	Constant for maximum N storage	0.05	0.05	0.05	0.15	0.05	0.05	Kattge et al. (2020) for phenology and parameter values from Smith et al. (2014) for evergreen (0.05) and deciduous plants (0.15)
$root_{L1}$	-	Fraction of roots between 0-50 cm of the soil horizon	0.69	0.87	0.65	0.77	0.64	0.45	Kattge et al. (2020)
$root_{L2}$	-	Fraction of roots between 50-150 cm of the soil horizon	0.31	0.13	0.35	0.23	0.36	0.55	Kattge et al. (2020)
$CN_{leaf,min}$	-	Minimum bound of C:N ratio in the leaves	29.1	46.8	13.9	19.8	40.5	34.5	Kattge et al. (2020)
$CN_{leaf,max}$	-	Maximum bound of C:N ratio in the leaves	34.7	58.6	20.9	21	61.4	38.9	Kattge et al. (2020)
e_{max}	mm day^{-1}	Maximum water transport capacity for transpiration	5.0	5.0	5.0	5.0	5.0	5.0	Sitch et al. (2003)
LM/RM	-	Allometric constant to transfer from leaf mass to root mass	1.0	1.0	1.0	1.0	1.0	1.0	Sitch et al. (2003)
WP	cm	Plant water potential at wilting point	23460	23460	23460	23460	23460	23460	Bartlett et al. (2012)

Table A.3.3 continued from previous page

r_{coef}	kgC kgN^{-1} day^{-1}	Respiration coefficient that accounts for the acclimation of plant respiration rates at average ambient temperatures (10°C)	0.066	0.066	0.066	0.066	0.066	0.066	Sitch et al. (2003)
LtS	-	Allometric constant to transfer from sapwood area to leaf area	8000	8000	8000	8000	8000	8000	Sitch et al. (2003)
WD	kgC m^{-3}	Wood density	624.2	597.8	606.7	637.4	623.3	668.3	Kattge et al. (2020)
a_2	-	Parameter in allometric equation that transfers stem diameter to plant height	28.36	2.29	6.7	11.26	8.68	3.59	Kattge et al. (2020)
a_3	-	Parameter in allometric equation that transfers stem diameter to plant height	0.67	0.67	0.67	0.67	0.67	0.67	Schaphoff et al. (2018)
a_1	-	Parameter in allometric equation that transfers stem diameter to crown area	22.65	29.16	21.05	21.21	32.15	30.16	Kattge et al. (2020)
r_{rp}	-	Parameter in allometric equation that transfers stem diameter to crown area	0.51	0.72	0.53	0.46	0.46	0.5	Kattge et al. (2020)
maxCA	m^2	Maximum possible crown area	36	39	29	30	82	40	Kattge et al. (2020)
seedMass	mg	Seed mass	34.35	20.11	13.42	37.77	25.24	40.6	Kattge et al. (2020)

Table A.3.3 continued from previous page

mean_{Disp}	m	Mean dispersal distance	48.01	2.76	9.25	17.18	31.26	4.83	Relationship between median plant height (Kattge et al., 2020) and dispersal distance (Thomson et al., 2011)
sd_{Disp}	m	Standard deviation of dispersal distance	2	2	2	2	2	2	assumed
p_{germ}	-	Germination probability	0.84	0.89	0.88	0.81	0.82	0.86	Kattge et al. (2020)
LAI_{ini}	-	Leaf area index of the sapling	1.5	1.5	1.5	1.5	1.5	1.5	Sitch et al. (2000)
t_{mort}	-	Yearly relative growth above which plant dies	0.98	0.98	0.98	0.98	0.98	0.98	assumed

A.3.3 Simulation experiments

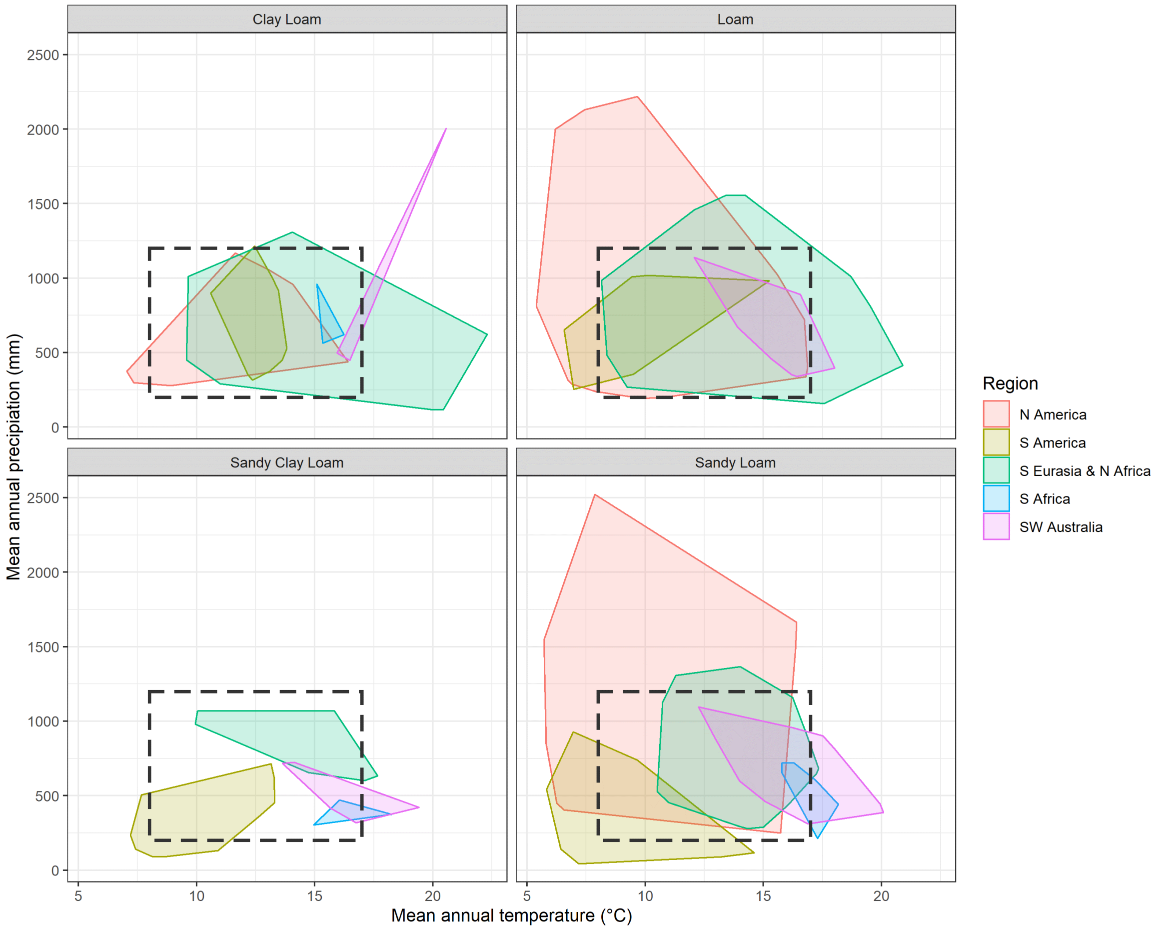


Figure A.3.3: Overview of the abiotic conditions found across Mediterranean-type ecosystems. Shown are ranges of mean annual precipitation and temperature (1901 – 2019, Harris et al., 2020) for the four most common soil textures (Koirala, 2012) and the five Mediterranean climatic regions (Csa and Csb, Kottek et al., 2006). Dashed rectangles depict the climatic ranges used for the simulation experiments.

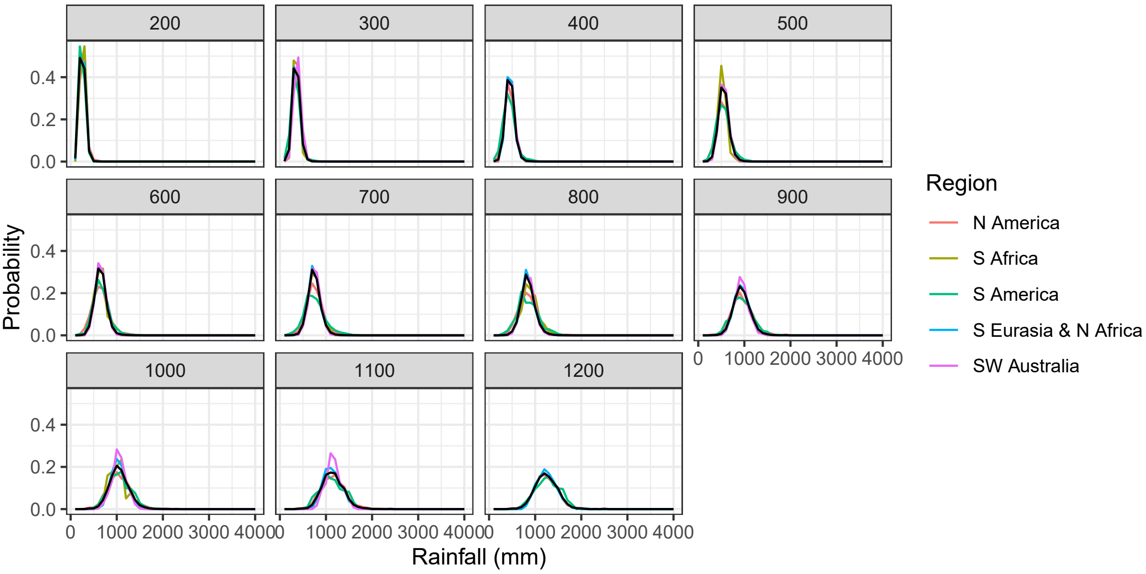


Figure A.3.4: Probability curves for each mean annual precipitation (panels) and each Mediterranean region (colors) derived from NOAA (2020b). Black line is probability curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

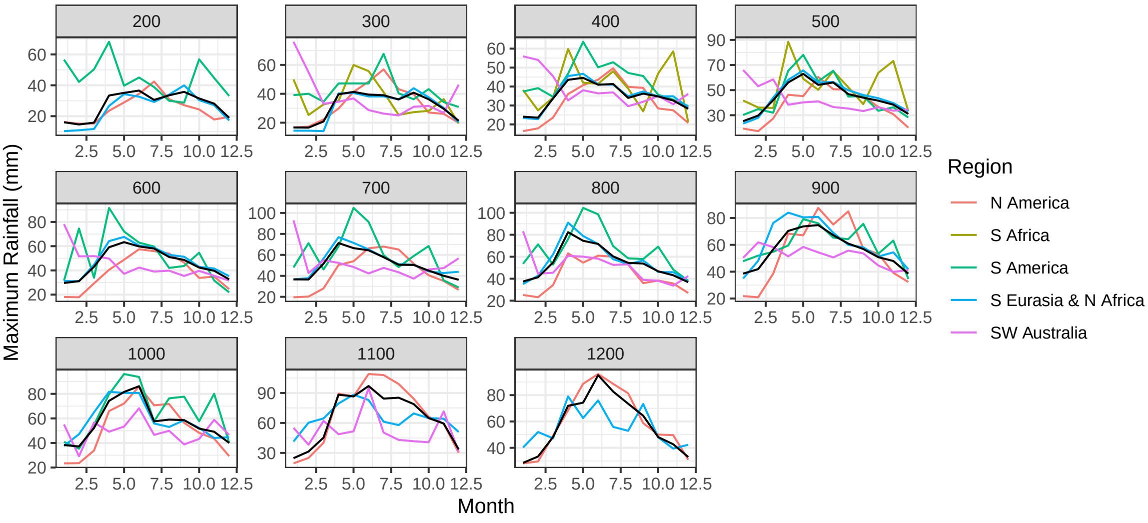


Figure A.3.5: Maximum rainfall per month for each mean annual precipitation (panels) and each Mediterranean region (colors) derived from NOAA (2020b). Black line is curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

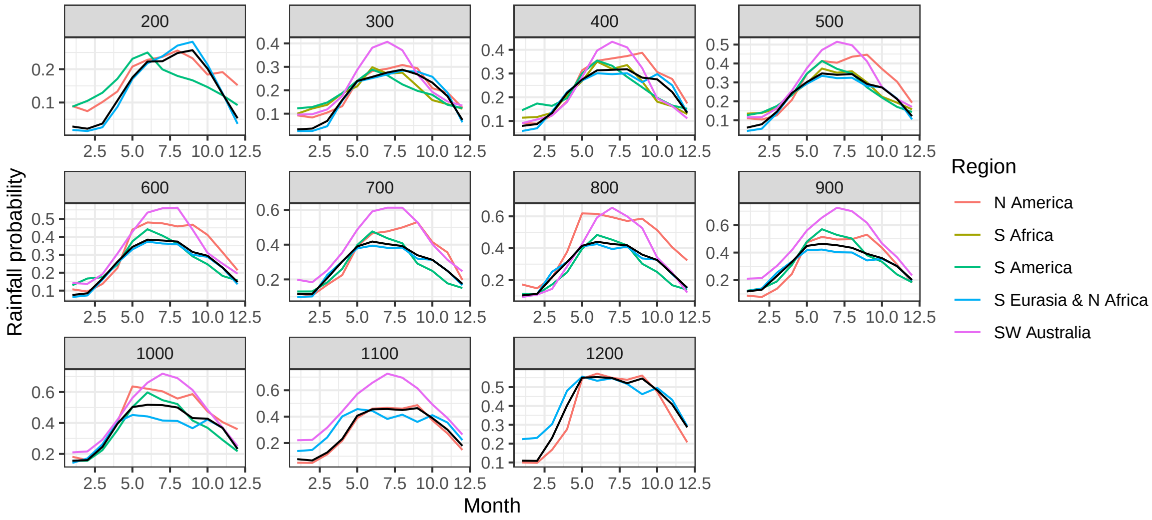


Figure A.3.6: Monthly rainfall probability for each mean annual precipitation (panels) and each Mediterranean region (colors) derived from NOAA (2020b). Black line is curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

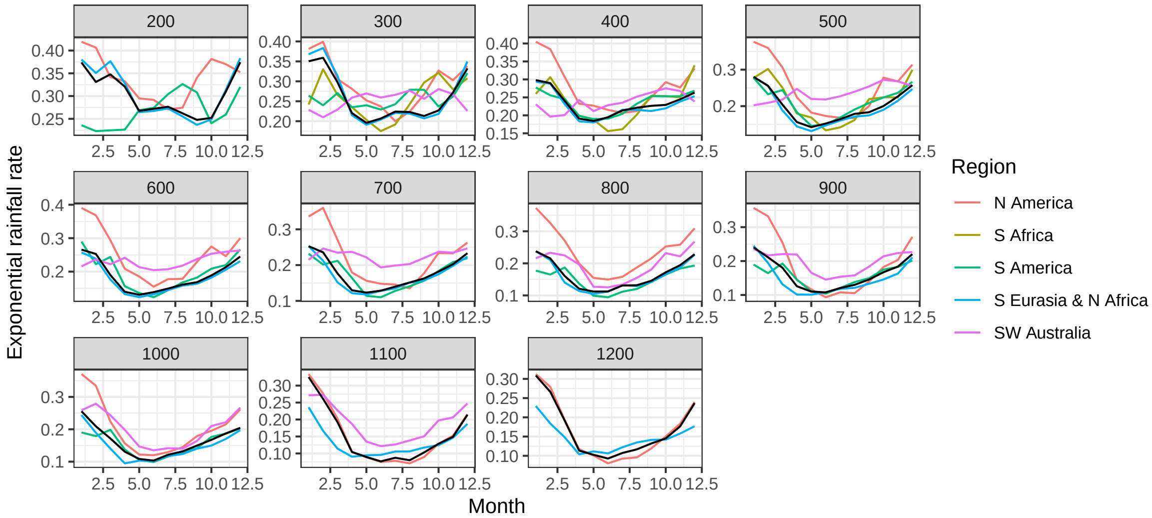


Figure A.3.7: Exponential rainfall rate per month for each mean annual precipitation (panels) and each Mediterranean region (colors) derived from NOAA (2020b). Black line is curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

