THE ROLE OF LEAF TRAITS IN FOREST ECOSYSTEMS: MEDIATORS IN THE RELATIONSHIP BETWEEN BIODIVERSITY AND ECOSYSTEM FUNCTIONS

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To Mariumti, your love carried me through this journey,
and for that, I am endlessly grateful.

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Zusammenfassung

Die Analyse von Blattmerkmalen ist ein wichtiger Bestandteil der modernen Waldökologie, da Ökosystemfunktionen wie Wachstum und Nährstoffkreisläufe eng mit dem Blattwerk der Bäume verbunden sind. Die merkmalsbasierte Ökologie konzentrierte sich traditionell auf Artunterschiede, was wichtige Erkenntnisse zu Wechselwirkungen mit Ökosystemfunktionen lieferte. Darüber hinaus konnte dieses Forschungsgebiet innerhalb der letzten Jahrzehnte durch die Miteinbeziehung der innerartlichen Variation von Blattmerkmalen weiter voran getrieben werden. Jedoch sind die Ursachen und Auswirkungen der Blattmerkmale innerhalb von Individuen, besonders in Waldökosystemen, wenig erforscht. Dabei könnte gerade hier die Untersuchung Intra-individueller Variation der Blattmerkmale dazu beitragen, unser Verständnis dieser Ökosysteme weiter zu verbessern. Trends die auf der Ebene eines kompletten Waldökosystems zu beobachten sind, gehen letztendlich auf Abwägungen zwischen Ressourcenerwerb und -erhaltung zurück, die individuell von einzelnen Individuen getroffen werden. Um diese Ökosystemprozesse zu verstehen, ist es daher entscheidend, diese Prozesse innerhalb von Individuen zu untersuchen.

Blattmerkmale und ihre Variation sind stark von der lokalen Lichtverfügbarkeit beeinflusst, welche wiederum von der Artenvielfalt abhängt. Es gibt einen ausgeprägten Lichtgradient innerhalb der Baumkronen, der einen entsprechenden Gradienten der Blattmerkmale verursacht. Die lokale Artenvielfalt – besonders der lokale Nachbar eines Baumes – die Blattmerkmale unabhängig von deren Einfluss auf die Lichtverfügbarkeit beeinflussen, etwa durch unterschiedliche Nutzung der Bodenressourcen. Jedoch fehlen Erkenntnisse, inwiefern sich diese Prozesse zwischen verschiedenen Klimazonen unterscheiden. Zudem sind Studien, die mehrere Arten einbeziehen um intraindividuelle Effekte zu verallgemeinern, rar.

Der Schwerpunkt der vorliegenden Arbeit liegt auf der Untersuchung der Rolle von Blattmerkmalen in Waldökosystemen. Insbesondere soll auf die Frage eingegangen werden, inwiefern Blattmerkmale und deren Variation innerhalb von Individuen auf die umliegende Artenvielfalt und die Lichtverfügbarkeit reagieren, und wie sich diese Prozesse auf das Baumwachstum auswirken. Kapitel zwei bis vier betrachten unterschiedliche Aspekte dieses Themas: vom Einfluss der Artenvielfalt auf Blattmerkmale, über deren Wechselwirkung mit Licht, bis zur Auswirkungen auf Baumwachstum. Die Kapitel stützen sich auf Biodiversitätsexperimente in verschiedenen Klimazonen, um breite Erkenntnisse für die Waldökologie abzuleiten.

Kapitel zwei basiert auf Studien im tropischen Regenwald (Sardinilla Biodiversitätsexperiment, Panama). Es wird untersucht, wie Blattmerkmale und ihre Variation auf Änderungen in der Artenvielfalt reagieren. Die vertikale Position in der

Baumkrone wurde als Quelle für die Blattmerkmalsvariation identifiziert. Dies impliziert, dass die lokale Lichtverfügbarkeit ein wichtiger Einflussfaktor für Blattmerkmale ist. Weiterhin wurde gezeigt, das die Variation mehrerer Blattmerkmale mit zunehmender Artenvielfalt abnimmt, sowohl auf Arten- als auch auf Individuen Ebene. Diese Ergebnisse deuten darauf hin, dass bei höherem Artenreichtum die Ressourcenaufnahme sowohl individuell als auch auf Ebene der gesamten Versuchsfläche optimiert wird.

In Kapitel drei werden Interaktionen zwischen Blattmerkmalen und Lichtverfügbarkeit im Kontext der Artenvielfalt untersucht. Die zugrunde liegenden Untersuchungen wurden im subtropischen BEF-China Biodiversitätsexperiment durchgeführt. In artenreichen Wäldern ist zu erwarten, dass das verfügbare Licht innerhalb der Baumkrone weitgehend absorbiert wird und der resultierende Lichtgradient die Blattmerkmale innerhalb der Krone beeinflusst. Tatsächlich konnte in diesem Kapitel durch detaillierte Messungen der lokalen Lichtverfügbarkeit und Blattmerkmale innerhalb einzelner Individuen gezeigt werden, dass der Lichtgradient innerhalb des Individuums die meisten Blattmerkmale stark beeinflusst, besonders in artenreichen Umgebungen. Zudem beeinflusst die lokale Artenvielfalt und der direkte Baumnachbar die Blattmerkmale auch jenseits ihrer Wirkung auf die Lichtverhältnisse.

Kapitel vier verknüpft Erkenntnisse über Blattmerkmalsvariation und Lichtverfügbarkeit mit deren Einfluss auf das Baumwachstum. Die zugrunde liegenden Untersuchungen wurden im Kreinitz Biodiversitätsexperiment (nahe Riesa, Sachsen) durchgeführt. Es konnte gezeigt werden, dass ein indirekter Zusammenhang zwischen Artenvielfalt und Baumwachstum besteht, der über die Variation der Blattmerkmale der einzelnen Bäume vermittelt wird. Darüber hinaus wird die Variation der Blattmerkmale innerhalb eines Individuums durch die Lichtverfügbarkeit modifiziert. In Monokulturen weisen Bäume eine höhere Blattmerkmalsvariation auf, die eine effizientere Ressourcennutzung ermöglichen könnte. Dies könnte dazu beitragen, einen Rückgang des Baumwachstums in Monokulturen zu kompensieren, sodass ein direkter Effekt der Artenvielfalt auf das Wachstum hier verdeckt wird.

Die Ergebnisse dieser Arbeit zeigen, dass Blattmerkmale und ihre Variation auf Ebene einzelner Individuen wichtige Faktoren sind, die Artenvielfalt und Ökosystemfunktionen miteinander verbinden. Die wichtigsten Anpassungen – vor allem die Abstimmung von Ressourcenerwerb und -erhaltung finden auf Blattebene statt. Diese Prozesse laufen offenbar unabhängig von Klimazone und Baumart, sowohl für immergrüne also auch für laubabwerfende Bäume ab. Diese Erkenntnisse betonen die Notwenigkeit, die Variation von Blattmerkmalen innerhalb von Individuen in die ökologische Forschung einzubeziehen.

Summary

The analysis of leaf traits is an integral part of modern forest ecology, since important ecosystem functions, such as growth and nutrient cycling are inherently linked to the trees' foliage. Traditional trait based ecology focused on species mean traits, which vastly improved our understanding of the interaction of leaf traits with ecosystem functions. Moreover, the topic of leaf trait variation within species received significant attention in the last decades, further progressing this field of research. However, the variation of leaf traits within individuals – especially in forest ecosystems – is still rarely accounted for. Yet, investigating within-individual leaf trait variation could help to improve our understanding of forest ecosystems. This is because trends at the ecosystem level naturally emerge from the individuals of the ecosystem. It is at the individual level, where essential trade-offs between resource acquisition and conservation are made. Hence, in order to understand ecosystems, it is important to understand individuals.

Leaf traits and their variations are influenced by the local light availability at the individual level, which is, in turn, affected by the surrounding biodiversity. Trees have a pronounced within-individual light gradient, which alters leaf traits along this gradient. Furthermore, the biodiversity surrounding an individual tree and especially its direct neighbour might influence the leaf traits beyond their dependency on light, such as through soil resource complementary. However, it is rarely taken into account how these processes differ between biomes. Furthermore, studies that generalize within-individual effects across multiple species and also incorporate possible differences emerging from different leaf habits are scarce.

This thesis analyses the role of leaf traits in forest ecosystems. Specifically their response to surrounding biodiversity and light availability and their impact on tree growth. Chapters 2 to 4 of the thesis focus on different aspects of the role of leaf traits in forest ecosystems. Beginning with the influence of biodiversity on leaf traits and their variation, over the interaction between leaf traits, biodiversity and light availability, to the impact of these factors on tree growth. The chapters are based on biodiversity experiments in different biomes, which helps to generalise the findings and draw broader implications for forest ecology.

Chapter 2 is located in the tropical rainforest plantation of the Sardinilla experiment in Panama. This chapter primarily addresses the question, how leaf traits and their variation respond to different levels of biodiversity, which is here represented in the form of the number of different tree species surrounding an individual. In a first step, the vertical location within a trees' crown is identified as one of the sources of trait variation of a leaf sample. This implies that the local light availability is an important

influencing factor on leaf traits, because of the inherent light gradient within tree crowns. In a second step it is demonstrated that the variation of several leaf traits decreases with increasing tree species richness, both on the species level and the individual level. These results suggest an increased niche partitioning with increased species richness, optimizing resource acquisition both at the community and individual plant levels.

In *Chapter 3*, the interaction between leaf traits and light availability, as well as their response to changes in tree species richness is further explored. The chapter is located in the highly diverse subtropical forest plantation of the BEF-China experiment. Such a species rich environment is expected to result in a high light utilisation within the canopy, which in turn influences its leaf traits. Indeed, by taking detailed measurements of local light availability and leaf traits at the within-individual level, this chapter clearly demonstrates that the within individual light gradient strongly influences most leaf traits, especially in species rich environments. Moreover, the chapter shows that the local biodiversity and the direct neighbour of an individual tree influence its leaf traits beyond the light-trait dependency. This is especially remarkable because it shows that the biodiversity impacts leaf traits in ways beyond just influencing light utilization.

Chapter 4 connects the concepts of leaf trait variation and importance of light availability from the previous chapters and analyses how these factors influence tree performance. This chapter is located in the temperate forest plantation of the Kreinitz experiment (Germany). It demonstrates that the relationship between tree species richness and tree growth is mediated via the leaf trait variation of the individual trees. Furthermore, within-individual leaf trait variation is modified by light availability. In particular, trees in monocultures show a higher within-individual leaf trait variation, which partly compensates for the lack in among-species leaf trait variation, and thus, affects the biodiversity-productivity relationship. These processes balance each other out on the plot level, which masks a potential overall effect of tree richness on productivity in this particular scenario.

In conclusion, the collective findings of this thesis demonstrate that leaf traits and their variation at the individual level are important factors that connect biodiversity and ecosystem functions. Critical adaptations – most importantly the trade-off between resource acquisition and conservation – are conducted at the leaf level. This processes appear to be a universal in forest ecosystems, irrespective of species, biome or leaf habit. This underscores the importance of including within-individual leaf trait variation in ecological research.

Chapter 1

General introduction

1.1 Introduction

Biodiversity and ecosystem functions in forest ecosystems

The functioning of natural ecosystems relays heavily on their biodiversity (Hooper et al. 2005, Tilman et al. 2014). This is especially relevant for plants as primary producers of terrestrial ecosystems (Cardinale et al. 2011, Isbell et al. 2011). Species-rich ecosystems provide more ecosystem services (Cardinale et al. 2012), are more productive (Piotto 2008), more resistant against disturbance and biological invasions (Levine et al. 2004, Quijas et al. 2010) and store more carbon (Chen et al. 2018). Especially in forest ecosystems, an increased biodiversity, which is typically expressed as tree species richness, has multiple beneficial effects that result in an overall increased productivity (Huang et al. 2018). For example, a high tree-species richness reduces infestation with leaf pathogens (Hantsch et al. 2014) and reduces herbivore damage (Schuldt et al. 2015). It also increases the temperature buffering effect, i.e. increases the minimum temperature, decreases the maximum temperature (Zhang et al. 2022), increases water supply (Jansen et al. 2021) and mitigates drought impacts (Fichtner et al. 2020). Furthermore, an increased tree species richness has been reported to increase the nutrient use efficiency (Lü et al. 2019) as well as the light availability for each individual (Pretzsch 2014).

Trait-based ecology

Globally, the most important ecosystem functions are connected to and mediated by functional traits (Díaz and Marceno 2001, Chapin 2003), which is why trait-based ecology has become a well established field of ecological research in the last decades (Zakharova et al. 2019). Functional traits are defined as morphological, physiological or phenological features measurable at the individual level, impacting fitness via their effects on growth, reproduction or survival (Violle et al. 2007). In particular, they might affect nutrient acquisition (Yan et al. 2015), plant growth and productivity (Roscher et al. 2012, Rawat et al. 2019), litter and wood decomposition (Jewell et al. 2015, Oberle et al. 2020), soil erosion prevention (Seitz et al. 2016), soil fertility (Laughlin et al. 2015) and drought tolerance (McGregor et al. 2021).

A subset of functional traits are leaf traits, which are chemical or morphological characteristics of leaves (Reich et al. 2003). The leaf economics spectrum (LES) is a globally coordinated set of leaf traits that indicates a general trade-off between resource acquisition and resource storage strategy in plants (Wright et al. 2004). According to a plant's leaf traits it can be positioned along a 'fast-slow continuum', where high values in acquisitive traits like leaf nutrients are correlated with fast growth (and fast return-of-invest) and high values in conservative leaf traits like structural traits are correlated with slow growth and slow return-on-invest of resources (Reich 2014). Leaf traits that are commonly considered as ‘acquisitive’ traits include a high specific leaf area (SLA) as well as a high mass-based leaf concentration of nitrogen (leaf N), phosphorus (leaf P), calcium (leaf Ca), potassium (leaf K), magnesium (leaf Mg) and sulphur (leaf S), because these traits are related to photosynthesis (Jackson and Volk 1968, Terry 1976, Hikosaka and Terashima 1996, Poorter and Bongers 2006, Tränkner et al. 2018, Wang et al. 2019). Additionally, leaves might include compounds to deter herbivores, for example tannin, phenolics and lignin. Tannin and phenolics as ‘defence traits’ are generally associated with a more acquisitive growth strategy (Eichenberg et al. 2015). Leaf traits commonly associated with a ‘conservative’ growth strategy include a high leaf dry matter content (LDMC), a high leaf carbon-to-nitrogen ratio (leaf CN), a high amount of leaf carbon (leaf C), lignin and cellulose, as these traits contribute to the structure and toughness of the leaves (Hikosaka and Terashima 1996, Lloyd et al. 2010, Grady et al. 2013).

Leaf trait variation across scales

When analysing the relationship between leaf traits and ecosystem functions, the use of community-weighted mean traits (CWMs, leaf traits weighted by species abundance within an ecosystem) is a commonly applied practice (Garnier et al. 2004, Lavorel et al. 2007, Ricotta and Moretti 2011). This approach can be derived from the mass-ratio hypothesis (Grime 1998) which postulates that the effect of a species’ traits is correlated to the species’ relative abundance in a community and that the most dominant traits are the most relevant factors for the ecosystem functions. The use of CWMs is generally considered a suitable approach for the analysis of the impact of leaf traits on ecosystem functions at large scales (Finegan et al. 2015, Pinho et al. 2018, Seyednasrollah and Clark 2020). However, the use of species mean trait values might become misleading if there is a considerable trait variation within species (intraspecific trait variation, ITV) (Siefert et al. 2015). Indeed, it has been shown that ITV can even exceed between-species variation in some cases (Fajardo and Siefert 2016). While it has been argued that the inclusion of ITV in global scale analyses might not be necessary in every case (Albert et al. 2011), for analyses of regional and local scale it is certainly relevant (Clark 2010). The magnitude of a species’ ITV reflects both the adaptability of genotypes within species as well as each single genotype’s ability to form different phenotypes. Thereby, with a higher ITV species expand their ecological niche (He et al. 2020). This can promote a higher biodiversity in an ecosystem, if multiple species can adjust their phenotype to the environmental conditions of this ecosystem (Crawford et al. 2019). At the same time, a high ITV also enables species coexistence, if the ITV difference in species is bigger than their difference in competitive ability (Turcotte and Levine 2016). Consequently, the topic of ITV is an rapidly advancing field of ecological research

(Westerband et al. 2021) and trait-based studies on regional or local scales typically include ITV (Lepš et al. 2011, Conti et al. 2018, Huang et al. 2022).

Closely related to ITV, is the topic of within-individual leaf trait variation. It is considered an emergent property of plants that results from their modular construction of physiologically independent leaves (Suomela and Ayres 1994). It has been shown that leaf traits can in some cases vary more within than between individuals (Wetzel and Meek 2019). It has been argued that a high amount of within-individual leaf trait variation can be beneficial for individual plants, which is why leaf traits and their variation should be considered as independent properties of individuals (Herrera 2009). However, this topic received much less attention than ITV, despite having similar relevance in ecological processes (Wetzel et al. 2016, Herrera 2017, Eisenring et al. 2020). Within-individual leaf trait variation is especially relevant in trees. Here, the adjustment of leaf traits to the changing light conditions in the crown is an important mechanism of optimising whole plant photosynthesis (Givnish 1988, Gutschick and Wiegel 1988, Koike et al. 2001).

It is unclear if leaf trait variation on all levels (between species, within species, within plants) is caused by the same underlaying process. In theory, effects that occur on higher levels of organisation (i.e. the ecosystem scale) should originally emerge form processes based on the local neighbourhood (Trogisch et al. 2021). In particular, the trade-off between construction cost and benefit could emerge at the leaf level and propagate to the ecosystem level (Gomarasca et al. 2023). However, to which degree within-individual leaf trait variation is relevant for higher-order ecological processes, is still largely unexplored.

Sources of leaf trait variation

At all scales, leaf traits are influenced by different factors that can be categorized as genetic variation, ontogenetic differences or responses to environmental factors (Weiner 2004, Auger et al. 2013, Russo and Kitajima 2016). In forest ecosystems, the response to environmental factors is by far the most relevant of these factors (Laughlin et al. 2017). Environmental factors can be further differentiated into biotic and abiotic factors. The specific biotic and abiotic factors that could influence leaf traits differ significantly between different biomes (for example between tropical, subtropical and temperate forest ecosystems). While the relationship between conservative and acquisitive leaf traits on the species level appears to be the same across biomes (Reich et al. 1999), there has been no attempt so far to test this relationship on lower levels of organisation.

Regarding the biotic factors, leaf traits can be influenced by herbivory (Xiao et al. 2019), by infections with pathogens (Gortari et al. 2018) and by interactions with neighbouring plants (Davrinche and Haider 2021). Especially the interactions between leaf traits and the surrounding biodiversity can be difficult to analyse, because the biodiversity interacts with other biotic and abiotic factors. However, in a planted biodiversity experiment the species richness is a controlled factor, which allows the causal inference between biodiversity and other factors (Kambach et al. 2019).

Abiotic factors that are known to influence leaf traits include for example nutrient availability (Fan et al. 2022), temperature (Yu et al. 2022) and water availability (Salehi et al. 2020). A majority of the factors that drive ITV is also likely to influence within-individual leaf trait variation (Herrera 2009). However, a factor that requires separate consideration for different scales is the availability of light. While it is also a relevant factor on the global scale (Lusk et al. 2013), it is especially relevant on the local scale, because light forms very steep gradients within local groups and within individuals (Matsuo et al. 2021).

Light availability in forest ecosystems

Light is an indispensable resource for all plant life and is one of the most limiting resources for tree growth in forest ecosystems (Scartazza et al. 2016). In forests it is also often considered to be the strongest influencing factor on leaf traits (Markesteijn et al. 2007, Legner et al. 2013). Consequently, leaf traits are adapted to the steep light gradient at the within-individual level (Escribano-Rocafort et al. 2016). The within-canopy light adjustment is considered to be a mechanism to optimise the whole plants' performance (Givnish 1988). Yet, it has been proposed that leaf traits respond to the within-canopy light gradient within the frame of the LES (Niinemets et al. 2015, Chen et al. 2020). Sun-exposed leaves are typically located on the conservative site of the LES and have a higher total photosynthetic capacity while shade-leaves are located on the acquisitive site of the LES and have a higher photosynthetic efficiency (Boardman 1977, Lichtenthaler et al. 1981).

The interaction between light and leaf traits is further modified by the biodiversity of a trees' local neighbourhood. Individuals of different species utilize the available crown space more efficiently than the same number of conspecific individuals (Ishii and Asano 2009). The enhanced crown packing leads to a better light interception and a steeper light gradient in the canopy (Pretzsch 2014). This can be observed in the form of a light-dependent leaf trait gradient, which is modified by the biodiversity of an ecosystem (Williams et al. 2020). Interestingly, the shift of light availability in the canopy, caused by an increased biodiversity, does not fully explain the observed shift in light-dependent leaf traits (Benomar et al. 2011, Cope et al. 2021). This apparent discrepancy implies that there are additional factors that modify the interaction between biodiversity, light and leaf traits and highlights the need for further research.

In the context of the within-individual trait-light relationship, it is also important to consider the relevance of the leaf habit. While the leaf traits of deciduous and evergreen species respond to changes in light conditions in a similar way (Lusk et al. 2008), they differ significantly in their mean leaf traits and should be located at opposing ends of the LES (Zhao et al. 2017, Oliveira et al. 2021). In several instances, deciduous and evergreen species have been reported to react with similar trait shifts to changes in environmental conditions (Tomlinson et al. 2013, Bai et al. 2015), which suggests that both are subject to comparable mechanisms and similar constraints on how much traits can shift independently of each other. However, these analyses were based on fully sun-exposed leaves. Yet, the main driver of within-individual leaf trait variation is the strong intra-canopy light gradient. Here, the higher flexibility of deciduous species in nitrogen allocation (Niinemets et al. 2015) and the stronger constraints of leaf morphology in evergreen species (Niinemets 2016) might lead to observations different from previous ones.

Practical considerations for the leaf trait analysis

When analysing leaf traits on the within-individual level, there are several practical implications that need to be considered. Firstly, trait analyses on finer scales require more samples to be analysed and are therefore more time consuming and expensive than analyses on larger scales (Baraloto et al. 2010). Secondly, commonly applied methods for the analysis of leaf traits (wet chemistry) are inherently destructive (Berry and Johnson 1966, Hagerman 1987, Van Soest et al. 1991, Graham 1992, Ayotte et al. 2019). Hence, a single leaf sample cannot be analysed for all traits with conventional means – which would be required for a multivariate analysis. Both problems can be avoided by analysing leaf traits via spectroscopic methods. The method of near-infrared spectroscopy (NIRS) was originally used for the analysis of agricultural products (Williams 1987) but quickly became an established alternative method for the analysis of leaf traits, as it is faster and more cost-effective than conventional methods (Foley et al. 1998). Another main advantage of this method is the ability to analyse the same leaf sample for multiple leaf traits, which enables the option of multivariate analyses (Bon et al. 2020). The method has proven its utility in ecological research (Trogisch et al. 2017). Furthermore, recent advances in sensor technology have enabled the option to include sections of the UV spectrum and visible light to the analysis ("Field Spectroscopy"), which has proven to further increase the utility of this method (Ge et al. 2019).

Aims and scope of the thesis

This dissertation aims at improving the current understanding of the role of leaf traits in forest ecosystems. The main premise of the thesis is that leaves are mediators in the relationship between biodiversity and ecosystem functions. In this regard, especially the role of within-individual leaf trait variation is largely underexplored. Yet, the understanding of within-individual processes might help to improve the understanding of higher-order processes. To test the relationship between biodiversity (expressed as tree species richness), ecosystem functions (in form of tree growth), leaf traits and their variation, I collected and analysed leaf samples across three large-scale planted forest biodiversity experiments in different climate zones at the within-individual level. In order to cope with the large number of samples, I analysed the leaves by means of spectroscopy. The following chapters address different aspects of leaf traits and consider them either as responses to biodiversity or as predictors of ecosystem functions. In particular, I will address the following questions: How are leaf traits and their variation at the individual level influenced by the biodiversity of an ecosystem? Which role plays the biodiversity on an ecosystem in the interaction between leaf traits and light availability? In which way are leaf traits connecting the biodiversity of an ecosystem functions like individual growth? Figure 1.1 shows a graphical thesis outline and depicts which aspects are analysed in which chapter.

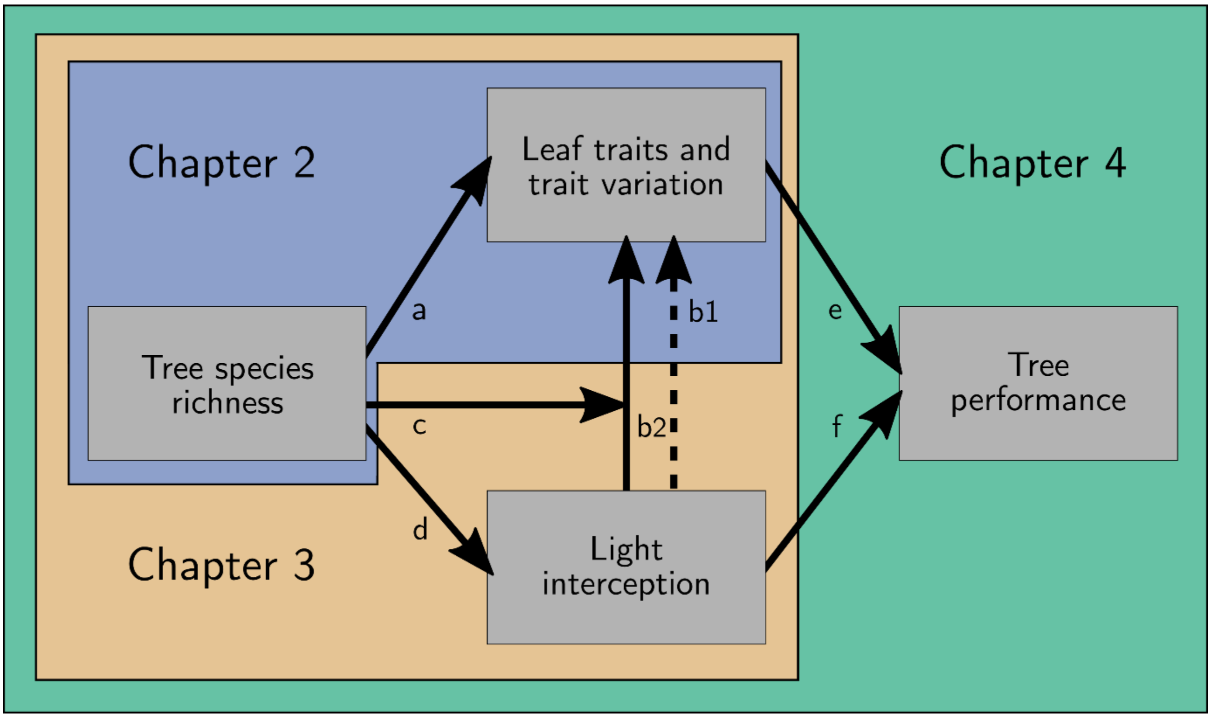

Figure 1.1. Graphical overview of the primary research questions that were addressed in this thesis. Different chapters are indicated by different colours. Arrows indicate the research questions of the chapters. The direction of the arrows indicates the direction of the assumed causality. Solid lines indicate direct measurements, dashed line indicates indirect measurement. *Chapter 2* (blue) investigates the influence of tree species richness on leaf trait variation (a) and to which degree leaf traits are influenced by sampling height, which is in this case an indirect measurement of light interception (b1). *Chapter 3* (brown) includes the directly measured leaf trait response to light (b2). It also investigates the question, to which degree the tree species richness modifies the light-trait relationship (c) and how tree species richness influences the light interception (d). *Chapter 4* (green) includes the questions to which degree light interception (f), leaf traits and their variation (e) influence tree performance. Note that that this overview is simplified for visualisation as the chapters use different metrics for tree species richness, light interception as well as leaf traits and their variation.

Chapter 2 is based on field work in the tropical lowland rainforest of the Sardinilla experiment in Panama. Here I measured the leaf traits along the outer canopy of five semi-deciduous tree species. The chapter addresses the questions, how leaf traits are dependent on the leaves' height in the crown and how the leaf trait variation is influenced by the species richness of the surrounding neighbourhood of an individual tree.

Chapter 3 investigates how leaf traits within individual trees are influenced by the differences in the light availability within the trees' crown and how this relationship is modified by the tree diversity of the local neighbourhood. The analysis is split into deciduous and evergreen tree species to highlight possible differences and similarities between leaf habits. Special emphasis is put on the question, whether the species richness of the local group or the direct partner of a tree dominates the light-trait interaction. The data for this chapter originates from the BEF-China experiment located in a subtropical climate, where I sampled leaves of six broadleaf evergreen and nine deciduous tree species.

Chapter 4 reiterates several design aspects of the second and third chapter and extends them to include the question, how the leaf trait-biodiversity relationship and the leaf trait-light relationship influence tree performance. This chapter is based on data that I collected from the temperate forest of the Kreinitz experiment (Germany) and includes four deciduous tree species. The chapter further investigates, how the findings form the previous chapters translates to the temperate biome.

Chapter 5 summarises the most important results of the previous chapters and discusses their broader implications. All chapters contribute to answer the question, how leaf traits on the within-individual level are influenced by the biodiversity of an ecosystem and how they are connected to critical ecosystem functions. As the chapters 2, 3 and 4 were based on data from different biomes, I identify and discuss patterns that emerged from the analyses. I further discuss the utility of the used method, the limitations of this project and perspectives for future research.

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Chapter 2

Drivers of within-tree leaf trait variation in a tropical planted forest varying in tree species richness

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2.1 Abstract

In plant ecology, community-weighted trait means are often used as predictors for ecosystem functions. More recently, also within-species trait variation has been confirmed to contribute to ecosystem functioning. We here go even further and assess within-individual trait variation, assuming that every leaf in a plant individually adjusts to its micro-environment. Using forest plots varying in tree species richness (Sardinilla experiment, Panama), we analysed how leaf traits within individual trees vary along the vertical crown gradient. Furthermore, we tested whether niche partitioning in mixed stands results in a decrease of within-species leaf trait variation and whether niche partitioning can be also observed at the level of individual trees. We focused on leaf traits that describe the growth strategy along the conservative-acquisitive spectrum of growth. We found a decrease in within-species variation of specific leaf area (SLA) with increasing neighbourhood species richness. Both sampling height and local neighbourhood richness contributed to explaining within-species leaf trait variation, which however, varied in importance among different species and traits. With increasing sampling height, leaf dry matter content (LDMC), carbon to nitrogen ratio and lignin content increased, while leaf nitrogen concentration (leaf N), SLA, cellulose and hemicellulose decreased. Variation in leaf N decreased with increasing neighbourhood species richness, while the magnitude of within-individual variation of most traits was unaffected by neighbourhood species richness. Our results suggest an increased niche partitioning with increasing species richness both in a plant community and at the level of individual plants. Our findings highlight the importance of including within-individual trait variation to understand biodiversity-ecosystem functioning relationships.

2.1.1 Keywords

Biodiversity; Leaf economics spectrum; Leaf traits; Niche theory; Sardinilla experiment; Trait variation; Tropical plantation forest

2.2 Introduction

In plant ecology, approaches based on functional traits are an important element of research (McGill, Enquist, Weiher & Westoby, 2006) as such traits might have an influence on plant fitness via their effects on growth, reproduction and survival (Violle et al., 2012). In the last decades, trait-based approaches significantly contributed to improve our understanding of ecosystem functions (Reich et al., 1999; Cornwell & Ackerly, 2009; Liu et al., 2016). For primary producers in terrestrial ecosystems, especially leaf traits are strongly associated with ecosystem functions (Wright et al., 2004). For example, mass-based leaf nitrogen concentration (leaf N) describes the overall nutrient availability (Donovan et al., 2014), leaf carbon to nitrogen ratio (C/N ratio) is an indicator for nitrogen use efficiency (Robertson, 1997), leaf area-to-mass ratio (specific leaf area, SLA, or its reciprocal, leaf mass per area, LMA) is a good predictor for growth strategy and biomass production (Poorter & Bongers, 2006). The mentioned traits locate plants along the fast-slow continuum of the leaf economics spectrum (Wright et al. 2004; Reich, 2014). While slow-growing plants (i.e. plants that follow a conservative growth strategy) typically have a high C/N ratio and high LDMC, fast-growing plants (i.e. plants that follow an acquisitive growth strategy) typically have high leaf N and high SLA (Reich, 2014). Furthermore, the amount of carbon invested in structural polymers in the leaves (lignin, cellulose, hemicellulose) drives litter decomposition rates and determines herbivory resistance (Hochuli, 1996; Berg, 2000).