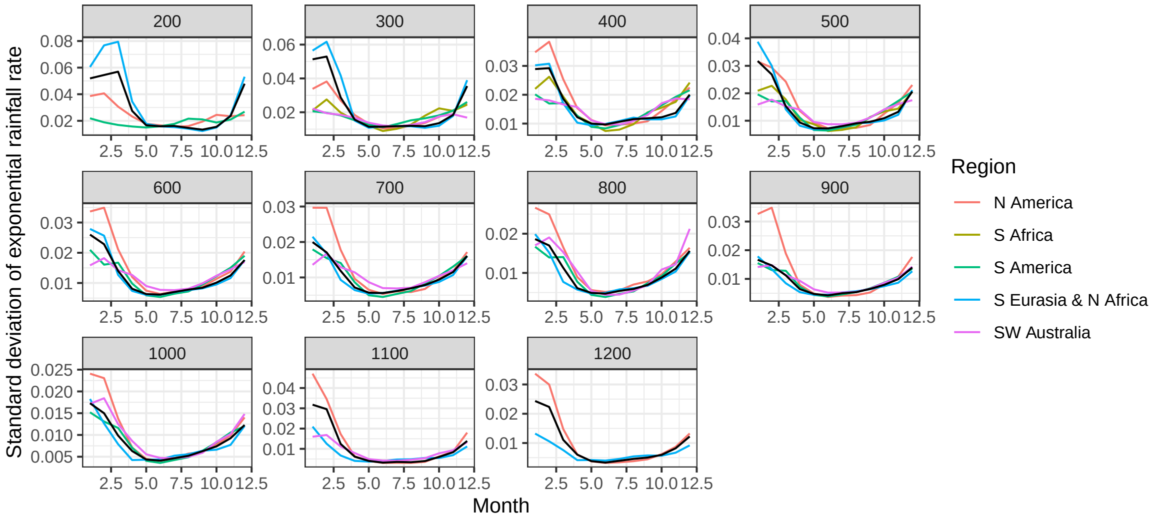


Figure A.3.8: Standard deviation of exponential rainfall rate per month for each mean annual precipitation (panels) and each Mediterranean region (colors) derived from NOAA (2020b). Black line is curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

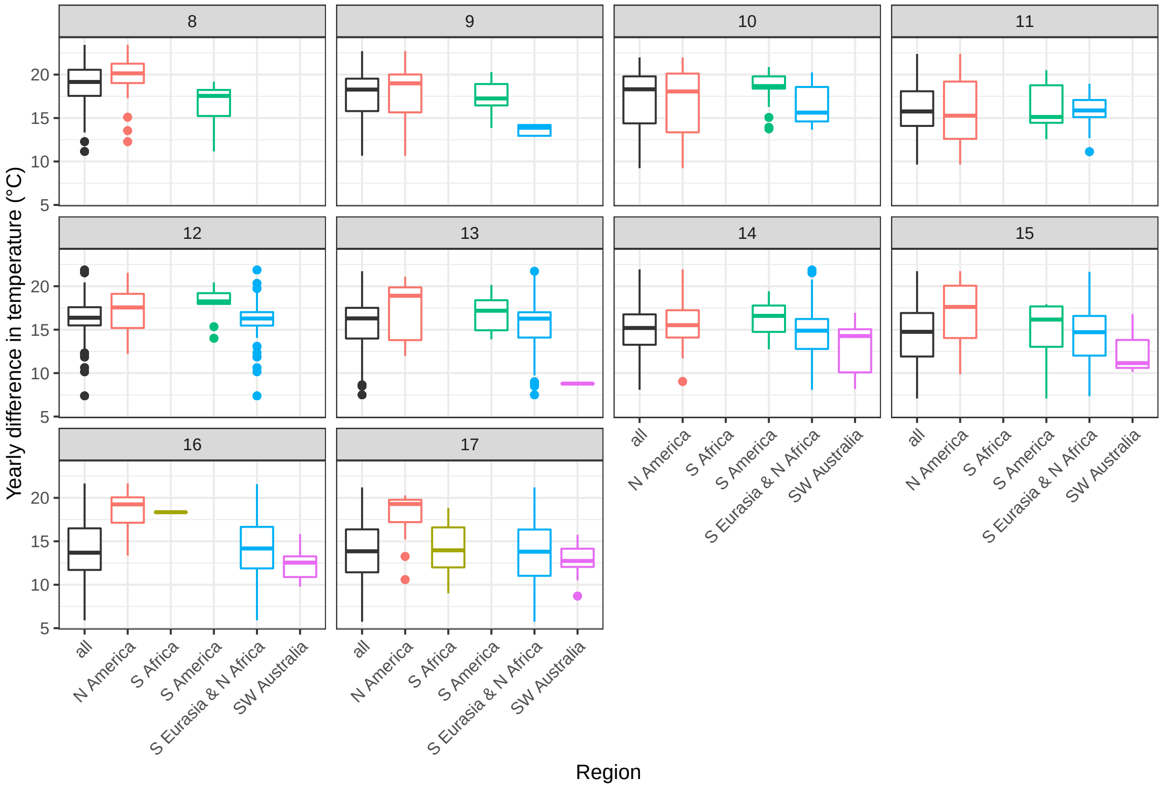


Figure A.3.9: Yearly difference in temperature for each mean annual temperature (panels) and each Mediterranean region (colors) derived from NOAA (2020a). Black line is curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

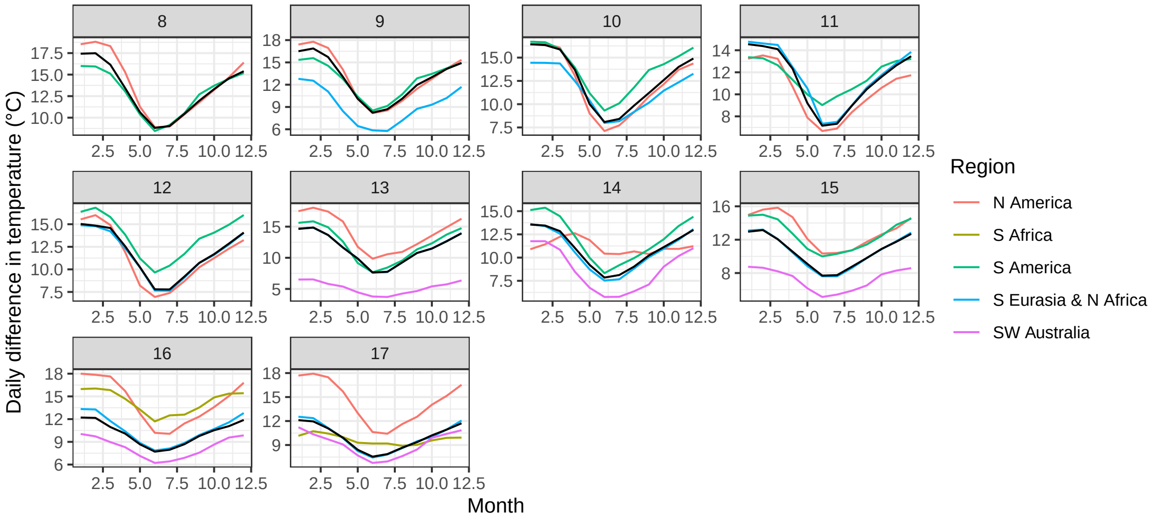


Figure A.3.10: Daily difference in temperature per month for each mean annual temperature (panels) and each Mediterranean region (colors) derived from NOAA (2020a). Black line is curve over all Mediterranean regions and serves as input for weather generation (see *Climate Scenarios* in main text).

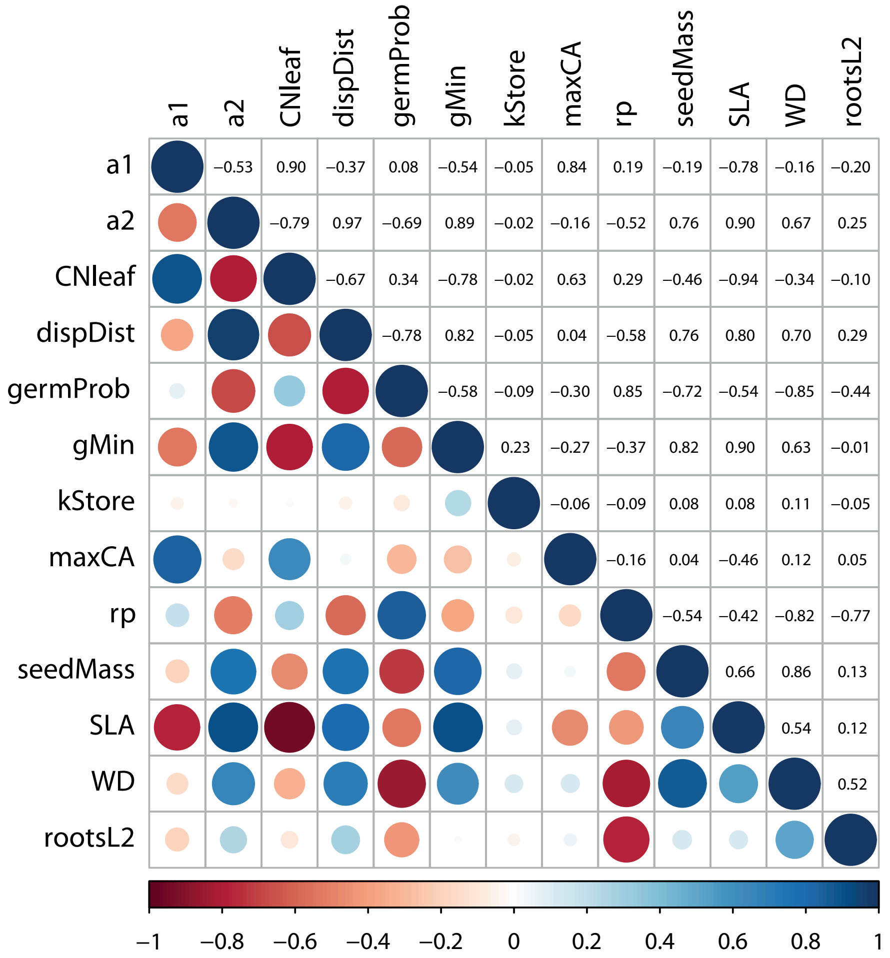


Figure A.3.11: Intrinsic community trait correlations. Shown are Spearman's rank correlations among community weighted mean plant traits across the mean simulated data set (see *Evaluation of simulation outcomes* in main text).

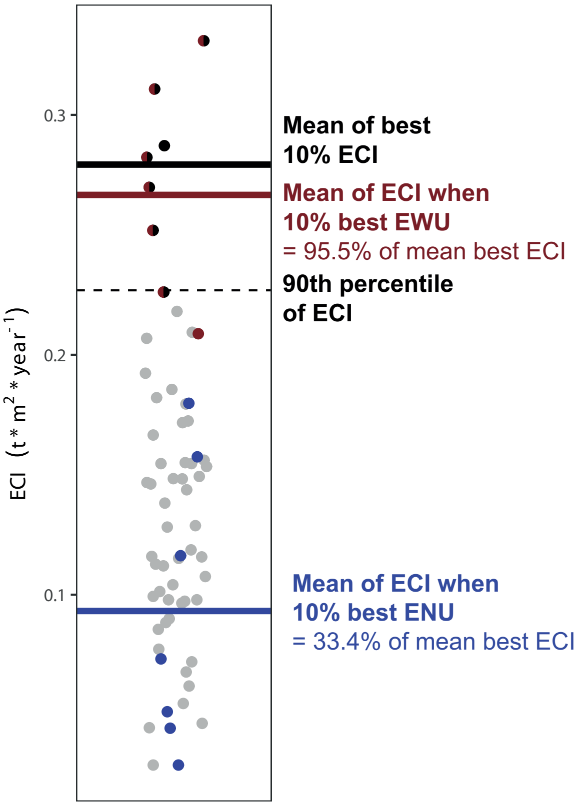


Figure A.3.12: Calculation of best ecosystem functioning per environmental context. Shown is mean (10 simulated years and 10 model repetitions) ecosystem carbon increment (ECI) for all 63 simulated PFT compositions (dots) and for one specific environmental context (here: MAP = 1200 mm, MAT = 8 °C, LAT = 40°, ST = sandy loam). Mean best ECI was obtained over all communities which provided 90% of maximum ECI or more (cp. Figure 4.2A). To understand trade-offs and synergies among the functions, mean best ECI was related to mean ECI of communities that provided 10% best functioning of EWU or ENU (cp. Figure 4.2B with percentage of mean best ECI).

Table A.3.4: Hypothesized links between environmental factors, plant traits, and ecosystem functions.

Link	From	To	Hypothesized link
	MAP	C:N ratio in leaves (CNleaf)	The higher MAP, the better N cycling, the less N limitation, the more leaf Nitrogen possible, the lower C:N ratio in the leaves.
	MAT		The higher MAT, the better N cycling but at the same time the less soil water due to higher evaporation with negative effects on decomposition with ultimately unclear effects on C:N ratio in the leaves.

Table A.3.4 continued from previous page

Link	From	To	Hypothesized link
	LAT (higher radiation)		The higher radiation, the higher evaporation, the lower soil water availability, the lower decomposition, the more N limitation, the more beneficial with higher C:N ratio in the leaves
	ST (higher sand content)		The higher sand content, the lower soil water availability, the lower decomposition, the more N limitation, the more beneficial with higher C:N ratio in the leaves
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAP:LAT:ST		
	MAT:LAT:ST		
	MAP	Deciduousness (kStore)	Drier conditions may be more favorable for drought-deciduous plants. Wetter conditions with higher water table favorable for evergreens to survive through droughts.
	MAT		The warmer, the less water availability, the more favorable for deciduous plants.
	LAT (higher radiation)		The more radiation, the higher evapotranspiration, the less water availability, the more deciduousness.
	ST (higher sand content)		The higher sand content, the lower water holding capacity, the less water availability, the less evergreens
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAP:LAT:ST		
	MAT:LAT:ST		

Table A.3.4 continued from previous page

Link	From	To	Hypothesized link
	MAP	Maximal crown area (maxCA)	The higher MAP, the less water limitation, the higher crown area.
	MAT		The higher MAT, the higher water limitation, the lower crown area.
	LAT (higher radiation)		The higher solar radiation, the higher evaporation, the higher water limitation, the lower crown area. At the same time, the less competition for light, the lower crown area.
	ST (higher sand content)		The higher sand content, the lower soil water availability, the higher water limitation, the lower crown area.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:ST		
	MAT:LAT:ST		
	MAP	Wood density (WD)	The higher MAP, the less limiting water, the lower WD, as higher WD more beneficial under drought.
	MAT		The higher MAT, the higher evaporation, the lower soil water availability, the higher WD.
	LAT (higher radiation)		The higher solar radiation, the higher evaporation, the lower soil water availability, the higher WD.
	ST (higher sand content)		The higher sand content, the lower soil water availability, the higher WD.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAT:LAT:ST		
	MAP	Rooting depth (rootsL2)	The higher MAP, the more soil water availability, the lower rooting depth.
	MAT		The higher MAT, the higher evaporation, the lower soil water availability, the higher rooting depth.

Table A.3.4 continued from previous page

Link	From	To	Hypothesized link
	LAT (higher radiation)		The higher radiation, the lower higher evaporation, the lower soil water availability, the higher rooting depth.
	ST (higher sand content)		The higher sand content, the lower soil water availability, the higher rooting depth.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:ST		
	MAP	Specific leaf area (SLA)	The higher MAP, the less conservative in water use, the higher SLA.
	MAT		The higher MAT, the higher evaporation, the less soil water availability, the more conservative in water use, the lower SLA.
	LAT (higher radiation)		The higher radiation, the higher evaporation, the less soil water availability, the more conservative in water use, the lower SLA.
	ST (higher sand content)		The higher sand content, the less soil water availability, the more conservative in water use, the lower SLA.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAP	EWU	The more rainfall, the less limiting water, the less important to efficiently use soil water.
	MAT		The warmer, the higher evaporation, the less soil water availability, the more important to efficiently use water.
	LAT (higher radiation)		The higher radiation, the more absorbed photosynthetic active radiation, the higher net primary productivity for the same amount of rainfall, if radiation is limiting.

Table A.3.4 continued from previous page

Link	From	To	Hypothesized link
	ST (higher sand content)		The sandier, the less soil water availability, the more important to efficiently use water.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAP:LAT:ST		
	MAT:LAT:ST		
	MAP:MAT:LAT:ST		
	MAP	ECI	The higher rainfall, the higher net primary productivity, the more plant carbon increment, the more litter. The more litter and soil water, the better decomposition, the more soil carbon increment.
	MAT		The higher temperature, the higher net primary productivity but also the higher evaporation, the lower soil water availability, the less net primary productivity, with unclear effects on plant carbon increment. The warmer, the better carbon decomposition, however at the same time drier conditions for decomposition, with unclear effects on soil carbon increment.
	LAT (higher radiation)		The higher radiation, the more absorbed photosynthetic active radiation, the higher net primary productivity.
	ST (higher sand content)		The more sand content, the less soil water moisture, the less net primary productivity and decomposition.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAP:LAT:ST		

Table A.3.4 continued from previous page

Link	From	To	Hypothesized link
	MAT:LAT:ST		
	MAP:MAT:LAT:ST		
	MAP	ENU	The higher soil water availability, the better decomposition, the more N availability.
	MAT		The higher soil temperature, the better decomposition, the more N availability.
	LAT (higher radiation)		The higher radiation, the more absorbed photosynthetic active radiation, the higher net primary productivity for the same amount of available soil N, if radiation is limiting.
	ST (higher sand content)		The more sand content, the less soil water moisture, the less decomposition, the less N availability.
	MAP:MAT		A pre-test by a linear regression of these factors revealed interactive effects of these abiotic factors on the trait.
	MAP:LAT		
	MAT:LAT		
	MAP:ST		
	MAT:ST		
	LAT:ST		
	MAP:MAT:LAT		
	MAP:MAT:ST		
	MAP:LAT:ST		
	MAT:LAT:ST		
Plant traits on ecosystem functions	Deciduousness (kStore)	EWU	The larger kStore (deciduous plants) the higher maximum N storage, the higher total N demand, the better buffered when N limited, the more optimal photosynthesis, the higher net primary productivity for the same amount of water.
	Maximal crown area (maxCA)		The higher maxCA, the higher maximum possible crown area, the higher absorbed photosynthetic active radiation and gross primary productivity, the higher also water use, the higher shading effects, the less evaporation.
	Wood density (WD)		The higher wood density, the lower sapwood area, the less sapflow, the lower net primary productivity and allocation for the same amount of available water.
	Rooting depth (rootsL2)		The more effective root distribution for the given soil moisture, the better water use.

Table A.3.4 continued from previous page

Link	From	To	Hypothesized link
	Specific leaf area (SLA)		The higher SLA, the higher leaf area index, the higher absorbed photosynthetic active radiation and gross primary productivity, the higher also water use.
	Deciduousness (kStore)	ECI	The larger kStore (deciduous plants) the higher maximum N storage, the higher total N demand, the better buffered when N limited, the better litter quality, the better soil and plant carbon increment.
	Maximal crown area (maxCA)		The higher maxCA, the higher maximum possible crown area, the higher absorbed photosynthetic active radiation and gross primary productivity, thus plant carbon increment.
	Wood density (WD)		The higher wood density, the lower sapwood area, the less sapflow, the lower net primary productivity and allocation, the lower plant carbon increment.
	Rooting depth (rootsL2)		The more effective root distribution for the given soil moisture, the better water use, the higher net primary productivity and thus plant carbon increment.
	Specific leaf area (SLA)		The higher SLA, the higher leaf area index, the higher absorbed photosynthetic active radiation and gross primary productivity, and thus plant carbon increment.
	C:N ratio in leaves (CNleaf)	ENU	The higher the C:N ratio in the leaves, the higher the demand for N uptake for the same amount of carbon allocated.
	Deciduousness (kStore)		The larger kStore (for deciduous plants), the higher maximum N storage, the higher total N demand, the better buffered when soil N is limited, the more optimal photosynthesis, the higher NPP for the same amount of soil N.
	Rooting depth (rootsL2)		The more effective root distribution for the given soil nitrogen, the more efficient nitrogen use.

A.3.4 Supporting results

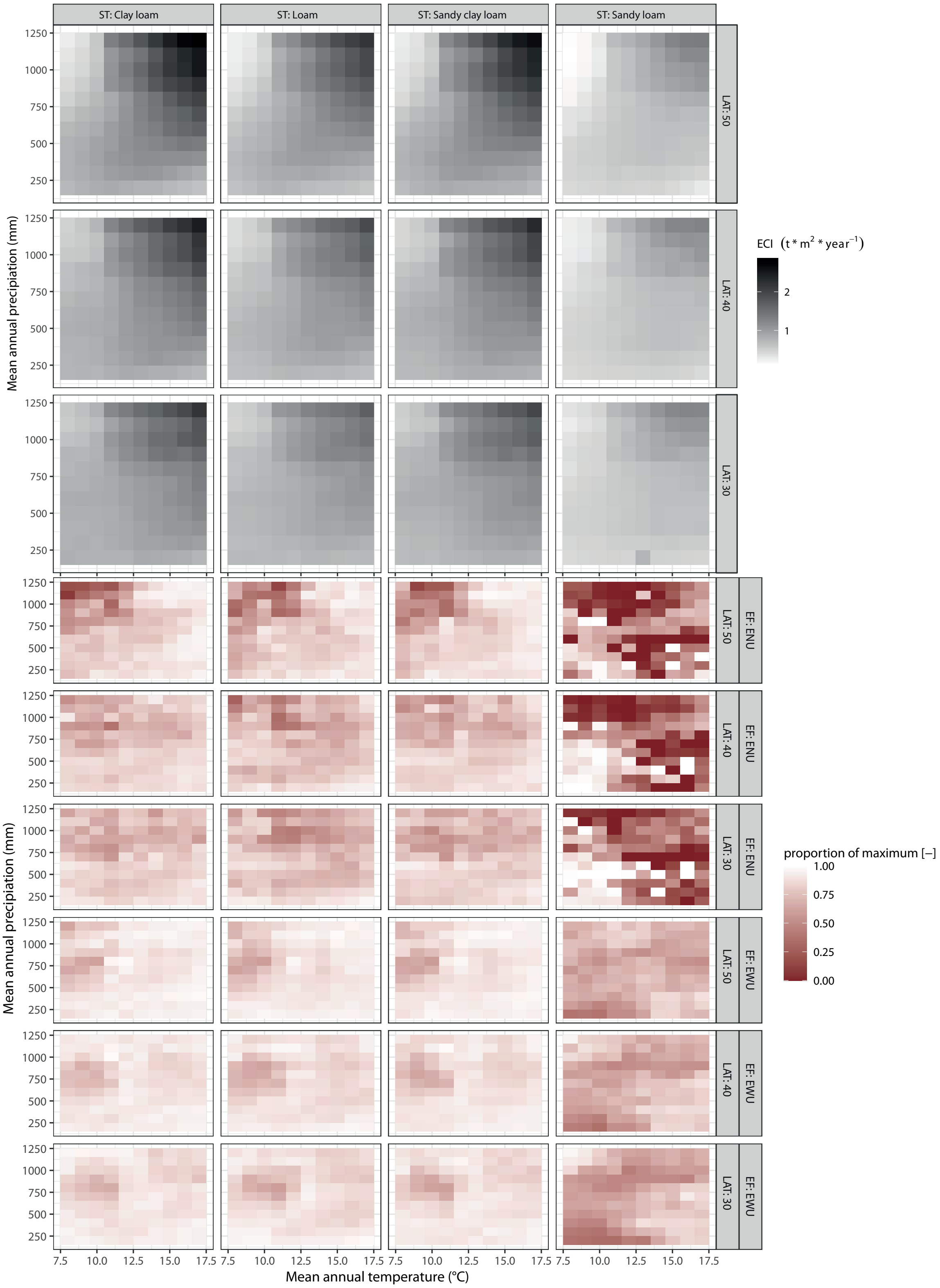


Figure A.3.13: Maximised provision of ecosystem carbon increment (ECI) (TOP) and proportion of its maximal possible provision when ecosystem water use efficiency (EWU) or ecosystem nitrogen use efficiency (ENU) is maximised for the same environmental context (BOTTOM) for different mean annual precipitations (y axis), mean annual temperatures (x axis), soil textures (columns), and different solar radiation resulting from different latitudes (rows). See further details in figure caption of Figure 4.2.

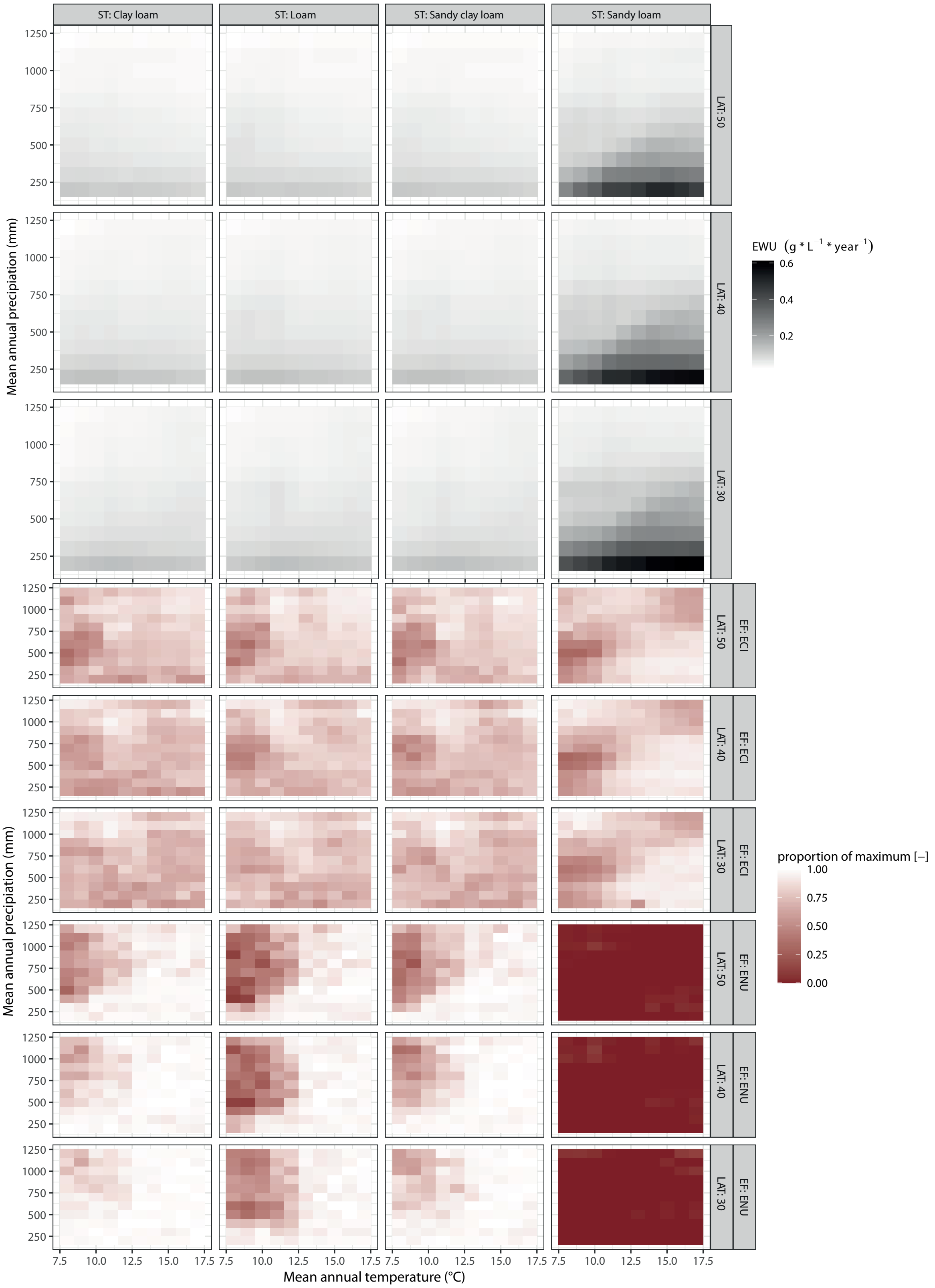


Figure A.3.14: Maximised provision of ecosystem water use efficiency (EWU) (TOP) and proportion of its maximal possible provision when ecosystem carbon increment (ECI) or ecosystem nitrogen use efficiency (ENU) is maximised for the same environmental context (BOTTOM) for different mean annual precipiations (y axis), mean annual temperatures (x axis), soil textures (columns), and different solar radiation resulting from different latitudes (rows). See further details in figure caption of Figure 4.2.

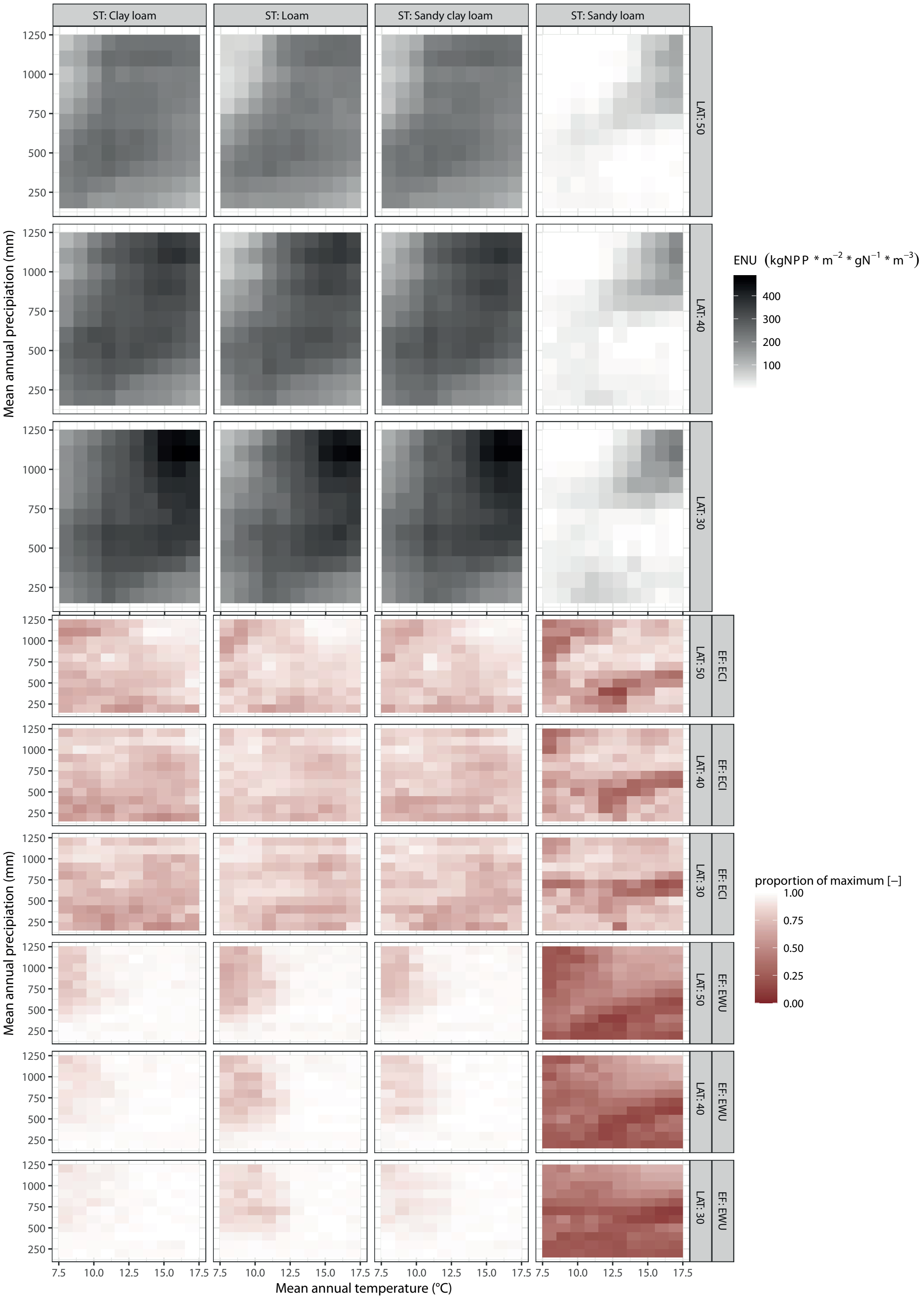


Figure A.3.15: Maximised provision of ecosystem nitrogen use efficiency (ENU) (TOP) and proportion of its maximal possible provision when ecosystem carbon increment (ECI) or ecosystem water use efficiency (EWU) is maximised for the same environmental context (BOTTOM) for different mean annual precipiations (y axis), mean annual temperatures (x axis), soil textures (columns), and different solar radiation resulting from different latitudes (rows). See further details in figure caption of Figure 4.2.