Because of their relevance for ecosystem functions, leaf traits have been studied intensely. However, leaf traits were often addressed only at the species level. While during the last years there has been a growing interest in within-species trait variation (e.g. Fajardo & Siefert, 2018; Hogan, Valverde-Barrantes, Ding, Xu & Baraloto, 2019), few attempts have been made to go beyond this level. In most studies, community weighted means (CWMs, plot-level traits weighted by species abundance) calculated from trait values at the species level are used as predictors for ecosystem functions (Garnier et al., 2004). One reason for this is that leaf traits often vary more among than within species (Garnier et al., 2001; Albert, Grassein, Schurr, Vieilledent & Violle, 2011). For example, for a Costa Rican dry forest Hulshof and Swenson (2010) described that up to 63% of variation in SLA can be explained by species identity, while 22% of variation was encountered among individual plants and 15% within individuals. However, depending on the environmental conditions, trait variation between species might be actually masked by trait variation within species (Laughlin et al., 2017). Thus, neglecting within-species variation may strongly underestimate the functional diversity of an ecosystem (Jung, Violle, Mondy, Hoffmann & Muller, 2010). Within-species trait variation is also an important factor in species coexistence as the theoretical model by Hart, Schreiber and Levine (2016) suggests that an increased within-species niche variation makes species coexistence more difficult.

One aspect that is still largely disregarded in the debate of within-species leaf trait variation is the variation within individual plants. However, for the herb species *Helleborus foetidus*, Herrera, Medrano and Bazaga (2015) showed that within-individual variation was even greater than among-individual variation. Even though the existence of within-individual leaf trait variation is generally acknowledged in plant ecology (cf. e.g. Cornelissen et al., 2003), it is unclear if the mechanisms that drive leaf trait variation between and within species are transferable to the within-individual scale. While the main sources of leaf trait variation between species are environmental and biotic filtering (Bruelheide et al., 2018), within-species variation can be brought about by both genetic adaptation and phenotypic adjustment of the plants to the local environment (Callaway, Pennings & Richards, 2003). This can be observed as a response to abiotic environmental conditions (e.g. to avoid stress), as response to biotic interactions (e.g. as a reaction to competitors (MacArthur & Levins, 1967)), or to a combination of these factors (Kichenin et al., 2013). Within-individual variation is solely the result of phenotypic plasticity, although it cannot be excluded that epigenetic adjustments might be involved (Grativol, Hemerly & Ferreira, 2012). Because of their size and leaf number, trees are an obvious object to study within-individual leaf trait variation. This approach complements the studies that have focused on shifts in mean trait values within individuals, such as the adjustment of SLA or leaf N to sunny or shady conditions (Ellsworth & Reich, 1993). Usually, such adjustments are interpreted as an individual's strategy of optimizing light capture (Legner, Fleck & Leuschner, 2013) but the connection between within-species and within-individual leaf trait variation is typically not addressed, even though they might have comparable mechanisms.

There are many possible abiotic drivers of within-species leaf trait variation, including environmental factors such as soil nutrient availability (Souto, Premoli & Reich, 2009), temperature (Choi, Jeong & Kim, 2019) and precipitation (Souza et al., 2018). However, the strongest above-ground abiotic driver of leaf trait variation is irradiation, which also drives within-individual leaf trait variation (Del Valle, Buide, Whittall & Narbona, 2018). Therefore, the foliage photosynthetic capacity (for example expressed as maximum photosynthesis rate A_{max} in µmol CO_2 m^{-2} s^{-1}), is a key factor in plant performance (Niinemets, 2007). Forest canopies show a vertical light gradient (Scartazza, Di Baccio, Bertolotto, Gavrichkova & Matteucci, 2016), with light availability decreasing from the top to the bottom of the crown. Consequently, the photosynthetic capacity also decreases downwards (Niinemets, Cescatti, Rodeghiero & Tosens, 2006). These differences in light availability influence leaf traits: for example, LMA and leaf C/N ratio are known to increase with increasing light availability (Böhnke & Bruelheide, 2013), while leaf N decreases (Zhao & Oosterhuis, 1998).

Regarding biotic interactions, the prevailing pattern described in the literature is that community trait space increases in species mixtures compared to monocultures (Siefert et al., 2015; Raffard, Santoul, Cucherousset & Blanchet, 2019; Tautenhahn, Grün-Wenzel, Jung, Higgins & Römermann, 2019). In contrast, the relationship between species richness of a community and within-species trait variation (the species niche breadth) has been discussed controversially. Figure 1 illustrates possible relationships between species niche breadths and species richness. First, the niche breadth of a species may remain unaffected by community species richness (Figs 1A and D). This corresponds to a null model according to which neither species niche breadth nor within-individual trait variation depends on community richness. In this case, the community trait space is just a sum of niche breadths that all species would show in a monoculture independent of species interactions (Fig. 1D). Alternatively, species niche breadths might also increase (Figs 1B and E) or decrease (Figs 1C and F) depending on community species richness. The former case could result from facilitation (Garcia-Cervigon, Linares, Aibar & Olano, 2015), which would allow species to display a wider range of trait values than in monoculture. For example, Benavides, Valladares, Wirth, Müller and Scherer-Lorenzen (2019) described greater within-species trait variability (increased species niche breadth) in mixed compared to species-poor European forests. Whether an extension of a species niche breadth is brought about by larger within-individual trait variation (Fig. 1E) or by less trait overlap between individuals of this species (Fig. 1B), remains an open question. In contrast, a meta-analysis by Siefert et al. (2015) showed that species occupy smaller proportions of the total community trait space (smaller species niche breadths) in species mixtures compared to monocultures. Decreasing species niche breadths might result either from smaller within-individual trait variation (Fig. 1F) or from higher trait overlap between individuals of this species (Fig. 1C). Niche theory (Hutchinson, 1957; MacArthur & Levins, 1967) predicts that niche overlap among species is reduced in order to decrease competition intensity (Carmona et al., 2019), as shown in Figs 1C and F. As competition acts on individual plants (Tilman, 1994), intraspecific competition could also reduce within-individual trait variation and thus trait overlap between individuals of the same species (Fig. 1F). Since within-individual trait variation has not been measured systematically in communities differing in species richness, it is yet unknown which of the scenarios described in Fig. 1 applies. Additionally, it has to be considered that within-species leaf trait variation may strongly depend on the trait considered and the species studied (Albert et al., 2011; Siebenkäs, Schumacher & Roscher, 2015).

While the abiotic environment often exerts direct effects on leaf traits, biotic interactions, which presumably vary with neighbourhood species richness, can be expected to affect leaf traits indirectly. In forests, trees will adjust their crown packing in order to use the light optimally (Pretzsch, 2014). The vertical structure of every single tree differs between tree species (Guisasola, Tang, Bauhus & Forrester, 2015) and between monocultures and species mixtures (Forrester et al., 2018). Thus, the availability of the abiotic resource light (which directly affects leaf traits) is modified by biotic interactions (Tremmel & Bazzaz, 1995). In diverse forests, trees can adjust their leaves better than in monocultures in order to avoid competition (Benavides, Valladares, Wirth, Müller & Scherer-Lorenzen, 2019) which also reduces the competition for light (Fichtner et al., 2018).

The aim of our study was to investigate biotic and abiotic effects on within-species and within-individual leaf trait variation in trees. We assumed that factors affecting leaf trait variation at the species level also play a role at the within-individual level. To capture the trait variation within tree individuals, we sampled leaves along the vertical crown gradient, thus capturing the response to irradiation as important abiotic driver. With respect to biotic drivers, we focused on the local tree species richness, which was manipulated and maintained at our study site, the Sardinilla tree diversity experiment in Panama, while keeping overall tree density constant. Assuming that competition is the most important biotic interaction, we assumed that (1) within-species leaf trait variation (species niche breadth) decreases with increasing tree species richness of the local neighbourhood (Figs 1C and F). We also hypothesized (2) that a considerable proportion of within-species leaf trait variation is explained by the vertical crown

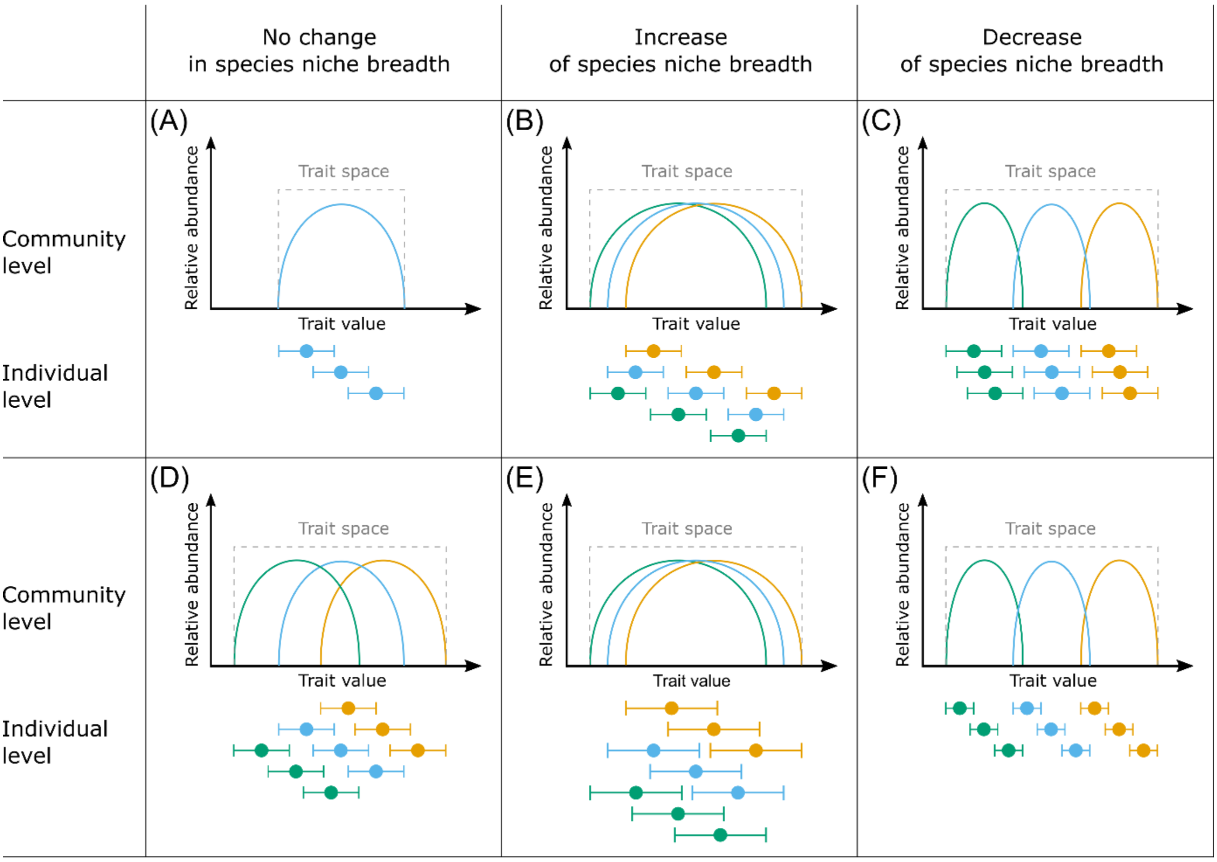

Fig. 1. Conceptual figure of how the variation in trait values differs between monocultures and species mixtures. Different colours indicate different species. Mixture refers to stands of the same density of individuals and equal proportions of tree numbers, resulting in the same reduction of conspecific density for every species. (A) Single species in monoculture for comparison with mixed stands. (B) Extended niche breadth of species in mixtures compared to monocultures, while the niche breadth of individuals within species remains unaffected. (C) Niche partitioning results in smaller niche breadths of species in mixtures compared to monocultures, while the niche breadth of individuals within species remains unaffected. (D) The niche breadths of the single species and individual plants remain unaffected by increased species richness. In consequence, there is a large overlap in species niches. (E) Extended niche breadths of both species and individuals within species in mixtures as compared to monocultures. (F) Niche partitioning results in smaller niche breadths of both species and individuals within species in mixtures as compared to monocultures.

gradient and (3) by tree species richness of the local neighbourhood. (4) Additionally, we expected that within-individual leaf trait variation decreases with increasing tree species richness of the local neighbourhood (Fig. 1F), thereby extending the niche theory to the level of individual plants.

2.3 Material and methods

2.3.1 Design of the Sardinilla experiment

The study took place in the main plantation of the Sardinilla tree diversity experiment in the lowlands of tropical Panama (9.3165°N, 79.6338°W). The experiment was established in 2001 on former agricultural land (Scherer-Lorenzen et al., 2005). The main plantation originally consisted of 24 plots (2025 m2 each) where six native tree species (*Cordia alliodora* (Boraginaceae), *Luehea seemannii* (Malvaceae), *Anacardium excelsum* (Anacardiaceae), *Hura crepitans* (Euphorbiaceae), *Cedrela odorata* (Meliaceae) and *Tabebuia rosea* (Bignoniaceae)) were planted (Supplementary material, Appendix A: Fig. A.1).

Plots represented three different diversity levels: twelve monocultures, six 3-species-mixtures and six 6-species-mixtures. Every species was planted in two monoculture plots, three different 3-species-mixtures and in all six 6-speciesmixtures. In each plot, on average 231 trees were planted. The sequence of species was kept fixed within the rows but shifted by one for every next line following a Latin square design (Appendix A: Fig. A.1). Thus, every tree had eight neighbour trees from up to five different species (Potvin & Dutilleul, 2009). For further details on the Sardinilla experiment see also Potvin, Whidden and Moore (2004) and references therein.

Species were a priori classified as light-demanding (*C. alliodora* and *L. seemannii*, which are considered as pioneer species), light-intermediate (*A. excelsum* and *H. crepitans*) and shade-tolerant (*C. odorata* and *T. rosea*), based on their performance on Barro Colorado Island (Condit et al., 2006).

2.3.2 Sampling design

Leaf sampling took place in May and June 2017. Due to high mortality of C. alliodora, this species was not included as target species in our study, however few individuals were part of the surrounding trees of the other species. Further, we excluded trees where the crown was unreachable by our means (>8 m from the ground), and trees with a vertically very narrow crown, where sampling at multiple height levels was not possible. In total, 195 trees were selected for sampling at all plot species richness levels, i.e. in monocultures (37 trees), 3-species- and 6-species-mixtures (82 and 76 trees, respectively; Appendix A: Table A.2). For each tree, we measured the circumference of every trunk at breast height to calculate the diameter at breast height (DBH) as a benchmark for tree size. Further we recorded how many different tree species directly surrounded the target tree (hereafter "neighbourhood richness"; see also Appendix A: Fig. A.1). To test the effect of neighbourhood richness on trait variation, we sampled trees always in pairs to make sure that they had at least one living neighbour.

Along the crown of every tree, leaves were sampled at up to three sampling points. The first sampling point was located at the lower border of the crown (not lower than 1.5 m), a second sampling point was set at around 8 m and a third sampling point was chosen between them (Appendix A: Fig: A.1). At each sampling point, up to five fully developed leaves without major damage from herbivores or pathogens were harvested (in total 1678 leaves from 560 sampling points). Directly after harvest, the leaves of each sampling point (hereafter "sample") were sealed in zip-lock bags and stored on ice until they were further processed on the same day.

2.3.3 Leaf trait analysis

We analysed eight morphological and chemical leaf traits representing the important dimensions of plant growth strategy (leaf economics spectrum; Reich, 2014) and litter decomposability (Schwarz, 2001): SLA, LDMC, leaf C, leaf N, C/N ratio, and the structural polymers lignin, cellulose and hemicellulose.

At the end of each field day, a subset of samples (see below for selection criteria; "calibration samples") was weighed fresh and leaf area was scanned with a flatbed scanner. Leaf area was calculated with the program WinFOLIA (v Pro 2004a Regent Instruments). The samples were dried for 72 hours at 60°C and weighed again to calculate SLA (leaf area per leaf dry mass) and LDMC (leaf fresh mass per leaf dry mass; Cornelissen et al., 2003). Further analyses were carried out later in the laboratory at Martin Luther University Halle-Wittenberg, Germany. For the analysis of lignin, cellulose and hemicellulose, leaf samples were shredded (2-3 mm) and analysed using an ANKOM200 Fiber Analyzer (ANKOM Technology, Macedon NY, USA). For the analysis of leaf C, leaf N and C/N ratio, samples were ground to a homogenous powder using a Retsch MM400 ball mill and analysed with a vario EL cube (Elementar, Hanau, Germany).

We chose the high-throughput method of Near-Infrared Spectroscopy (NIRS) to determine trait values for the majority of samples. NIRS is a rapid, cost-effective and well established method for plant analysis (Trogisch et al., 2017). To apply a prediction method with NIRS, at the day of harvest every single fresh leaf (in total 1678 leaves) was scanned three times with an ASD "FieldSpec4" Wide-Res Field Spectroradiometer (Malvern Panalytical Ltd, Almelo, Netherlands). We used a contact probe head ("Hi-Brite" with an integrated 6.5 W halogen light source) which was calibrated with a diffuse reflectance target (Zenith "LITE 95%"). The FieldSpec features three sensors

(VNIR, 350-700 nm; SWIR1, 700-1400 nm and SWIR2, 1400-2500 nm) and acquires spectral data with a resolution of 3 nm (VNIR) and 30 nm (SWIR1 and SWIR2), respectively. These scans resulted in spectral files to which a splice correction was applied to minimize intersection noise between the three sensors of the FieldSpec.

For a subset of 137 samples ("calibration samples") spectral data of individual leaves were averaged at the level of the sampling point. The calibration samples were equally distributed across all study species, plot diversity levels and sampling heights along the vertical crown gradient to represent the full range of trait values. The merged spectral data were linked to the corresponding trait values analysed in the laboratory and a prediction model for every leaf trait was created using partial least squares regression (after trait-specific data-transformation) in the Opus QUANT2 calibration software. For each model, test-set-validation was applied: approximately half of the data was used for model building, while the remaining data was used to evaluate the quality of the predictions (R2). The quality of our models was good or very good (according to e.g. Saeys, Mouazen & Ramon, 2005), with R2 for LDMC 0.96, SLA 0.93, leaf C 0.85, leaf N 0.90, C/N ratio 0.91, lignin 0.89, cellulose 0.90, hemicellulose 0.80. The prediction models proved to be very robust: no outliers had to be removed. Leaf traits were predicted for all 1678 leaves.

2.3.4 Statistical analysis

All statistical analyses were performed in the R statistical environment version 3.5.0 (R Core Team, 2018). A principal component analysis (PCA, "prcomp" function) was conducted to reveal the relationships between the leaf traits and the similarity between species. To identify trait differences between species, we calculated an analysis of variance (Anova, "aov" function), further applying Tukey's Honest Significant Differences Test ("HSD.test" function in the agricolae package, de Mendiburu, 2019).

To assess species niche breadths, and therefore testing our first hypothesis, we analysed the effects of neighbourhood richness on within-species leaf trait variation, by calculating for each species the standard deviation (SD) of each trait across all leaves of all trees and plots for each neighbourhood richness level. For each leaf trait, a linear model was fitted with the standard deviation of a trait as response variable, and species, neighbourhood richness and their interaction as predictors.

Second, we tested within species how traits varied along the vertical crown gradient and with tree species richness of the local neighbourhood (hypotheses 2 and 3). We fitted linear mixed-effects models ("lmer" function) for every leaf trait, using the lmerTest package (Kuznetsova, Brockhoff & Christensen, 2017). The models contained the mean trait value per sampling point as response variable, and species, sampling height, neighbourhood richness and all possible 2-way-interactions as fixed effects. We further added the random factor of tree individual nested in tree pair nested in plot to account for the spatial structure of the sampling design. Since interactions including species were significant in the majority of models (also in the linear models testing the first hypothesis), they were further explored by re-fitting all models separately for each species.

To quantify how much trait variation was caused by the different components, we conducted a variance partitioning, using the “calcVarPart” function of the variancePartition package (Hoffman & Schadt, 2016). This function allows to calculate the individual proportion of explained variance for each fixed and random factor of the mixed-effects models described above.

In order to test our fourth hypothesis, we determined the within-individual leaf trait variation by calculating the SD from all leaves from a given tree. For each leaf trait, a linear mixed-effects model was fitted, using the standard deviation of a particular trait across all measured leaves of an individual tree as response variable, and species, neighbourhood richness and their interaction as fixed effects. Tree pair nested in plot was included as random factor to account for the spatial structure of the sampling design.

Further, linear mixed-effects models were fitted, which contained tree DBH as response variable, tree mean leaf traits, neighbourhood richness and their interaction as fixed effects, and species and the tree pair nested in plot as crossed random factors. For all mixed-effects models, we visually checked if model requirements were met, but no data transformations were necessary. Significance of fixed factors was assessed with Anova, using type 1 sum of squares and Satterthwaite approximation for estimating the denominator degrees of freedom.

2.4 Results

2.4.1 Trait relationships and species differences

The observed leaf traits differed significantly between species (Supplementary material, Appendix B: Table B.1). This was also reflected in the PCA (Fig. 2) where, in most cases, different species covered more or less isolated parts of the total trait space. A considerable overlap in trait values was only encountered for the light-demanding species *L. seemannii* and the shade-tolerant species *C. odorata*. Shade-tolerant or light-intermediate species did not appear to share the same trait space.

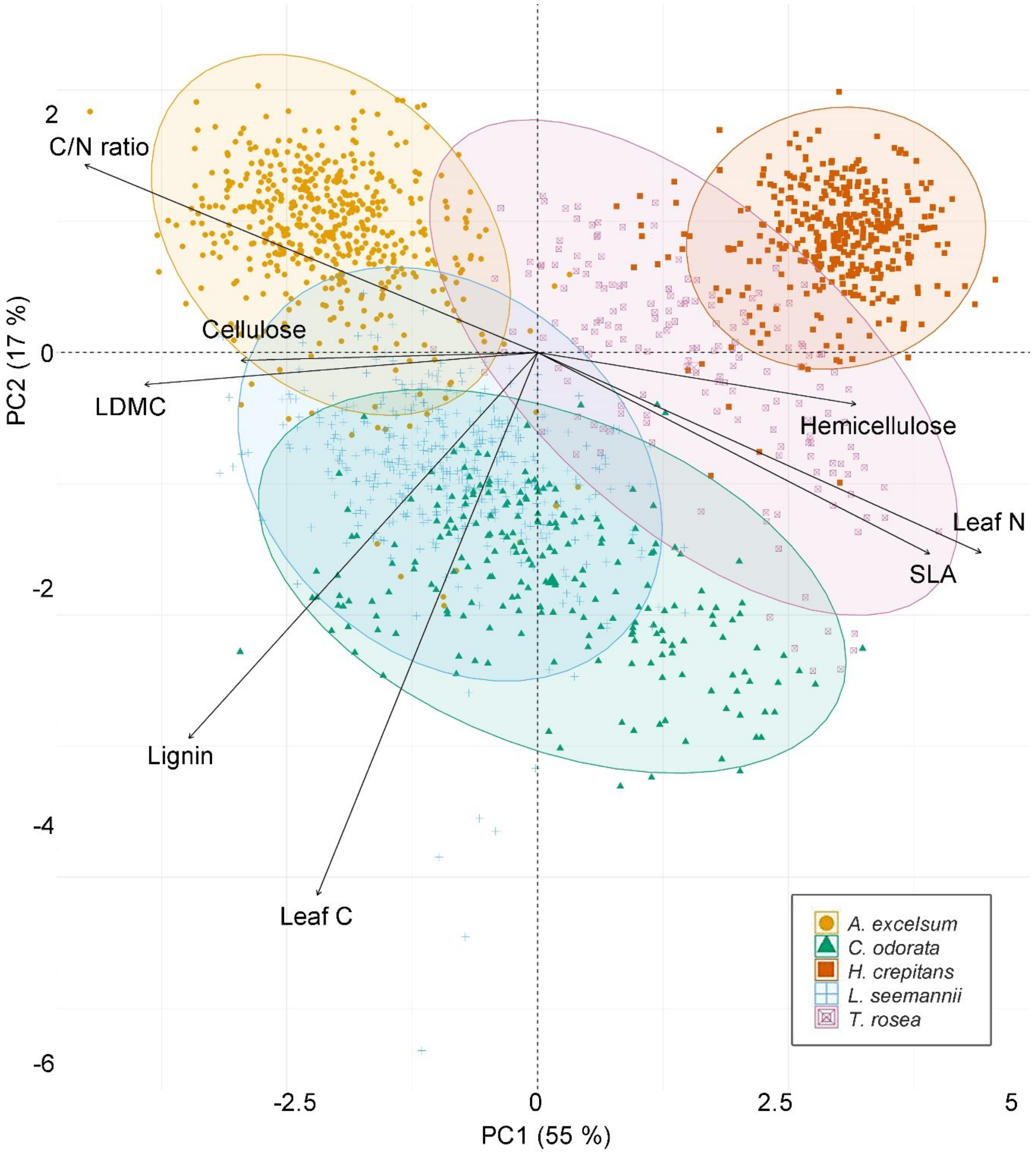

Fig. 2. Principal component analysis of leaf traits (first and second axis shown). Data points are single leaves on which traits were measured. Different colours and symbols represent different species. Ellipses contain 95% of the data points per species. Proportions of explained variance for the first and second axis were 0.55 and 0.17, respectively (for other axes see Appendix B: Table B.2).

Considering the first two PCA axes, there was no overlap between both light-intermediate species *H. crepitans* and *A. excelsum*, and only slight overlap between both shade-tolerant species *C. odorata* and *T. rosea*.

The first axis of the PCA was strongly related to LDMC, cellulose and hemicellulose (with loadings -0.38, -0.29 and 0.31, respectively, Appendix B: Table B.2). Less strongly, but also related to the first axis of the PCA, were C/N ratio, SLA and leaf N (with loadings -0.44, 0.38 and 0.43, respectively). The second axis of the PCA was mainly related to lignin and leaf C (with loadings -0.51 and -0.72, respectively).

2.4.2 Within-species leaf trait variation (species niche breadth)

We found a significant decrease of within-species trait variation with increasing neighbourhood richness for SLA (Fig. 3; Appendix B: Table B.3) but not for the other traits (Appendix B: Fig. B.4). Variation of LDMC, SLA, C/N ratio, leaf N and cellulose differed significantly between species. C/N ratio, lignin and cellulose also showed a significant species-by-neighbourhood richness interaction. Testing the species separately (Appendix B: Table B.5), we found for *H. crepitans* a significant decrease of within-species variation of LDMC and SLA with increasing neighbourhood richness, as well as an increase of within-species variation of cellulose for *T. rosea* (Appendix B: Fig. B.4 and Table B.5).

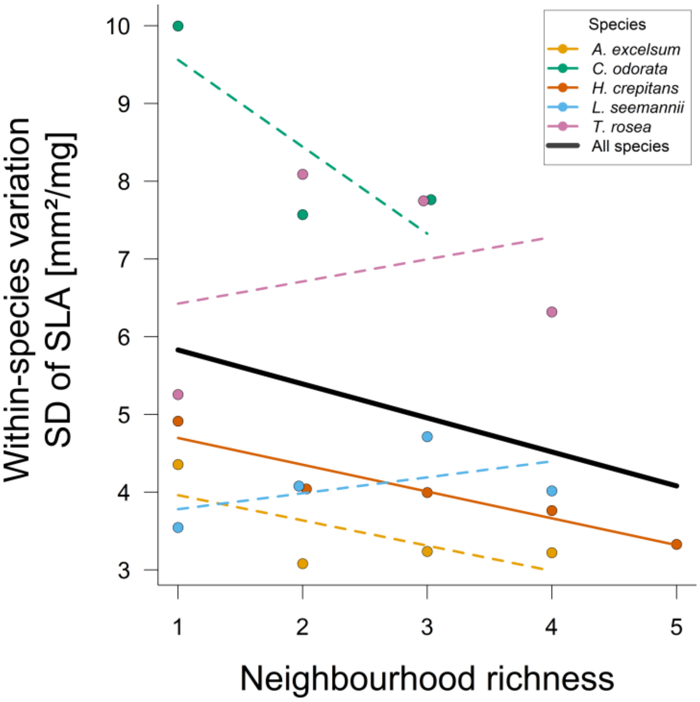

Fig. 3. Effect of neighbourhood species richness on within-species variation (measured as standard deviation) of SLA. The black line results from model predictions, including all species. Different colours represent different species. Continuous lines indicate significant relationships, dashed lines indicate non-significant ones. For the other traits and the numerical results of the models see Appendix B: Tables B.3 and B.5 and Fig. B.4.

2.4.3 Trait responses to species identity, sampling height and neighbourhood richness

All observed leaf traits except for leaf C showed a significant height dependency (Fig. 4, Appendix B: Table B.6). LDMC, C/N ratio, and lignin increased, while SLA, leaf N, cellulose and hemicellulose decreased with increasing sampling height. In case of leaf N, this was only significant for the species *H. crepitans* (Appendix B: Table B.7). For LDMC, SLA and C/N ratio the effect of sampling height was primary driven by *A. excelsum*, *L. seemannii* (only for SLA), and *H. crepitans*. With increasing neighbourhood richness, C/N ratio increased, while leaf N and hemicellulose decreased for *A. excelsum* (Appendix B: Figs B.8 C, D, H and Table B.7). We did not detect an

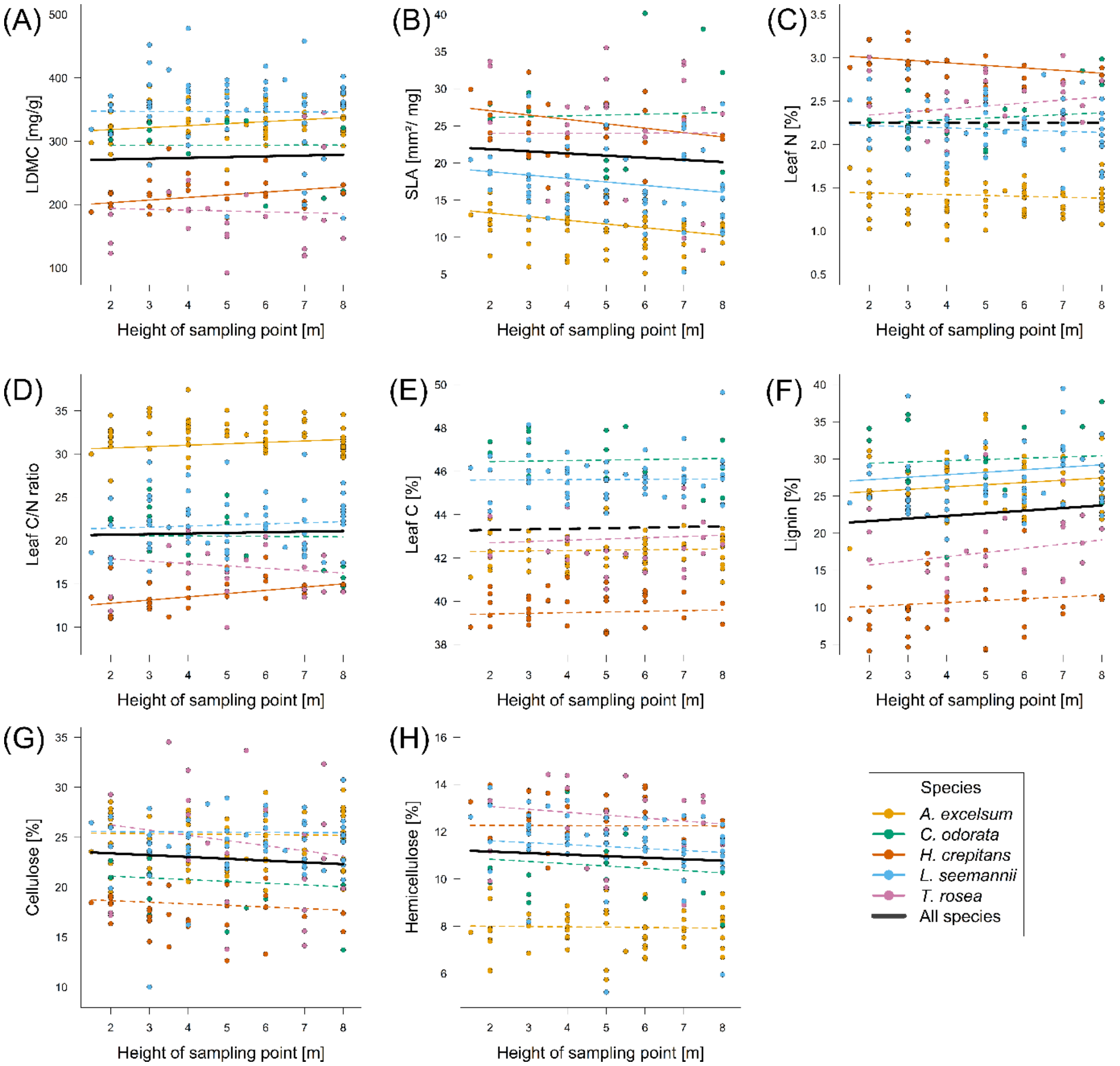

Fig. 4. Trait changes along the vertical crown gradient. All graphs are displayed for neighbourhood species richness level of 3. The black line indicates the predictions from the model including all species. Coloured points represent trait values averaged per sampling point, coloured lines represent predictions from models fitted separately for each species. Continuous lines indicate significant relationships, therefore showing an increase or decrease of the leaf trait with increasing sampling height. Dashed lines indicate non-significant correlations. For the numerical results of the models see Appendix B: Tables B.6 and B.7).

effect of neighbourhood richness for any of the other species or for all species together (Appendix B: Table B.6 and Table B.7). For *C. odorata* there was a significant interaction between sampling height and neighbourhood richness. The increase of LDMC with sampling height was strongest in monocultures and disappeared towards higher diversity levels (Fig. 5).