Table A.3.5: Effect sizes (standardized SEM regression coefficients) of the direct and indirect effects of the abiotic factors, as well as proportion of indirect effect from the respective direct effect.

Ecosystem function	**Environmental factor**	**Direct**	**Plant trait**	**Indirect**	**Proportion of indirect effect from direct effect**
ECI	MAP	-0.6	kStore	-0.0861	0.14
ECI	MAP	-0.6	maxCA	NA	NA
ECI	MAP	-0.6	WD	0.0126	0.02
ECI	MAP	-0.6	rootsL2	-0.0304	0.05
ECI	MAP	-0.6	SLA	-0.0775	0.13
ECI	MAP	-0.6	CNleaf	NA	NA
ECI	MAT	-0.26	kStore	-0.0126	0.05
ECI	MAT	-0.26	maxCA	NA	NA
ECI	MAT	-0.26	WD	0.0033	0.01
ECI	MAT	-0.26	rootsL2	-0.0088	0.03
ECI	MAT	-0.26	SLA	0.0248	0.1
ECI	MAT	-0.26	CNleaf	NA	NA
ECI	ST	0.14	kStore	0.0336	0.24
ECI	ST	0.14	maxCA	NA	NA
ECI	ST	0.14	WD	NA	NA
ECI	ST	0.14	rootsL2	-0.0176	0.13
ECI	ST	0.14	SLA	-0.093	0.66
ECI	ST	0.14	CNleaf	NA	NA
ECI	MAP x MAT	1.53	kStore	0.0714	0.05
ECI	MAP x MAT	1.53	maxCA	NA	NA
ECI	MAP x MAT	1.53	WD	-0.0114	0.01
ECI	MAP x MAT	1.53	rootsL2	0.0256	0.02
ECI	MAP x MAT	1.53	SLA	NA	NA
ECI	MAP x MAT	1.53	CNleaf	NA	NA
ECI	MAP x ST	NA	kStore	-0.0399	no direct effect
ECI	MAP x ST	NA	maxCA	NA	NA
ECI	MAP x ST	NA	WD	NA	NA
ECI	MAP x ST	NA	rootsL2	0.02	no direct effect
ECI	MAP x ST	NA	SLA	0.1209	no direct effect
ECI	MAP x ST	NA	CNleaf	NA	NA
ECI	MAT x ST	-0.18	kStore	-0.0798	0.44

Table A.3.5 continued from previous page

Ecosystem function	Environmental factor	Direct	Plant trait	Indirect	Proportion of indirect effect from direct effect
ECI	MAT x ST	-0.18	maxCA	NA	NA
ECI	MAT x ST	-0.18	WD	0.0078	0.04
ECI	MAT x ST	-0.18	rootsL2	0.0184	0.1
ECI	MAT x ST	-0.18	SLA	0.1426	0.79
ECI	MAT x ST	-0.18	CNleaf	NA	NA
ECI	MAP x MAT x ST	-0.13	kStore	0.0672	0.52
ECI	MAP x MAT x ST	-0.13	maxCA	NA	NA
ECI	MAP x MAT x ST	-0.13	WD	-0.0072	0.06
ECI	MAP x MAT x ST	-0.13	rootsL2	-0.0184	0.14
ECI	MAP x MAT x ST	-0.13	SLA	-0.155	1.19
ECI	MAP x MAT x ST	-0.13	CNleaf	NA	NA
EWU	MAP	-0.3	kStore	-0.1107	0.37
EWU	MAP	-0.3	maxCA	0.028	0.09
EWU	MAP	-0.3	WD	-0.021	0.07
EWU	MAP	-0.3	rootsL2	-0.0076	0.03
EWU	MAP	-0.3	SLA	-0.1525	0.51
EWU	MAP	-0.3	CNleaf	NA	NA
EWU	MAT	-0.23	kStore	-0.0162	0.07
EWU	MAT	-0.23	maxCA	NA	NA
EWU	MAT	-0.23	WD	-0.0055	0.02
EWU	MAT	-0.23	rootsL2	-0.0022	0.01
EWU	MAT	-0.23	SLA	0.0488	0.21
EWU	MAT	-0.23	CNleaf	NA	NA
EWU	ST	0.49	kStore	0.0405	0.08
EWU	ST	0.49	maxCA	0.039	0.08
EWU	ST	0.49	WD	NA	NA
EWU	ST	0.49	rootsL2	-0.0044	0.01
EWU	ST	0.49	SLA	-0.183	0.37
EWU	ST	0.49	CNleaf	NA	NA
EWU	MAP x MAT	0.57	kStore	0.0945	0.17
EWU	MAP x MAT	0.57	maxCA	NA	NA
EWU	MAP x MAT	0.57	WD	0.019	0.03
EWU	MAP x MAT	0.57	rootsL2	0.0064	0.01
EWU	MAP x MAT	0.57	SLA	NA	NA
EWU	MAP x MAT	0.57	CNleaf	NA	NA
EWU	MAP x ST	-0.4	kStore	-0.0513	0.13

Table A.3.5 continued from previous page

Ecosystem function	Environmental factor	Direct	Plant trait	Indirect	Proportion of indirect effect from direct effect
EWU	MAP x ST	-0.4	maxCA	-0.042	0.11
EWU	MAP x ST	-0.4	WD	NA	NA
EWU	MAP x ST	-0.4	rootsL2	0.005	0.01
EWU	MAP x ST	-0.4	SLA	0.2379	0.59
EWU	MAP x ST	-0.4	CNleaf	NA	NA
EWU	MAT x ST	NA	kStore	-0.0999	no direct effect
EWU	MAT x ST	NA	maxCA	-0.046	no direct effect
EWU	MAT x ST	NA	WD	-0.013	no direct effect
EWU	MAT x ST	NA	rootsL2	0.0046	no direct effect
EWU	MAT x ST	NA	SLA	0.2806	no direct effect
EWU	MAT x ST	NA	CNleaf	NA	NA
EWU	MAP x MAT x ST	NA	kStore	0.0837	no direct effect
EWU	MAP x MAT x ST	NA	maxCA	0.045	no direct effect
EWU	MAP x MAT x ST	NA	WD	0.012	no direct effect
EWU	MAP x MAT x ST	NA	rootsL2	-0.0044	no direct effect
EWU	MAP x MAT x ST	NA	SLA	-0.305	no direct effect
EWU	MAP x MAT x ST	NA	CNleaf	NA	NA
ENU	MAP	-0.67	kStore	-0.0492	0.07
ENU	MAP	-0.67	maxCA	NA	NA
ENU	MAP	-0.67	WD	NA	NA
ENU	MAP	-0.67	rootsL2	-0.0152	0.02
ENU	MAP	-0.67	SLA	NA	NA
ENU	MAP	-0.67	CNleaf	-0.1216	0.18
ENU	MAT	-0.37	kStore	-0.0072	0.02
ENU	MAT	-0.37	maxCA	NA	NA
ENU	MAT	-0.37	WD	NA	NA

Table A.3.5 continued from previous page

Ecosystem function	**Environmental factor**	**Direct**	**Plant trait**	**Indirect**	**Proportion of indirect effect from direct effect**
ENU	MAT	-0.37	rootsL2	-0.0044	0.01
ENU	MAT	-0.37	SLA	NA	NA
ENU	MAT	-0.37	CNleaf	0.0646	0.17
ENU	ST	-0.38	kStore	0.018	0.05
ENU	ST	-0.38	maxCA	NA	NA
ENU	ST	-0.38	WD	NA	NA
ENU	ST	-0.38	rootsL2	-0.0088	0.02
ENU	ST	-0.38	SLA	NA	NA
ENU	ST	-0.38	CNleaf	-0.0798	0.21
ENU	MAP x MAT	1.33	kStore	0.042	0.03
ENU	MAP x MAT	1.33	maxCA	NA	NA
ENU	MAP x MAT	1.33	WD	NA	NA
ENU	MAP x MAT	1.33	rootsL2	0.0128	0.01
ENU	MAP x MAT	1.33	SLA	NA	NA
ENU	MAP x MAT	1.33	CNleaf	-0.0494	0.04
ENU	MAP x ST	0.14	kStore	-0.0228	0.16
ENU	MAP x ST	0.14	maxCA	NA	NA
ENU	MAP x ST	0.14	WD	NA	NA
ENU	MAP x ST	0.14	rootsL2	0.01	0.07
ENU	MAP x ST	0.14	SLA	NA	NA
ENU	MAP x ST	0.14	CNleaf	0.114	0.81
ENU	MAT x ST	NA	kStore	-0.0444	no direct effect
ENU	MAT x ST	NA	maxCA	NA	NA
ENU	MAT x ST	NA	WD	NA	NA
ENU	MAT x ST	NA	rootsL2	0.0092	no direct effect
ENU	MAT x ST	NA	SLA	NA	NA
ENU	MAT x ST	NA	CNleaf	0.114	no direct effect
ENU	MAP x MAT x ST	-0.33	kStore	0.0372	0.11
ENU	MAP x MAT x ST	-0.33	maxCA	NA	NA
ENU	MAP x MAT x ST	-0.33	WD	NA	NA
ENU	MAP x MAT x ST	-0.33	rootsL2	-0.0088	NA
ENU	MAP x MAT x ST	-0.33	SLA	NA	NA
ENU	MAP x MAT x ST	-0.33	CNleaf	-0.1254	0.38

B

Bibliography

Achat, D. L., Augusto, L., Gallet-Budynek, A., and Loustau, D. (2016). Future challenges in coupled C–N–P cycle models for terrestrial ecosystems under global change: a review. *Biogeochemistry*, 131:173–202.

Acosta, A., Izzi, C., and Stanisci, A. (2006). Comparison of native and alien plant traits in Mediterranean coastal dunes. *Community Ecology*, 7:35–41.

Ahrens, C. W., Andrew, M. E., Mazanec, R. A., Ruthrof, K. X., Challis, A., Hardy, G., Byrne, M., Tissue, D. T., and Rymer, P. D. (2020). Plant functional traits differ in adaptability and are predicted to be differentially affected by climate change. *Ecology and Evolution*, 10:232–248.

Alessandri, A., Felice, M. D., Zeng, N., Mariotti, A., Pan, Y., Cherchi, A., Lee, J.-Y., Wang, B., Ha, K.-J., Ruti, P., and Artale, V. (2015). Robust assessment of the expansion and retreat of Mediterranean climate in the 21st century. *Scientific Reports*, 4:7211.

Ali, A., Yan, E.-R., Chang, S. X., Cheng, J.-Y., and Liu, X.-Y. (2016). Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. *Science of the Total Environment*, 574:654–662.

Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Bl€, N., B€, S., Grassein, F., H€, N., Klaus, V. H., Kleinebecker, T., Morris, E. K., Oelmann, Y., Prati, D., Renner, S. C., Rillig, M. C., Schaefer, M., Schloter, M., Schmitt, B., Sch€, I., Schrumpf, M., Solly, E., Sorkau, E., Steckel, J., Steffen-Dewenter, I., Stempfhuber, B., Tschapka, M., Weiner, C. N., Weisser, W. W., Werner, M., Westphal, C., Wilcke, W., and Fischer, M. (2015). Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology Letters*, 18:834–843.

Ashbacher, A. C. and Cleland, E. E. (2015). Native and exotic plant species show differential growth but similar functional trait responses to experimental rainfall. *Ecosphere*, 6:art245.

Augustin, C. and Cihacek, L. J. (2016). Relationships between soil carbon and soil texture in the Northern Great Plains. *Soil Science*, 181:386–392.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., and Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9:1146–1156.

Bardgett, R. D., Mommer, L., and Vries, F. T. D. (2014). Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29:692–699.

Bartlett, M. K., Scoffoni, C., and Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: A global meta-analysis. *Ecology Letters*, 15:393–405.

Batriu, E., Ninot, J. M., and Pino, J. (2015). Filtering of plant functional traits is determined by environmental gradients and by past land use in a Mediterranean coastal marsh. *Journal of Vegetation Science*, 26:492–500.

Benayas, J. M. R., Fernández, A., and Aubenau, A. (2007). Clipping herbaceous vegetation improves early performance of planted seedlings of the Mediterranean shrub Quercus coccifera. *Web Ecology*, 7:120–131.

Benayas, J. M. R., Newton, A. C., Diaz, A., and Bullock, J. M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. *Science*, 325:1121–1124.

Benke, K. K., Norng, S., Robinson, N. J., Benke, L. R., and Peterson, T. J. (2018). Error propagation in computer models: analytic approaches, advantages, disadvantages and constraints. *Stochastic Environmental Research and Risk Assessment*, 32:2971–2985.

Bennett, E. M., Peterson, G. D., and Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services. *Ecology Letters*, 12:1394–1404.

Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., and Garnier, E. (2012). Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, 100:1422–1433.

Berzaghi, F., Wright, I. J., Kramer, K., Oddou-Muratorio, S., Bohn, F. J., Reyer, C. P., Sabaté, S., Sanders, T. G., and Hartig, F. (2020). Towards a new generation of trait-flexible vegetation models. *Trends in Ecology & Evolution*, 35:191–205.

Birouste, M., Kazakou, E., Blanchard, A., and Roumet, C. (2012). Plant traits and decomposition: are the relationships for roots comparable to those for leaves? *Annals of Botany*, 109:463–472.

Blondel, J., Aronson, J., Bodiou, J.-Y., and Boeuf, G. (2010). *The Mediterraneaen Region - Biological Diversity in Space and Time*. Oxford University Press, 2nd edition.

Blumler, M. (2005). Three conflated definitions of Mediterranean climates. *Middle States Geographer*, 38:52–60.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., and Vries, W. D. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, 20:30–59.

Bonet, A. (2004). Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. *Journal of Arid Environments*, 56:213–233.