For all traits except for SLA, variance partitioning revealed species identity as the most important explanatory variable (Fig. 6A; Appendix B: Table B.9). The combined random factors (i.e. the sampled tree, the pair to which the tree belonged and the plot in with the pair was located) explained the second largest proportion, again with the exception of SLA, where these relations were reversed. Across all species, neighbourhood richness explained up to 1.5% of the trait variation (in case of SLA). At the species level (Figs 6C to G; Appendix B: Table B.10), it explained up to 13% of the trait values (C/N ratio of *A. excelsum*, Fig. 6C). Although the sampling height had a significant influence on most traits (see above), its proportion of variation explained was small. Across all species it explained up to 0.6% (in case of lignin, Fig. 6A) and at the species level a maximum of 6% for LDMC of *H. crepitans* (Fig. 6E). The traits differed in their magnitude of variation and (coefficient of variation, CV) and the most variable trait SLA had six-fold the CV of the least variable trait leaf C (Fig. 6B).

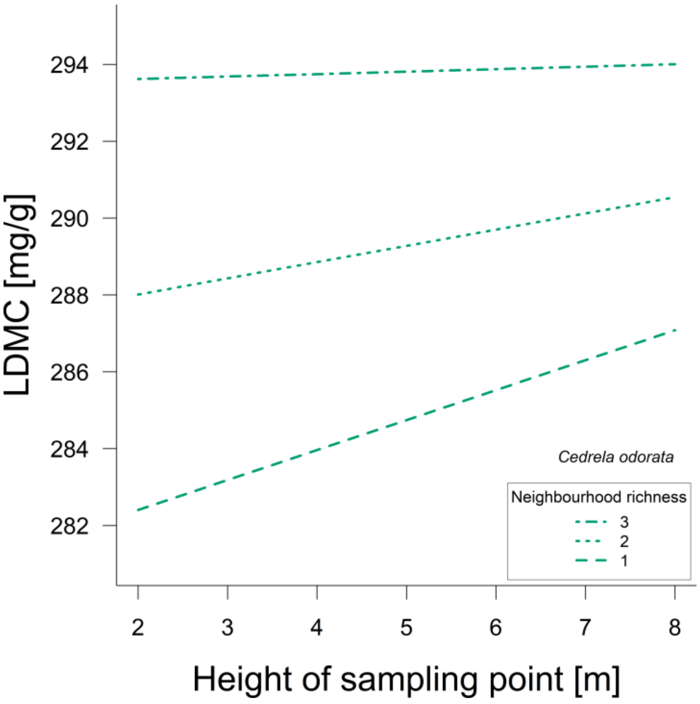

Fig. 5. Interacting effect of sampling height and neighbourhood richness on LDMC for *Cedrela odorata*. Different line types indicate different neighbourhood richness levels. For the numerical results of the model see Appendix B: Table B.7.

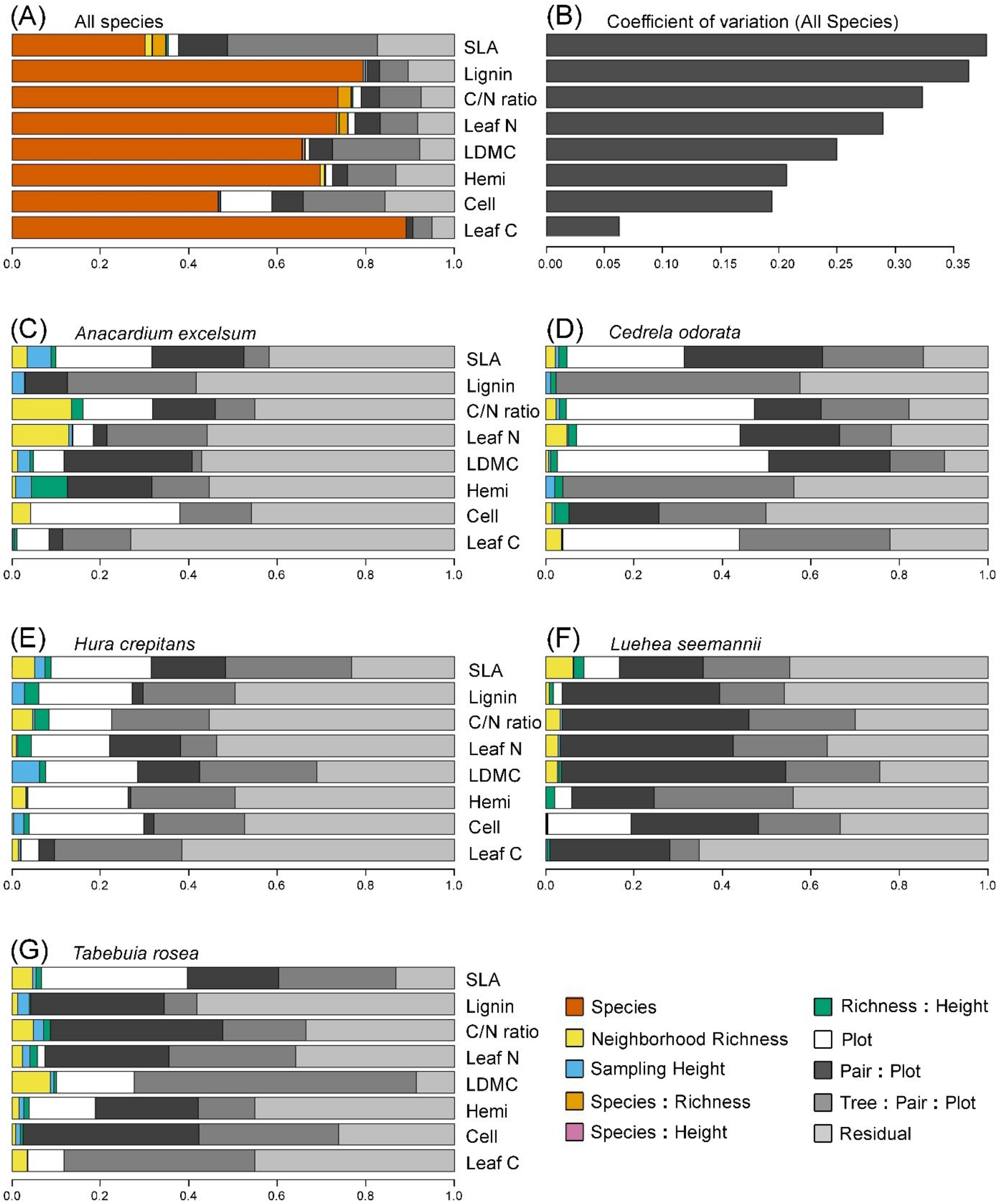

Fig. 6. Proportions of explained variance for leaf traits across all species (A) and for each species separately (C to G). Traits are sorted by their coefficient of variation across all species (B). Coloured bars indicate fixed effects and their interactions, shades of gray and white indicate random effects. For numerical values see Appendix B: Tables B.9 and B.10.

2.4.4 Within-individual leaf trait variation

For most traits (LDMC, SLA, leaf C, C/N ratio, lignin, cellulose and hemicellulose) within-individual variation was not influenced by neighbourhood richness (Appendix B: Fig. B.11, Table B.12). The only exception was leaf N concentration, which decreased significantly with increasing neighbourhood richness (Fig. 7). The lack of a significant species-by-neighbourhood richness interaction indicates that this relationship was not driven by particular species (Appendix B: Table B.12). This finding was also supported by the species-specific results, where the SD of none of the traits decreased significantly with increasing neighbourhood richness (Appendix B: Table B.13); however, there were marginal effects for *C. odorata* and *T. rosea.* Within-individual variation significantly differed between species for LDMC, SLA, lignin and cellulose, but not for C/N ratio, leaf C and hemicellulose (Appendix B: Table B.12). The species *L. seemannii* and *T. rosea*, which were classified as light-demanding and shade-tolerant, respectively, had the lowest DBH (Appendix B: Table B.1). The shade-tolerant *C. odorata* had higher DBH than the light intermediate *H. crepitans*, but not a higher DBH than the light-intermediate *A. excelsum*, which showed the highest DBH of all species. In most cases, leaf traits and species richness did not explain tree size. However, in higher diversity levels DBH was positively corelated with cellulose and negatively corelated hemicellulose (Appendix B: Table B.14).

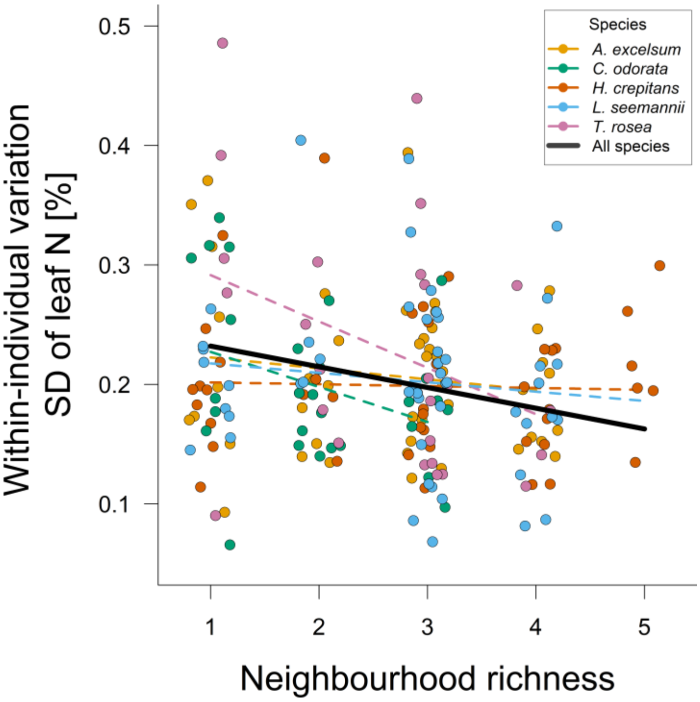

Fig. 7. Within-individual variation (measured as standard deviation) of leaf N as response to neighbourhood species richness. The black line indicates the predictions from the significant model including all species. Coloured points represent individual trees, coloured, dashed lines represent the non-significant species-specific models. For the other traits and the numerical results of the models see Appendix B: Tables B.12, B.13 and Fig. B.11.

2.5 Discussion

With regard to specific leaf area (SLA), within-species trait variation (that is, species niche breadth) decreased with increasing neighbourhood species richness. According to the niche theory (Hutchinson, 1957; MacArthur & Levins, 1967), narrower species niches might be a strategy to reduce competition intensity with other species (Carmona et al., 2019). In contrast, within-species trait variation did not change with neighbourhood species richness for the other traits measured. Thus, the niche breadth mostly followed the null model visualized in Fig. 1D. For leaf N we found indications that niche theory might be expanded to the level of individual plants: within-individual leaf trait variation of leaf N decreased with increasing neighbourhood richness. While our study revealed that a large amount of leaf trait variation is related to species identity or caused randomly, a considerable part of within-individual leaf trait variation was brought about by the vertical crown gradient and neighbourhood species richness.

2.5.1 Within-species leaf trait variation

As for most traits within-species variation did not change with neighbourhood species richness, we could not unequivocally confirm our first hypothesis that a species' niche breadth decreases with increasing tree species richness of the local neighbourhood. However, we found support for this relationship for SLA. Here, the smaller niche breadth of SLA in species mixtures might be explained by niche partitioning with different species exploiting different sections of the light gradient (Fig. 1C). On the other hand, SLA was the trait with the highest overall coefficient of variation, which might be the prerequisite to optimally adjust to a steeper light gradient within monocultures. Our findings that the magnitude of within-species variation strongly depends on the trait considered has been also pointed out also in other studies (Albert et al., 2011). For example, Siebenkäs, Schumacher & Roscher (2015) found that in grass and forb species, within-species variation of SLA and leaf N was higher than for LDMC. For woody species, Garnier et al. (2001) reported that within-species variability was high for SLA, low for LDMC and intermediate for leaf N concentration. These trait-specific responses are consistent with our findings.

2.5.2 Sources and magnitude of within-individual leaf trait variation

All traits except for leaf C varied significantly along the tree crown gradient, thus supporting our second hypothesis. Especially in tropical rainforests, leaves of the top canopy are exposed to high levels of radiation and a high water vapor deficit (Chazdon & Fetcher, 1984), which explains the need to construct leaves with more structural support as provided by the lignification of leaf cell walls (Moura, Bonine, de Oliveira Fernandes Viana, Dornelas & Mazzafera, 2010). This was also shown for herbaceous species, and, for example, *Calamagrostis epigejos* which produced more lignin in its leaves when exposed to an increased amount of UV-B radiation (Rozema et al., 1997). By producing more lignin in the leaves in the upper crown, plants can sustain higher turgor loss without suffering cell wall damage (Le Gall et al., 2015). In the lower crown where less light is available, this mechanism is not necessary, and a larger proportion of carbon can be allocated to other structural polymers (hemicellulose and cellulose).

Here, trees produce thinner leaves (i.e. high SLA, low LDMC) with more proteins (i.e. higher leaf N) which allow a positive net photosynthesis rate.

Our observation of changing leaf traits along the vertical crown gradient is most likely a consequence of the changing light conditions within the crown. However, it is also highly dependent on the individual species. Most of these effects were observed for the two species that had been classified as light-intermediate (*A. excelsum* and *H. crepitans*). In contrast, both species classified as shade-tolerant (*C. odorata* and *T. rosea*) showed no height dependency of their leaf traits. These findings correspond to an overall lower leaf trait variation of conservative species, as found for Chinese subtropical trees by Böhnke and Bruelheide (2013). Interestingly, both light-intermediate species were very unequal regarding their leaf traits: in most cases they were on the opposite edge of the observed trait spectrum and showed no overlap in the first PCA axis. In addition, both shade-tolerant species showed only a very small overlap in the PCA. Thus, niche differentiation in leaf traits was strongest between species with similar light adaptations.

We found only limited support for our third hypothesis, as only one trait responded to tree species richness of the local neighbourhood. In the case of LDMC, the trait variation along the vertical crown gradient was modified by the diversity of the local neighbourhood, and a positive relationship between LDMC and sampling height in monocultures disappeared with increasing neighbourhood richness. This might indicate that with increasing diversity, the light gradient becomes less steep and the influence of the vertical structure on the trait becomes less relevant. This leads to the conclusion that, given the standardized age and density of the Sardinilla experiment, light attenuation is weaker in more diverse communities, and thus, more light is available in the lower canopies, as compared to monospecific stands.

At the scale of individual trees, the variation of most leaf traits did not change with neighbourhood species richness. Therefore, we also could not unequivocally confirm our fourth hypothesis. However, variation of leaf N significantly decreased with increasing neighbourhood species richness. A decreased variation of leaf N within trees in mixtures indicates a reduction in competition intensity (Fichtner et al., 2018). In contrast, in monocultures every plant is competing with plants of very similar phenotypes. In order to use as many resources as possible, plants tend to modify their phenotype to avoid within-species competition. Thus, the lower within-individual variation of leaf N indicates that in mixed communities plants avoid trait overlap, while the overall species niche breadth remained unaffected, thus partitioning the total trait space at the community level among individuals within species. One reason why this pattern was only observed for leaf N may be the combination of strong differences between species but sufficiently high within-species variation. While soil nitrogen is often a limiting factor (e.g. Tamm, 1991), leaf N is very mobile within the crown (Swanston & Myrold, 1998), which facilitates a high within-individual variation. Trait relationships Values of SLA and leaf N were higher in *T. rosea*, which was a priori categorized as a shade-tolerant species, than in the light-demanding *L. seemannii*. One would expect this relationship for SLA but the opposite for leaf N as shade-tolerant plants should display higher values of SLA and lower values of leaf N (Mooney & Gulmon, 1979). A possible explanation for this finding might be that *T. rosea* develops its leaves slightly later in the season than do the other species (Sapijanskas, Paquette, Potvin, Kunert & Loreau, 2004). Therefore, the leaf samples of *T. rosea* were in an earlier ontogenetic stage than those of the other sampled species, which could explain their higher values in leaf N.

2.6 Conclusions

We investigated trait variation at two different scales and identified sources of within-individual trait variation: variation along the vertical crown gradient and along the neighbourhood species richness gradient. Although we could not demonstrate niche partitioning among individuals within species for all traits, our findings point to the existence of this mechanism. Thus, our study showed for the first time that the total trait space of mixed communities might not only be divided among species but also among individuals within species. We therefore conclude that factors affecting leaf trait variation at the species level might also play a role at the individual level and that niche partitioning could also apply to the level of individual plants.

2.7 Acknowledgements

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Appendix A: Supporting information to the methods

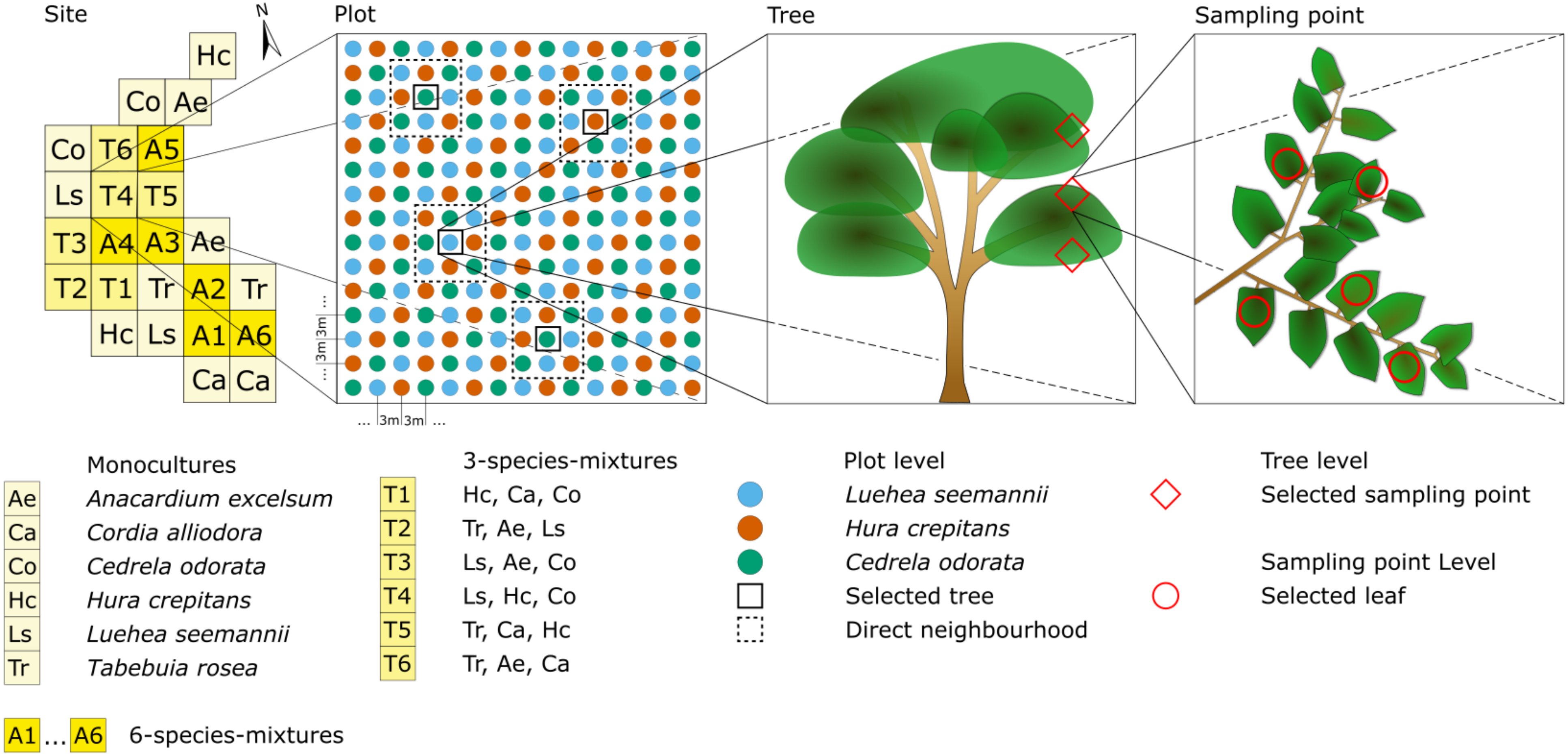

Fig. A.1: Experimental setup and sampling design. (A) Overview of the 24 plots of the main experiment of the Sardinilla plantation. Plots were established in three different diversity levels: twelve monocultures (Ae, Ca, Co, Hc, Ls and Tr), six 3-species-mixtures (T1-T6) and six 6-species-mixtures (A1-A6). Due to high mortality of C. alliodora, the Ca monocultures were abandoned. (B) Overview of a selected plot. In each plot, on average 231 trees were planted in a distance of 3 m (and a diagonal distance of 4.2 m, respectively). The sequence of species was kept fixed within the rows but shifted by one for every next line following a Latin square design. The eight trees directly adjacent to a focal tree were considered as its local neighbourhood. (C) Sampling took place along the vertical crown gradient, starting at the lower border of the crown (but not lower than 1.5 m). A second sampling point was set at around 8 m and a third sampling point was chosen between them. (D) At each sampling point, up to five fully developed leaves without major damage from herbivores or pathogens were harvested for trait measurement.

Table A.2 Number of focal trees and collected leaves per planted plot diversity. Number of tree species surrounding the target tree („neighbourhood richness“) for each of the five investigated species, *Anacardium excelsum*, *Cedrela odorata*, *Hura crepitans*, *Luehea seemannii* and *Tabebuia rosea*, respectively.

	A. excelsum	*C. odorata*	*H. crepitans*	*L. seemannii*	*T. rosea*
Focal trees - plot diversity 1	8	8	8	8	5
Focal trees - plot diversity 3	20	15	17	22	8
Focal trees - plot diversity 6	20	5	18	20	13
Collected leaves - plot diversity 1	96	63	81	86	30
Collected leaves - plot diversity 3	192	117	132	167	54
Collected leaves - plot diversity 6	219	39	159	156	87
Focal trees - neighbourhood richness 1	9	9	10	9	5
Focal trees - neighbourhood richness 2	9	11	5	5	5
Focal trees - neighbourhood richness 3	20	8	12	24	12
Focal trees - neighbourhood richness 4	10	0	10	12	4
Focal trees - neighbourhood richness 5	0	0	6	0	0

Appendix B: Supporting information to the results

Table B.1 Characteristics for each of the five investigated species, *Anacardium excelsum*, *Cedrela odorata*, *Hura crepitans*, *Luehea seemannii* and *Tabebuia rosea*, respectively. Values are averaged at the level of individual trees and then tested for significant differences between species. Letters in brackets below the species mean values indicate significant differences between species based on Tukey's Honest Significant Difference test.

	A. excelsum	*C. odorata*	*H. crepitans*	*L. seemannii*	*T. rosea*	All species
Light adaptation	Light-intermediate	Shade-tolerant	Light-intermediate	Light-demanding	Shade-tolerant	-
Mean DBH [cm]	21.82 (a)	21.50 (a)	16.81 (b)	13.88 (b c)	11.77 (c)	18.15
Mean height [m]	15.31 (a)	13.49 (b)	10.56 (b)	16.52 (a)	11.40 (b)	13.66
Mean SLA [mm^2/mg]	12.80 (c)	22.58 (a)	25.16 (a)	16.92 (b)	23.44 (a)	18.91
Mean LDMC [mg/g]	323.70 (a)	297.12 (b)	214.77 (c)	248.79 (a)	196.82 (c)	289.28
Mean Leaf N [%]	1.44 (d)	2.53 (b)	2.92 (a)	2.16 (c)	2.46 (b)	2.19
Mean C/N ratio	30.57 (a)	18.97 (c)	13.71 (d)	22.01 (b)	17.38 (c)	21.89
Mean Leaf C [%]	42.31 (d)	46.68 (a)	39.45 (e)	45.53 (b)	43.04 (c)	43.11
Mean Lignin [%]	26.47 (c)	30.56 (a)	10.90 (e)	28.41 (b)	17.73 (d)	23.13
Mean Cellulose [%]	25.12 (a)	19.71 (b)	18.10 (b)	25.46 (a)	24.99 (a)	22.93
Mean Hemicellulose [%]	8.05 (d)	10.29 (c)	12.32 (a)	11.42 (b)	12.85 (a)	10.60

Table B.2 Results of the principal component analysis. Standard deviation, proportion of variance and cumulative proportion for each of the first eight PCA axes, trait names and values of trait contributions (loadings) to the first (PC1) to eighth (PC8) PCA axis are given.

Importance of PC	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Standard deviation	2.0985	1.1646	0.9904	0.8675	0.4492	0.3918	0.3349	0.1979
Proportion of variance	0.5505	0.1695	0.1226	0.0941	0.0252	0.0192	0.0140	0.0049
Cumulative proportion	0.5505	0.7200	0.8426	0.9367	0.9619	0.9811	0.9951	1.0000
Traits								
LDMC	-0.3802	-0.0425	-0.4274	-0.3827	-0.2227	-0.4715	-0.4906	-0.1090
SLA	0.3791	-0.2682	0.3624	0.2713	0.3351	-0.4996	-0.4661	-0.0176
Leaf N	0.4287	-0.2669	-0.0754	-0.1087	-0.5524	0.0726	-0.1186	0.6349
C/N ratio	-0.4380	0.2503	0.1253	0.0025	0.3948	-0.0577	-0.0841	0.7507
Leaf C	-0.2133	-0.7233	-0.1524	-0.0573	0.3176	0.5048	-0.2215	-0.0107
Lignin	-0.3375	-0.5142	0.2621	-0.0040	-0.1708	-0.4414	0.5713	0.0507
Cellulose	-0.2867	-0.0104	-0.2276	0.8673	-0.3040	0.0227	-0.1429	0.0169
Hemicellulose	0.3076	-0.0689	-0.7217	0.1118	0.3933	-0.2633	0.3536	0.1351

Table B.3 Effect of neighbourhood richness on within-species leaf trait variation (measured as standard deviation, SD). For each leaf trait, a linear model was fitted with the standard deviation of a trait as response variable, and species, neighbourhood richness and their interaction as predictors. Given are the outputs of the model (F-statistics, *p*-values), significant results (*p*-value <0.05) are highlighted in bold.

Trait	Factor	F-value	*p*-value
LDMC	Species	5.05	0.017
	Neighbourhood richness	1.94	0.193
	Neighbourhood richness : Species	0.64	0.648
SLA	Species	21.84	<0.001
	Neighbourhood richness	7.83	0.018
	Neighbourhood richness : Species	1.40	0.302
Leaf N	Species	4.07	0.032
	Neighbourhood richness	1.55	0.241
	Neighbourhood richness : Species	0.68	0.621
C/N ratio	Species	5.38	0.014
	Neighbourhood richness	0.08	0.783
	Neighbourhood richness : Species	4.11	0.031
Leaf C	Species	1.08	0.414
	Neighbourhood richness	1.79	0.210
	Neighbourhood richness : Species	0.16	0.953
Lignin	Species	1.87	0.192
	Neighbourhood richness	0.01	0.932
	Neighbourhood richness : Species	4.11	0.031
Cellulose	Species	70.15	<0.001
	Neighbourhood richness	2.07	0.180
	Neighbourhood richness : Species	12.29	<0.001
Hemicellulose	Species	2.34	0.119
	Neighbourhood richness	0.45	0.516
	Neighbourhood richness : Species	0.72	0.597

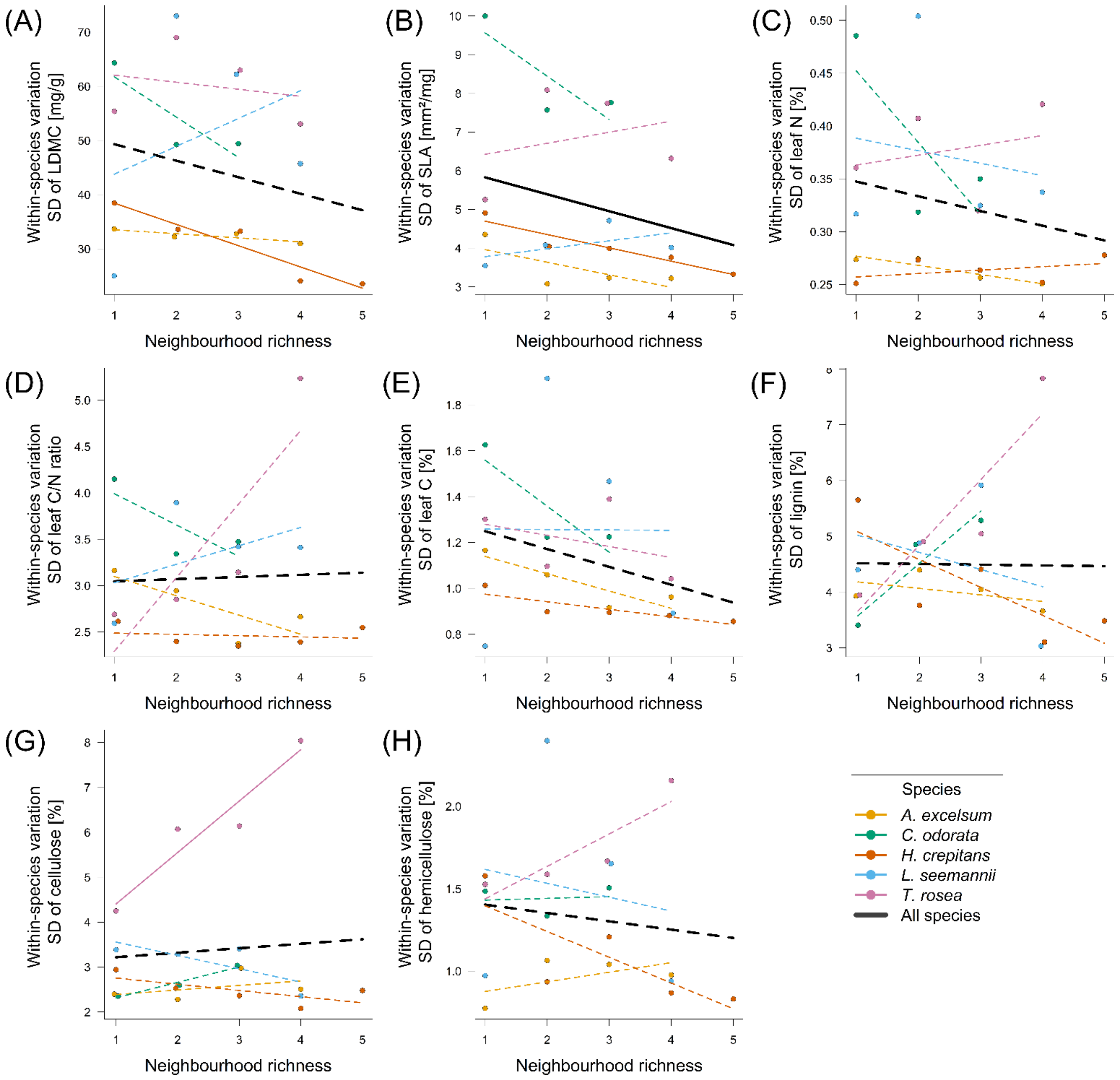

Fig. B.4: Effect of neighbourhood richness on within-species leaf trait variation (measured as standard deviation). The black line represents the models across all species. Coloured points represent the species' SD for the given neighbourhood richness, coloured lines represent predictions from linear models. Continuous lines indicate significant effects, dashed lines indicate non-significant effects. For the numerical values see Tables B.3 and B.5.

Table B.5 Effect of neighbourhood richness on within-species leaf trait variation (measured as standard deviation, SD). Separate models were applied for each species. Given are the outputs of the models (F-statistics, *p*-values), significant results (*p*-value <0.05) are highlighted in bold.