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrodt, F., Mahecha, M. D., Peet, R. K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., Khan, M. A. A., Attorre, F., Aubin, I., Baraloto, C., Barroso, J. G., Bauters, M., Bergmeier, E., Biurrun, I., Bjorkman, A. D., Blonder, B., Čarni, A., Cayuela, L., Černý, T., Cornelissen, J. H. C., Craven, D., Dainese, M., Derroire, G., Sanctis, M. D., Díaz, S., Doležal, J., Farfan-Rios, W., Feldpausch, T. R., Fenton, N. J., Garnier, E., Guerin, G. R., Gutiérrez, A. G., Haider, S., Hattab, T., Henry, G., Hérault, B., Higuchi, P., Hölzel, N., Homeier, J., Jentsch, A., Jürgens, N., Kącki, Z., Karger, D. N., Kessler, M., Kleyer, M., Knollová, I., Korolyuk, A. Y., Kühn, I., Laughlin, D. C., Lens, F., Loos, J., Louault, F., Lyubenova, M. I., Malhi, Y., Marcenò, C., Mencuccini, M., Müller, J. V., Munzinger, J., Myers-Smith, I. H., Neill, D. A., Ülo Niinemets, Orwin, K. H., Ozinga, W. A., Penuelas, J., Pérez-Haase, A., Petřík, P., Phillips, O. L., Pärtel, M., Reich, P. B., Römermann, C., Rodrigues, A. V., Sabatini, F. M., Sardans, J., Schmidt, M., Seidler, G., Espejo, J. E. S., Silveira, M., Smyth, A., Sporbert, M., Svenning, J. C., Tang, Z., Thomas, R., Tsiripidis, I., Vassilev, K., Violle, C., Virtanen, R., Weiher, E., Welk, E., Wesche, K., Winter, M., Wirth, C., and Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature Ecology and Evolution*, 2:1906–1917.

Bugalho, M. N., Caldeira, M. C., Pereira, J. S., Aronson, J., and Pausas, J. G. (2011). Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. *Frontiers in Ecology and the Environment*, 9:278–286.

Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F., and Rey-Benayas, J. M. (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology & Evolution*, 26:541–549.

Bureau of Meteorology (2019). Climate data. http://www.bom.gov.au/.

Bureau of Meterology (2015). Daily climate data for Pingelly. http://www.bom.gov.au/.

Burylo, M., Rey, F., Bochet, E., and Dutoit, T. (2012). Plant functional traits and species ability for sediment retention during concentrated flow erosion. *Plant and Soil*, 353:135–144.

Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., Banerjee, A., Atkin, O. K., Kattge, J., Amiaud, B., Blonder, B., Boenisch, G., Bond-Lamberty, B., Brown, K. A., Byun, C., Campetella, G., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., Craven, D., de Vries, F. T., Díaz, S., Domingues, T. F., Forey, E., González-Melo, A., Gross, N., Han, W., Hattingh, W. N., Hickler, T., Jansen, S., Kramer, K., Kraft, N. J. B., Kurokawa, H., Laughlin, D. C., Meir, P., Minden, V., Ülo Niinemets, Onoda, Y., Peñuelas, J., Read, Q., Sack, L., Schamp, B., Soudzilovskaia, N. A., Spasojevic, M. J., Sosinski, E., Thornton, P. E., Valladares, F., van Bodegom, P. M., Williams, M., Wirth, C., and Reich, P. B. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences*, 114:E10937–E10946.

Butterfield, B. J. and Suding, K. N. (2013). Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology*, 101:9–17.

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E., and Duffy, J. E. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods in Ecology and Evolution*, 5:111–124.

Cademus, R., Escobedo, F., McLaughlin, D., and Abd-Elrahman, A. (2014). Analyzing trade-offs, synergies, and drivers among timber production, carbon sequestration, and water yield in Pinus elliotii forests in southeastern USA. *Forests*, 5:1409–1431.

Cadotte, M. W. (2017). Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters*, 20:989–996.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., and Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486:59–67.

Cardinale, B. J., Nelson, K., and Palmer, M. A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91:175–183.

Carlucci, M. B., Brancalion, P. H. S., Rodrigues, R. R., Loyola, R., and Cianciaruso, M. V. (2020). Functional traits and ecosystem services in ecological restoration. *Restoration Ecology*, 28:1372–1383.

Castro, H., Fortunel, C., and Freitas, H. (2010a). Effects of land abandonment on plant litter decomposition in a Montado system: relation to litter chemistry and community functional parameters. *Plant and Soil*, 333:181–190.

Castro, H., Lehsten, V., Lavorel, S., and Freitas, H. (2010b). Functional response traits in relation to land use change in the Montado. *Agriculture, Ecosystems & Environment*, 137:183–191.

Castro-Díez, P., Valle, G., González-Muñoz, N., and Álvaro Alonso (2014). Can the life-history strategy explain the success of the exotic trees Ailanthus altissima and Robinia pseudoacacia in Iberian floodplain forests? *PLoS ONE*, 9:e100254.

Cebrián-Piqueras, M. A., Trinogga, J., Trenkamp, A., Minden, V., Maier, M., and Mantilla-Contreras, J. (2021). Digging into the roots: understanding direct and indirect drivers of ecosystem service trade-offs in coastal grasslands via plant functional traits. *Environmental Monitoring and Assessment*, 193:271.

Chamizo, S., Cantón, Y., Rodríguez-Caballero, E., and Domingo, F. (2016). Biocrusts positively affect the soil water balance in semiarid ecosystems. *Ecohydrology*, 9:1208–1221.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405:234–242.

Charrad, M., Ghazzali, N., Boiteau, V., and Niknafs, A. (2014). NbClust: An R package for determining the relevant number of clusters in a data set. *Journal of Statistical Software*, 61:1–36.

Choi, Y. D., Temperton, V. M., Allen, E. B., Grootjans, A. P., Halassy, M., Hobbs, R. J., Naeth, M. A., and Torok, K. (2008). Ecological restoration for future sustainability in a changing environment. *Ecoscience*, 15:53–64.

Cochrane, A., Hoyle, G. L., Yates, C. J., Wood, J., and Nicotra, A. B. (2015). The phenotypic response of co-occurring banksia species to warming and drying. *Plant Ecology*, 216:27–39.

Cornwell, W. K. and Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79:109–126.

Cortez, J., Garnier, E., Pérez-Harguindeguy, N., Debussche, M., and Gillon, D. (2007). Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant and Soil*, 296:19–34.

Costa-Saura, J. M., Martínez-Vilalta, J., Trabucco, A., Spano, D., and Mereu, S. (2016). Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species. *Perspectives in Plant Ecology, Evolution and Systematics*, 21:23–30.

Cowling, R. M., Rundel, P. W., Lamont, B. B., Arroyo, M. K., and Arianoutsou, M. (1996). Plant diversity in Mediterranean-climate regions. *TREE*, 11:362–366.

Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A., Lange, M. A., Lionello, P., Llasat, M. C., Paz, S., Peñuelas, J., Snoussi, M., Toreti, A., Tsimplis, M. N., and Xoplaki, E. (2018). Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change*, 8:972–980.

Crawford, M., Jeltsch, F., May, F., Grimm, V., and Schlägel, U. E. (2019). Intraspecific trait variation increases species diversity in a trait-based grassland model. *Oikos*, 128:441–455.

Cregger, M. A., McDowell, N. G., Pangle, R. E., Pockman, W. T., and Classen, A. T. (2014). The impact of precipitation change on nitrogen cycling in a semi-arid ecosystem. *Functional Ecology*, 28:1534–1544.

Crescente, M. F., Gratani, L., and Larcher, W. (2002). Shoot growth efficiency and production of Quercus ilex L. in different climates. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 197:2–9.

Cruz-Alonso, V., Ruiz-Benito, P., Villar-Salvador, P., Rey-Benayas, J. M., Móstoles, R. J. C., and Cruz-Alonso, S. C. V. (2019). Long-term recovery of multifunctionality in Mediterranean forests depends on restoration strategy and forest type. *Journal of Applied Ecology*, 56.

Daily, G. C. (1997). *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press.

Daroub, S. H., Gerakis, A., Ritchie, J. T., Friesen, D. K., and Ryan, J. (2003). Development of a soil-plant phosphorus simulation model for calcareous and weathered tropical soils. *Agricultural Systems*, 76:1157–1181.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., Chave, J., Wright, S. J., Sheremet'ev, S. N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J. S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M. D., and Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529:167–171.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg, M. P., Cipriotti, P., Feld, C. K., Hering, D., da Silva, P. M., Potts, S. G., Sandin, L., Sousa, J. P., Storkey, J., Wardle, D. A., and Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19:2873–2893.

de la Riva, E. G., Olmo, M., Poorter, H., Ubera, J. L., and Villar, R. (2016a). Leaf mass per area (LMA) and its relationship with leaf structure and anatomy in 34 Mediterranean woody species along a water availability gradient. *PLOS ONE*, 11:e0148788.

de la Riva, E. G., Tosto, A., Pérez-Ramos, I. M., Navarro-Fernández, C. M., Olmo, M., Anten, N. P., Marañón, T., and Villar, R. (2016b). A plant economics spectrum in Mediterranean forests along environmental gradients: Is there coordination among leaf, stem and root traits? *Journal of Vegetation Science*, 27:187–199.

de la Riva, E. G., Violle, C., Pérez-Ramos, I. M., Marañón, T., Navarro-Fernández, C. M., Olmo, M., and Villar, R. (2018). A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody communities. *Ecosystems*, 21:248–262.

DeAngelis, D. L. and Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000Prime Reports*, 6.

del Cacho, M., Peñuelas, J., and Lloret, F. (2013). Reproductive output in Mediterranean shrubs under climate change experimentally induced by drought and warming. *Perspectives in Plant Ecology, Evolution and Systematics*, 15:319–327.

Dentener, F., Drevet, J., Lamarque, J. F., Bey, I., Eickhout, B., Fiore, A. M., Hauglustaine, D., Horowitz, L. W., Krol, M., Kulshrestha, U. C., Lawrence, M., Galy-Lacaux, C., Rast, S., Shindell, D., Stevenson, D., Noije, T. V., Atherton, C., Bell, N., Bergman, D., Butler, T., Cofala, J., Collins, B., Doherty, R., Ellingsen, K., Galloway, J., Gauss, M., Montanaro, V., Müller, J. F., Pitari, G., Rodriguez, J., Sanderson, M., Solmon, F., Strahan, S., Schultz, M., Sudo, K., Szopa, S., and Wild, O. (2006). Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation. *Global Biogeochemical Cycles*, 20.

Deyn, G. B. D., Cornelissen, J. H. C., and Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, 11:516–531.

Dias, T., Oakley, S., Alarcón-Gutiérrez, E., Ziarelli, F., Trindade, H., Martins-Loução, M. A., Sheppard, L., Ostle, N., and Cruz, C. (2013). N-driven changes in a plant community affect leaf-litter traits and may delay organic matter decomposition in a Mediterranean maquis. *Soil Biology and Biochemistry*, 58:163–171.

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K., and Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, 104:20684–20689.

Ding, J., Travers, S. K., Delgado-Baquerizo, M., and Eldridge, D. J. (2020). Multiple trade-offs regulate the effects of woody plant removal on biodiversity and ecosystem functions in global rangelands. *Global Change Biology*, 26:709–720.

Dobarro, I., Carmona, C. P., and Peco, B. (2013). Dissecting the effects of simulated cattle activity on floristic composition and functional traits in Mediterranean grasslands. *PLoS ONE*, 8:e79822.

Doblas-Miranda, E., Alonso, R., Arnan, X., Bermejo, V., Brotons, L., de las Heras, J., Estiarte, M., Hódar, J., Llorens, P., Lloret, F., López-Serrano, F., Martínez-Vilalta, J., Moya, D., Peñuelas, J., Pino, J., Rodrigo, A., Roura-Pascual, N., Valladares, F., Vilà, M., Zamora, R., and Retana, J. (2017). A review of the combination among global change factors in forests, shrublands and pastures of the Mediterranean region: Beyond drought effects. *Global and Planetary Change*, 148:42–54.

Domènech, R. and Vilà, M. (2008). Response of the invader Cortaderia selloana and two coexisting natives to competition and water stress. *Biological Invasions*, 10:903–912.

Eastburn, D. J., O'Geen, A. T., Tate, K. W., and Roche, L. M. (2017). Multiple ecosystem services in a working landscape. *PLOS ONE*, 12:e0166595.

Esther, A., Groeneveld, J., Enright, N. J., Miller, B. P., Lamont, B. B., Perry, G. L. W., Tietjen, B., and Jeltsch, F. (2011). Low-dimensional trade-offs fail to explain richness and structure in species-rich plant communities. *Theoretical Ecology*, 4:495–511.

Everard, K., Seabloom, E. W., Harpole, W. S., and de Mazancourt, C. (2010). Plant water use affects competition for nitrogen: why drought favors invasive species in California. *The American naturalist*, 175:85–97.

Eviner, V. T. and III, F. S. C. (2003). Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution, and Systematics*, 34:455–485.

FAO and Plan Bleu (2013). *State of Mediterranean forests 2013.* FAO.

FAO and Plan Bleu (2018). *State of Mediterranean Forests 2018.* FAO.

Fiedler, S., Monteiro, J. A., Hulvey, K. B., Standish, R. J., Perring, M. P., and Tietjen, B. (2021). Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. *Journal of Applied Ecology.*

Fiedler, S., Monteiro, J. A., Perring, M. P., and Tietjen, B. (2020). ModEST v1.0: Modelling ecosystem functions and services based on traits. https://zenodo.org/record/4034790.

Fiedler, S., Perring, M. P., and Tietjen, B. (2018). Integrating trait-based empirical and modeling research to improve ecological restoration. *Ecology and Evolution*, 8:6369–6380.

Fried, J. S., Torn, M. S., and Mills, E. (2004). The impact of climate change on wildfire severity: A regional forecast for northern California. *Climatic Change*, 64:169–191.

Fry, D. L., Stephens, S. L., Collins, B. M., North, M. P., Franco-Vizcaíno, E., and Gill, S. J. (2014). Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. *PLoS ONE*, 9:e88985.

Fu, B., Wang, S., Su, C., and Forsius, M. (2013). Linking ecosystem processes and ecosystem services. *Current Opinion in Environmental Sustainability*, 5:4–10.

Funk, J. L., Cleland, E. E., Suding, K. N., and Zavaleta, E. S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution*, 23:695–703.

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L., and Wright, J. (2017). Revisiting the holy grail: using plant functional traits to understand ecological processes. *Biological Reviews*, 92:1156–1173.

Fyllas, N. M. and Troumbis, A. Y. (2009). Simulating vegetation shifts in north-eastern Mediterranean mountain forests under climatic change scenarios. *Global Ecology and Biogeography*, 18:64–77.

Gaertner, M., Breeyen, A. D., Hui, C., and Richardson, D. M. (2009). Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography: Earth and Environment*, 33:319–338.

Gahrooee, F. R. (1998). Impacts of elevated atmospheric CO2 on litter quality, litter decomposability and nitrogen turnover rate of two oak species in a Mediterranean forest ecosystem. *Global Change Biology*, 4:667–677.

Gaines, L. A. G., Olds, A. D., Henderson, C. J., Connolly, R. M., Schlacher, T. A., Jones, T. R., and Gilby, B. L. (2020). Linking ecosystem condition and landscape context in the conservation of ecosystem multifunctionality. *Biological Conservation*, 243:108479.

Gamfeldt, L. and Roger, F. (2017). Revisiting the biodiversity–ecosystem multifunctionality relationship. *Nature Ecology & Evolution*, 1:0168.

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., and Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, 27.

Garcia-Serrano, H., Caño, L., Escarré, J., Fleck, I., and Sans, F. (2009). Physiological comparison of alien Senecio inaequidens and S. pterophorus and native S. malacitanus: Implications for invasion. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 204:445–455.

Garnier, E., Bellmann, A., Navas, M.-L., Roumet, C., and Laurent, G. (2004). The leaf-height-seed plant ecology strategy scheme as applied to species from a Mediterranean old-field succession. page 16.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V. P., Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thebault, A., Vile, D., and Zarovali, M. P. (2007).

Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99:967–985.

Garnier, E., Navas, M.-L., and Grigulis, K. (2016). *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties.* Oxford University Press.

Giannini, T. C., Giulietti, A. M., Harley, R. M., Viana, P. L., Jaffe, R., Alves, R., Pinto, C. E., Mota, N. F. O., Caldeira, C. F., Imperatriz-Fonseca, V. L., Furtini, A. E., and Siqueira, J. O. (2017). Selecting plant species for practical restoration of degraded lands using a multiple-trait approach. *Austral Ecology*, 42:510–521.

Giling, D. P., Beaumelle, L., Phillips, H. R. P., Cesarz, S., Eisenhauer, N., Ferlian, O., Gottschall, F., Guerra, C., Hines, J., Sendek, A., Siebert, J., Thakur, M. P., and Barnes, A. D. (2019). A niche for ecosystem multifunctionality in global change research. *Global Change Biology*, 25:763–774.

Godoy, O., Castro-Díez, P., Logtestijn, R. S. P. V., Cornelissen, J. H. C., and Valladares, F. (2010). Leaf litter traits of invasive species slow down decomposition compared to Spanish natives: a broad phylogenetic comparison. *Oecologia*, 162:781–790.

Godoy, O., Castro-Díez, P., Valladares, F., and Costa-Tenorio, M. (2009a). Different flowering phenology of alien invasive species in Spain: evidence for the use of an empty temporal niche? *Plant Biology*, 11:803–811.

Godoy, O., de Lemos-Filho, J. P., and Valladares, F. (2011). Invasive species can handle higher leaf temperature under water stress than Mediterranean natives. *Environmental and Experimental Botany*, 71:207–214.

Godoy, O., Richardson, D. M., Valladares, F., and Castro-Díez, P. (2009b). Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems. *Annals of Botany*, 103:485–494.

Gratani, L., Varone, L., Ricotta, C., and Catoni, R. (2013). Mediterranean shrublands carbon sequestration: environmental and economic benefits. *Mitigation and Adaptation Strategies for Global Change*, 18:1167–1182.

Grime, J. P. (1997). Biodiversity and ecosystem function: The debate deepens. *Science*, 277:1260–1261.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86:902–910.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T., and Deangelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, 310:987–991.

Grünzweig, J. M. and Dumbur, R. (2012). Seed traits, seed-reserve utilization and offspring performance across pre-industrial to future CO2 concentrations in a Mediterranean community. *Oikos*, 121:579–588.

Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, M., Gotelli, N. J., and Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, 1:0132.

Grotkopp, E. and Rejmanek, M. (2007). High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany*, 94:526–532.

Guijarro, J. (2019). climatol: Climate tools (series homogenization and derived products). R package version 3.1.2.

Gutiérrez-Girón, A. and Gavilán, R. (2013). Plant functional strategies and environmental constraints in Mediterranean high mountain grasslands in central Spain. *Plant Ecology & Diversity*, 6:435–446.

Hallett, L. M., Standish, R. J., and Hobbs, R. J. (2011). Seed mass and summer drought survival in a Mediterranean-climate ecosystem. *Plant Ecology*, 212:1479–1489.

Hanisch, M., Schweiger, O., Cord, A. F., Volk, M., and Knapp, S. (2020). Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *Journal of Applied Ecology*, 57:1535–1550.

Harris, I., Osborn, T. J., Jones, P., and Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, 7:109.

Harris, J. A., Hobbs, R. J., Higgs, E., and Aronson, J. (2006). Ecological restoration and global climate change. *Restoration Ecology*, 14:170–176.

Harris, R. J. and Standish, R. J. (2008). Ant dispersal and predation affects the availability of seeds for old-field recolonisation in Western Australia. *Journal of the Royal Society of Western Australia*, 91:301–311.

Hartig, F., Dyke, J., Hickler, T., Higgins, S. I., O'Hara, R. B., Scheiter, S., and Huth, A. (2012). Connecting dynamic vegetation models to data - an inverse perspective. *Journal of Biogeography*, 39:2240–2252.

Hartig, F., Minunno, F., and Paul, S. (2019). BayesianTools: General-purpose MCMC and SMC samplers and tools for Bayesian statistics. R package version 0.1.6.

Henn, J. J., Buzzard, V., Enquist, B. J., Halbritter, A. H., Klanderud, K., Maitner, B. S., Michaletz, S. T., Pötsch, C., Seltzer, L., Telford, R. J., Yang, Y., Zhang, L., and Vandvik, V. (2018). Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, 9.

Hänel, S. and Tielbörger, K. (2015). Phenotypic response of plants to simulated climate change in a long-term rain-manipulation experiment: a multi-species study. *Oecologia*, 177:1015–1024.

Hobbs, R. J. (1998). Impacts of land use on biodiversity in Southwestern Australia. pages 81–106. Springer.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4:1–23.

Holman, I., Brown, C., Janes, V., and Sandars, D. (2017). Can we be certain about future land use change in Europe? A multi-scenario, integrated-assessment analysis. *Agricultural Systems*, 151:126–135.

Hooper, D. U. and Dukes, J. S. (2010). Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology*, 98:764–777.

Hope, P., Abbs, D., Bhend, J., Chiew, F., Church, J., Ekström, M., Kirono, D., Lenton, A., Lucas, C., McInnes, K., Moise, A., Monselesan, D., Mpelasoka, F., Timbal, B., Webb, L., and Whetton, P. (2015). *Southern and South-Western Flatlands Cluster Report.* CSIRO and Bureau of Meteorology, Australia.

Hopfe, C. J. and Hensen, J. L. (2011). Uncertainty analysis in building performance simulation for design support. *Energy and Buildings*, 43:2798–2805.

Houerou, H. N. L. (2000). Restoration and rehabilitation of arid and semiarid Mediterranean ecosystems in North Africa and West Asia: A review. *Arid Soil Research and Rehabilitation*, 14:3–14.

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., and Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429:651–654.

Inbar, M., Tamir, M., and Wittenberg, L. (1998). Runoff and erosion processes after a forest fire in Mount Carmel, a Mediterranean area. *Geomorphology*, 24:17–33.

IPBES (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.* IPBES secretariat.

IPCC (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press.

IPCC (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* IPCC.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S., and Loreau, M. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, 477:199–202.

Jaunatre, R., Buisson, E., and Dutoit, T. (2014). Can ecological engineering restore Mediterranean rangeland after intensive cultivation? A large-scale experiment in southern France. *Ecological Engineering*, 64:202–212.

Jing, G., Cheng, J., Su, J., Wei, L., Hu, T., and Li, W. (2019). Community-weighted mean traits play crucial roles in driving ecosystem functioning along long-term grassland restoration gradient on the Loess Plateau of China. *Journal of Arid Environments*, 165:97–105.

Johnson, I. R., Chapman, D. F., Snow, V. O., Eckard, R. J., Parsons, A. J., Lambert, M. G., and Cullen, B. R. (2008). DairyMod and EcoMod: biophysical pasture-simulation models for Australia and New Zealand. *Australian Journal of Experimental Agriculture*, 48:621.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology*, 98:1134–1140.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., C, C. A., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M. M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D. M. G., Ashman, T., Asmara, D. H., Asner, G. P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W. J., Bakker, J. P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D. R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M. L., Berenguer, E., Bergamin, R., Bergmann, J., Carlucci, M. B., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A. D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K. T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C. C. F., Bordin, K., Boughton, E. H., Boukili, V., Bowman, D. M. J. S., Bravo, S., Brendel, M. R., Broadley, M. R., Brown, K. A., Bruelheide, H., Brumnich, F., Bruun, H. H., Bruy, D., Buchanan, S. W., Bucher, S. F., Buchmann, N., Buitenwerf, R., Bunker, D. E., Bürger, J., Burrascano, S., Burslem, D. F. R. P., Butterfield, B. J., Byun, C., Marques, M., Scalon, M. C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J. J., Campany, C., Campetella, G., Campos, J. A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J. A., Cavender-Bares, J., Cerabolini, B. E. L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F. S., Chelli, S., Chen, S., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C. G., Conti, L., Coomes, D., Cornelissen, J. H. C., Cornwell, W. K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J. P. G. M., Csecserits, A., Cufar, K., Cuntz, M., Silva, A. C., Dahlin, K. M., Dainese, M., Dalke, I., Fratte, M. D., Dang-Le, A. T., Danihelka, J., Dannoura, M., Dawson, S., Beer, A. J., Frutos, A. D., Long, J. R. D., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A. S., Diaz-Toribio, M. H., Dimitrakopoulos, P. G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R. L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M. B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T. F., Fagan, W. F., Fagúndez, J., Falster, D. S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T. J., Flynn, D. F. B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G. T., Fry, E. L., Fyllas, N. M., Mazzochini, G. G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J. L., Gasper, A. L., Gea-Izquierdo, G., Gibson, D., Gillison, A. N., Giroldo, A., Glasenhardt, M., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J. L., González-Melo, A., González-Robles, A., Graae, B. J., Granda, E., Graves, S., Green, W. A., Gregor, T., Gross, N., Guerin, G. R., Günther, A., Gutiérrez, A. G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S. P., Hattingh, W., Hawes, J. E., He, T., He, P., Heberling, J. M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A. L., Hirons, A., Hock, M., Hogan, J. A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K. A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C. M., Izquierdo, J., Jackson, R. B., Jackson, B., Jactel, H., Jagodzinski, A. M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J. R. P., Jiang, G., Johansen, J. L., Johnson, D., Jokela, E. J., Joly, C. A., Jordan, G. J., Joseph, G. S., Junaedi, D., Junker, R. R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M. I., Kinlock, N. L., Kissling, W. D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J. M. H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N. J. B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D. J., Laughlin, D., Bagousse-Pinguet, Y. L., Maire, G., Roux, P. C., Roux, E., Lee, T., Lens, F., Lewis, S. L., Lhotsky, B., Li, Y., Li, X., Lichstein, J. W., Liebergesell, M., Lim, J. Y., Lin, Y., Linares, J. C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., Álvaro López-García, Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B. A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Pereira, C. M. R., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A. C. M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T. J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M. L., McCulloh, K., McFadden, I. R., McGill, B. J., McPartland, M. Y., Medeiros, J. S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F. P. L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S. T., Michelaki, C., Migalina, S., Milla, R., Miller, J. E. D., Minden, V., Ming, R., Mokany, K., Moles, A. T., Molnár, A., Molofsky, J., Molz, M., Montgomery, R. A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A. S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C. D., Müller, S. C., Munoz, F., Myers-Smith, I. H., Myster, R. W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A. S., Neuschulz, E. L., Ni, J., Niedrist, G., Nieto, J., Ülo Niinemets, Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Nystuen, K. O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M. E., Onipchenko, V., Onoda, Y., Onstein, R. E., Ordonez, J. C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G. E., Ozinga, W. A., Pahl, A. T., Paine, C. E. T., Pakeman, R. J., Papageorgiou, A. C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J. G., Peco, B., Penuelas, J., Perea, A., Peri, P. L., Petisco-Souza, A. C., Petraglia, A., Petritan, A. M., Phillips, O. L., Pierce, S., Pillar, V. D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A. S., Power, S. A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C. A., Reich, P. B., Reichstein, M., Reid, D. E. B., Réjou-Méchain, M., Dios, V. R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M. C., Riviera, F., Robert, E. M. R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A. V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J. A., Rosenfield, M. F., Rossi, C., Roy, D. B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S. B., Rusch, G. M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A. C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J. V., Schowanek, S. D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Garvizu, G. S., Semchenko, M., Seymour, C., Sfair, J. C., Sharpe, J. M., Sheppard, C. S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T. A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N. G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M. V., Sosinski, E. E., Soudzilovskaia, N. A., Souza, A. F., Spasojevic, M., Sperandii, M. G., Stan, A. B., Stegen, J., Steinbauer, K., Stephan, J. G., Sterck, F., Stojanovic, D. B., Strydom, T., Suarez, M. L., Svenning, J., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P. E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M. G., Tng, D. Y. P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J. M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J. L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., Bodegom, P. M., Breugel, M., Cleemput, E. V., Weg, M., Merwe, S., Plas, F., Sande, M. T., Kleunen, M., Meerbeek, K. V., Vanderwel, M., Vanselow, K. A., Vårhammar, A., Varone, L., Valderrama, M. Y. V., Vassilev, K., Vellend, M., Veneklaas, E. J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A. P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J. T., Wei, L., Weigelt, P., Weiher, E., Wells, A. W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P. J., Whitten, M., Williams, M., Winkler, D. E., Winter, K., Womack, C., Wright, I. J., Wright, S. J., Wright, J., Pinho, B. X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K. J., Zanne, A. E., Zelený, D., Zhao, Y., Zheng, J., Zheng, J., Ziemińska, K., Zirbel, C. R., Zizka, G., Zo-Bi, I. C., Zotz, G., and Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26:119–188.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Bodegom, P. M. V., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., III, F. S. C., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Guiterrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Lluisà, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., Müller, S. C., Nardowski, K., Naeem, S., Niinemetes, ., Nöllert, S., Nüske, A., Ogaya, R., Olesksyn, J., Onipchenko, V. G., Onoda, Y., Ordonez, J., Overbeck, G., Ozinga, W. A., Patino, S., Paula, S., Pausas, J. G., Penuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinisch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., and Wirth, C. (2011). TRY - a global database of plant traits. *Global Change Biology*, 17:2905–2935.

Kaufman, L. and Rousseeuw, P. J. (1990). Finding groups in data an introduction to cluster analysis.

Kazakou, E., Vile, D., Shipley, B., Gallet, C., and Garnier, E. (2006). Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology*, 20:21–30.

Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., and Garnier, E. (2009). Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. *Annals of Botany*, 104:1151–1161.

Köchy, M. (2006). Stochastic time series of daily precipitation for the interior of Israel. *Israel Journal of Earth Sciences*, 55:103–109.

Keeley, J. E. (2001). Fire and invasive species in Mediterranean-climate ecosystems of California. pages 81–94.

Kemanian, A. R., Julich, S., Manoranjan, V. S., and Arnold, J. R. (2011). Integrating soil carbon cycling with that of nitrogen and phosphorus in the watershed model SWAT: Theory and model testing. *Ecological Modelling*, 222:1913–1921.

Koirala, S. (2012). Effect of soil texture classification on global hydrology. *Proceedings of Annual Conference - Japan Society of Hydrology and Water Resources*, 25:240.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., and Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, 15:259–263.

Köppen, W. (1900). Versuch einer Klassifikation der Klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. *Geographische Zeitschrift*, 6:593–611.

Körner, C. and Miglietta, F. (1994). Long term effects of naturally elevated CO2 on Mediterranean grassland and forest trees. *Oecologia*, 99:343–351.

Laliberté, E., Legendre, P., and Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Laliberte, E. and Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91:299–305.

Landuyt, D., Perring, M., Seidl, R., Taubert, F., Verbeeck, H., and Verheyen, K. (2018). Modelling understorey dynamics in temperate forests under global change–challenges and perspectives. *Perspectives in Plant Ecology, Evolution and Systematics*, 31:44–54.

Laughlin, D. C. (2014a). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, 17:771–784.

Laughlin, D. C. (2014b). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102:186–193.

Lavergne, S., Garnier, E., and Debussche, M. (2003). Do rock endemic and widespread plant species differ under the leaf-height-seed plant ecology strategy scheme? *Ecology Letters*, 6:398–404.

Lavorel, S. and Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology*, 16:545–556.

Lavorel, S. and Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, 100:128–140.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G., and Douzet, R. (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, 99:135–147.

Lavorel, S., McIntyre, S., and Grigulis, K. (1999). Plant response to disturbance in a Mediterranean grassland: How many functional groups? *Journal of Vegetation Science*, 10:661–672.

Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., Hensel, M. J. S., Hector, A., Cardinale, B. J., and Duffy, J. E. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications*, 6:6936.

LeRoy, C. J., Wymore, A. S., Davis, R., and Marks, J. C. (2014). Indirect influences of a major drought on leaf litter quality and decomposition in a southwestern stream. *Fundamental and Applied Limnology*, 184:1–10.

Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J., and Li, B. (2008). Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist*, 177:706–714.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M. J., and Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, 259:698–709.

Liu, S. and Ng, G.-H. C. (2020). The role of spatiotemporal plant trait variability in model predictions of ecohydrological responses to climate change in a desert shrubland. *Journal of Hydrology*, 588:125088.