	A. excelsum		*C. odorata*		*H. crepitans*		*L. seemannii*		*T. rosea*	
Trait	F-value	*p*-value	F-value	*p*-value	F-value	*p*-value	F-value	*p*-value	F-value	*p*-value
LDMC	5.70	0.140	2.84	0.341	30.31	0.012	0.22	0.683	0.11	0.771
SLA	2.00	0.292	2.19	0.378	23.16	0.017	0.87	0.450	0.17	0.720
Leaf N	13.40	0.067	1.40	0.447	0.65	0.479	0.06	0.829	0.15	0.738
C/N ratio	3.16	0.218	1.55	0.431	0.11	0.760	0.25	0.526	5.84	0.136
Leaf C	6.77	0.121	2.97	0.335	8.58	0.061	0.00	0.996	0.33	0.622
Lignin	0.64	0.507	10.27	0.193	5.06	0.111	0.25	0.670	9.70	0.089
Cellulose	0.46	0.568	34.96	0.107	2.85	0.190	2.72	0.241	20.45	0.046
Hemicellulose	0.97	0.429	0.01	0.929	4.93	0.113	0.05	0.842	7.26	0.115

Table B.6 Effects of neighbourhood richness and sampling height on leaf traits. The models contained all species. Given are the outputs of the models (Degrees of Freedom (DF), F-statistics, *p*-values), significant results (*p*-value <0.05) are highlighted in bold.

Trait		Species	Neighbourhood richness	Height	Species : Richness	Species : Height	Richness : Height
LDMC	DF	129.46	40.43	393.45	127.17	382.49	371.19
	F-value	91.45	0.24	11.18	1.41	2.97	0.51
	p-value	<0.001	0.624	0.001	0.233	0.020	0.475
SLA	DF	118.47	28.84	395.42	107.77	386.98	373.89
	F-value	52.29	0.47	32.81	1.99	3.48	0.92
	p-value	<0.001	0.498	<0.001	0.101	0.008	0.337
Leaf N	DF	120.4	30.65	406.4	122.13	404.94	387.68
	F-value	189.00	2.99	1.54	5.13	4.63	0.11
	p-value	<0.001	0.094	0.216	0.001	0.001	0.741
C/N ratio	DF	127.47	33.75	404.49	115.85	401.41	385.08
	F-value	247.50	2.84	7.51	6.88	4.24	0.79
	p-value	<0.001	0.101	0.006	<0.001	0.002	0.376
Leaf C	DF	164.05	98.34	416.24	147.56	421.06	399.05
	F-value	433.64	1.11	1.03	0.89	0.20	1.70
	p-value	<0.001	0.296	0.311	0.474	0.94	0.194
Lignin	DF	114.97	29.09	419.55	122.41	426.53	402.35
	F-value	218.93	1.30	19.98	0.59	0.37	0.41
	p-value	<0.001	0.264	<0.001	0.669	0.828	0.521
Cellulose	DF	141.34	58.12	404.62	115.42	399.08	382.35
	F-value	45.26	0.46	7.33	0.69	2.32	0.29
	p-value	<0.001	0.501	0.007	0.602	0.056	0.591
Hemicellulose	DF	123.27	33.15	412.77	113.07	416.37	394.51
	F-value	129.48	6.88	5.28	1.47	0.95	0.89
	p-value	<0.001	0.013	0.022	0.217	0.433	0.346

Table B.7 Effects of neighbourhood richness and sampling height on leaf traits. Separate models were applied for each species. Given are the outputs of the models (Degrees of Freedom (DF), F-statistics, *p*-values), significant results (*p*-value <0.05) are highlighted in bold.

Trait		*A. excelsum*			*C. odorata*			*H. crepitans*			*L. seemannii*			*T. rosea*		
		Richness	Height	Richness: Height	Richness	Height	Richness: Height	Richness	Height	Richness: Height	Richness	Height	Richness: Height	Richness	Height	Richness: Height
LDMC	DF	37.17	136.03	132.52	23.3	47.66	48.96	16.42	86.6	86.41	40.61	92.76	91.6	11.24	30.69	30.34
	F-value	0.98	16.46	1.04	0.01	2.38	4.34	0.78	29.72	0.89	1.69	0.01	0.27	2.49	0.62	0.27
	p-value	0.329	<0.001	0.311	0.925	0.130	0.042	0.389	<0.001	0.349	0.201	0.925	0.607	0.142	0.435	0.604
SLA	DF	33.5	125.92	121.73	16.74	48.74	50.79	15.64	85.56	85.38	23.87	105.75	100.5	15.33	32.02	30.81
	F-value	1.89	37.51	1.42	0.76	0.09	3.26	0.89	35.99	0.62	2.89	8.51	0.64	1.46	0.11	0.69
	p-value	0.178	<0.001	0.236	0.395	0.764	0.077	0.359	<0.001	0.434	0.102	0.004	0.426	0.245	0.739	0.413
Leaf N	DF	17.75	128.68	124.62	23.11	50.1	51.83	15.45	95.26	95.2	40.48	96.97	95.26	11.73	35.48	34.08
	F-value	12.96	2.29	0.12	2.02	1.91	2.04	0.04	12.96	0.82	1.66	2.20	0.02	0.70	3.47	1
	p-value	0.002	0.133	0.733	0.169	0.173	0.160	0.844	0.001	0.369	0.205	0.142	0.886	0.419	0.071	0.324
C/N ratio	DF	30.67	127.49	123.51	21.47	50.59	52.46	11.12	94.64	94.41	38.14	94.63	93.03	21.61	35.72	34.12
	F-value	10.75	5.76	0.76	1.12	0.21	3.30	0.93	21.12	1.53	1.80	1.98	0.00	2.10	2.96	0.47
	p-value	0.003	0.018	0.384	0.302	0.650	0.075	0.355	<0.001	0.219	0.188	0.163	0.953	0.162	0.094	0.499
Leaf C	DF	18.35	133.26	128.24	17.98	49.8	51.92	13.27	90.33	90.13	31.11	106.34	101.69	11.44	35.58	34.43
	F-value	0.26	0.14	3.00	1.10	0.73	0.00	1.21	1.87	0.15	0.81	0.08	0.35	1.30	0.31	0.00
	p-value	0.615	0.710	0.086	0.308	0.397	0.976	0.291	0.175	0.695	0.374	0.780	0.558	0.278	0.584	0.948
Lignin	DF	16.72	125.61	121.86	26.51	58.27	64.23	14.84	94.81	94.63	30.21	100.83	97.64	18.82	46.18	46.73
	F-value	0.12	11.06	0.00	0.80	0.75	0.49	1.88	2.76	3.01	0.15	4.59	0.42	0.26	1.89	0.07
	p-value	0.729	0.001	0.956	0.380	0.390	0.489	0.190	0.100	0.086	0.699	0.035	0.518	0.617	0.176	0.791
Cellulose	DF	38.3	129.21	124.7	13.96	56.16	58.29	17.79	93.61	93.39	30.95	94.25	92.22	11.87	34.25	32.95
	F-value	2.76	0.48	0.01	0.03	3.65	1.92	1.14	3.60	0.66	0.15	0.10	1.23	0.12	2.76	0.23
	p-value	0.105	0.491	0.924	0.859	0.061	0.171	0.299	0.061	0.418	0.704	0.749	0.271	0.739	0.106	0.635
Hemicellulose	DF	22.63	125.07	120.9	26.79	57.93	63.74	13.7	93.06	93.02	19.99	96.22	93.07	14.81	43.62	43.03
	F-value	11.76	0.21	3.79	1.53	1.15	0.42	1.71	0.01	0.17	0.65	3.30	1.05	0.68	0.81	0.90
	p-value	0.002	0.645	0.054	0.227	0.288	0.521	0.213	0.925	0.685	0.428	0.073	0.309	0.424	0.372	0.347

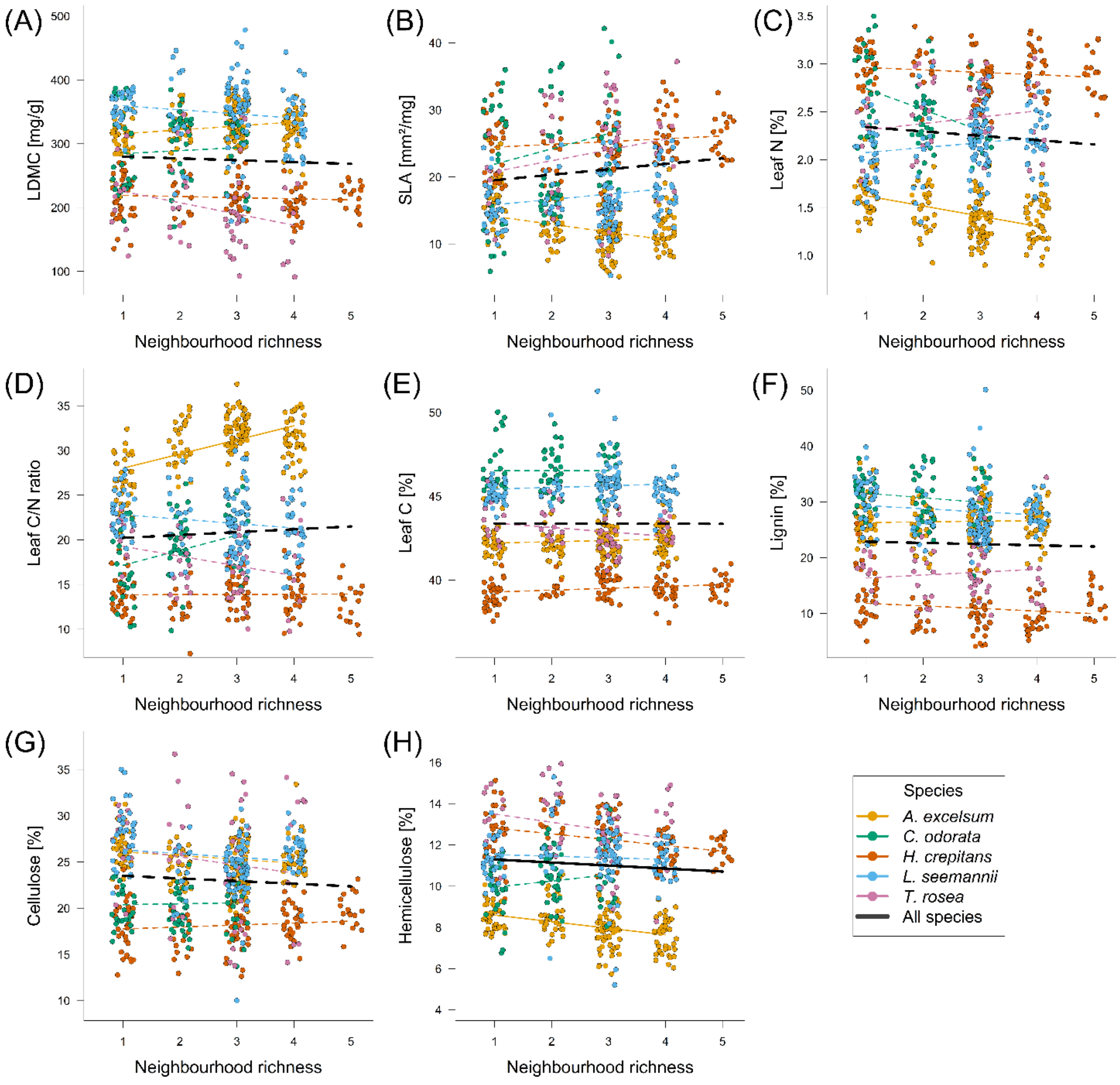

Fig. B.8: Effect of neighbourhood richness on trait values. The black lines represent the models across all species. Coloured points represent individual sampling points, coloured lines represent predictions from linear mixed-effects models for each species separately. Continuous lines indicate significant effects. Dashed lines indicate non-significant effects. For the numerical results of the models see Tables B.6 and B.7.

Table B.9 Results of the variance partitioning – All species. Individual proportion of explained variance for each fixed factor (Species, neighbourhood richness, height, and their two-way interactions) and each random factor (Plot, Tree Pair, Tree, and their interactions), as well as the unexplained variance (Residual). Additionally, the coefficient of variation (CV) illustrates the overall variability of the traits.

Trait	Species	Neighbourhood richness	Height	Species: Richness	Species Height	Richness: Height	Plot	Pair: Plot	Tree: Pair : Plot	Residual	CV
LDMC	0.6546	0.0003	0.0023	0.0043	0.0006	0.0005	0.0095	0.0529	0.1956	0.0794	0.2498
SLA	0.3008	0.0156	0.0005	0.0296	0.0014	0.0047	0.0230	0.1110	0.3393	0.1741	0.3788
Leaf N	0.7333	0.0053	0.0002	0.0190	0.0013	0.0009	0.0143	0.0571	0.0855	0.0831	0.2899
C/N ratio	0.7358	0.0008	0.0001	0.0292	0.0009	0.0035	0.0193	0.0403	0.0939	0.0762	0.3234
Leaf C	0.8900	0.0001	0.0001	<0.0001	<0.0001	0.0005	<0.0001	0.0142	0.0429	0.0513	0.0622
Lignin	0.7928	0.0001	0.0055	<0.0001	<0.0001	0.0006	0.0034	0.0276	0.0648	0.1052	0.3634
Cellulose	0.4648	<0.0001	0.0030	<0.0001	0.0006	0.0006	0.1154	0.0721	0.1849	0.1566	0.1939
Hemicellulose	0.6965	0.0095	0.0003	<0.0001	<0.0001	0.0015	0.0167	0.0326	0.1096	0.1333	0.2066

Table B.10 Results of the variance partitioning – species-wise. Individual proportion of explained variance for each fixed factor (Neighbourhood richness, height, and their interaction) and each random factor (plot, tree pair, tree, and their interactions), as well as the unexplained variance (residual).

Species	Trait	Neighbourhood richness	Height	Richness : Height	Plot	Pair : Plot	Tree : Pair : Plot	Residual
A. excelsum	LDMC	0.0133	0.0276	0.0078	0.0681	0.2908	0.0203	0.5721
	SLA	0.0339	0.0537	0.0118	0.2164	0.2088	0.0563	0.4191
	Leaf N	0.1284	0.0079	0.0014	0.0462	0.0310	0.2267	0.5584
	C/N ratio	0.1342	<0.0001	0.0268	0.1568	0.1420	0.0883	0.4519
	Leaf C	0.0018	0.0028	0.0071	0.0714	0.0313	0.1544	0.7312
	Lignin	0.0008	0.0278	0.0012	0.0028	0.0916	0.2928	0.5830
	Cell	0.0416	0.0003	0.0004	0.3365	<0.0001	0.1620	0.4592
	Hemi	0.0087	0.0347	0.0818	<0.0001	0.1904	0.1293	0.5552
C. odorata	LDMC	0.0068	0.0043	0.0151	0.4777	0.2739	0.1234	0.0987
	SLA	0.0214	0.0081	0.0191	0.2642	0.3122	0.2286	0.1464
	Leaf N	0.0475	0.0044	0.0185	0.3694	0.2251	0.1160	0.2192
	C/N ratio	0.0242	0.0072	0.0147	0.4258	0.1500	0.1990	0.1792
	Leaf C	0.0367	0.0011	0.0014	0.3992	<0.0001	0.3390	0.2226
	Lignin	0.0010	0.0109	0.0117	<0.0001	<0.0001	0.5511	0.4253
	Cell	0.0141	0.0062	0.0330	<0.0001	0.2015	0.2424	0.5029
	Hemi	0.0004	0.0198	0.0182	<0.0001	<0.0001	0.5221	0.4395
H. crepitans	LDMC	0.0003	0.0618	0.0138	0.2077	0.1405	0.2649	0.3110
	SLA	0.0514	0.0234	0.0133	0.2269	0.1681	0.2844	0.2326
	Leaf N	0.0091	0.0037	0.0303	0.1770	0.1600	0.0829	0.5370
	C/N ratio	0.0470	0.0040	0.0332	0.1414	<0.0001	0.2193	0.5551
	Leaf C	0.0138	0.0050	0.0021	0.0393	0.0353	0.2886	0.6159
	Lignin	0.0010	0.0264	0.0325	0.2117	0.0249	0.2079	0.4956
	Cell	0.0033	0.0239	0.0117	0.2589	0.0234	0.2044	0.4744
	Hemi	0.0315	0.0013	0.0033	0.2257	0.0060	0.2368	0.4954

L. seemannii	LDMC	0.0259	0.0033	0.0068	<0.0001	0.5064	0.2123	0.2453
	SLA	0.0619	0.0012	0.0234	0.0797	0.1895	0.1968	0.4476
	Leaf N	0.0281	0.0041	0.0001	<0.0001	0.3918	0.2117	0.3642
	C/N ratio	0.0324	0.0043	<0.0001	<0.0001	0.4232	0.2394	0.3007
	Leaf C	0.0001	0.0028	0.0074	<0.0001	0.2705	0.0653	0.6538
	Lignin	0.0079	0.0001	0.0090	0.0201	0.3564	0.1463	0.4601
	Cell	0.0020	0.0012	0.0019	0.1874	0.2890	0.1839	0.3346
	Hemi	0.0005	0.0005	0.0199	0.0383	0.1856	0.3147	0.4406
T. rosea	LDMC	0.0870	0.0073	0.0067	0.1787	<0.0001	0.6335	0.0869
	SLA	0.0460	0.0078	0.0131	0.3289	0.2056	0.2665	0.1321
	Leaf N	0.0231	0.0178	0.0168	0.0160	0.2815	0.2856	0.3592
	C/N ratio	0.0484	0.0226	0.0162	<0.0001	0.3884	0.1891	0.3352
	Leaf C	0.0342	0.0002	0.0015	0.0815	<0.0001	0.4318	0.4508
	Lignin	0.0120	0.0269	0.0023	<0.0001	0.3027	0.0740	0.5820
	Cell	0.0080	0.0100	0.0060	0.0089	0.3906	0.3154	0.2611
	Hemi	0.0155	0.0104	0.0128	0.1492	0.2331	0.1281	0.4509

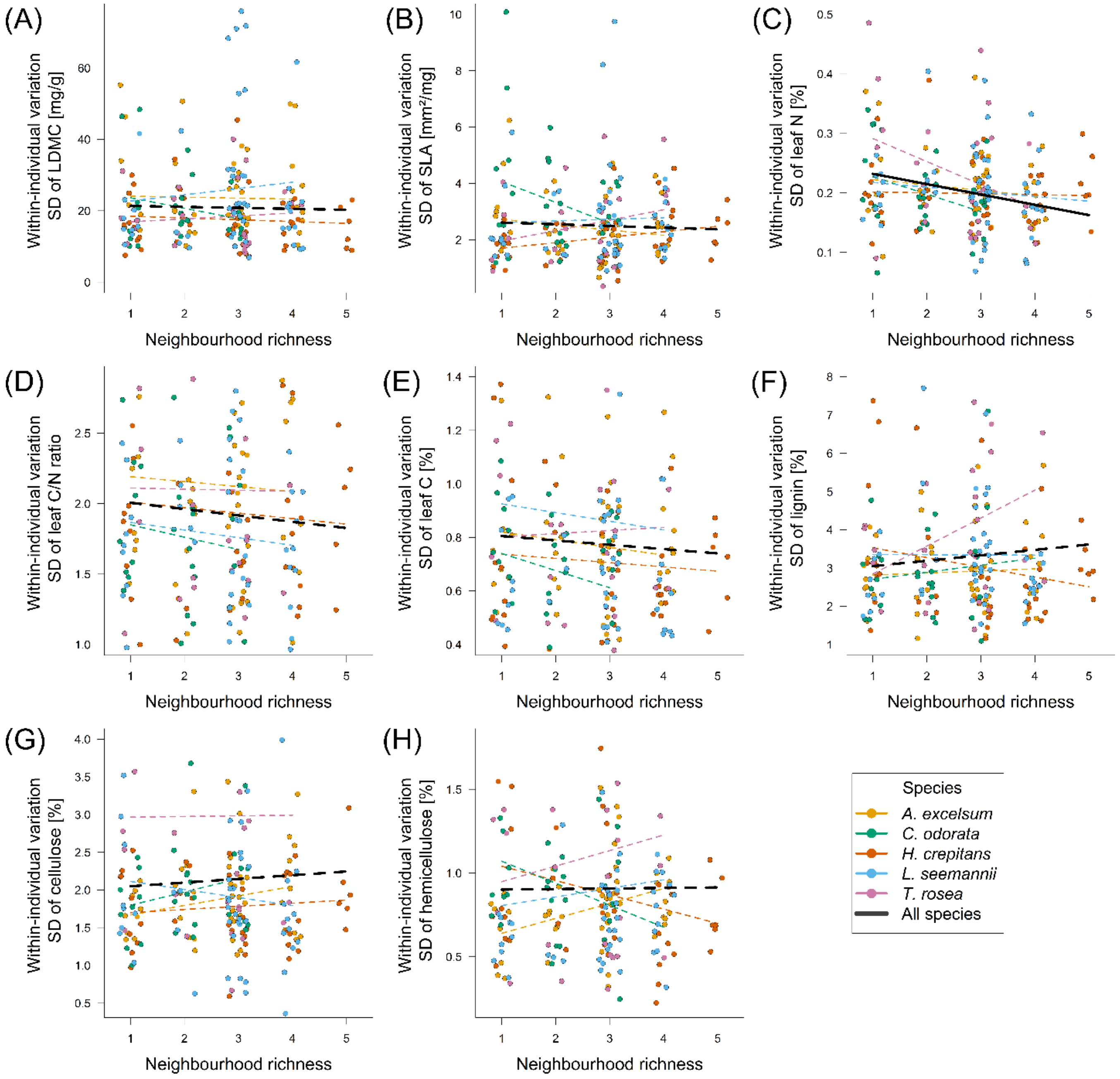

Fig. B.11: Effect of neighbourhood richness on within-individual leaf trait variation (measured as standard deviation). The black lines represent the models across all species. Coloured points represent individual trees, coloured lines represent predictions from linear mixed-effects models. Continuous lines indicate significant effects, dashed lines indicate non-significant effects. For the numerical values see Tables B.12 and B.13.

Table B.12 Effect of neighbourhood richness on within-individual leaf trait variation (measured as standard deviation, SD). Models contained all species. Given are the outputs of the models (Degrees of Freedom (DF), F-statistics, *p*-values), significant results (*p*-value <0.05) are highlighted in bold.

Trait		DF	F-value	*p*-value
LDMC	Species	140.4	3.17	0.016
	Neighbourhood richness	47.16	0.00	0.975
	Neighbourhood richness : Species	130.37	0.49	0.744
SLA	Species	185	3.68	0.007
	Neighbourhood richness	185	0.07	0.795
	Neighbourhood richness : Species	185	2.14	0.078
Leaf N	Species	185	0.96	0.429
	Neighbourhood richness	185	5.26	0.023
	Neighbourhood richness : Species	185	1.60	0.176
C/N ratio	Species	185	2.09	0.084
	Neighbourhood richness	185	0.68	0.410
	Neighbourhood richness : Species	185	0.03	0.998
Leaf C	Species	147.39	0.92	0.455
	Neighbourhood richness	48.09	0.36	0.550
	Neighbourhood richness : Species	128.4	0.07	0.992
Lignin	Species	134.57	2.67	0.035
	Neighbourhood Richness	49.5	0.02	0.893
	Neighbourhood richness : Species	126.92	1.95	0.106
Cellulose	Species	139.72	8.10	<0.001
	Neighbourhood Richness	44.14	0.23	0.636
	Neighbourhood richness : Species	122.48	0.50	0.733
Hemicellulose	Species	145.64	1.67	0.160
	Neighbourhood Richness	49.28	0.00	0.973
	Neighbourhood richness : Species	143.95	1.54	0.194

Table B.13 Effects of neighbourhood richness on within-individual leaf trait variation (measured as standard deviation, SD). Separate models were applied for each species. Given are the outputs of the models (Degrees of Freedom (DF), F-statistics, *p*-values).

	A. excelsum			*C. odorata*			*H. crepitans*			*L. seemannii*			*T. rosea*		
Trait	DF	F-value	*p*-value	DF	F-value	*p*-value	DF	F-value	*p*-value	DF	F-value	*p*-value	DF	F-value	*p*-value
LDMC	9.77	0.01	0.916	18.44	1.81	0.195	27.32	0.65	0.429	30.23	0.00	0.996	11.49	0.18	0.678
SLA	46	1.44	0.237	18.84	2.58	0.125	41	3.72	0.061	41.14	0.00	0.996	24	1.67	0.209
Leaf N	21.24	0.83	0.371	26	3.39	0.077	41	0.05	0.817	48	0.62	0.435	12.11	3.63	0.081
C/N ratio	22.68	0.04	0.849	9.04	0.02	0.899	41	0.17	0.681	48	0.34	0.560	24	0.00	0.970
Leaf C	18.39	0.70	0.412	11.88	0.22	0.647	23.5	0.97	0.336	19.31	0.05	0.828	14.98	1.76	0.204
Lignin	32.94	0.10	0.751	18.92	0.16	0.693	41	2.41	0.128	21.58	0.00	0.976	24	3.29	0.082
Cellulose	12.4	1.62	0.226	26	1.57	0.221	13.74	0.06	0.807	20.93	0.58	0.455	10.97	0.00	0.979
Hemicellulose	21.74	3.44	0.077	26	1.60	0.218	14.74	4.20	0.059	22.68	0.42	0.522	24	0.29	0.592

Table B.14 Effects of leaf traits and neighbourhood richness on tree sizes (measured as DBH). Models contain all species. Given are the outputs of the models (Degrees of Freedom (DF), F-statistics, *p*-values), significant results (*p*-value <0.05) are highlighted in bold.

Trait	DF	F-value	*p*-value
LDMC	163.54	3.55	0.061
Neighbourhood richness	188.10	0.66	0.419
LDMC : Neighbourhood richness	186.92	0.07	0.790
SLA	171.79	0.06	0.805
Neighbourhood richness	189.28	0.81	0.368
SLA : Neighbourhood richness	188.77	0.21	0.644
Leaf N	76.20	0.00	0.968
Neighbourhood richness	189.50	0.74	0.391
Leaf N : Neighbourhood richness	188.56	3.56	0.061
C/N Ratio	75.45	0.65	0.422
Neighbourhood richness	188.68	0.88	0.349
C/N Ratio : Neighbourhood richness	187.18	2.36	0.126
Leaf C	25.04	0.70	0.409
Neighbourhood richness	52.07	0.98	0.328
Leaf C : Neighbourhood richness	166.22	0.42	0.517
Lignin	49.09	0.11	0.745
Neighbourhood richness	188.79	1.11	0.294
Lignin : Neighbourhood richness	189.66	2.31	0.130
Cellulose	165.29	1.12	0.292
Neighbourhood richness	189.41	0.83	0.363
Cellulose : Neighbourhood richness	188.14	6.61	0.011
Hemicellulose	84.68	0.64	0.425
Neighbourhood richness	190.91	0.75	0.387
Hemicellulose : Neighbourhood richness	188.37	5.61	0.019

Chapter 3

Within-individual leaf trait response to local light availability and biodiversity in a subtropical forest experiment

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Abstract

Leaf traits are important indicators of ecosystem functions. Trait values can vary widely between species, and a considerable amount of variation also occurs within species. However, within-individual variation is often neglected due to the limitations of traditional measurement tools. Many leaf trait values respond to light availability, which, in turn, is affected by the surrounding vegetation. Additionally, there is a strong within-individual light gradient, especially in tree canopies. In the BEF-China (Biodiversity–Ecosystem Functioning China) subtropical forest plantation, we analyzed how leaf trait values respond to light availability and neighboring tree species richness at the within-individual level. We sampled across the vertical light gradient formed by neighboring trees planted at varying diversity levels from monocultures to 24-species mixtures. We closely paired the leaf samples with sensor-based measurements of light availability. We used visible and near-infrared spectroscopy (spectral range: 350–2500 nm) to predict 14 leaf traits across 4981 leaves from 15 native tree species. Using a key feature of spectroscopy—deriving multiple leaf traits from a single spectral measurement of a sample—we assessed all traits simultaneously at the leaf level. We investigated whether an individual tree's direct neighbor or the surrounding tree species richness had a stronger influence on the light–trait relationship. Most trait values responded to light availability, though this response differed between deciduous and evergreen species. We found that tree species richness and a tree's direct neighbor could modify the light–trait relationship at the individual level. In some instances, a focal tree's direct neighbor influenced its leaf trait values more than the tree species richness in its local neighborhood. Specifically, in conspecific tree pairs of evergreens, specific leaf area and leaf nitrogen displayed a stronger response to changing light conditions. This response to light availability suggests a mechanism for avoiding within-species competition that is observable at the within-individual level. Our results show that biodiversity influences ecosystem functions through its effects on within-individual leaf trait variation. The fact that the interplay between light availability, biodiversity, and leaf traits can be observed within-individual trees highlights the importance of within-individual leaf trait variation in biodiversity research.

Keywords

BEF-China, FieldSpec, leaf habit, leaf trait variation, leaf traits, light availability, NIRS, phenotypic plasticity, subtropical forest, Vis/NIR spectroscopy

1. Introduction

Trait-based studies have become an integral part of plant ecology, as ecosystem functions are reflected in and mediated through functional traits (Laughlin, 2014; Poorter & Bongers, 2006; Violle et al., 2007). Leaf traits are particularly relevant because of their role in various ecological processes. Some of these leaf traits align with the leaf economics spectrum (LES), which characterizes a plant's return-on-investment strategy (Wright et al., 2004). The LES categorizes plant species along a continuum from fast-growing/acquisitive to slow-growing/conservative, based on their leaf trait values (Reich, 2014). One of the key indicators of the LES is specific leaf area (SLA), with high SLA values generally being associated with an acquisitive strategy. Such acquisitive leaves also tend to have higher concentrations of leaf macronutrients (Delpiano et al., 2020; Freschet et al., 2013), including high trait values for mass-based concentration of leaf nitrogen (leaf N), magnesium (leaf Mg), phosphorus (leaf P), potassium (leaf K), calcium (leaf Ca), and sulfur (leaf S), which are linked to metabolic processes such as photosynthesis and growth (Bird et al., 1973; Jackson & Volk, 1968; Poorter et al., 2009; Terry, 1976; Tränkner et al., 2018; Wang et al., 2019). Moreover, plants with an acquisitive growth strategy tend to have higher values in chemical defense traits such as phenolics and tannins, as they typically lack structural defenses (Coley et al., 1985; Eichenberg et al., 2015). Although not all of the traits mentioned are directly involved in resource acquisition, high values of these traits are typically observed in the plants on the acquisitive side of the LES (Wright et al., 2004). Given the strong correlations between high SLA, macronutrient concentrations, and chemical defense traits, we consider them a group of correlated traits in the framework of this study (hereafter “acquisitive traits”).

By contrast, many leaf traits show high values on the conservative side of the LES (hereafter “structural traits”). For example, high values in leaf dry matter content (LDMC), cellulose, and the mass-based carbon content (leaf C) facilitate structural integrity (Kitajima et al., 2016; Xing et al., 2021). Furthermore, plants may adjust the leaf lignin content in response to drought stress, while lignin also serves as a physical defense against pathogens (Liu et al., 2018). Finally, the leaf carbon-to-nitrogen ratio (CN ratio) reflects the role of N in structural compounds and metabolic processes (Xu et al., 2023) and has been reported to be positively correlated with other structural traits (Proß et al., 2021).

Leaf traits are often assessed as species mean traits (Garnier et al., 2001; McGill et al., 2006). However, within-species leaf trait variation may contribute a substantial amount to the total variability observed within a community (Siefert et al., 2015; Violle et al., 2012). The most important drivers of within-species leaf trait variation are ontogenetic shifts (Dayrell et al., 2018) as well as genetic variation and phenotypic plasticity (Callaway et al., 2003; Coleman et al., 1994). The latter is often caused by abiotic factors like gradients of precipitation, temperature, or elevation (Choi et al., 2019; Kühn et al., 2021; Souza et al., 2018). Within-individual variation is rarely addressed in current studies, but existing literature indicates that it is a major contributor to overall leaf trait variation (Escribano-Rocafort et al., 2016; Herrera, 2017; Messier et al., 2010). In forest stands, the progressive decrease in light availability from the top to the bottom of a tree's crown likely represents the most important environmental gradient (Scartazza et al., 2016). As many leaf traits are influenced by light availability (Böhnke & Bruelheide, 2013; Poorter et al., 2019), the light gradient drives the within-individual variation in leaf trait values through adjustments in morphology and physiology (Coble & Cavaleri, 2014), particularly, in traits related to photosynthesis (Koike et al., 2001; Terashima et al., 2001; Wyka et al., 2012). Yet, changes in light conditions within the crown might affect traits idiosyncratically (Givnish, 1988). In order to maintain a net positive photosynthesis rate under low-light conditions (i.e., at the bottom of the crown), leaves should have high values of acquisitive leaf traits and low values for structural leaf traits (Shipley et al., 2006). By contrast, under full light conditions (i.e., at the top of the crown), optimization for photosynthesis promotes thicker leaves, resulting in higher values in structural traits (Björkman, 1981).