Lloret, F., Médail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P., and Hulme, P. E. (2005). Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology*, 93:512–520.

Lorilla, R., Poirazidis, K., Kalogirou, S., Detsis, V., and Martinis, A. (2018). Assessment of the spatial dynamics and interactions among multiple ecosystem services to promote effective policy making across Mediterranean island landscapes. *Sustainability*, 10:3285.

Lovell, S. T. and Johnston, D. M. (2009). Creating multifunctional landscapes: How can the field of ecology inform the design of the landscape? *Frontiers in Ecology and the Environment*, 7:212–220.

Luo, Y., Cadotte, M. W., Burgess, K. S., Liu, J., Tan, S., Zou, J., Xu, K., Li, D., and Gao, L. (2019). Greater than the sum of the parts: how the species composition in different forest strata influence ecosystem function. *Ecology Letters*, 22:1449–1461.

Luo, Y., El-Madany, T., Ma, X., Nair, R., Jung, M., Weber, U., Filippa, G., Bucher, S. F., Moreno, G., Cremonese, E., Carrara, A., Gonzalez-Cascon, R., Escudero, Y. C., Galvagno, M., Pacheco-Labrador, J., Martín, M. P., Perez-Priego, O., Reichstein, M., Richardson, A. D., Menzel, A., Römermann, C., and Migliavacca, M. (2020). Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. *Global Change Biology*, 26:4379–4400.

Luo, Y., Gerten, D., Maire, G. L., Parton, W. J., Weng, E., Zhou, X., Keough, C., Beier, C., Ciais, P., Cramer, W., Dukes, J. S., Emmett, B., Hanson, P. J., Knapp, A., Linder, S., Nepstad, D., and Rustad, L. (2008). Modeled interactive effects of precipitation, temperature, and CO2 on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, 14:1986–1999.

Lázaro-Nogal, A., Forner, A., Traveset, A., and Valladares, F. (2013). Contrasting water strategies of two Mediterranean shrubs of limited distribution: uncertain future under a drier climate. *Tree Physiology*, 33:1284–1295.

Mace, G. M., Norris, K., and Fitter, A. H. (2012). Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology & Evolution*, 27:19–26.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K. (2021). cluster: Cluster analysis basics and extensions. R package version 2.1.2.

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-baquerizo, M., García-gómez, M., a Bowker, M., Soliveres, S., Escolar, C., García-palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., a Conceição, A., and Cabrera, O. (2012a). Plant species richness and ecosystems multifunctionality in global drylands. *Science*, 335:2014–2017.

Maestre, F. T., Salguero-Gómez, R., and Quero, J. L. (2012b). It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367:3062–3075.

Manning, P., Newington, J. E., Robson, H. R., Saunders, M., Eggers, T., Bradford, M. A., Bardgett, R. D., Bonkowski, M., Ellis, R. J., Gange, A. C., Grayston, S. J., Kandeler, E., Marhan, S., Reid, E., Tscherko, D., Godfray, H. C. J., and Rees, M. (2006). Decoupling the direct and indirect effects of nitrogen deposition on ecosystem function. *Ecology Letters*, 9:1015–1024.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., Whittingham, M. J., and Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, 2:427–436.

Martin-StPaul, N. K., Limousin, J.-M., Vogt-Schilb, H., Rodríguez-Calcerrada, J., Rambal, S., Longepierre, D., and Misson, L. (2013). The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a throughfall exclusion experiment. *Global Change Biology*, 19:2413–2426.

Mastrotheodoros, T., Pappas, C., Molnar, P., Burlando, P., Keenan, T. F., Gentine, P., Gough, C. M., and Fatichi, S. (2017). Linking plant functional trait plasticity and the large increase in forest water use efficiency. *Journal of Geophysical Research: Biogeosciences*, 122:2393–2408.

Matteucci, G., Cammarano, M., Dezi, S., Mancini, M., Mugnozza, G. S., and Magnani, F. (2013). Climate change impacts on forests and forest products in the Mediterranean area. *Regional Assessment of Climate Change in the Mediterranean*, pages 71–100.

May, F., Grimm, V., and Jeltsch, F. (2009). Reversed effects of grazing on plant diversity: the role of below-ground competition and size symmetry. *Oikos*, 118:1830–1843.

McGill, B., Enquist, B., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21:178–185.

McLauchlan, K. K. (2006). Effects of soil texture on soil carbon and nitrogen dynamics after cessation of agriculture. *Geoderma*, 136:289–299.

Médail, F. and Quézel, P. (1997). Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. *Annals of the Missouri Botanical Garden*, 84:112–127.

Medlyn, B. E., Zaehle, S., Kauwe, M. G. D., Walker, A. P., Dietze, M. C., Hanson, P. J., Hickler, T., Jain, A. K., Luo, Y., Parton, W., Prentice, I. C., Thornton, P. E., Wang, S., Wang, Y.-P., Weng, E., Iversen, C. M., Mccarthy, H. R., Warren, J. M., Oren, R., and Norby, R. J. (2015). Using ecosystem experiments to improve vegetation models the assumption-centred approach. *Nature Publishing Group.*

Medrano, H., Flexas, J., and Galmés, J. (2009). Variability in water use efficiency at the leaf level among Mediterranean plants with different growth forms. *Plant and Soil*, 317:17–29.

Messier, J., McGill, B. J., Enquist, B. J., and Lechowicz, M. J. (2017). Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography*, 40:685–697.

Meyer, S. T., Ptacnik, R., Hillebrand, H., Bessler, H., Buchmann, N., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Halle, S., Klein, A.-M., Oelmann, Y., Roscher, C., Rottstock, T., Scherber, C., Scheu, S., Schmid, B., Schulze, E.-D., Temperton, V. M., Tscharntke, T., Voigt, W., Weigelt, A., Wilcke, W., and Weisser, W. W. (2018). Biodiversity–multifunctionality relationships depend on identity and number of measured functions. *Nature Ecology & Evolution*, 2:44–49.

Meyer-Grünefeldt, M., Friedrich, U., Klotz, M., Oheimb, G. V., and Härdtle, W. (2015). Nitrogen deposition and drought events have non-additive effects on plant growth – evidence from greenhouse experiments. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 149:424–432.

Millennium Ecosystem Assessment (2005). Ecosystems and human well-being: Synthesis.

Monteith, J. (1995). Accommodation between transpiring vegetation and the convective boundary layer. *Journal of Hydrology*, 166:251–263.

Moore, A. D. and Noble, I. R. (1990). An individualistic model of vegetation stand dynamics. *Journal of Environmental Management*, 31:61–81.

Mori, A. S., Furukawa, T., and Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, 88:349–364.

Morillas, L., Bellucco, V., Cascio, M. L., Marras, S., Spano, D., and Mereu, S. (2017). Contribution of biological crust to soil CO2 efflux in a Mediterranean shrubland ecosystem. *Geoderma*, 289:11–19.

Moriondo, M., Good, P., Durao, R., Bindi, M., Giannakopoulos, C., and Corte-Real, J. (2006). Potential impact of climate change on fire risk in the Mediterranean area. *Climate Research*, 31:85–95.

Mouillot, F., Rambal, S., and Lavorel, S. (2001). A generic process-based SImulator for Mediterranean landscApes (SIERRA): design and validation exercises. *Forest Ecology and Management*, 147:75–97.

Muler, A. L., Canham, C. A., van Etten, E. J., Stock, W. D., and Froend, R. H. (2018). Using a functional ecology approach to assist plant selection for restoration of Mediterranean woodlands. *Forest Ecology and Management*, 424:1–10.

Murphy, B. P., Russel-Smith, J., and Prior, L. D. (2010). Frequent fires reduce tree growth in northern Australian savannas: implications for tree demography and carbon sequestration. *Global Change Biology*, 16:331–343.

Myers, N. (1990). The biodiversity challenge: Expanded hot-spots analysis. *The Environmentalist*, 10:243–256.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403:853–858.

Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R. E., Lehner, B., Malcolm, T. R., and Ricketts, T. H. (2008). Global mapping of ecosystem services and conservation priorities. *Proceedings of the National Academy of Sciences*, 105:9495–9500.

Nainggolan, D., Termansen, M., Reed, M. S., Cebollero, E. D., and Hubacek, K. (2013). Farmer typology, future scenarios and the implications for ecosystem service provision: a case study from south-eastern Spain. *Regional Environmental Change*, 13:601–614.

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Chan, K. M., Daily, G. C., Goldstein, J., Kareiva, P. M., Lonsdorf, E., Naidoo, R., Ricketts, T. H., and Shaw, M. R. (2009). Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, 7:4–11.

NOAA (2020a). CPC global daily temperature. https://psl.noaa.gov/data/gridded/data.cpc.globaltemp.html.

NOAA (2020b). CPC global unified gauge-based analysis of daily precipitation. https://psl.noaa.gov/data/gridded/data.cpc.globalprecip.html.

Norby, R. J. (2011). Ecological and evolutionary lessons from free air carbon enhancement (FACE) experiments. *Annual Review of Ecology, Evolution, and Systematics*, 42.

Norby, R. J., Kauwe, M. G. D., Domingues, T. F., Duursma, R. A., Ellsworth, D. S., Goll, D. S., Lapola, D. M., Luus, K. A., MacKenzie, A. R., Medlyn, B. E., Pavlick, R., Rammig, A., Smith, B., Thomas, R., Thonicke, K., Walker, A. P., Yang, X., and Zaehle, S. (2016). Model–data synthesis for the next generation of forest free-air CO2 enrichment (FACE) experiments. *New Phytologist*, 209:17–28.

Nunes, L., Gower, S. T., Peckham, S. D., Magalhaes, M., Lopes, D., and Rego, F. C. (2015). Estimation of productivity in pine and oak forests in northern Portugal using Biome-BGC. *Forestry*, 88:200–212.

Ochoa-Hueso, R., Maestre, F. T., de los Ríos, A., Valea, S., Theobald, M. R., Vivanco, M. G., Manrique, E., and Bowker, M. A. (2013). Nitrogen deposition alters nitrogen cycling and reduces soil carbon content in low-productivity semiarid Mediterranean ecosystems. *Environmental Pollution*, 179:185–193.

Ochoa-Hueso, R. and Stevens, C. J. (2015). European semiarid Mediterranean ecosystems are sensitive to nitrogen deposition: Impacts on plant communities and root phosphatase activity. *Water, Air, & Soil Pollution*, 226:5.

Oijen, M. V., Rougier, J., and Smith, R. (2005). Bayesian calibration of process-based forest models: bridging the gap between models and data. *Tree Physiology*, 25:915–927.

Oreskes, N., Shrader-Frechette, K., and Belitz, K. (1994). Verification, validation, and confirmation of numerical models in the earth sciences. *Science*, 263:641–646.

Pacala, S. W. and Deutschman, D. H. (1995). Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos*, 74:357.

Padilla, F. M., Ortega, R., Sánchez, J., and Pugnaire, F. I. (2009). Rethinking species selection for restoration of arid shrublands. *Basic and Applied Ecology*, 10:640–647.

Palahi, M., Mavsar, R., Gracia, C., and Birot, Y. (2008). Mediterranean forests under focus. *International Forestry Review*, 10:676–688.

Paula, S. and Pausas, J. G. (2008). Burning seeds: germinative response to heat treatments in relation to resprouting ability. *Journal of Ecology*, 96:543–552.

Pausas, J. G. (1999). Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach. *Journal of Vegetation Science*, 10:717–722.

Pausas, J. G., Bladé, C., Valdecantos, A., Seva, J. P., Fuentes, D., Alloza, J. A., Vilagrosa, A., Bautista, S., Cortina, J., and Vallejo, R. (2004). Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice – a review. *Plant Ecology*, 171:209–220.

Peel, M. C., Finlayson, B. L., and McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11:1633–1644.

Pereira, J. S., Mateus, J. A., Aires, L. M., Pita, G., Pio, C., David, J. S., Andrade, V., Banza, J., David, T. S., Paço, T. A., and Rodrigues, A. (2007). Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems – the effect of drought. *Biogeosciences*, 4:791–802.

Perring, M. P., Standish, R. J., Hulvey, K. B., Lach, L., Morald, T. K., Parsons, R., Didham, R. K., and Hobbs, R. J. (2012). The Ridgefield multiple ecosystem services experiment: Can restoration of former agricultural land achieve multiple outcomes? *Agriculture, Ecosystems & Environment*, 163:14–27.

Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof, K. X., Whiteley, A. S., Valentine, L. E., and Hobbs, R. J. (2015). Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere*, 6:art131.

Pescador, D. S., de Bello, F., Valladares, F., and Escudero, A. (2015). Plant trait variation along an altitudinal gradient in Mediterranean high mountain grasslands: Controlling the species turnover effect. *PLOS ONE*, 10:e0118876.

Peterson, R. A. and Cavanaugh, J. E. (2020). Ordered quantile normalization: a semiparametric transformation built for the cross-validation era. *Journal of Applied Statistics*, 47:2312–2327.

Pierce, L. L., Running, S. W., and Walker, J. (1994). Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. *Ecological Applications*, 4:313–321.

Pillar, V. D. (1999). On the identification of optimal plant functional types. *Journal of Vegetation Science*, 10:631–640.

Plas, F., Allan, E., Fischer, M., Alt, F., Arndt, H., Binkenstein, J., Blaser, S., Blüthgen, N., Böhm, S., Hölzel, N., Klaus, V. H., Kleinebecker, T., Morris, K., Oelmann, Y., Prati, D., Renner, S. C., Rillig, M. C., Schaefer, H. M., Schloter, M., Schmitt, B., Schöning, I., Schrumpf, M., Solly, E. F., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Weiner, C. N., Weisser, W. W., Werner, M., Westphal, C., Wilcke, W., and Manning, P. (2019). Towards the development of general rules describing landscape heterogeneity–multifunctionality relationships. *Journal of Applied Ecology*, 56:168–179.

Plas, F. V. D., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D. A., Coppi, A., Bestias, C. C., Dawud, S. M., Wandeler, H. D., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F. X., Jucker, T., Koricheva, J., Milligan, H., Mueller, S., Muys, B., Nguyen, D., Pollastrini, M., Ratcliffe, S., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielinski, D., and Fischer, M. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences*, 113:E2549–E2549.

Porada, P., Weber, B., Elbert, W., Pöschl, U., and Kleidon, A. (2013). Estimating global carbon uptake by lichens and bryophytes with a process-based model. *Biogeosciences*, 10:6989–7033.

Pérez-Camacho, L., Rebollo, S., Hernández-Santana, V., García-Salgado, G., Pavón-García, J., and Gómez-Sal, A. (2012). Plant functional trait responses to interannual rainfall variability, summer drought and seasonal grazing in Mediterranean herbaceous communities. *Functional Ecology*, 26:740–749.

Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Roupsard, O., Thammahacksa, C., and Stokes, A. (2015). Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology*, 103:361–373.

R Core Team (2021). R: A language and environment for statistical computing.

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Chećko, E., Dawud, S. M., Wandeler, H. D., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L., and Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, 20:1414–1426.

Rawls, W. J., Ahuja, L. R., Brakensiek, D. L., and Shirmohammadi, A. (1992). Infiltration and soil water movement. McGraw-Hill Professional, 1 edition.

Rawls, W. J., Gimenez, D., and Grossman, R. (1998). Use of soil texture, bulk density, and slope of the water retention curve to predict saturated hydraulic conductivity. *Transactions of the ASAE*, 41:983–988.

Reinecke, R., Schmied, H. M., Trautmann, T., Andersen, L. S., Burek, P., Flörke, M., Gosling, S. N., Grillakis, M., Hanasaki, N., Koutroulis, A., Pokhrel, Y., Thiery, W., Wada, Y., Yusuke, S., and Döll, P. (2021). Uncertainty of simulated groundwater recharge at different global warming levels: a global-scale multi-model ensemble study. *Hydrology and Earth System Sciences*, 25:787–810.

Resch, M. C., Schütz, M., Buchmann, N., Frey, B., Graf, U., Putten, W. H., Zimmermann, S., and Risch, A. C. (2021). Evaluating long-term success in grassland restoration: an ecosystem multifunctionality approach. *Ecological Applications*, 31.

Reuter, H., Jopp, F., Breckling, B., Lange, C., and Weigmann, G. (2011). How valid are model results? assumptions, validity range and documentation. pages 323–340. Springer.

Rick, T., Ángel Cau Ontiveros, M., Jerardino, A., Mariotti, A., Méndez, C., and Williams, A. N. (2020). Human-environmental interactions in Mediterranean climate regions from the Pleistocene to the Anthropocene. *Anthropocene*, 31:100253.

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, 48:1–36.

Rouget, M., Richardson, D. M., Cowling, R. M., Lloyd, J., and Lombard, A. T. (2003). Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape floristic region, South Africa. *Biological Conservation*, 112:63–85.

Rout, M. E. and Callaway, R. M. (2009). An invasive plant paradox. *Science*, 324:734–735.

Ruget, F., Brisson, N., Delécolle, R., and Faivre, R. (2002). Sensitivity analysis of a crop simulation model, stics, in order to choose the main parameters to be estimated. *Agronomie*, 22:133–158.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., and Zavala, M. A. (2014). Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography*, 23:311–322.

Ruiz-Benito, P., Lines, E. R., Gómez-Aparicio, L., Zavala, M. A., and Coomes, D. A. (2013). Patterns and drivers of tree mortality in Iberian forests: Climatic effects are modified by competition. *PLoS ONE*, 8:e56843.

Rundel, P. W. (1998). Landscape disturbance in Mediterranean-type ecosystems: An overview. pages 3–22. Springer.

Rundel, P. W. and Cowling, R. M. (2013). Mediterranean-climate ecosystems. volume 5, pages 212–222. Elsevier.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., and Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126:543–562.

Sala, O. E. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287:1770–1774.

Sans, F., Garcia-Serrano, H., and Afán, I. (2004). Life-history traits of alien and native senecio species in the Mediterranean region. *Acta Oecologica*, 26:167–178.

Santini, M., Collalti, A., and Valentini, R. (2014). Climate change impacts on vegetation and water cycle in the Euro-Mediterranean region, studied by a likelihood approach. *Regional Environmental Change*, 14:1405–1418.

Sargent, R. G. (2013). Verification and validation of simulation models. *Journal of Simulation*, 7:12–24.

Sariyildiz, T., Anderson, J., and Kucuk, M. (2005). Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biology and Biochemistry*, 37:1695–1706.

Schaphoff, S., von Bloh, W., Rammig, A., Thonicke, K., Biemans, H., Forkel, M., Gerten, D., Heinke, J., Jägermeyr, J., Knauer, J., Langerwisch, F., Lucht, W., Müller, C., Rolinski, S., and Waha, K. (2018). LPJmL4 – a dynamic global vegetation model with managed land – part 1: Model description. *Geoscientific Model Development*, 11:1343–1375.

Schwarz, M. T., Bischoff, S., Blaser, S., Boch, S., Schmitt, B., Thieme, L., Fischer, M., Michalzik, B., Schulze, E.-D., Siemens, J., and Wilcke, W. (2014). More efficient aboveground nitrogen use in more diverse Central European forest canopies. *Forest Ecology and Management*, 313:274–282.

Shackelford, N., Hobbs, R. J., Burgar, J. M., Erickson, T. E., Fontaine, J. B., Laliberté, E., Ramalho, C. E., Perring, M. P., and Standish, R. J. (2013). Primed for change: Developing ecological restoration for the 21st century. *Restoration Ecology*, 21:297–304.

Simpson, K. J., Ripley, B. S., Christin, P., Belcher, C. M., Lehmann, C. E. R., Thomas, G. H., and Osborne, C. P. (2016). Determinants of flammability in savanna grass species. *Journal of Ecology*, 104:138–148.

Sitch, S., Prentice, I. C., Smith, B., Cramer, W., Kaplan, J. O., Lucht, W., Sykes, M., Thonicke, K., and Venevsky, S. (2000). LPJ - a coupled model of vegetation dynamics and the terrestrial carbon cycle. *The Role of Vegetation Dynamics in the Control of Atmospheric CO2 Content, Ph.D. Thesis.*

Sitch, S., Smith, B., Prentice, I. C., a. Arneth, a. Bondeau, Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, 9:161–185.

Smith, B., Prentice, I. C., and Sykes, M. T. (2001). Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, 10:621–637.

Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, 11:2027–2054.

Smith, N. G. and Dukes, J. S. (2013). Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO2. *Global Change Biology*, 19:45–63.

Society for Ecological Restoration (2004). The SER international primer on ecological restoration.

Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Hölzel, N., Jung, K., Klaus, V. H., Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E. K., Müller, J., Oelmann, Y., Overmann, J., Pašalić, E., Rillig, M. C., Schaefer, H. M., Schloter, M., Schmitt, B., Schöning, I., Schrumpf, M., Sikorski, J., Socher, S. A., Solly, E. F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Türke, M., Venter, P. C., Weiner, C. N., Weisser, W. W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M., and Allan, E. (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, 536:456–459.

Southon, G. E., Field, C., Caporn, S. J. M., Britton, A. J., and Power, S. A. (2013). Nitrogen deposition reduces plant diversity and alters ecosystem functioning: Field-scale evidence from a nationwide survey of UK heathlands. *PLoS ONE*, 8:e59031.

Stanisci, A., Acosta, A. T. R., Iorio, A. D., and Vergalito, M. (2010). Leaf and root trait variability of alien and native species along adriatic coastal dunes (Italy). *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 144:47–52.

Stekhoven, D. J. and Buhlmann, P. (2012). Missforest–non-parametric missing value imputation for mixed-type data. *Bioinformatics*, 28:112–118.

Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B., and Schwartz, K. Z. S. (2015). Committing to ecological restoration. *Science*, 348:638–640.

Suding, K. N. and Goldstein, L. J. (2008). Testing the holy grail framework: using functional traits to predict ecosystem change. *New Phytologist*, 180:559–562.

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., and Navas, M.-L. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14:1125–1140.

Sun, J. and Du, W. (2017). Effects of precipitation and temperature on net primary productivity and precipitation use efficiency across China's grasslands. *GIScience & Remote Sensing*, 54:881–897.

Targetti, S., Messeri, A., Staglianò, N., and Argenti, G. (2013). Leaf functional traits for the assessment of succession following management in semi-natural grasslands: a case study in the North Apennines, Italy. *Applied Vegetation Science*, 16:325–332.

Tavares, A., Dias, C., Rosado, B. H. P., Bello, F. D., Pistón, N., and Mattos, E. A. D. (2020). Alternative plant designs: consequences for community assembly and ecosystem functioning. *Annals of Botany*, 125:391–398.

Teixeira, L. H., Oliveira, B. F., Krah, F.-S., Kollmann, J., and Ganade, G. (2020). Linking plant traits to multiple soil functions in semi-arid ecosystems. *Journal of Arid Environments*, 172:104040.

Thomas, H. J., Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Kattge, J., Diaz, S., Vellend, M., Blok, D., Cornelissen, J. H., Forbes, B. C., Henry, G. H., Hollister, R. D., Normand, S., Prevéy, J. S., Rixen, C., Schaepman-Strub, G., Wilmking, M., Wipf, S., Cornwell, W. K., Beck, P. S., Georges, D., Goetz, S. J., Guay, K. C., Rüger, N., Soudzilovskaia, N. A., Spasojevic, M. J., Alatalo, J. M., Alexander, H. D., Anadon-Rosell, A., Angers-Blondin, S., te Beest, M., Berner, L. T., Björk, R. G., Buchwal, A., Buras, A., Carbognani, M., Christie, K. S., Collier, L. S., Cooper, E. J., Elberling, B., Eskelinen, A., Frei, E. R., Grau, O., Grogan, P., Hallinger, M., Heijmans, M. M., Hermanutz, L., Hudson, J. M., Johnstone, J. F., Hülber, K., Iturrate-Garcia, M., Iversen, C. M., Jaroszynska, F., Kaarlejarvi, E., Kulonen, A., Lamarque, L. J., Lantz, T. C., Lévesque, E., Little, C. J., Michelsen, A., Milbau, A., Nabe-Nielsen, J., Nielsen, S. S., Ninot, J. M., Oberbauer, S. F., Olofsson, J., Onipchenko, V. G., Petraglia, A., Rumpf, S. B., Shetti, R., Speed, J. D., Suding, K. N., Tape, K. D., Tomaselli, M., Trant, A. J., Treier, U. A., Tremblay, M., Venn, S. E., Vowles, T., Weijers, S., Wookey, P. A., Zamin, T. J., Bahn, M., Blonder, B., van Bodegom, P. M., Bond-Lamberty, B., Campetella, G., Cerabolini, B. E., Chapin, F. S., Craine, J. M., Dainese, M., Green, W. A., Jansen, S., Kleyer, M., Manning, P., Niinemets, Onoda, Y., Ozinga, W. A., Peñuelas, J., Poschlod, P., Reich, P. B., Sandel, B., Schamp, B. S., Sheremetiev, S. N., and de Vries, F. T. (2020). Global plant trait relationships extend to the climatic extremes of the tundra biome. *Nature Communications*, 11.

Thomson, F. J., Moles, A. T., Auld, T. D., and Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, 99:1299–1307.

Tietjen, B., Jeltsch, F., Zehe, E., Classen, N., Groengroeft, A., Schiffers, K., and Oldeland, J. (2009a). Effects of climate change on the coupled dynamics of water and vegetation in drylands. *Ecohydrology*, 3:226–237.

Tietjen, B., Zehe, E., and Jeltsch, F. (2009b). Simulating plant water availability in dry lands under climate change: A generic model of two soil layers. *Water Resources Research*, 45:W01418.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277:1300–1302.

USDA (2020). Soil texture calculator. https://www.nrcs.usda.gov.

Valencia, E., Maestre, F. T., Bagousse-Pinguet, Y. L., Quero, J. L., Tamme, R., Börger, L., García-Gómez, M., and Gross, N. (2015). Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist*, 206:660–671.

Valera-Burgos, J., Zunzunegui, M., and Díaz-Barradas, M. C. (2013). Do leaf traits and nitrogen supply affect decomposability rates of three Mediterranean species growing under different competition levels? *Pedobiologia*, 56:113–119.

Vallejo, R., Aronson, J., Pausas, J. G., and Cortina, J. (2001). Restoration of Mediterranean woodlands. pages 193–207. Blackwell Science.

Vallejo, V. R., Allen, E. B., Aronson, J., Pausas, J. G., Cortina, J., and Gutiérrez, J. R. (2012). Restoration of Mediterranean-type woodlands and shrublands. pages 1–22. Wiley-Blackwell, 2nd edition.

van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D., Coppi, A., Bastias, C. C., Dawud, S. M., Wandeler, H. D., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Koricheva, J., Milligan, H., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielínski, D., and Fischer, M. (2016). Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in european forests. *Nature communications*, 7:11109.

van der Plas, F., Schröder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R. L., Buchmann, N., de Kroon, H., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Gleixner, G., Hildebrandt, A., Koller-France, E., Leimer, S., Milcu, A., Mommer, L., Niklaus, P. A., Oelmann, Y., Roscher, C., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Schmid, B., Schulze, E.-D., Temperton, V., Tscharntke, T., Voigt, W., Weisser, W., Wilcke, W., and Wirth, C. (2020). Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution*, 4:1602–1611.

van Lissa, C. J. (2021). tidySEM: Tidy structural equation modeling. R package version 0.1.8.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., and Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14:702–708.

Vilà, M. and Sardans, J. (1999). Plant competition in Mediterranean-type vegetation. *Journal of Vegetation Science*, 10:281–294.

Vilà-Cabrera, A., Martínez-Vilalta, J., and Retana, J. (2015). Functional trait variation along environmental gradients in temperate and Mediterranean trees. *Global Ecology and Biogeography*, 24:1377–1389.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116:882–892.

Vourlitis, G. L., Pasquini, S. C., and Mustard, R. (2009). Effects of dry-season N input on the productivity and N storage of Mediterranean-type shrublands. *Ecosystems*, 12:473–488.

Vries, F. T. D. and Bardgett, R. D. (2016). Plant community controls on short-term ecosystem nitrogen retention. *New Phytologist*, 210:861–874.

Walker, A. P., Kauwe, M. G. D., Medlyn, B. E., Zaehle, S., Iversen, C. M., Asao, S., Guenet, B., Harper, A., Hickler, T., Hungate, B. A., Jain, A. K., Luo, Y., Lu, X., Lu, M., Luus, K., Megonigal, J. P., Oren, R., Ryan, E., Shu, S., Talhelm, A., Wang, Y.-P., Warren, J. M., Werner, C., Xia, J., Yang, B., Zak, D. R., and Norby, R. J. (2019). Decadal biomass increment in early secondary succession woody ecosystems is increased by CO2 enrichment. *Nature Communications*, 10:454.

Walter, H. and Lieth, H. (1967). *Klimadiagramm-Weltatlas.* Gustav Fischer Verlag.

Wang, C., Zhang, H., Liu, H., Jian, S., Yan, J., and Liu, N. (2020). Application of a trait-based species screening framework for vegetation restoration in a tropical coral island of China. *Functional Ecology*, 34:1193–1204.

Wen, Z., Zheng, H., Smith, J. R., Zhao, H., Liu, L., and Ouyang, Z. (2019). Functional diversity overrides community-weighted mean traits in linking land-use intensity to hydrological ecosystem services. *Science of the Total Environment*, 682:583–590.

Werner, C., Zumkier, U., Beyschlag, W., and Máguas, C. (2010). High competitiveness of a resource demanding invasive acacia under low resource supply. *Plant Ecology*, 206:83–96.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199:213–227.

Wolkovich, E. M., Lipson, D. A., Virginia, R. A., Cottingham, K. L., and Bolger, D. T. (2010). Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. *Global Change Biology*, 16:1351–1365.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Ülo Niinemets, Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428:821–827.

Wright, J. P. and Sutton-Grier, A. (2012). Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology*, 26:1390–1398.

Wu, L., McGechan, M., McRoberts, N., Baddeley, J., and Watson, C. (2007). Spacsys: Integration of a 3D root architecture component to carbon, nitrogen and water cycling—model description. *Ecological Modelling*, 200:343–359.

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., Kattge, J., Norby, R. J., van Bodegom, P. M., and Xu, X. (2014). Plant functional types in earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany*, 114:1–16.

Xu, Z., Shimizu, H., Yagasaki, Y., Ito, S., Zheng, Y., and Zhou, G. (2013). Interactive effects of elevated CO2, drought, and warming on plants. *Journal of Plant Growth Regulation*, 32:692–707.

Yates, M. J., Verboom, G. A., Rebelo, A. G., and Cramer, M. D. (2010). Ecophysiological significance of leaf size variation in proteaceae from the Cape floristic region. *Functional Ecology*, 24:485–492.

Zakharova, L., Meyer, K. M., and Seifan, M. (2019). Trait-based modelling in ecology: A review of two decades of research. *Ecological Modelling*, 407:108703.

Zirbel, C. R., Bassett, T., Grman, E., and Brudvig, L. A. (2017). Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *Journal of Applied Ecology*, 54:1070–1079.

Zirbel, C. R., Grman, E., Bassett, T., and Brudvig, L. A. (2019). Landscape context explains ecosystem multifunctionality in restored grasslands better than plant diversity. *Ecology*, 100:1–11.

Zwetsloot, M. J., Leeuwen, J., Hemerik, L., Martens, H., Josa, I. S., Broek, M., Debeljak, M., Rutgers, M., Sandén, T., Wall, D. P., Jones, A., and Creamer, R. E. (2021). Soil multifunctionality: Synergies and trade-offs across european climatic zones and land uses. *European Journal of Soil Science*, 72:1640–1654.