Another factor influencing leaf traits is plant–plant interactions, which occur aboveground and belowground (Callaway et al., 2003; Davrinche & Haider, 2021; Le Bagousse-Pinguet et al., 2013). Aboveground, light availability is a primary driver, which is itself influenced by the structure and density of the forest canopy (Pretzsch, 2014). In stands with higher species richness, spatial complementarity of tree crowns leads to more efficient crown space utilization compared to monocultures (Jucker et al., 2015; Williams et al., 2017). This results in a steeper vertical gradient of light availability, which, in turn, drives variation in light-dependent leaf traits (Williams et al., 2020). Such biodiversity-mediated light effects on leaf traits should be visible already at the very small scale because light availability changes drastically even across short distances (Escribano-Rocafort et al., 2016). Moreover, in a recent study, Davrinche and Haider (2021) demonstrated that local species richness can influence multiple leaf traits, with the strongest effects often arising from a tree's closest neighbor rather than the surrounding community, hence suggesting a scale dependency of light-mediated biodiversity effects.

Belowground interactions also influence leaf traits, albeit through different mechanisms than aboveground interactions. High species richness can enhance the availability of belowground resources through complementary resource use of different root systems (McKane et al., 2002; Turner, 2008). Belowground resource use complementarity may shift leaf trait values toward more acquisitive strategies in environments with higher species richness (Richards et al., 2010). To make use of additional belowground resources, a sufficient amount of light is necessary for photosynthesis (Freschet et al., 2015; Meziane & Shipley, 1999). Therefore, biodiversity effects on leaf traits might be stronger under full light conditions, where plants can fully utilize the enhanced resources provided in a species-rich environment. By contrast, under low-light conditions, the influence of biodiversity on leaf traits might decrease, as physiological constraints could outweigh the benefits of increased belowground resource availability (Dewar et al., 2012; Lloyd et al., 2010; Niinemets, 2012).

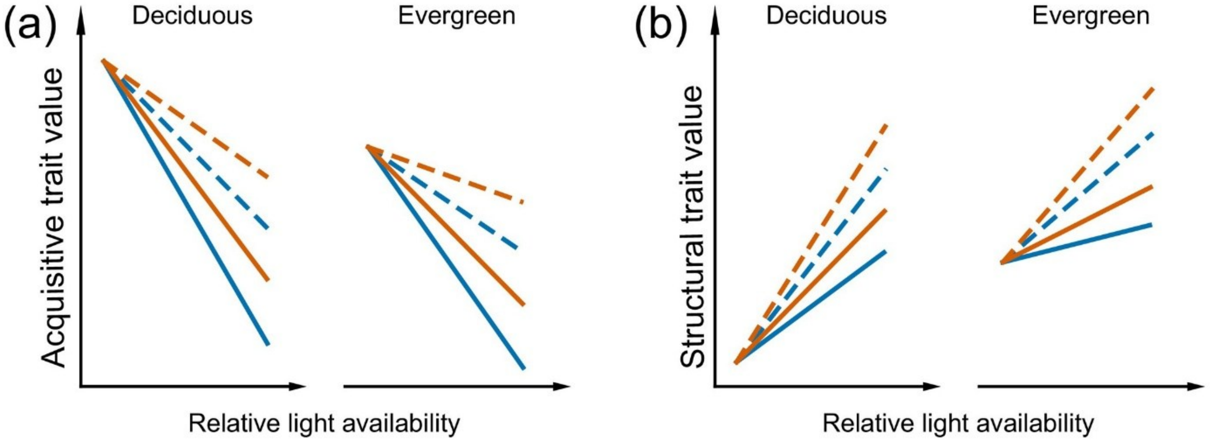

Figure 1: Conceptual figure of the expected interacting effects of leaf habit, light availability, and different biodiversity factors on (a) acquisitive traits, for example, leaf nitrogen content and specific leaf area; (b) structural traits, for example, leaf dry matter content and leaf carbon content. The line type indicates whether the closest neighbor of the target tree is conspecific (solid line) or heterospecific (broken line), and the line color indicates the neighborhood species richness (blue line for low, red line for high species richness). Three hypotheses are tested: H1 states that the light responsiveness of leaf traits is more pronounced in deciduous species than in evergreen species, as reflected in steeper slopes in deciduous species. H2 states that neighborhood species richness strongly affects leaf traits under full light conditions, while this effect weakens under low-light conditions. This is visualized by all lines intersecting at low light while diverging toward full light. H3 states that the effect of the direct neighbor tree on leaf trait variation is greater than the effect of the surrounding neighborhood. This is symbolized by the broken line for heterospecific direct neighbors taking more different trait values than the solid lines for conspecific neighbors, irrespective of line color representing different species richness of the wider neighborhood.

When analyzing the light availability effect on leaf traits, it is also important to take into account the leaf habit of the tree species, as leaves of deciduous and evergreen trees strongly differ in their trait values. Deciduous trees typically have higher values in acquisitive traits and lower ones in structural traits than evergreen trees (Qin et al., 2024; Ye et al., 2022). Furthermore, there is some indication that in deciduous trees, some leaf traits respond more plastically to changing light conditions than in evergreens (Böhnke & Bruelheide, 2013; Wyka et al., 2012). In both deciduous and evergreen trees, trait responses to changes in light conditions are limited by the leaf structure (Niinemets et al., 2006; Oguchi et al., 2005). However, this limitation appears to be stronger in evergreen trees than in deciduous trees (Niinemets, 2016b). We therefore expect that leaf traits of evergreen trees will show a weaker response to the light gradient within a tree crown than that of deciduous trees. We studied leaf trait responses to light availability in the subtropical BEF-China experiment (Biodiversity-Ecosystem Functioning China) in forest plots differing in species richness. The aim of this study is to reveal the relationship between light availability and leaf trait values at the within-individual level and how this relationship is mediated by local biodiversity, including the effect of the directly adjacent tree as well as the tree species richness of the surrounding neighborhood. We investigated to what extent the leaf habit of a tree might influence these interactions, assuming that leaves of evergreen trees are generally less acquisitive but possess higher values of structural traits. Further assuming that values of acquisitive traits increase with decreasing light availability (vice versa for structural traits, see Figure 1), we hypothesized that (1) the light responsiveness of leaf traits is more pronounced in deciduous species than in evergreen species. Assuming a positive effect of neighborhood species richness on acquisitive traits (vice versa for structural traits), we expected that (2) the effect of neighborhood species richness on leaf traits is more pronounced under full light conditions than under low-light conditions. Thereby, (3) the effect of the direct neighbor tree on leaf trait variation is greater than the effect of the surrounding neighborhood.

2. Material and methods

2.1 Study Site

The study took place in the BEF-China experiment (Bruelheide et al., 2014), which is located in southeast China near the city of Xingangshan (Jiangxi province). The experimental site is characterized by a subtropical climate with a mean annual temperature of 16.7°C and an average annual precipitation of 1821 mm (Yang et al., 2013). The main experiment is subdivided into two experimental sites (Sites A and B). Our study took place on Site A (29.1241° N, 117.9079° E), which was established in 2009 on land that was previously covered with a forest dominated by *Pinus massoniana* Lamb. The site has a total area of 18.4 ha and consists of 271 square-shaped plots with an area of 667 m^2 each, corresponding to the Chinese unit of 1 mu. In each plot, 400 trees were planted in a square grid pattern with a grid distance of 1.29 m between the trees. The plots consisted of monocultures and mixtures of 2, 4, 8, 16, and 24 native tree species, with species randomly assigned to positions within the grid. In the main random extinction scenario used in this study, the species of the monocultures and in the 2-, 4-, 8-, and 16-species mixtures were drawn from the same pool of 16 species, ensuring that all 16 species were equally represented at each of these diversity levels. The 24-species mixture included an additional eight species that occurred in two other random extinction scenarios but were not part of the other mixtures included in our study. Spontaneously emerging woody plants were cut every year to maintain the experimental design.

2.2 Sampling Design

Sampling took place in August and September 2017 in 66 plots across all plot diversity levels. We focused on the species that were present in the diversity levels up to 16 species. However, because of the high mortality of *Koelreuteria bipinnata* throughout the experimental site, we excluded it from the sampling. In total, 400 trees from the remaining 15 species (9 broad-leaved deciduous and 6 broad-leaved evergreen species, Appendix S1: Table S1) were selected for sampling. Trees were sampled in pairs (tree species pairs, hereafter, TSPs). TSPs consist either of two trees of the same or different species and are referred to as "Mono TSPs" and "Mixed TSPs," respectively. While we paid attention to choose TSPs with a mostly complete neighborhood, that is, a low mortality of neighbors, the final choice of the TSPs within the plots was random.

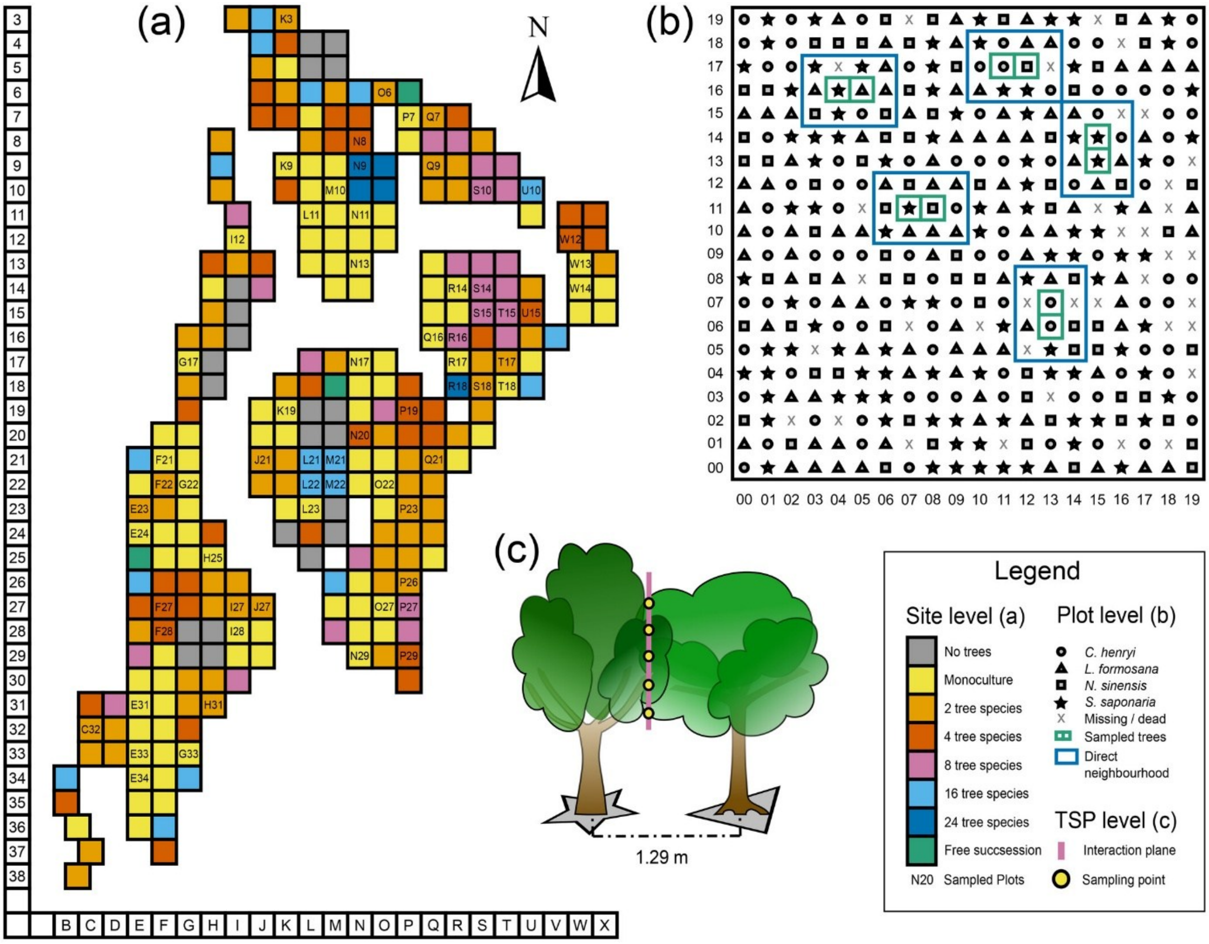

Figure 2: Graphical overview on the experimental design. (a) Overview of Site A of the BEF-China main experiment near Xingangshan. The plots that were selected for sampling are marked with their x- and y-coordinates (characters for x and numbers for y coordinates). The plots are color-coded according to their initial diversity level. (b) Example for the sampling design within a plot (here Plot P19). Different species are indicated by different symbols, and dead or missing trees are indicated with X. Sampled trees (tree species pairs [TSPs]) are marked with green rectangles and the corresponding local neighborhood with blue rectangles. (c) Example for sampling within a TSP (here TSP 0416-0516), showing the relationship between the focal tree and its TSP partner. Sampling took place along the vertical interaction plane of both individuals, indicated by the vertical line. Along the interaction plane, up to five sampling points (yellow points) were chosen from which at least three fully developed leaves were sampled from each tree. The illustration was created by Tobias Proß using Inkscape version 1.0.

Mono TSPs were sampled throughout all plot diversity levels, and mixed TSPs were sampled in all but monocultures. The species compositions of the mixed TSPs included all possible species compositions that were present in the four-species mixture plots (see Appendix S1: Table S2 for species pairings and Table S3 for number of samples). These species combinations also occur in the 2-, 8-, 16-, and 24-species plots. Tree species richness was assessed at the TSP level. The number of different tree species directly neighboring a TSP (with a theoretical maximum of 10 different species) was considered as a measure of its species richness (hereafter "neighborhood species richness"). The observed neighborhood species richness of the TSPs ranged from 1 to 7 for both mono and mixed TSPs. Leaf samples were taken on the side which faced the other TSP partner. The TSP partner is considered as the "direct neighbor." Sampling was done along the vertical interaction plane of the crown between the two tree individuals of a TSP. Depending on the height of the trees, one to five sampling points were chosen in areas where crowns were intermingled. Sampling points were located between 30 cm and 8 m aboveground, with a minimum distance of 30 cm between them. From every sampling point, we aimed to collect at least three fully developed leaves from both TSP partners. Leaves were harvested without petioles, sealed in a zip-lock bag, and stored cool until further processing in the laboratory on the same day (total sample size of 4981 leaves). For a graphical overview of the study site and the sampling design, see Figure 2.

2.3 Light measurement

We recorded the local light availability at each sampling point using a LI-1400 logger with a LI-190SA quantum sensor (LI-COR Biosciences Inc., Lincoln, NE, USA). A single reading per sampling point was used for both trees of the TSP. To account for different light conditions caused by changes in weather conditions, an identical device was located outside of the experimental site (position 29.1200° N, 117.9060° E) and fully exposed to the open sky as a reference logger. The horizontal distance between the sampling points and the reference logger ranged from 93 to 856 m. Both devices were synchronized in time (synchronization accuracy approximately 1 s) to record the photosynthetically active radiation (PAR in micromoles of photons per square meter per second) between 400 and 700 nm. The quotient of both values was used as a measure of the relative light availability at the sampling point. The method of linking two loggers was used to minimize the influence of differences in sky conditions during measurements; however, under variable sky conditions, differences might not have been fully compensated, particularly at longer distances.

2.4 Leaf trait analysis

We acquired visible and near-infrared spectra (Vis/NIR spectra, 350–2500 nm) from the adaxial side of each harvested leaf. Each leaf was scanned threefold with an ASD

FieldSpec 4 WideRes Field Spectroradiometer (Malvern Panalytical Ltd., Almelo, the Netherlands) fitted with a "high-bright" contact probe, including an internal 6.5 watt halogen light source. For scanning, we placed the samples between the contact probe of the FieldSpec and a black background. The three scans were averaged into single spectra in order to reduce instrument noise. A subset of 190 randomly chosen samples were analyzed for leaf traits via conventional means in the laboratory (see Appendix S1: Table S4 for reference methods). We analyzed 14 leaf traits, including LDMC, SLA, CN ratio as well as the mass-based concentrations of leaf C, leaf N, lignin, cellulose, leaf Mg, leaf Ca, leaf K, leaf P, leaf S, phenolics, and tannin. Trait-specific prediction models were developed via partial least squares regression (PLS regression) using "The Unscrambler X" (Version 10.1, Camo Analytics, Oslo, Norway) and "OPUS QUANT2" (Version 7.0 Bruker Optics Ltd., Billerica, MA, USA) calibration software. The models were subsequently applied to the spectral data of all leaves, yielding predicted values for each leaf trait.

2.6 Statistical analyses

Statistical analysis was conducted using R version 4.0.3 (The R Core Team, 2020).

2.6.1 Exploratory analysis

To identify the key drivers of leaf trait variation in our dataset, we fitted a linear mixed-effects model ("lmer" function in "lmerTest" package version 3.1-3; Kuznetsova et al., 2017) for each leaf trait. The response variable in the models was the trait value predicted by Vis/NIR spectroscopy at the level of individual scan files. The fixed effects included light availability at the sampling point, TSP type (Mono TSP vs. Mixed TSP), and neighborhood species richness, along with all possible interactions between these variables. The model further captured how the two types of tree strategies with respect to leaf habit (deciduous and evergreen) and the different species responded differently to light availability (random slope for light across leaf habits and tree species), as well as how different species responded to differences in neighborhood species richness (random slope for neighborhood species richness across tree species).

The possible baseline differences in leaf trait values among species and leaf habits were considered (random intercept). To address the hierarchical structure of the dataset, a nested random effect was included in the models: The ID of each individual leaf was nested within the sampling point, which was nested within the individual tree, which was nested within the TSP identity, and further nested within the plot. We calculated the proportion of variance explained by each effect in the models ("calcVarPart" function in "variancePartition" package version 1.28.7; Hoffman & Schadt, 2016). To explore the relationship between the leaf traits, we calculated the pairwise correlations and performed a principal components analysis (PCA) at the sampling point level.

2.6.2 Hypothesis testing

For every leaf trait, linear mixed-effects models were fitted ("lmer" function in "lmerTest" package version 3.1-3; Kuznetsova et al., 2017). The response variable in the models was the trait value at each sampling point. The fixed effects included light availability at the sampling point, TSP type (Mono TSP vs. Mixed TSP), and neighborhood species richness, along with all possible interactions between these variables. Additionally, leaf habit (deciduous or evergreen) was added as the fourth fixed effect, and we allowed its interaction with light availability. This model structure captured how species may respond differently to light availability or neighborhood species richness by allowing these variables to vary across species (random slope model). Furthermore, the models accounted for possible baseline differences in leaf traits among species (random intercept model). To address the hierarchical structure of the spatial sampling, a nested random effect was included in the models: The ID of each tree individual was nested within TSP identity, which was further nested within the plot.

Since we found significant leaf habit-by-light interactions for many leaf traits—which suggests that the relationship between light availability and trait values differs with leaf habit—we fitted separate linear mixed-effects models for deciduous and evergreen species, with otherwise identical model parameters. In all models, TSP type was distinguished with binary values (mono TSP = 0, mixed TSP = 1). The values of the other fixed effects (i.e., light and neighborhood richness) were scaled by dividing them by two times their SD, as this treatment makes them directly comparable to binary values (Gelman, 2008). Type 1 analysis of variance using Satterthwaite approximation for estimation of the denominator degrees of freedom was used to assess the significance of the fixed effects. All hypotheses were tested by assessing the significant effects on leaf traits in the models that were separately fitted for evergreen and deciduous species. To confirm H1, traits needed to be significantly influenced by light. To confirm H2, models should show a significant light-by-species richness interaction, and to confirm H3 models, it should show a significant effect of the TSP.

3. Results

3.1 Leaf trait prediction models

We were able to fit a prediction model for each of the leaf traits. Model performance ranged from 0.44 for leaf K to 0.95 for SLA based on the coefficient of determination from model validation. For other performance metrics and detailed information on the prediction models, see Appendix S1: Table S5. Appendix S1: Figure S1 shows the PLS regression coefficients for every leaf trait prediction model across all wavelengths. Each leaf trait is predicted by distinct wavelengths, with some traits utilizing broader wavelength ranges than others.

3.2 Leaf trait variation and relationship between leaf traits

All leaf traits showed strong variation between species, within-species, and within-individual trees (Figure 3 and Appendix S1: Figure S2). While a large portion of the variation was explained by species, species also responded differently to light, TSP type, and neighborhood richness. The unexplained variance ("residual" in Figure 3), which includes both systematic biases (i.e., model limitations) and random noise in individual predictions, is quite small compared to the other effects in the trait-specific models.

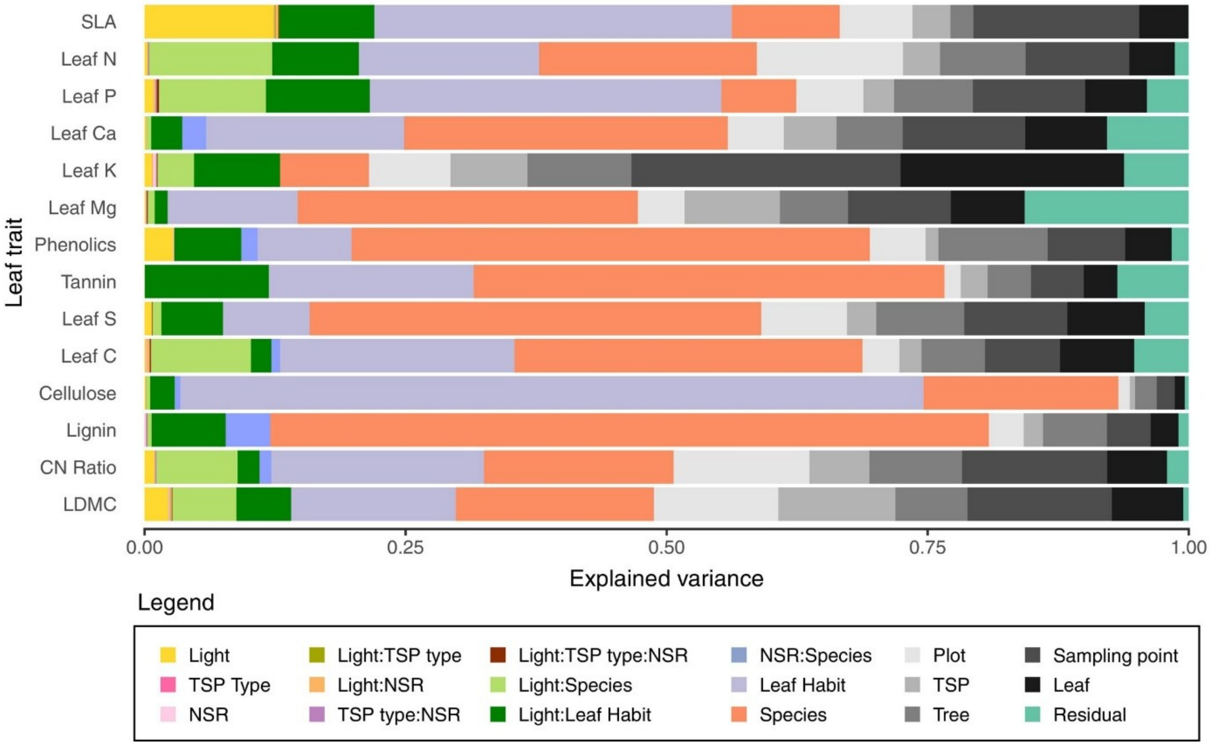

Figure 3: Proportions of explained variance for each leaf trait. Fixed effects include light, TSP type (tree species pair type), and NSR (neighborhood species richness), as well as all possible interactions (Light:TSP type, Light:NSR, TSP type:NSR, Light:TSP type:NSR). The model also accounts for species-specific and leaf habit-specific trait responses to light (Light:Species, Light:Leaf habit), as well as species-specific leaf trait response to neighborhood species richness (NSR:Species). Random factors are nested: species within leaf habit, leaf within sampling point, sampling point within tree, tree within TSP, and TSP within plot. Residual represents unexplained variance.

Analysis of the leaf traits revealed that nearly all acquisitive traits were strongly correlated with one another, except for lignin and cellulose. Similarly, most structural traits exhibited strong intercorrelations (Appendix S1: Figure S3). In the PCA (Appendix S1: Figure S4), all structural traits showed positive loadings, and all acquisitive traits showed negative loadings on the first principal component. However, these traits had varying contributions to the second principal component. Only the chemical defense traits were major contributors to the third principal component.

3.3 Leaf trait response to light availability for different leaf habits

Light availability strongly influenced many leaf traits. In particular, SLA, leaf K and CN ratio, phenolics, leaf C, and LDMC responded to changes in light availability (significant main effects, see Appendix S1: Table S6). However, for 7 of the 14 leaf traits, the influence of light also depended on the leaf habit (significant light-by-leaf habit interaction, Appendix S1: Table S6). Separate analyses for evergreen and deciduous species (Figure 4; Appendix S1: Figure S5 and Table S7) revealed that values of acquisitive traits in evergreen species, such as SLA and tannin, decreased (Figure 4a,c) while leaf N increased (Appendix S1: Figure S5a) with increasing light availability. By contrast, values of structural traits leaf C, lignin, and CN ratio decreased (Appendix S1: Figure S5h,j,k) with increasing light availability. For acquisitive traits of deciduous species, SLA, leaf P, leaf K, and leaf S decreased (Figure 4a and Appendix S1: Figure S5b,d,g) with increasing light availability. The structural trait LDMC increased with increasing light availability (Figure 4b). SLA decreased in both leaf habits, with deciduous trees showing a stronger reaction (steeper slope, Figure 4a). Finally, phenolics increased in both leaf habits, with no significant difference between the slopes (Appendix S1: Figure S5f).

3.4 Influence of biodiversity and light availability on leaf traits

In most cases, biodiversity alone did not directly affect the leaf traits. However, biodiversity mediated the effect of light on leaf traits, as separate analyses for evergreen and deciduous species revealed multiple interactions between light and TSP type as well as between light and neighborhood species richness. For evergreen species, the observed light effect on SLA, CN ratio, and leaf N was significantly stronger in mono TSPs than in mixed TSPs (visible as steeper slopes of mono TSPs in Figure 4a and Appendix S1: Figure S5a,k). By contrast, CN ratio in deciduous trees decreased with increasing light availability in species-rich neighborhoods, while no light effect was observed in low-species-richness environments (Appendix S1: Figure S5k). However, the TSP type further influenced this relationship, and mono TSPs showed an increase, while mixed TSPs showed a stronger decrease of the CN ratio in dependency on light availability (Appendix S1: Figure S5k). For evergreen species, neighborhood species richness mediated the decrease in leaf tannin content with increasing light availability: The effect of light was significantly stronger in species-rich neighborhoods (Figure 4c).

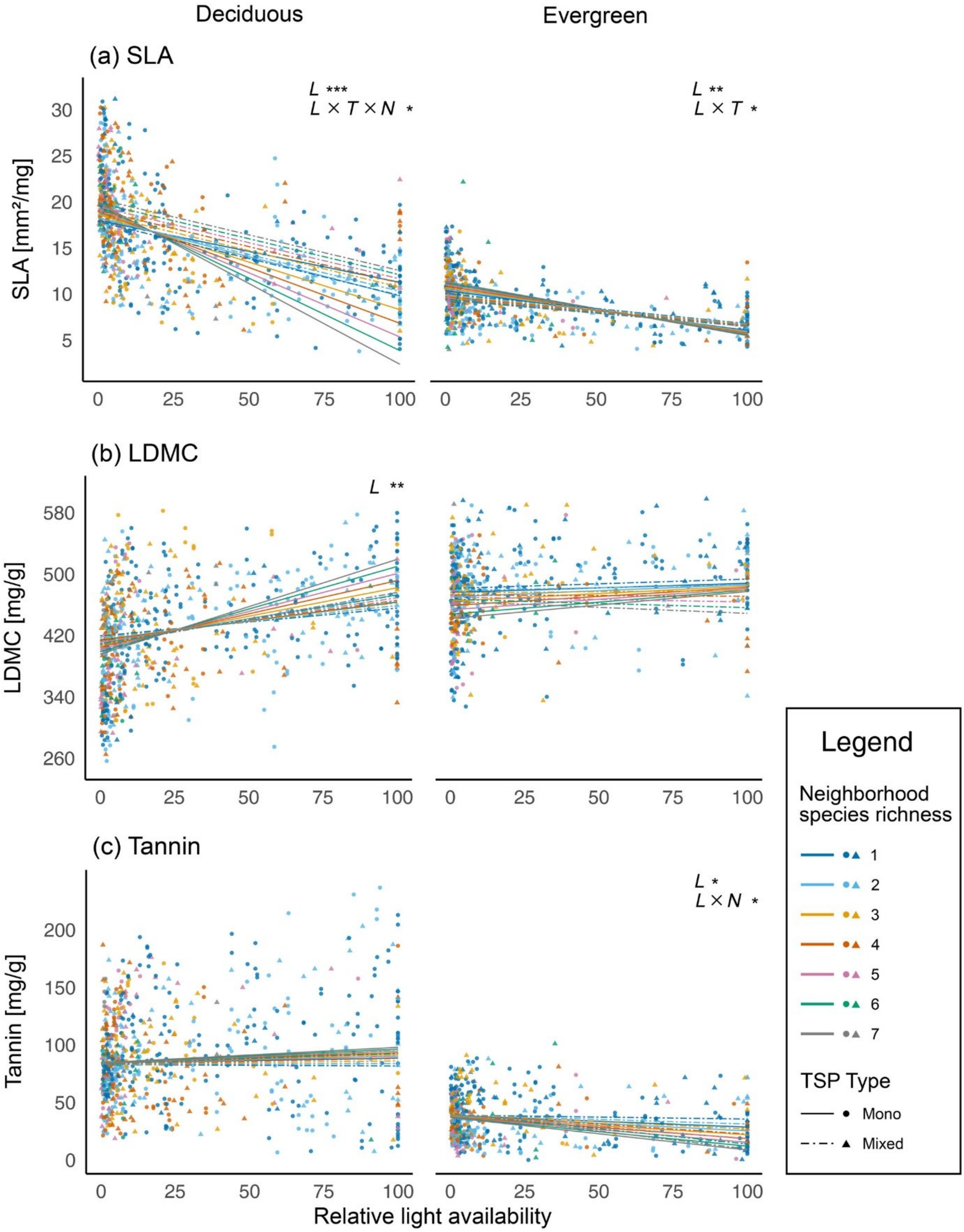

Figure 4: Leaf traits as functions of light availability, modified by TSP type (tree species pair type) and neighborhood species richness. Separate graphs display results for deciduous and evergreen species. Continuous lines represent monospecific TSPs; dashed lines represent mixed TSPs. Line colors correspond to different levels of tree species richness. Letters indicate significant main effects and interactions (L = light, T = TSP type, N = neighborhood species richness, x = interaction, *p < 0.05; **p < 0.01; ***p < 0.001). For the numerical results of the underlying models, see Appendix S1: Table S7. LDMC, leaf dry matter content.

4. Discussion

Overall, coupling intra-crown leaf trait variation with detailed light measurements and tree diversity gradients demonstrates how strongly trait values adjust to local light conditions.

4.1 Effectiveness of Vis/NIR spectroscopy for leaf trait analysis across scales

Our findings demonstrate that Vis/NIR spectroscopy can be effectively used for leaf trait analyses, especially when applied to large leaf-to-ecosystem datasets. While prediction accuracy varies across traits, the key limitation lies in the fact that some traits are inherently less predictable from spectral data than others. Nonetheless, this does not diminish the overall utility of the method. Some models performed exceptionally well. For example, the model for SLA achieved a very low Normalized Root Mean Square Error of 0.073 (NRMSE, which expresses the root mean square error relative to the mean of the observed values). By contrast, the model for tannin had the highest NRMSE with 0.556, indicating an average prediction error of 55.6 percent of the mean tannin value. However, our variance partitioning analysis revealed that the trait variance for tannin, as well as for most other traits, was primarily driven by species identity, leaf habit, light availability, and special variables, that is, the location of the sampled leaf, the individual tree, and the plot within the experimental site. In most cases, the residual variance was smaller than what the NRMSE of the prediction model might suggest. This implies that even for traits with moderate predictive accuracy, such as tannin, the inaccuracy of the prediction model contributes little to the unexplained variance. This is likely because the prediction errors are largely random rather than systematic, which allows the trait predictions to retain a sufficiently strong signal to reflect the underlying ecological variation.

A striking result of this study is that even the predicted values of the least accurate model (tannin) revealed significant ecological interactions when used in a linear mixed-effects model. These results highlight a key advantage of using Vis/NIR spectroscopy for large-scale ecological studies: Even with moderate prediction errors at the sample level, each trait prediction still retains a meaningful signal to detect ecological patterns across biological and ecological scales.

Another strength of Vis/NIR spectroscopy is that it enables the simultaneous prediction of multiple leaf traits from a single spectral measurement. This makes it a highly effective tool in large-scale ecological studies where traditional trait measurements would be infeasible. However, concerns may arise regarding the potential nonindependence of trait predictions (Kothari & Schweiger, 2022), since all traits are derived from the same reflectance spectrum. If multiple traits were predicted from identical spectral features, this could artificially inflate trait–trait correlations. In practice, though, this concern is unwarranted. The spectral ranges used by the models to predict different traits vary considerably, and even when overlapping regions are used, the models assign different weights to spectral features (Appendix S1: Figure S1). This indicates that the predictions are based on trait-specific spectral signatures. Therefore, while some level of correlation between the predicted traits is expected—especially for functionally related traits—the models still capture biologically meaningful and largely independent information.

4.2 Relationship between leaf traits

All observed leaf traits showed strong alignment with the first PCA axis, with acquisitive and structural traits pointing toward opposing directions. This observation is consistent with previous studies (Delpiano et al., 2020; Domínguez et al., 2012). Hence, the first PCA axis is in our case a good representation of the LES. Additionally, traits differ in their alignment with the second PCA axis, which indicates that their variation is further influenced by other variables beyond the conservative–acquisitive trade-off. Finally, the alignment of phenolics and tannin with the first and third PCA axis, respectively, suggests that defense traits do correlate with high values of acquisitive traits but are still influenced by another independent variable.

4.3 Varying trait responses of evergreen and deciduous species to light

We expected that the light dependency of leaf traits was stronger in deciduous trees than in evergreens, which was the case for SLA. Furthermore, LDMC responded to changes in light conditions in deciduous, but not in evergreen, species. While the trait responses differed between evergreen and deciduous species, the overall patterns suggest that leaves of deciduous species are morphologically more adjustable to changes in light conditions, or in other words, that the response of leaves of evergreen species is more physiologically restricted, as proposed by Niinemets (2016a). The other traits (leaf P, leaf K, and leaf S) that showed a light dependency only in deciduous but not in evergreen species are all macronutrients and key elements in photosynthesis. On average, trees relocate larger proportions of phosphorus, potassium, and sulfur from their leaves before senescence compared to calcium and magnesium (Hagen-Thorn et al., 2006). If the proportion of the recovered macronutrients can be interpreted as an indicator of their general mobility in the plant, this would be consistent with our observation that leaf P, leaf K, and leaf S respond to light conditions only in deciduous trees. A possible explanation for this pattern is that these macronutrients are essential for optimizing photosynthetic efficiency. Phosphorus plays a central role in energy metabolism, and in nucleic acid synthesis, potassium regulates stomatal conductance and enzyme activation, and sulfur is involved in amino acid and protein metabolism (Lambers et al., 2008; Terry, 1976). As light availability declines, deciduous trees may prioritize the redistribution of these elements to maximize short-term photosynthetic gains. This greater plasticity in nutrient allocation supports faster growth and ensures efficient resource use in environments with fluctuating light conditions. The stronger adjustment of the photosynthesis-related leaf traits in deciduous species could be a crucial mechanism to maintain plant growth under sub-ideal conditions and hence to overall follow a faster growth strategy (Givnish, 2002). Leaves of deciduous trees represent the acquisitive side of the leaf economics spectrum (Zhao et al., 2017). As they have a shorter lifespan than leaves of evergreen trees, it is likely that the corresponding leaf traits are inherently more flexible in deciduous trees, especially in the darker sections of the crown.

However, contrary to our expectations, the light dependency of leaf N, tannin, leaf C, lignin, and CN ratio appeared to be stronger in evergreen trees. Yet, these leaf traits could be influenced by factors other than the local light availability. For lignin and tannin, a possible explanation could be found in their role as chemical defense agents.

Deciduous trees have been reported to lose more leaf area to herbivory than evergreen trees, and one contributing factor is their higher SLA (Pérez-Harguindeguy et al., 2003; Silva et al., 2015). To counter this vulnerability, deciduous trees tend to accumulate more chemical defenses (Eichenberg et al., 2015), which is in line with our observation of higher base levels of phenolics and tannin in deciduous species. By contrast, leaves of evergreen trees are generally better protected against herbivory due to their lower SLA (Silva et al., 2015). However, we still observed an increased SLA with decreased light availability. We speculate that evergreen trees only apply chemical defenses selectively, that is, in the darker sections of the crown, where the SLA of their leaves is highest, potentially explaining our observed stronger light dependency in evergreen trees.

An alternative explanation may lie in the seasonal dynamics of carbon acquisition (Xu et al., 2024). Unlike deciduous species, evergreen trees retain their foliage year-round, allowing them to sequester carbon dioxide outside the main growing season. Under shaded conditions, the increased SLA observed in evergreen trees indicates a strategic shift to enhance light capture. By producing thinner, more efficient leaves in low-light conditions, evergreens can optimize carbon gain in shaded parts of the canopy while still maintaining their ability to gain carbon during cooler months. This suggests that, despite following a generally conservative strategy, evergreen species retain some degree of plasticity in leaf structure to balance light acquisition, seasonal carbon economy, and leaf longevity, much like the more acquisitive strategy seen in deciduous species.

A possible explanation for the observed increase in leaf C with decreasing light availability could be that, in leaves of evergreen trees, changes in leaf C are primarily driven by changes in lignin, which shows a similar pattern in response to light availability. The observed leaf N decrease in darker locations could be simply a dilution effect, resulting as a secondary effect from the increase in carbon compounds in these areas (Niinemets, 1997). Given these mixed results, we can only partially confirm our first hypothesis, and while light availability seems to be an important driver mainly for structural leaf traits, it has only indirect or no effects on traits associated with defense or biochemical activity.

4.4 Influence of local biodiversity

4.4.1 Effect of neighborhood species richness in different light regimes

In most cases, leaf traits did not depend on light availability alone but also on one of the biodiversity variables (neighborhood species richness or TSP type) or a combination of both. We expected that a biodiversity effect on leaf traits would be primarily visible in full light and weaken under low-light conditions. Tannin showed this pattern in evergreen trees, and we found lower trait values in full light conditions, especially in high species richness. A possible interpretation is that tannin allocation in forest ecosystems is a response to herbivore pressure (Hunter & Schultz, 1993), which itself depends on the tree species richness and leaf morphology (Schuldt et al., 2015; Stiegel et al., 2017), with the latter being further modified by light availability (Poorter et al., 2019). Tannin is an effective defense component against insect herbivores (Barbehenn & Constabel, 2011). However, plants might allocate resources to tannin only if necessary because they are subject to a “growth-defense trade-off” (Herms & Mattson, 1992), in which growth is typically prioritized over the production of secondary metabolites (Tuomi et al., 1991). In low-light conditions, tannin content was generally higher than in full light, with no differences between levels of tree species richness. Under low-light conditions, leaves also had higher SLA, which makes them more vulnerable to herbivory, thus making a generally higher allocation of tannin necessary. By contrast, in full-light conditions, we found higher tannin concentrations in environments with low tree species richness than in species-rich environments. In full light, leaves had lower SLA values, which means that they can at least partially rely on structural defense. However, in full light, tannin concentration additionally depended on the level of tree species richness, with lower tannin concentrations being observed at higher levels of tree species richness.

For the CN ratio of deciduous species, we confirmed the predicted light-dependent biodiversity effect. In full light, leaves in species-rich environments had a lower CN ratio than those in monocultures, while we could not detect a biodiversity effect under low-light conditions. This is consistent with our second hypothesis. As the relative response of leaf N to biodiversity is higher than the response of leaf C, we might consider the change in CN ratio as primarily driven by changes in leaf N (Xu et al., 2023). Other studies reported an increase in leaf N with increasing biodiversity (Lang et al., 2013; Oelmann et al., 2010), possibly resulting from increasing niche partitioning in nitrogen uptake among tree species (Liu et al., 2022). However, these studies typically do not account for within-individual trait variation (Lang et al., 2013; Liu et al., 2022; Oelmann et al., 2010). Our results suggest that a potential increase in available nitrogen due to increased species richness could result in an accumulation of nitrogen in the more sun-exposed areas of the tree crown, where it would be utilized for photosynthesis. However, for all other leaf traits, we did not observe the predicted relationship. While many traits depended on both light and biodiversity, this relationship was not consistent.

4.4.2 Effect of the direct neighbor compared to the surrounding neighborhood

We predicted that the biodiversity influence on the light–leaf trait relationship would be greater by the direct neighbor than the species richness of the local neighborhood. When analyzing evergreen and deciduous trees together, we were not able to observe the predicted pattern. However, when analyzing leaf habits separately, we observed the predicted relationship in evergreen trees for SLA, leaf N, and CN ratio. For these traits, trees with a conspecific partner reacted stronger to changes in light conditions than those in mixed TSPs (visible as steeper slopes of the trait–light curve).

The stronger reaction of monospecific TSPs to changes in light conditions could be interpreted as a mechanism to mitigate within-species competition between the TSP partners, which can be observed at the within-individual level. The steeper trait–light curve indicates a greater trait variation along the light gradient, thus allowing the individuals to cover a larger trait space. A similar concept has been established among species in limiting similarity theory (MacArthur & Levins, 1967) that suggests that two species cannot coexist in the same habitat if they are too similar regarding their occupied niche. In this case, similar resource requirements would lead to greater competition. However, an increase in trait variation typically leads to a relaxation of the competition between species (Beltrán et al., 2012; Tilman, 1977), thereby enabling coexistence. Additionally, there are hints that this principle could also apply to the level of within-species competition, that is, two individuals of the same species experience greater competition than heterospecific individuals because they are too similar regarding their resource requirements (Asay et al., 2020; File et al., 2012). By modifying their leaf traits in the presence of a conspecific competitor, both individuals can broaden their trait space. While this might not necessarily result in reduced competition, it could lead to a more efficient resource usage for both individuals. Clark (2010) demonstrated that individual-level variation allows species to persist in competitive environments by enabling them to respond differently to environmental conditions, even when populations show no mean differences. Our observation is consistent with Proß et al. (2021) who showed that individuals of the same species show increased leaf trait variation when grown in monoculture. In our case, the observed trait shift occurs in monospecific TSPs when two individuals of the same species—that have very similar resource requirements—compete for the same aboveground resources. However, it remains unclear whether this increased intraspecific trait variation is an adaptive response that improves performance or simply a consequence of resource heterogeneity (i.e., differences in light availability or nutrient competition). Further research is needed to disentangle these possibilities. Controlled experiments would be needed that manipulate both competition intensity and resource availability to assess whether trait variation confers a competitive advantage or merely reflects environmental constraints.

Our results are further consistent with findings from Davrinche and Haider (2021) who demonstrated that leaf traits are more strongly influenced by a tree's closest neighbor than by the surrounding community. This is especially relevant because their study was conducted on the same research platform, using a similar sampling design. In species-rich neighborhoods, they observed a shift toward a more acquisitive growth strategy for mono TSPs and attributed it to aboveground spatial niche complementarity (Davrinche & Haider, 2021). Our results indicate that apart from species richness, light availability, which itself depends on species richness, appears to be the second important driver of trait variation. This aligns with previous findings by Ellsworth and Reich (1993), who demonstrated a light-dependent trait gradient in forest canopies, emphasizing the strong influence of light on leaf trait expression. Our findings are consistent with Williams et al. (2020) who demonstrated at the community level that leaf trait expression is mediated by light availability and biodiversity. Our results provide novel evidence that the same mechanisms are in place at the individual level.

5. Conclusion

Our study demonstrated that within-individual leaf trait values respond to changes in light conditions and to tree species richness of the local neighborhood. Such within-individual leaf trait variation has rarely been recorded in this detail, yet our findings highlight the importance of this approach. Leaf traits of deciduous and evergreen species responded differently to changes in light conditions, which reflects the acquisitive or conservative growth strategy of the species. The leaf trait–light gradient within individuals was influenced by the surrounding neighborhood and the direct partner of a focal tree. This is an important distinction, as more leaf traits responded to the direct neighbor. While these findings provide insights into the potential mechanisms of species interactions, their direct role in species coexistence has yet to be demonstrated. In our case, conspecific tree pairs experienced a stronger light influence on leaf traits. The coexistence of conspecific individuals within an ecosystem is inherently hampered, as they have similar resource requirements. In this case, increased leaf trait variation could be a means of complementary resource usage and thereby enable coexistence. Additionally, our study highlights the value of Vis/NIR spectroscopy as a powerful tool for leaf trait analysis. A key advantage of this method is its ability to capture multiple leaf traits simultaneously with a single measurement, making it highly efficient for large-scale studies. This capacity is particularly useful when applied to extensive leaf-to-ecosystem datasets, allowing for a more comprehensive understanding of trait variation across different spatial scales.

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Authors' contributions

HB and SH conceived and designed the experiment. TP conducted field work and analyzed the data. TP wrote the first draft of the manuscript under the supervision of SH. All authors contributed to the interpretation of the results and the revision and final version of the manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.

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Appendix

Supplementary information

Journal: Ecology

Title: Within-individual leaf trait response to local light availability and biodiversity in a subtropical forest experiment

Authors: Tobias Proß, Helge Bruelheide, Sylvia Haider

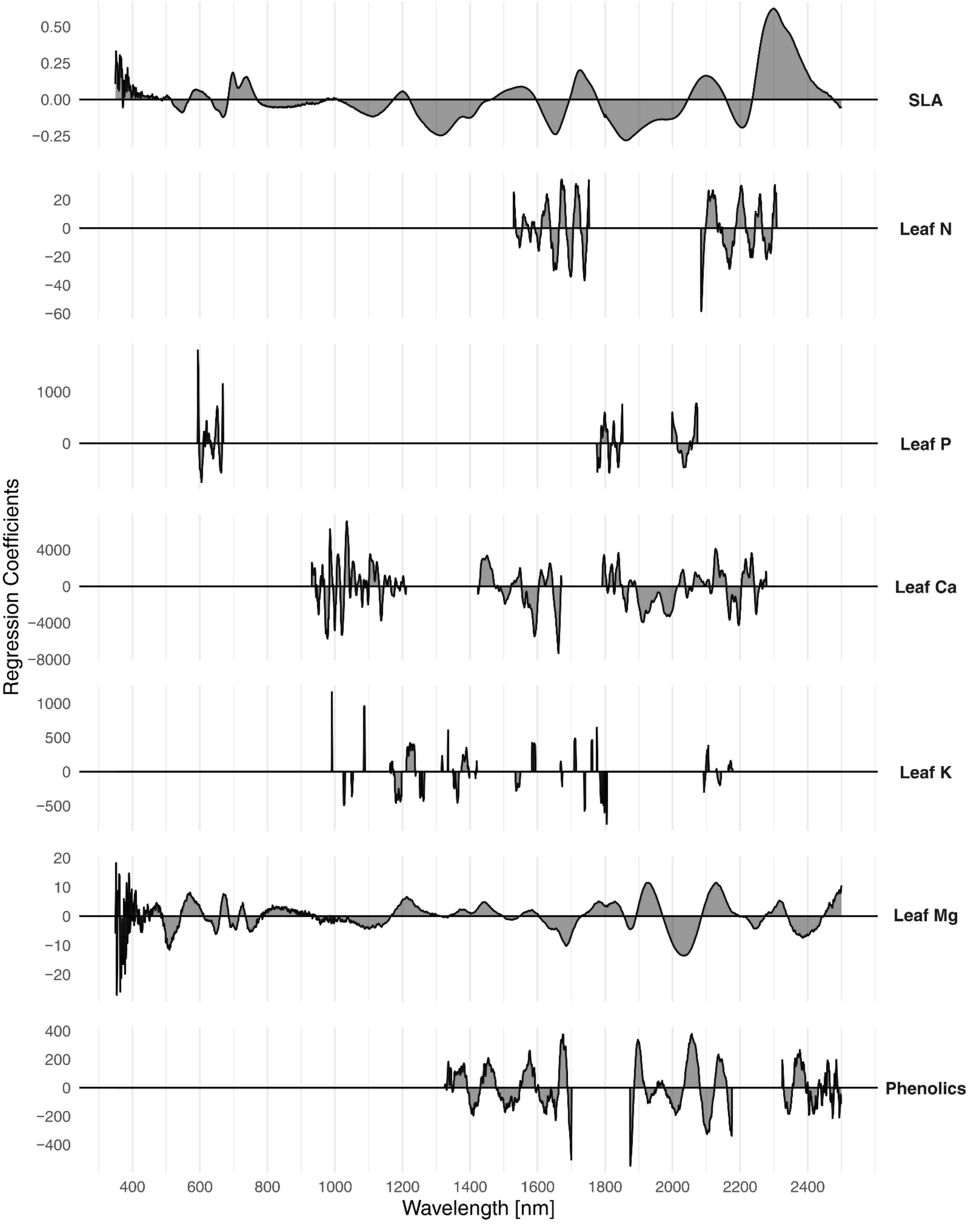


Figure S1. Regression coefficients for the highest rank of the leaf trait prediction models. For model ranks see table S5.

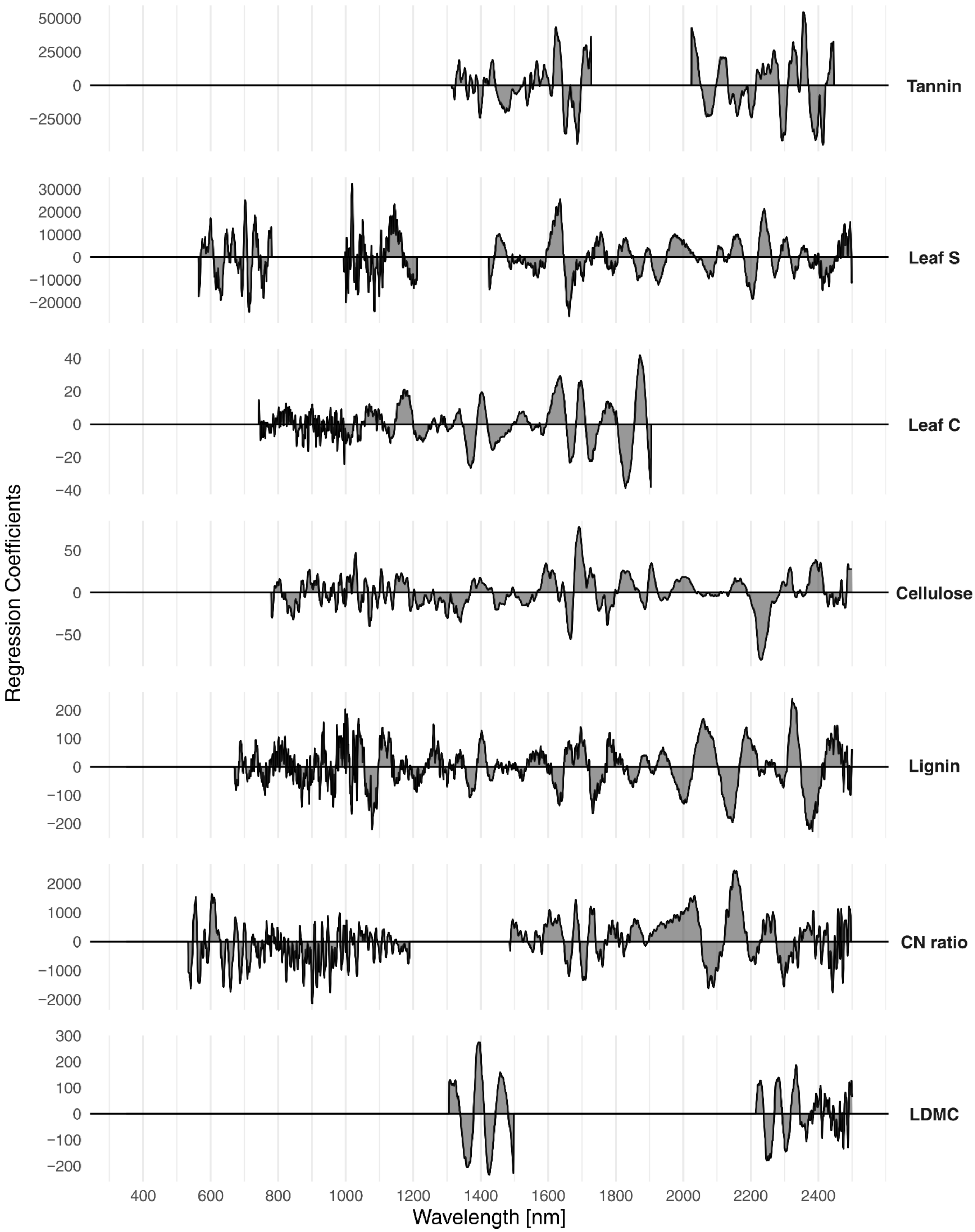


Figure S1 (cont.). Regression coefficients for the highest rank of the leaf trait prediction models. For model ranks see table S5.

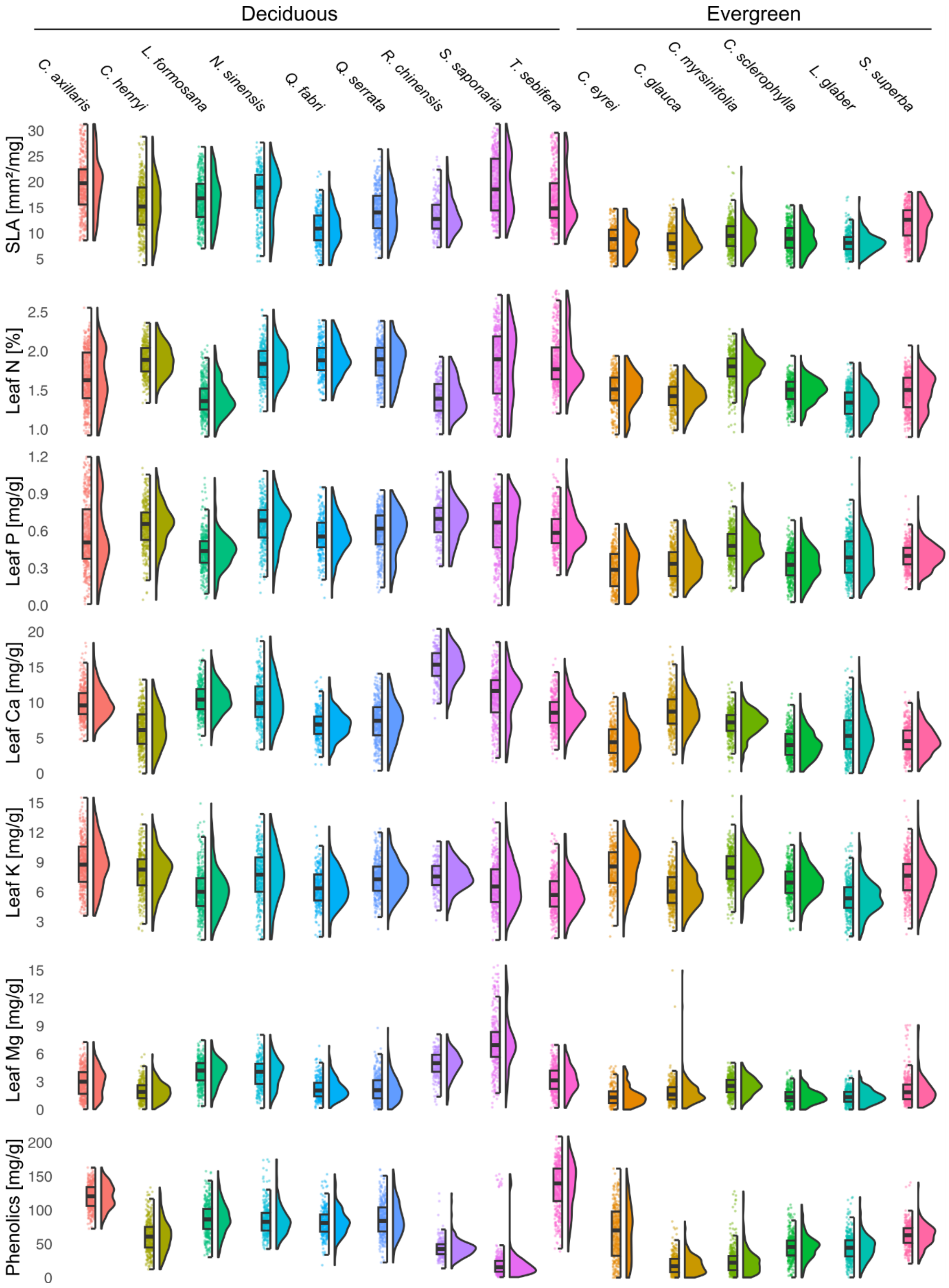


Figure S2. Species-wise overview of leaf traits. Each datapoint represents a separate leaf. For full species names, see table S1.

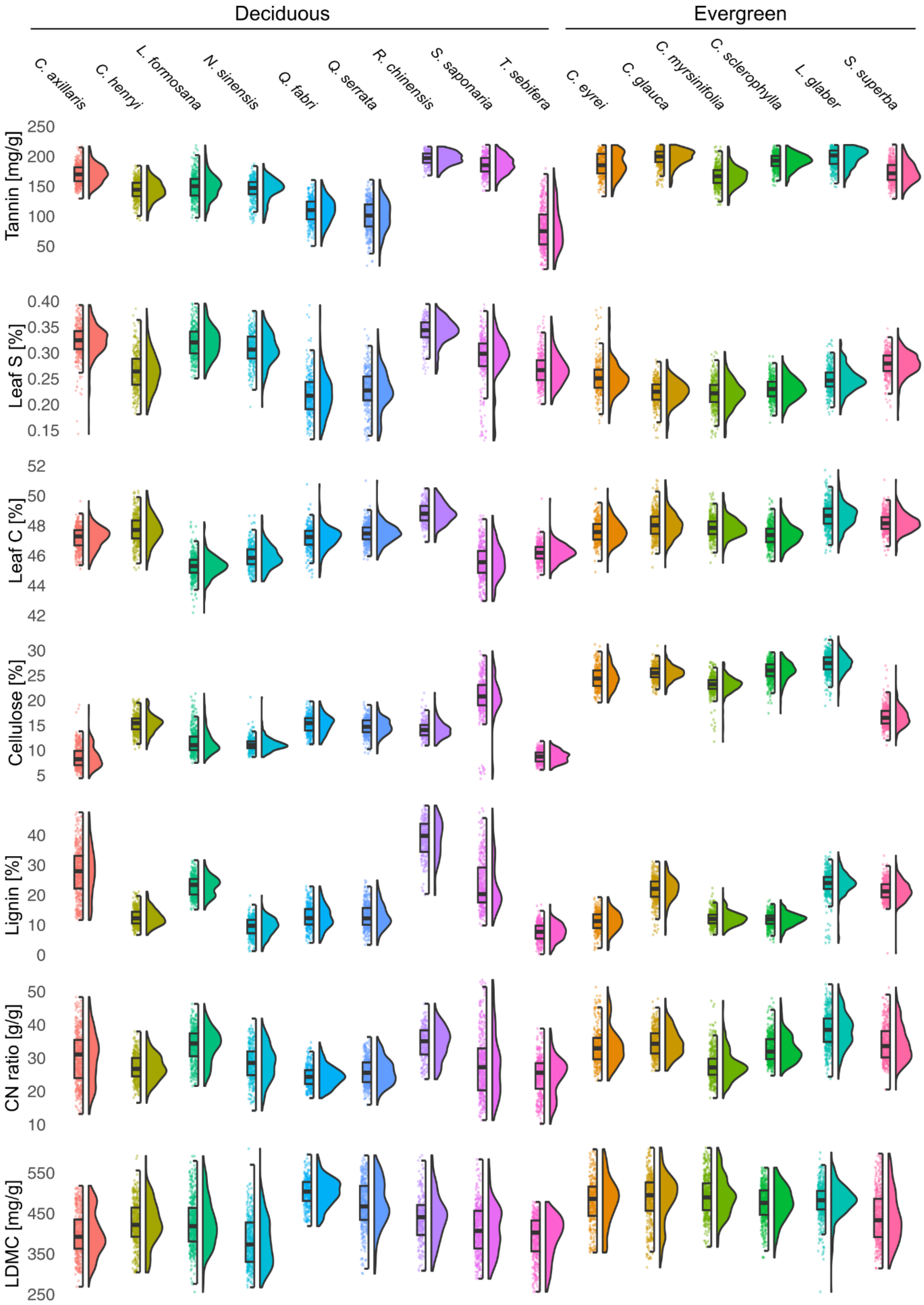
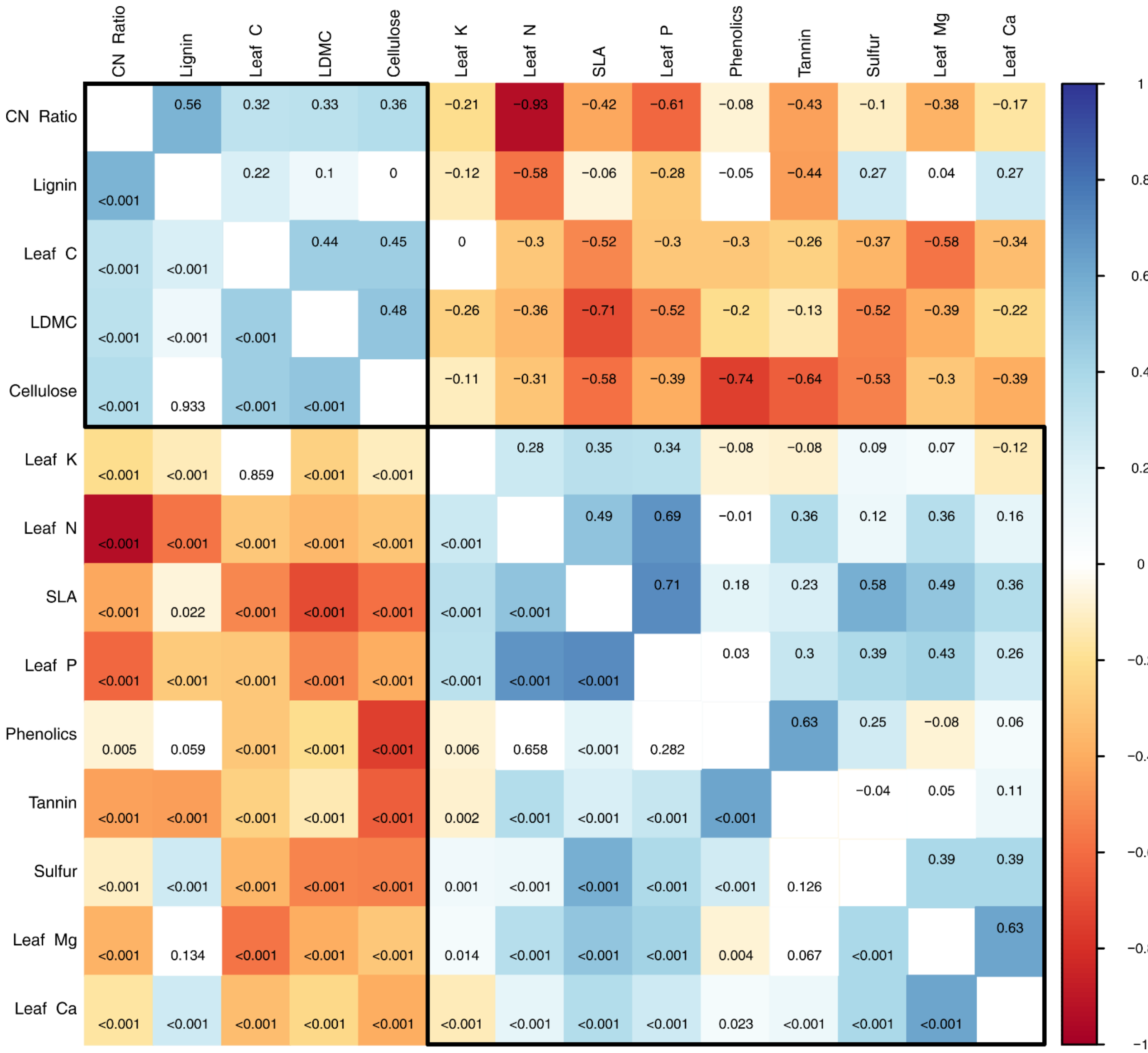


Figure S2 (cont). Species-wise overview of leaf traits. Each datapoint represents a separate leaf. For full species names, see Table S1.



	CN Ratio	Lignin	Leaf C	LDMC	Cellulose	Leaf K	Leaf N	SLA	Leaf P	Phenolics	Tannin	Sulfur	Leaf Mg	Leaf Ca
CN Ratio		0.56	0.32	0.33	0.36	−0.21	−0.93	−0.42	−0.61	−0.08	−0.43	−0.1	−0.38	−0.17
Lignin	<0.001		0.22	0.1	0	−0.12	−0.58	−0.06	−0.28	−0.05	−0.44	0.27	0.04	0.27
Leaf C	<0.001	<0.001		0.44	0.45	0	−0.3	−0.52	−0.3	−0.3	−0.26	−0.37	−0.58	−0.34
LDMC	<0.001	<0.001	<0.001		0.48	−0.26	−0.36	−0.71	−0.52	−0.2	−0.13	−0.52	−0.39	−0.22
Cellulose	<0.001	0.933	<0.001	<0.001		−0.11	−0.31	−0.58	−0.39	−0.74	−0.64	−0.53	−0.3	−0.39
Leaf K	<0.001	<0.001	0.859	<0.001	<0.001		0.28	0.35	0.34	−0.08	−0.08	0.09	0.07	−0.12
Leaf N	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		0.49	0.69	−0.01	0.36	0.12	0.36	0.16
SLA	<0.001	0.022	<0.001	<0.001	<0.001	<0.001	<0.001		0.71	0.18	0.23	0.58	0.49	0.36
Leaf P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		0.03	0.3	0.39	0.43	0.26
Phenolics	0.005	0.059	<0.001	<0.001	<0.001	0.006	0.658	<0.001	0.282		0.63	0.25	−0.08	0.06
Tannin	<0.001	<0.001	<0.001	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001		−0.04	0.05	0.11
Sulfur	<0.001	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	0.126		0.39	0.39
Leaf Mg	<0.001	0.134	<0.001	<0.001	<0.001	0.014	<0.001	<0.001	<0.001	0.004	0.067	<0.001		0.63
Leaf Ca	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.023	<0.001	<0.001	<0.001	

Figure S3. Correlation between all measured leaf traits. Each of the possible trait pairings is present twice: Top values and colors indicate magnitude and direction of the pairwise correlation between leaf traits. Bottom values indicate p-values to identify significant correlations. Calculations are based on Pearson's product moment correlation coefficient. Black boxes indicate the two most similar groups of traits, based on hierarchical cluster analysis.

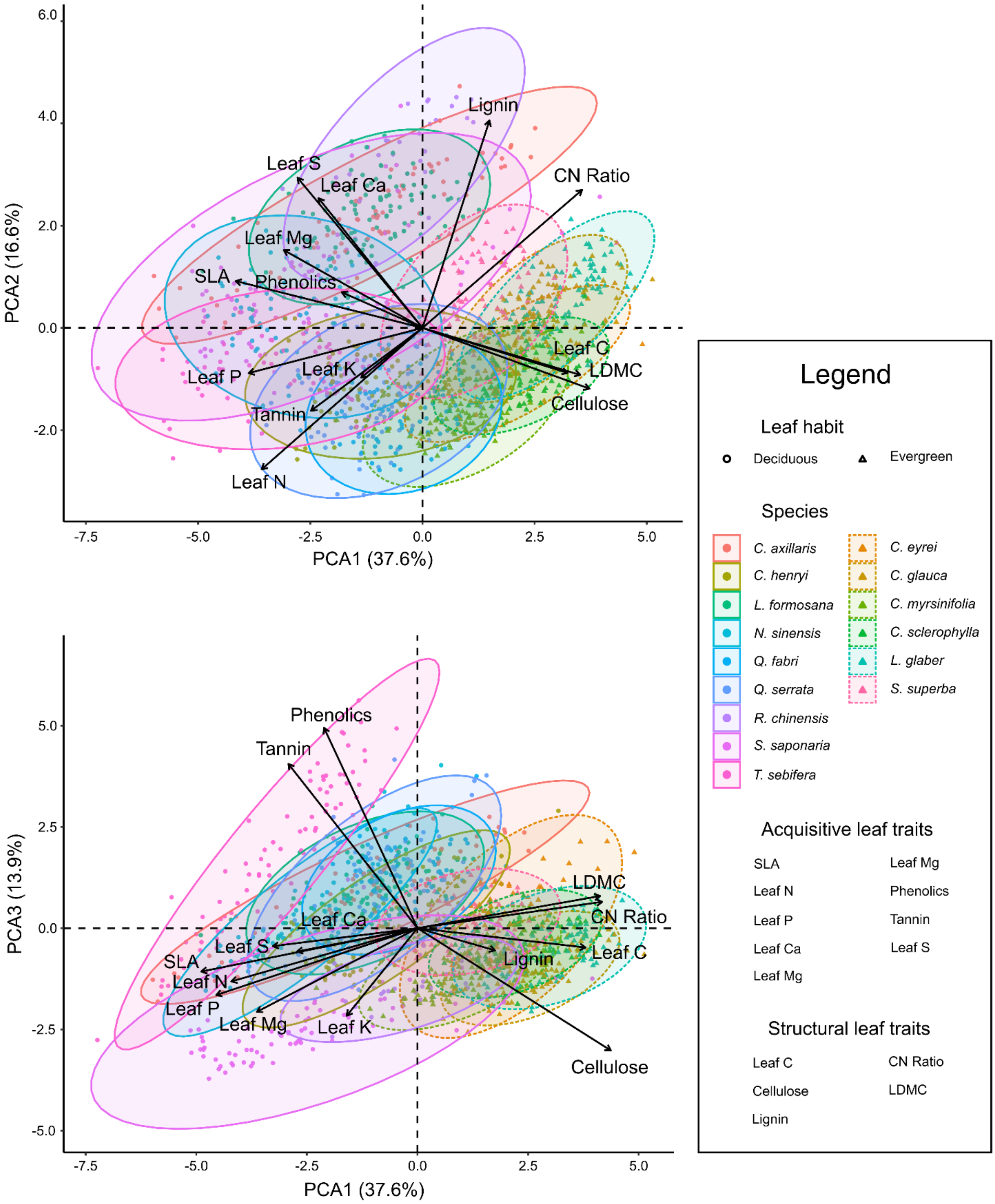


Figure S4. Principal component analysis of all measured leaf traits. Top: first vs. second axis. Bottom: first vs. third axis. Each datapoint represents a separate sampling point. Ellipses contain 95% of the datapoints of each species. Colors indicate different species, shapes and ellipse line types indicate their leaf habit. For full species names, see Table S1.

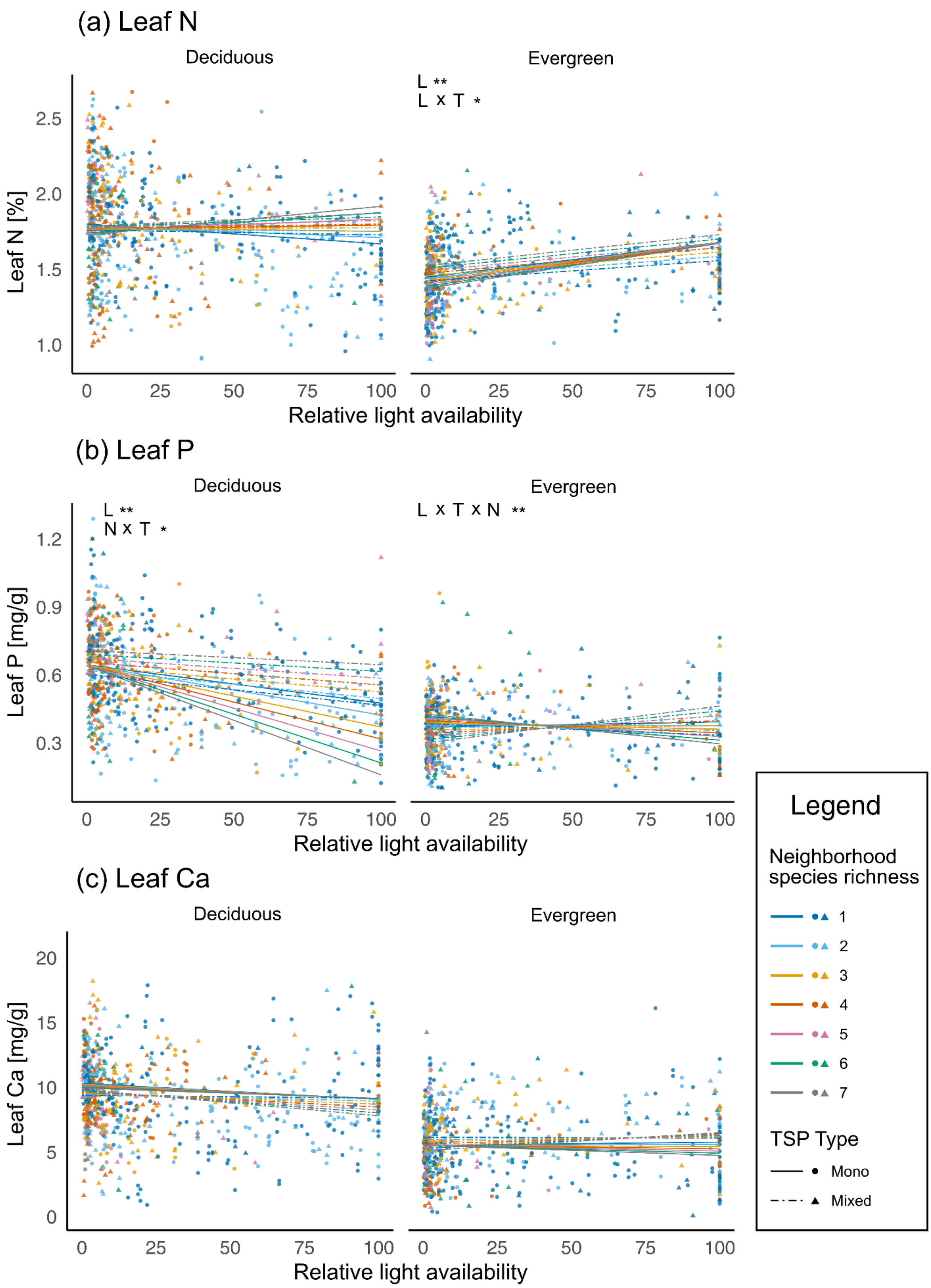


Figure S5 (a-c). Leaf traits as functions of light availability, modified by TSP type (Tree species pair type) and neighborhood species richness. Separate graphs for deciduous and evergreen species. The continuous lines indicate monospecific TSPs, dashed lines indicate mixed TSPs. Different colors indicate different levels of neighborhood species richness. Letters indicate significant main effects and interactions (L = Light, T = TSP type, N = Neighborhood species richness, x = interaction, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). For the numeric results of the underlaying models see Table S7.

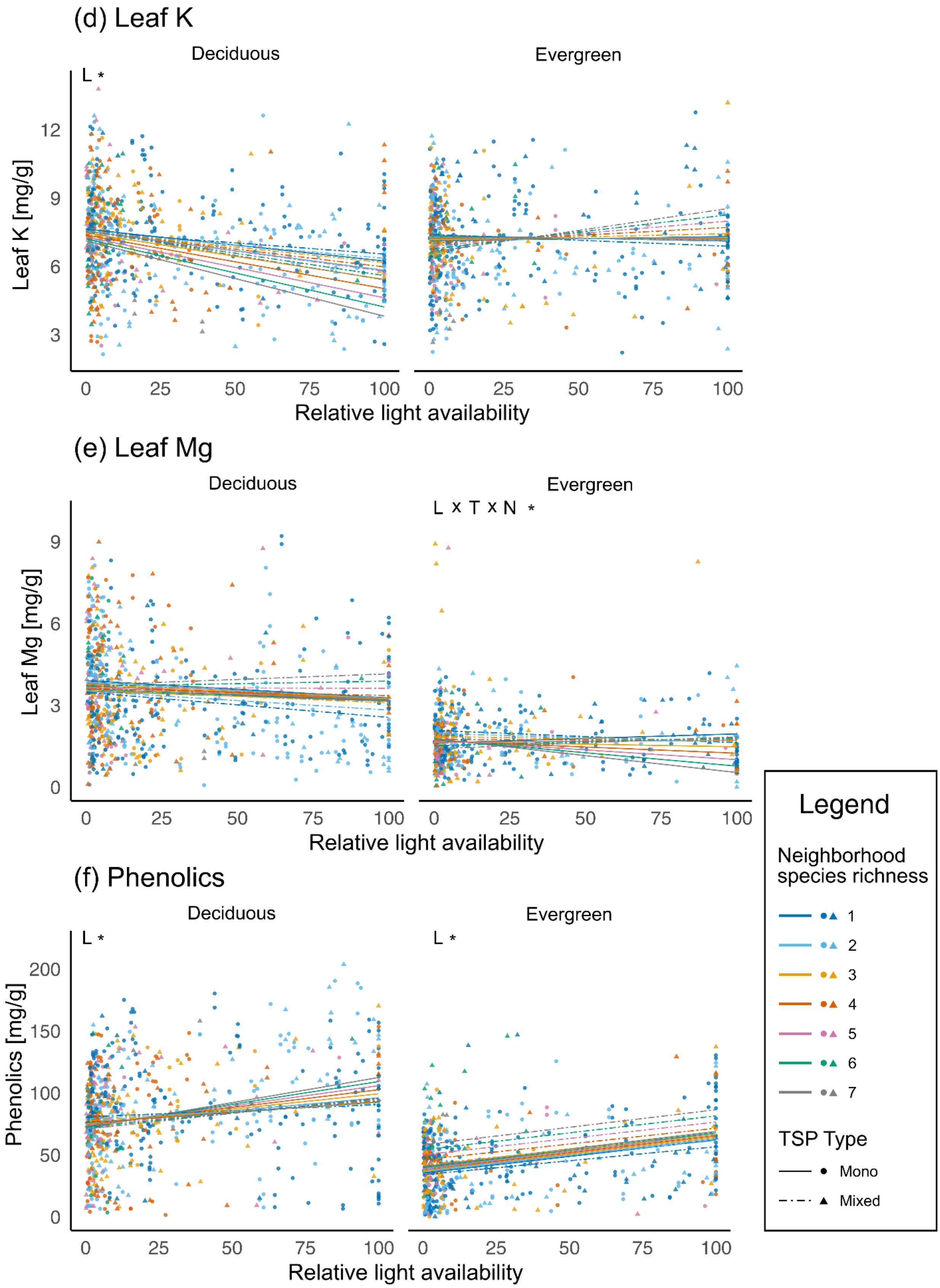


Figure S5 (d-f). Leaf traits as functions of light availability, modified by TSP type (Tree species pair type) and neighborhood species richness. Separate graphs for deciduous and evergreen species. The continuous lines indicate monospecific TSPs, dashed lines indicate mixed TSPs. Different colors indicate different levels of neighborhood species richness. Letters indicate significant main effects and interactions (L = Light, T = TSP type, N = Neighborhood species richness, x = interaction, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). For the numeric results of the underlaying models see Table S7.

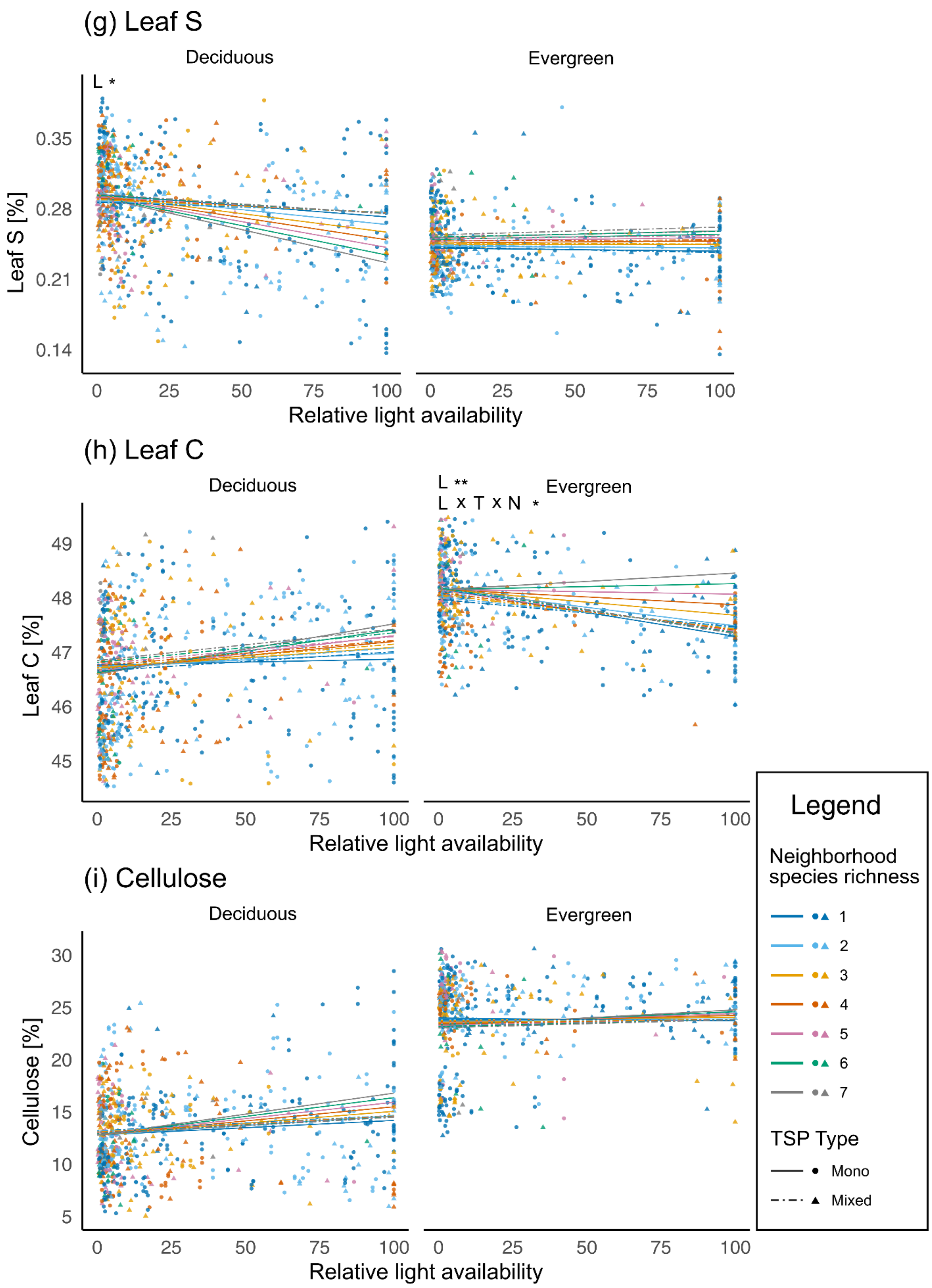


Figure S5 (g-i). Leaf traits as functions of light availability, modified by TSP type (Tree species pair type) and neighborhood species richness. Separate graphs for deciduous and evergreen species. The continuous lines indicate monospecific TSPs, dashed lines indicate mixed TSPs. Different colors indicate different levels of neighborhood species richness. Letters indicate significant main effects and interactions (L = Light, T = TSP type, N = Neighborhood species richness, x = interaction, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). For the numeric results of the underlaying models see Table S7.

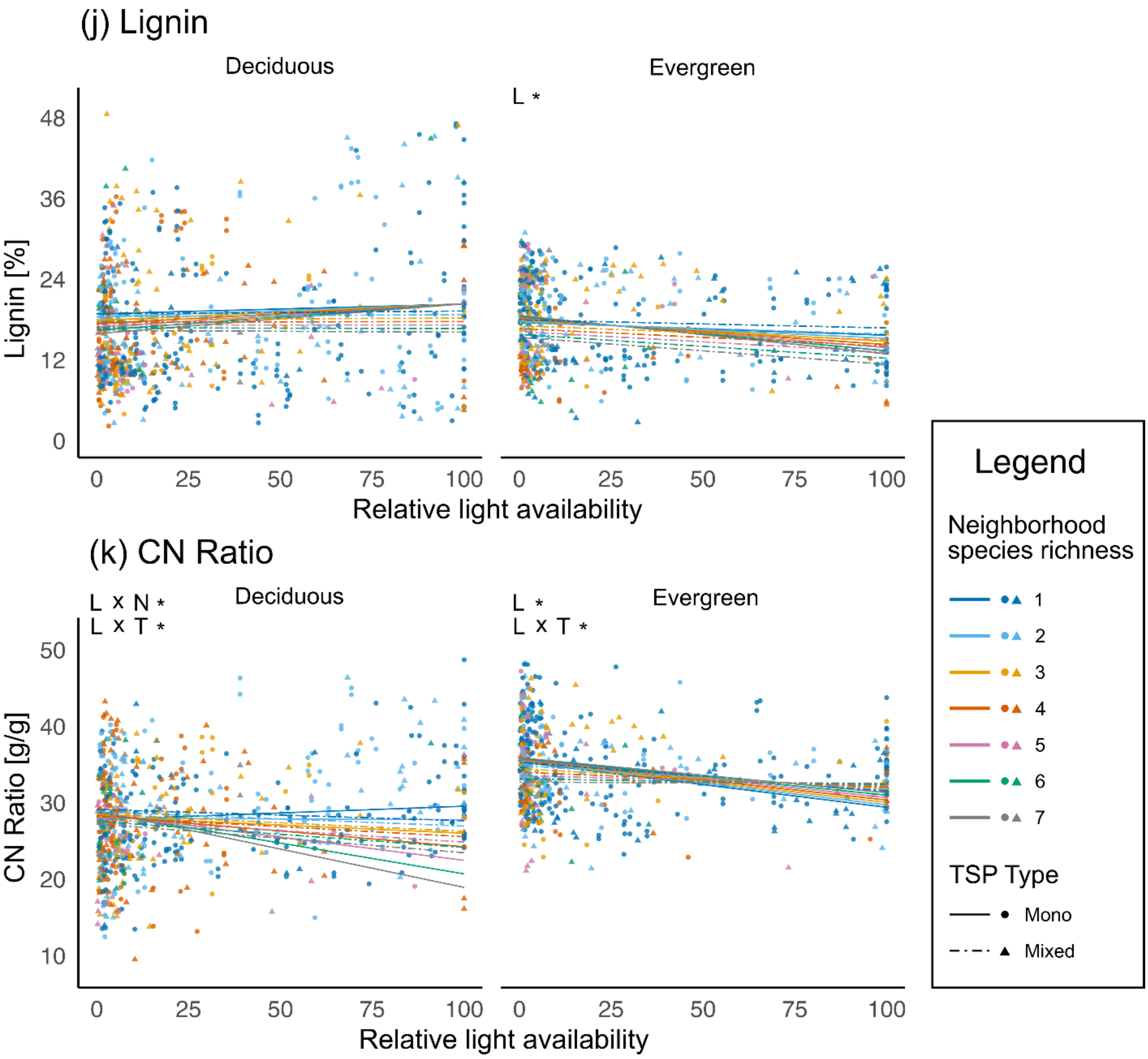


Figure S5 (j-k). Leaf traits as functions of light availability, modified by TSP type (Tree species pair type) and neighborhood species richness. Separate graphs for deciduous and evergreen species. The continuous lines indicate monospecific TSPs, dashed lines indicate mixed TSPs. Different colors indicate different levels of neighborhood species richness. Letters indicate significant main effects and interactions (L = Light, T = TSP type, N = Neighborhood species richness, x = interaction, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). For the numeric results of the underlaying models see Table S7.

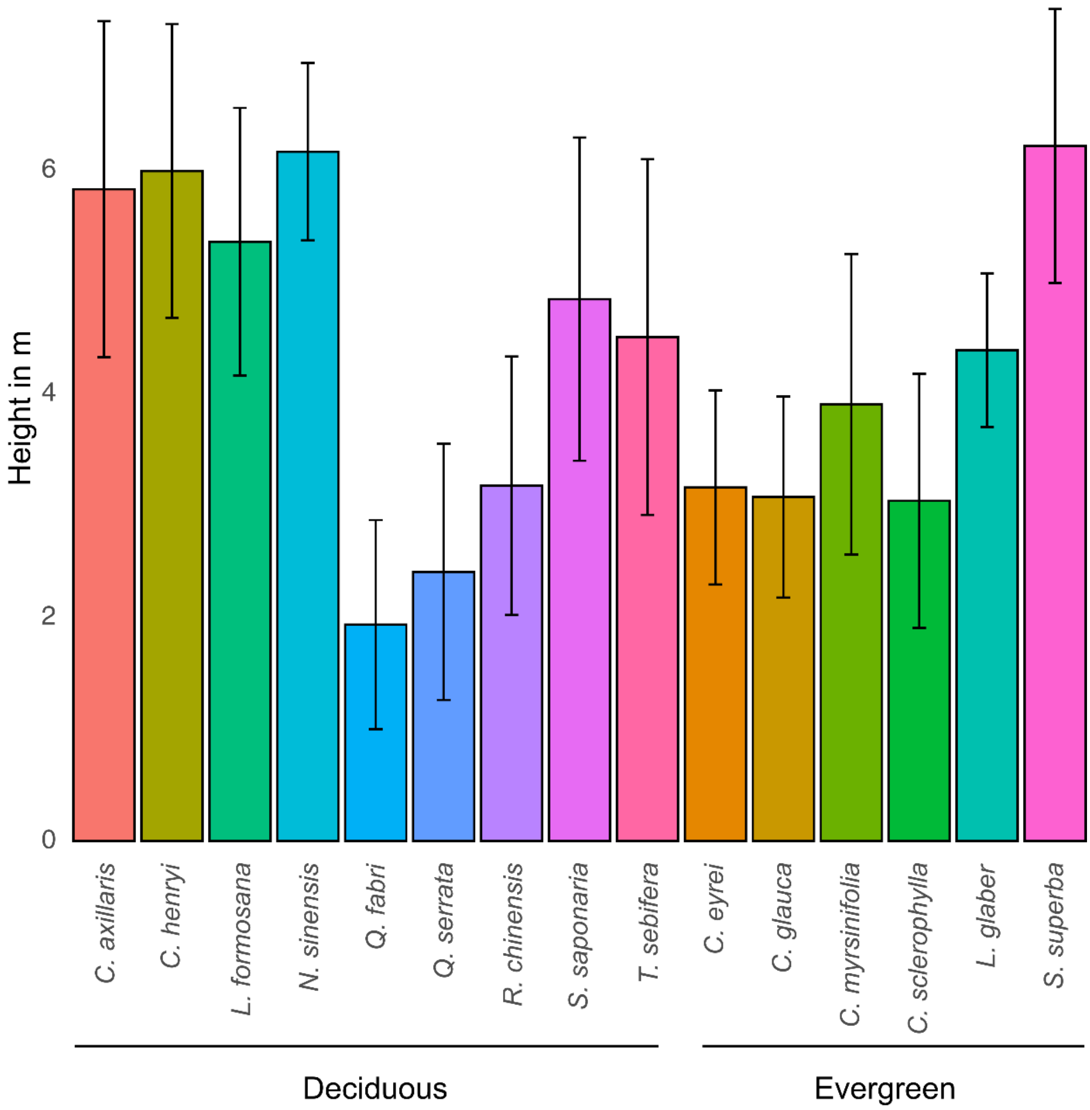


Figure S6. Approximate height of the sampled trees. Colored bars indicate the average height per species, the error bars indicate the standard deviation. For full species names, see Table S1.

Table S1. Species list. Note that some of the species have been described under multiple names or have undergone taxonomic revisions, including reassignments to different genera. While alternative classifications may exist in other taxonomic sources, the species names throughout this publication follow the nomenclature and classification used in the Flora of China (Brach and Song 2006; eFloras 2008).

Species	Abbreviation	Family	Leaf habit
Choerospondias axillaris (ROXB.) B.L.BURTT & A.W.HILL	*C. axillaris*	Anacardiaceae	Deciduous
Castanea henryi (SKAN) REHDER & E.H.WILSON	*C. henryi*	Fagaceae	Deciduous
Liquidambar formosana HANCE	*L. formosana*	Altingiaceae	Deciduous
Nyssa sinensis OLIVER	*N. sinensis*	Nyssaceae	Deciduous
Quercus fabri HANCE	*Q. fabri*	Fagaceae	Deciduous
Quercus serrata MURRAY	*Q. serrata*	Fagaceae	Deciduous
Rhus chinensis MILLER	*R. chinensis*	Anacardiaceae	Deciduous
Sapindus saponaria GAERTNER	*S. saponaria*	Sapindaceae	Deciduous
Triadica sebifera (LINNAEUS) SMALL	*T. sebifera*	Euphorbiaceae	Deciduous
Castanopsis eyrei (CHAMPION EX BENTHAM) HUTCHINSON	*C. eyrei*	Fagaceae	Evergreen
Cyclobalanopsis glauca (THUNBERG) OERSTED	*C. glauca*	Fagaceae	Evergreen
Cyclobalanopsis myrsinifolia (BLUME) OERSTED	*C. myrsinifolia*	Fagaceae	Evergreen
Castanopsis sclerophylla (LINDLEY & PAXTON) SCHOTTKY	*C. sclerophylla*	Fagaceae	Evergreen
Lithocarpus glaber (THUNBERG) NAKAI	*L. glaber*	Fagaceae	Evergreen
Schima superba GARDNER & CHAMPION	*S. superba*	Theaceae	Evergreen

Table S2. Number of sampled trees by species. The selection of the species pairings is based on the species combinations that occur in 4-species mixture plots. The # Trees refers to the first species of the pair and indicates how many individuals of this species are paired with the corresponding species. For full species names, see table S1.

Species pairing	# Trees	Species pairing	# Trees	Species pairing	# Trees
C. axillaris - C. axillaris	18	*C. sclerophylla - C. sclerophylla*	18	*Q. serrata - Q. serrata*	18
C. axillaris - C. sclerophylla	3	*C. sclerophylla - C. axillaris*	3	*Q. serrata - C. axillaris*	3
C. axillaris - Q. serrata	3	*C. sclerophylla - Q. serrata*	6	*Q. serrata - C. sclerophylla*	6
C. axillaris - T. sebifera	6	*C. sclerophylla - T. sebifera*	3	*Q. serrata - T. sebifera*	2
C. eyrei - C. eyrei	8	*L. formosana - L. formosana*	18	*R. chinensis - R. chinensis*	6
C. eyrei - C. myrsinifolia	4	*L. formosana - C. henryi*	3	*R. chinensis - C. glauca*	3
C. eyrei - L. glaber	4	*L. formosana - N. sinensis*	3	*R. chinensis - K. bipinnata*	1
C. eyrei - K. bipinnata	0	*L. formosana - S. saponaria*	6	*R. chinensis - S. superba*	1
C. glauca - C. glauca	18	*L. glaber - L. glaber*	18	*S. saponaria - S. saponaria*	18
C. glauca - Q. fabri	6	*L. glaber - C. eyrei*	4	*S. saponaria - C. henryi*	3
C. glauca - R. chinensis	3	*L. glaber - C. myrsinifolia*	3	*S. saponaria - L. formosana*	6
C. glauca - S. superba	3	*L. glaber – K. bipinnata*	3	*S. saponaria - N. sinensis*	3
C. henryi - C. henryi	18	*N. sinensis - N. sinensis*	16	*T. sebifera - T. sebifera*	16
C. henryi - L. formosana	3	*N. sinensis - C. henryi*	7	*T. sebifera - C. axillaris*	6
C. henryi - N. sinensis	7	*N. sinensis - L. formosana*	3	*T. sebifera - C. sclerophylla*	3
C. henryi - S. saponaria	3	*N. sinensis - S. saponaria*	3	*T. sebifera - Q. serrata*	2
C. myrsinifolia - C. myrsinifolia	18	*Q. fabri - Q. fabri*	18	*S. superba - S. superba*	18
C. myrsinifolia - C. eyrei	4	*Q. fabri - C. glauca*	6	*S. superba - C. glauca*	3
C. myrsinifolia - K. bipinnata	3	*Q. fabri - K. bipinnata*	1	*S. superba - Q. fabri*	2
C. myrsinifolia - L. glaber	3	*Q. fabri - S. superba*	2	*S. superba - R. chinensis*	1

Table S3. Number of samples by species and neighborhood species richness level (NSR). For full species names, see table S1.

Species	**Samples per NSR level (Mono)**							**Samples per NSR level (Mixed)**						
	1	**2**	**3**	**4**	**5**	**6**	**7**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
C. axillaris	20	11	0	16	0	0	0	3	10	4	10	5	3	0
C. henryi	23	8	0	0	0	0	0	12	10	0	4	4	4	0
L. formosana	24	27	7	0	7	0	0	6	11	18	0	3	0	3
N. sinensis	23	16	8	0	5	4	0	0	13	6	10	2	2	3
Q. fabri	23	0	6	7	0	0	0	13	9	3	3	4	3	0
Q. serrata	31	16	0	24	0	0	0	0	10	7	13	3	2	0
R. chinensis	22	23	7	17	0	0	0	3	8	8	11	0	11	0
S. saponaria	40	8	7	0	8	0	0	7	15	5	0	4	8	0
T. sebifera	16	15	6	7	0	0	0	0	17	4	6	5	5	4
C. eyrei	28	8	6	0	12	0	0	2	11	10	0	0	0	0
C. glauca	29	13	5	7	0	0	5	0	8	4	14	2	0	0
C. myrsinifolia	10	0	0	0	0	0	0	0	0	8	0	4	0	0
C. sclerophylla	14	17	0	12	0	3	0	3	4	10	9	8	0	0
L. glaber	29	9	0	5	4	0	0	2	10	7	7	10	0	0
S. superba	42	8	7	0	8	0	0	4	4	14	0	0	0	4

Table S4. Reference methods for leaf trait analysis. The samples were rehydrated and weighted freshly and scanned with a flatbed scanner on the day of harvest. The samples were dried for 72 hours at 60 °C and weighed again. LDMC was calculated as dry weight per unit fresh weight and SLA was calculated as leaf area per unit dry mass. As a preparation for other analyses, calibration samples were ground to a homogenous powder using a Retsch MM400 ball mill. Ground samples were further treated via nitric acid digestion and diluted with a Cs/Ln buffer solution. Reference samples and phenolics and tannin data for calibration were kindly provided by Eichenberg et al. (2014).

Leaf trait	Method, instrument or software	Reference
LDMC	Weighting of fresh and dried leaves with precision scale (Sartorius, Göttingen, Germany)	Pérez-Harguindeguy et al. 2016
SLA	Leaf area calculation with WinFOLIA (v Pro 2004a Regent Instruments)	Pérez-Harguindeguy et al. 2016
Lignin, Cellulose	Van Soest analysis using a ANKOM200 Fiber Analyzer (ANKOM Technology, Macedon NY, USA)	Van Soest et al. 1991
Leaf C, Leaf N, Leaf S, CN ratio	Gas chromatography using a vario EL cube (Elementar, Hanau, Germany)	-
Leaf Ca, Leaf Mg, Leaf K,	Atomic absorption spectrometry using a SpectrAA 300 (Analytik Jena GmbH, Jena, Germany)	Schinkel 1984
Leaf P	Molybdenum blue assay using a GENESYS 140 Spectrophotometer (Thermo Fisher Scientific Inc., Waltham MA, USA)	Murphy and Riley 1958
Phenolics	Modified Prussian-blue assay	Graham 1992; Price and Butler 1977; Eichenberg et al. 2014
Tannin	Protein-precipitation based radial diffusion assay	Hagerman 1987; Eichenberg et al. 2014

Table S5. Details of the leaf trait prediction models. A separate model was created for each leaf trait. The dataset, consisting of 190 samples, was divided into two subsets: a calibration (training) set and a validation (test) set. Each subset contained 95 samples, ensuring that all species were represented in both sets. For most models, spectral data underwent pre-treatment, with the optimal method chosen empirically for each leaf trait. Several pre-treatment methods were tested, including standard normal variate (SNV), multiplicative scatter correction (MSC), first and second derivative using Savitzky-Golay algorithm (1D, 2D), min-max normalization (MMN) as well as a combination of these (+), or no data pre-treatment (RAW). Relevant spectral regions were selected empirically to optimize predictive performance. The models were trained using the calibration dataset and subsequently validated using the independent test dataset. The final model for each trait was selected based on the lowest root mean square error of prediction (RMSEP). Additional performance metrics are reported, including normalized root mean square error (NRMSE, i.e. RMSEP divided by mean trait value), coefficient of determination (R^2), ratio of standard deviation of the sample to standard error of the prediction (RPD). The model rank indicates the number of latent factors in the regression. For regression coefficients figure S1.

Leaf trait	Mean trait value	RMSEP	NRMSE	R^2	RPD	Rank	Data pre-treatment	Spectral regions in nm
SLA	13.23 mm²/mg	0.96	0.0726	0.95	4.51	6	SNV	350-2500
Leaf N	1.64 %	0.12	0.0731	0.85	2.56	15	MSC	1530-1752; 2085-2307
Leaf P	0.49 mg/g	0.15	0.3042	0.63	1.65	13	1D	991-1855; 2069-2177
Leaf Ca	7.69 mg/g	1.81	0.2354	0.79	2.19	13	1D	924-1210; 1424-167 1793-2285
Leaf K	7.07 mg/g	2.13	0.3012	0.44	1.33	15	MSC	991-1099
Leaf Mg	2.71 mg/g	0.76	0.2801	0.88	2.90	15	RAW	350-2500
Phenolics	65.76 mg/g	23.00	0.3498	0.75	1.98	13	MMN	1325-1700; 1875-2175; 2325-2500
Tannin	65.88 mg/g	36.60	0.5556	0.66	1.73	7	1D + MSC	1315-1727; 2025-2445
Leaf S	0.26 mg/g	0.06	0.2266	0.61	1.59	19	MSC	565-780; 995-1210; 1425-2500
Leaf C	47.23 %	0.90	0.0191	0.74	1.97	11	MSC	743-1904
Cellulose	18.00 %	2.38	0.1323	0.87	2.77	9	1D + SNV	780-2500
Lignin	17.37 %	3.04	0.1750	0.87	2.79	24	RAW	671-2500
CN ratio	30.67 g/g	2.04	0.0665	0.89	3.01	15	1D	530-1188; 1487-2500
LDMC	446.77 mg/g	18.04	0.0404	0.91	3.38	9	SNV	1307-1497; 2215-2500

Table S6. Results of the type I ANOVA of linear mixed-effects models including both leaf habits (n=1314) for each leaf trait. Models were fitted with the trait values as response variables and light availability, TSP type (Tree species pair type), neighborhood species richness and leaf habit as fixed effects. Colons indicate interactions between fixed effects, significant results ($p < 0.05$) are highlighted in bold.

Trait	Predictors	*F*-value	*p*-value
SLA	Light availability	93.61	**< 0.001**
	TSP type	2.79	0.098
	Neighborhood species richness	12.63	**0.001**
	Leaf habit	45.37	**< 0.001**
	Light availability : TSP type	1.96	0.162
	Light availability : Neighborhood species richness	6.35	**0.012**
	TSP type : Neighborhood species richness	0.01	0.913
	Light availability : Leaf habit	12.28	**0.005**
	Light availability : TSP type : Neighborhood species richness	2.73	0.099
Leaf N	Light availability	2.03	0.177
	TSP type	0.39	0.532
	Neighborhood species richness	2.93	0.090
	Leaf habit	7.37	**0.017**
	Light availability : TSP type	0.03	0.872
	Light availability : Neighborhood species richness	0.72	0.398
	TSP type : Neighborhood species richness	0.51	0.477
	Light availability : Leaf habit	9.65	**0.009**
	Light availability : TSP type : Neighborhood species richness	0.22	0.637
Leaf P	Light availability	4.47	0.052
	TSP type	0.43	0.515
	Neighborhood species richness	3.10	0.088
	Leaf habit	31.49	**< 0.001**
	Light availability : TSP type	0.96	0.327
	Light availability : Neighborhood species richness	1.77	0.184
	TSP type : Neighborhood species richness	0.49	0.487
	Light availability : Leaf habit	6.05	**0.028**
	Light availability : TSP type : Neighborhood species richness	11.24	**< 0.001**
Leaf Ca	Light availability	0.45	0.512
	TSP type	0.06	0.812
	Neighborhood species richness	2.90	0.095
	Leaf habit	11.33	**0.005**
	Light availability : TSP type	0.21	0.646
	Light availability : Neighborhood species richness	1.15	0.285
	TSP type : Neighborhood species richness	0.26	0.609
	Light availability : Leaf habit	2.38	0.147
	Light availability : TSP type : Neighborhood species richness	0.14	0.708
Leaf K	Light availability	4.94	**0.043**
	TSP type	0.28	0.597

Trait	**Predictors**	***F*-value**	***p*-value**
	Neighborhood species richness	0.94	0.334
	Leaf habit	0.32	0.578
	Light availability : TSP type	0.00	0.952
	Light availability : Neighborhood species richness	0.76	0.385
	TSP type : Neighborhood species richness	0.08	0.777
	Light availability : Leaf habit	6.10	**0.028**
	Light availability : TSP type : Neighborhood species richness	1.38	0.241
Leaf Mg	Light availability	0.90	0.354
	TSP type	0.00	0.995
	Neighborhood species richness	2.54	0.115
	Leaf habit	8.23	**0.013**
	Light availability : TSP type	0.81	0.369
	Light availability : Neighborhood species richness	0.21	0.648
	TSP type : Neighborhood species richness	0.06	0.808
	Light availability : Leaf habit	3.37	0.087
	Light availability : TSP type : Neighborhood species richness	6.44	**0.011**
Phenolics	Light availability	20.81	< **0.001**
	TSP type	2.74	0.100
	Neighborhood species richness	3.78	0.061
	Leaf habit	3.57	0.081
	Light availability : TSP type	0.80	0.370
	Light availability : Neighborhood species richness	0.35	0.555
	TSP type : Neighborhood species richness	0.17	0.680
	Light availability : Leaf habit	0.49	0.496
	Light availability : TSP type : Neighborhood species richness	0.00	0.951
Tannin	Light availability	0.00	0.967
	TSP type	0.12	0.733
	Neighborhood species richness	5.23	**0.029**
	Leaf habit	8.42	**0.013**
	Light availability : TSP type	0.00	1.000
	Light availability : Neighborhood species richness	0.55	0.459
	TSP type : Neighborhood species richness	0.11	0.742
	Light availability : Leaf habit	1.30	0.276
	Light availability : TSP type : Neighborhood species richness	0.09	0.770
Leaf S	Light availability	3.58	0.079
	TSP type	0.63	0.430
	Neighborhood species richness	3.49	0.067
	Leaf habit	4.64	0.051
	Light availability : TSP type	1.39	0.238
	Light availability : Neighborhood species richness	0.04	0.852
	TSP type : Neighborhood species richness	0.00	0.993
	Light availability : Leaf habit	3.54	0.084
	Light availability : TSP type : Neighborhood species richness	0.84	0.360
Leaf C	Light availability	6.44	**0.023**

Trait	**Predictors**	***F*-value**	***p*-value**
	TSP type	0.46	0.498
	Neighborhood species richness	2.01	0.164
	Leaf habit	6.83	**0.021**
	Light availability : TSP type	0.65	0.421
	Light availability : Neighborhood species richness	10.10	**0.002**
	TSP type : Neighborhood species richness	1.75	0.187
	Light availability : Leaf habit	22.03	**< 0.001**
	Light availability : TSP type : Neighborhood species richness	4.31	**0.038**
Cellulose	Light availability	0.71	0.414
	TSP type	1.61	0.207
	Neighborhood species richness	19.90	**< 0.001**
	Leaf habit	27.43	**< 0.001**
	Light availability : TSP type	0.03	0.873
	Light availability : Neighborhood species richness	5.62	**0.018**
	TSP type : Neighborhood species richness	0.02	0.884
	Light availability : Leaf habit	1.92	0.191
	Light availability : TSP type : Neighborhood species richness	1.50	0.220
Lignin	Light availability	0.01	0.938
	TSP type	2.15	0.146
	Neighborhood species richness	0.49	0.487
	Leaf habit	0.03	0.865
	Light availability : TSP type	0.55	0.457
	Light availability : Neighborhood species richness	0.85	0.357
	TSP type : Neighborhood species richness	0.23	0.629
	Light availability : Leaf habit	2.71	0.124
	Light availability : TSP type : Neighborhood species richness	0.60	0.441
CN ratio	Light availability	14.33	**0.001**
	TSP type	0.46	0.499
	Neighborhood species richness	3.71	0.057
	Leaf habit	8.70	**0.010**
	Light availability : TSP type	0.26	0.607
	Light availability : Neighborhood species richness	0.28	0.594
	TSP type : Neighborhood species richness	0.56	0.458
	Light availability : Leaf habit	15.46	**0.002**
	Light availability : TSP type : Neighborhood species richness	0.00	0.997
LDMC	Light availability	16.36	**0.001**
	TSP type	0.04	0.844
	Neighborhood species richness	4.99	**0.027**
	Leaf habit	7.26	**0.018**
	Light availability : TSP type	1.54	0.215
	Light availability : Neighborhood species richness	2.18	0.141
	TSP type : Neighborhood species richness	0.16	0.688
	Light availability : Leaf habit	6.65	**0.025**
	Light availability : TSP type : Neighborhood species richness	1.25	0.265

Table S7. Results of the type I ANOVA. Linear mixed-effects models were fitted for each leaf trait and for both deciduous (n=725) and evergreen (n=589) trees separately. The trait values are response variables and light availability, TSP type (Tree species pair type) and neighborhood species richness (NSR) are fixed effects. Colons indicate interactions between fixed effects, significant results ($p < 0.05$) are highlighted in bold.

		Deciduous species		Evergreen species	
Trait	**Predictor**	***F*-value**	***p*-value**	***F*-value**	***p*-value**
SLA	Light	59.67	**< 0.001**	26.13	**0.004**
	TSP Type	0.90	0.347	1.05	0.312
	NSR	0.80	0.387	0.00	0.955
	Light : TSP Type	0.40	0.530	6.26	**0.013**
	Light : NSR	3.43	0.065	0.19	0.663
	TSP Type : NSR	1.61	0.207	1.48	0.228
	Light : TSP Type : NSR	4.07	**0.044**	0.49	0.483
Leaf N	Light	0.79	0.394	17.77	**0.008**
	TSP Type	0.14	0.714	0.07	0.795
	NSR	0.01	0.917	0.18	0.675
	Light : TSP Type	2.99	0.085	6.19	**0.013**
	Light : NSR	2.61	0.107	0.15	0.699
	TSP Type : NSR	0.30	0.584	2.46	0.122
	Light : TSP Type : NSR	0.48	0.490	0.00	0.988
Leaf P	Light	10.99	**0.008**	0.00	0.952
	TSP Type	1.60	0.210	1.22	0.275
	NSR	0.25	0.625	0.04	0.857
	Light : TSP Type	1.68	0.196	0.02	0.900
	Light : NSR	0.78	0.377	0.00	0.979
	TSP Type : NSR	5.52	**0.021**	1.12	0.294
	Light : TSP Type : NSR	3.23	0.073	7.15	**0.008**
Leaf Ca	Light	2.48	0.144	0.32	0.595
	TSP Type	3.22	0.076	1.16	0.287
	NSR	0.01	0.909	0.42	0.530
	Light : TSP Type	0.14	0.710	0.11	0.745
	Light : NSR	0.09	0.759	0.00	0.995
	TSP Type : NSR	0.12	0.732	0.32	0.575
	Light : TSP Type : NSR	0.46	0.500	0.99	0.320
Leaf K	Light	9.17	**0.013**	0.04	0.855
	TSP Type	0.09	0.760	0.01	0.916
	NSR	0.92	0.340	0.03	0.866
	Light : TSP Type	0.01	0.931	0.05	0.828
	Light : NSR	1.14	0.286	0.46	0.499
	TSP Type : NSR	0.62	0.432	0.27	0.605
	Light : TSP Type : NSR	0.08	0.783	1.87	0.172
Leaf Mg	Light	3.51	0.079	0.08	0.782
	TSP Type	1.10	0.296	0.72	0.400
	NSR	0.00	0.977	0.92	0.353
	Light : TSP Type	0.01	0.944	2.84	0.093

		Deciduous species		Evergreen species	
Trait	**Predictor**	***F*-value**	***p*-value**	***F*-value**	***p*-value**
	Light : NSR	1.00	0.317	1.23	0.269
	TSP Type : NSR	1.08	0.301	0.58	0.449
	Light : TSP Type : NSR	0.33	0.567	5.04	**0.025**
Phenolics	Light	6.15	**0.034**	16.05	**0.010**
	TSP Type	0.08	0.778	2.17	0.146
	NSR	0.26	0.615	3.83	0.095
	Light : TSP Type	0.19	0.666	1.94	0.164
	Light : NSR	1.62	0.204	0.00	0.981
	TSP Type : NSR	0.47	0.493	2.69	0.105
	Light : TSP Type : NSR	0.08	0.774	0.04	0.835
Tannin	Light	0.15	0.705	6.89	**0.049**
	TSP Type	0.40	0.529	0.58	0.449
	NSR	0.08	0.778	0.57	0.483
	Light : TSP Type	0.11	0.740	0.37	0.543
	Light : NSR	0.54	0.461	5.81	**0.016**
	TSP Type : NSR	0.00	0.958	0.05	0.821
	Light : TSP Type : NSR	0.02	0.895	0.29	0.589
Leaf S	Light	5.96	**0.036**	0.30	0.611
	TSP Type	0.03	0.863	1.00	0.321
	NSR	0.01	0.915	2.66	0.110
	Light : TSP Type	1.49	0.223	0.03	0.857
	Light : NSR	1.34	0.247	0.58	0.447
	TSP Type : NSR	1.00	0.319	0.03	0.875
	Light : TSP Type : NSR	0.67	0.414	0.02	0.894
Leaf C	Light	2.71	0.129	22.26	**0.007**
	TSP Type	0.41	0.522	0.53	0.468
	NSR	0.09	0.768	0.63	0.442
	Light : TSP Type	1.15	0.285	1.38	0.241
	Light : NSR	1.49	0.223	2.33	0.128
	TSP Type : NSR	0.50	0.483	0.00	0.992
	Light : TSP Type : NSR	0.38	0.538	4.35	**0.038**
Cellulose	Light	2.84	0.126	0.05	0.835
	TSP Type	0.81	0.371	0.72	0.398
	NSR	0.01	0.929	0.45	0.510
	Light : TSP Type	0.00	0.955	0.49	0.483
	Light : NSR	0.96	0.327	1.97	0.161
	TSP Type : NSR	0.47	0.496	0.04	0.838
	Light : TSP Type : NSR	0.92	0.337	0.28	0.596
Lignin	Light	1.20	0.298	6.97	**0.039**
	TSP Type	1.37	0.251	0.59	0.446
	NSR	1.24	0.300	0.64	0.441
	Light : TSP Type	2.12	0.146	1.83	0.177
	Light : NSR	0.22	0.641	2.90	0.089

		Deciduous species		Evergreen species	
Trait	**Predictor**	***F*-value**	***p*-value**	***F*-value**	***p*-value**
	TSP Type : NSR	0.00	0.965	2.71	0.106
	Light : TSP Type : NSR	0.54	0.465	0.10	0.756
CN ratio	Light	0.00	0.985	25.75	**0.003**
	TSP Type	0.24	0.627	0.07	0.789
	NSR	0.50	0.487	0.21	0.654
	Light : TSP Type	4.62	**0.032**	8.02	**0.005**
	Light : NSR	5.70	**0.018**	1.03	0.310
	TSP Type : NSR	0.34	0.562	1.00	0.322
	Light : TSP Type : NSR	2.14	0.144	0.19	0.666
LDMC	Light	16.39	**0.002**	3.17	0.142
	TSP Type	0.08	0.772	0.07	0.793
	NSR	0.20	0.654	1.93	0.173
	Light : TSP Type	0.42	0.520	0.62	0.432
	Light : NSR	2.79	0.096	0.01	0.921
	TSP Type : NSR	0.00	0.989	0.07	0.786
	Light : TSP Type : NSR	0.43	0.513	1.04	0.308

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Chapter 4

Leaf trait variation within individuals mediates the relationship between tree species richness and productivity

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Abstract

In forest ecosystems, many ecosystem functions such as tree growth are affected by tree species richness. This biodiversity-productivity relationship (BPR) is mediated by leaf traits, which themselves are known to be influenced by tree species richness; at the same time, as the primary organs of light capture, they are an important factor for tree growth. However, how tree growth is influenced by a tree's ability to phenotypically adjust its leaf traits to the within-individual light gradient has largely been unexplored. Furthermore, it is not known how such impacts of within-tree leaf trait variation on individual tree growth sums up to productivity at the community scale. In this study we tested, how tree species richness, a tree's mean leaf traits, within-tree leaf trait variation and the light extinction coefficient within a tree crown influence tree growth. We measured these variables in the temperate forest plantation of the Kreinitz biodiversity experiment. We found that the relationship between tree species richness and tree growth is mediated via the leaf trait variation of the individual trees, which in turn was modified by light availability. In particular, trees in monocultures show a higher within-individual leaf trait variation, which partly compensates for the lack in among-species leaf trait variation, and thus affects the BPR. It seems that tree richness operates both through increased acquisitive trait values and within-individual leaf trait variation, two processes that cancelled out each other and resulted in the absence of a significant effect of tree richness on productivity in our study. In conclusion, to understand the BPR, it is important to study the underlying processes and to know which ones reinforce or oppose each other. In particular, our study highlights the importance of including within-individual leaf trait variation in ecological research as one important moderator in the BPR.

Keywords

biodiversity-ecosystem-functioning experiment, diversity-productivity relationship, leaf traits, light availability, near-infrared spectroscopy (NIRS), temperate forest plantation

Introduction

The diversity-productivity relationship in forest ecosystems

In ecological research, the relationship between tree species richness and productivity of forest ecosystems biodiversity-productivity relationship (BPR) has been intensively studied. While the driving mechanisms are still poorly understood, current research suggests a generally positive BPR (Chisholm and Gupta 2023). For natural forests, literature indicates a positive BPR (Zhang et al. 2012, Ruiz-Benito et al. 2014, Liang et al. 2016), especially when control for biome, climate and environmental conditions is applied (Paquette and Messier 2011, van der Plas 2019, Ratcliffe et al. 2017). In planted biodiversity-ecosystem-functioning experiments, however, the pattern is less clear (Kambach et al. 2019). While there are multiple studies that reported a positive BPR in planted forests (Potvin and Gotelli 2008, Huang et al. 2018, Zemp et al. 2019), some studies described a negative (Firn et al. 2007) or no significant BPR (Nguyen et al. 2012, Staples et al. 2019). These divergent findings highlight that, in addition to a direct effect of biodiversity on productivity, indirect effects may determine the outcome of a BPR.

In general, there are multiple possible mechanisms that connect species richness and tree productivity (Ammer 2019, Trogisch et al. 2021). For example, in species-rich environments, higher tree growth might be related to stronger facilitation effects among species (Hooper et al. 2005) as well as to weaker effects of species-specific pathogens (Maron et al. 2011, Schnitzer et al. 2011). Furthermore, selection effects can cause positive BPRs (Tatsumi 2020). Selection effects might occur when well-performing species become more abundant in mixtures. Additionally, the biodiversity of primary producers in a community reduces the competition among them through niche partitioning (Tilman 1977). Competition is most severe for plants that are similar regarding their resource requirements and uptake strategy, which is in particular the case for plants of the same species (MacArthur and Levins 1967). Consequently, an increased biodiversity can lead to reduced competition for resources (Tilman 1994), and therefore, to increased resource availability for each individual plant. This in turn results in increased productivity of the community (Fichtner et al. 2018).

Competition for light and optimisation of light capturing

In closed canopy forests, light is the resource that trees most compete for (Oliver and Larson 1996, Kohyama et al. 2012, Rüger et al. 2012). Hence, forest canopies are optimized for light capture (Reich 2012). In particular, a higher structural complexity appears to be linked to greater photosynthetic capacity of the forest (Seidel and Ammer 2023). Optimization for light capture occurs at all organisation levels of the community. There are differences between species in light demand and shade tolerance, differences between individuals of the same species and even differences in the adjustment of leaves to light conditions within a single tree (Lichtenthaler et al. 1981, Givnish 1988, Bassow and Bazzaz 1997, Valladares and Niinemets 2008). A highly diverse forest should be more effective in partitioning the available light than a monoculture (Morin et al. 2011). Hence, diverse tree communities should be more productive than monocultures (Williams et al. 2021)

Leaf traits

The amount of light captured by an individual tree is dependent on the total leaf mass (Galia Selaya et al. 2008) and its leaf traits (Terashima and Hikosaka 1995). Numerous leaf traits are related to photosynthesis and light capture, including specific leaf area (SLA) and the concentration of nitrogen (leaf N) (Evans and Poorter 2001), calcium (leaf Ca) (Wang et al. 2019), potassium (leaf K) (Leigh and Wyn Jones 1984), magnesium (leaf Mg) (Shaul 2002) and phosphate (leaf P) (Plaxton and Carswell 1999) in the leaves. However, when analysing leaf traits, the optimisation of light capture also involves the trade-off between these photosynthesis-related traits and the construction cost of the leaves (Zhang et al. 2017). Therefore, relevant traits also include leaf dry matter content (LDMC), leaf carbon content (leaf C) and ratio of leaf carbon to leaf nitrogen (CN ratio). On the species level, this trade-off is described by the leaf economics spectrum (LES) (Wright et al. 2004). Traits related to the LES allow ranking plant species along the fast-slow growth spectrum according to their acquisitive or conservative strategy, with photosynthesis-related traits associated with an acquisitive strategy and structural traits associated with a conservative strategy (Reich 2014). Indeed, several studies clearly demonstrated the link between acquisitive leaf traits and fast tree growth (Poorter and Bongers 2006, Chaturvedi et al. 2011, Li et al. 2017).

Leaf trait variation

Leaf traits of the LES have been traditionally considered at the species level (Garnier et al. 2001, Díaz et al. 2016). However, mean trait values may fail to predict tree growth (Paine et al. 2015) which is why besides the average leaf trait values of a species, the ability of a species to adjust its leaf traits (leaf trait variation) has also been linked to tree growth (Laforest-Lapointe et al. 2014, Lusk 2019, Asefa et al. 2021). Indeed, the topic of intraspecific leaf trait variation has received much attention in the recent years (Albert et al. 2010, Messier et al. 2010, Violle et al. 2012). The link between intraspecific leaf trait variation and tree growth has been described in the context of the ability of a species to adjust its leaf traits to environmental gradients (Hikosaka et al. 2021, Kühn et al. 2021, O'Sullivan et al. 2022). Furthermore, leaf trait adjustments on smaller scales might be also relevant, albeit as responses to different factors. For forest ecosystems, the leaf trait variation within individual trees (within-individual leaf trait variation) could be especially relevant, as here every tree is subject to a strong within-individual light gradient (Binkley et al. 2013). Plants respond to the within-individual light gradient with leaf trait value adjustments at the within-individual level (de Kroon et al. 2005, Kawamura 2010). The consequence is a strong individual leaf trait variation in tree crowns (Chmura and Tjoelker 2008). Irrespective of a species' position on the LES spectrum, it would be beneficial to adjust the leaf traits to the sun-shade gradient along the crown, thus making best use of the given light conditions by making sun and shade leaves. At the level of individual trees, this ability of leaf trait adjustment would be seen in an increased leaf trait variation. Yet, studies that link individual leaf trait variation to tree growth are rare (Feng et al. 2022 studied the vertical variation in leaf traits to understand the coexistence of tree species).

A major hurdle for such analyses is the high effort of analysing the required amount of samples. A possible solution is the usen of near-infrared spectroscopy (NIRS) in ecological research (Trogisch et al. 2017), as it offers a rapid and effective method for the analysis of leaf traits (Foley et al. 1998).

In this study, we investigated whether a higher individual trait variation allows an individual tree to better adjust to the within-individual light gradient in order to optimise its light capture. We analysed a wide arrange of leaf traits with a focus on those related to the LES. While the LES is a framework that describes between-species trait correlation, there is a strong indication that it can be extended to the trait coordination within tree canopies (Niinemets et al. 2015). Thus, we applied the LES concept to within-individual trait values.

Aim and Hypotheses

The aim of this study is to identify the key underlying mechanism of the BPR in a temperate forest ecosystem. In the Kreinitz tree diversity experiment (Saxony, Germany), we analysed the growth of all 2880 trees over a three-year period. For a subset of 283 individuals we measured leaf traits, leaf trait variation and the light extinction coefficient at the within-individual level. We predicted a generally positive relationship between tree species richness and tree growth (H1). We expected to find this relationship both at the plot level (H1a) and at the individual level (H1b). While H1a tests for a positive net biodiversity effect on tree growth, H1b assumes that tree richness has a positive effect on growth of the majority of tree species. Moreover, we expected that tree-level mean trait values of the LES and within-individual trait variation are driven by tree species richness (H2a) and a tree's light extinction coefficient (H2b). Furthermore, we hypothesized that individual tree growth depends on leaf traits (H3), and trees grow better with a more acquisitive mean LES trait value (H3a) and a higher LES trait variation (H3b). Finally, we expected that mean trait values and trait variation are mediating factors of how tree species richness affects tree growth (H4a). We also tested whether the way light is intercepted along the crown mediates the relationship of tree species richness with mean trait values and trait variation (H4b). The mediating effects in H4 were tested with a structural equation model (SEM) (see Supporting information for the tested relationships within the model).

Material and methods

Experimental site

The Kreinitz experiment is located in central Germany near the city of Riesa, Saxony (51°23′08″N, 13°15′41″E). The experimental site was established in 2005 on former agricultural land (humic cambisol) and is partially surrounded by pine forest. The experiment covers six common European tree species: European beech *Fagus sylvatica*, European ash *Fraxinus excelsior*, Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, sessile oak *Quercus petraea* and small-leaved linden *Tilia cordata*. The 2880 tree individuals are distributed over 98 plots in two blocks of 49 plots each (Supporting information). Each block consists of one plot each for all monocultures, one plot each for all possible two, three and five species mixtures, one plot for the six species mixture, as well as one control plot without trees. The position of the plots within blocks is random. The number of different tree species planted in a plot is referred to as 'tree species richness'. Each plot covers an area of 25 m2, on which 30 individuals are planted in five rows of six individuals. The planting distance is 80 cm between individuals within rows and 100 cm between rows with a horizontal offset of 40 cm for every second row, which results in a hexagonal planting pattern. For further information on the Kreinitz experiment, see Hantsch et al. (2014).

Sampling

Biometry and leaf sampling

Tree height and basal area of all trees in the Kreinitz experiment were measured in winter 2013/2014 and winter 2016/2017. Woody biomass of the trees was calculated according to Annighöfer et al. (2016) using species-specific factors (Supporting information). Tree growth was calculated as the relative increase of the above-ground woody biomass between the two measurement periods. This method suggested negative growth values for six individuals. While negative growth is not implausible (Pastur et al. 2007), e.g. owing to die-back of the main stem and thus decline in tree height, we cannot rule out that this is a result of measurement errors. However, we decided not to remove these values from the dataset as suggested by Pastur et al. (2007) and Sheil et al. (2016), because in sum, negative and positive measurement errors can be assumed to cancel each other out. Therefore, selectively removing negative growth values might add a significant bias to the dataset (Sheil et al. 2016).

We applied multiple methods to calculate tree growth, in order to answer the question of how dead trees would influence plot level performance. The mortality rate of the trees does not necessarily correspond to the productivity of the forest, because even a high mortality might be compensated for by increased growth of the surviving trees (Guerrero-Ramírez et al. 2017).

First, we calculated the 'absolute growth on plot level' expressed as increase of woody biomass in kg between the surveys. The absolute growth refers to the difference of the sum of the woody biomasses of all trees of a plot that were alive during the particular survey. Thus, the trees that died between the surveys (140 out of 2660 individuals) were considered as part of the total woody biomass during the first but not the second survey.

Second, we calculated the 'relative growth on plot level' expressed as relative increase of woody biomass in relation to the first survey. The relative growth refers to the difference of the sum of the woody biomasses of all trees of a plot divided by the woody biomass of the first survey. In this case, the woody biomass did not contain trees that were not alive during both surveys.

Finally, we calculated the 'relative growth on individual level' analogue to the calculation on the plot level. Here, the relative growth refers to the difference in woody biomasses for each tree, divided by that tree's' woody biomass of the first survey. This calculation also did not include trees that were not alive during both surveys.

Leaf sampling took place in July/August 2017. A subset of 283 individuals (48 in monocultures, 83 in two species mixtures, 81 in three species mixtures, 59 in five species mixtures and 12 in six species mixtures) was selected for leaf sampling. For each tree, up to five sampling points were chosen, which were evenly distributed along the outer crown of the tree. At each sampling point up to eight fully developed leaves without visible damage were harvested (total sample size = 3656 leaves), sealed in moist plastic bags and stored cold until further analysis on the same day.

Light measurement

At each sampling point we took light measurements directly above the subsequently sampled leaves using an LI-1400 data logger in combination with a LI-190SA quantum sensor. As a reference, a second identical setup was placed outside of the experiment, exposed to the open sky. Light was measured as the photosynthetic active radiation (PAR; 400–700 nm) expressed in µmol s^{-1} m^{-2}. The relative light availability was calculated as the quotient of both values (PAR sampling point/PAR open sky). In each tree, the increase of relative light availability with measurement height was considered to follow the Lambert-Beer law (as demonstrated by Vose et al. (1995) or Kitajima et al. (2005)) and was therefore fitted as an exponential curve according to Eq. 1:

$$y = c \cdot a^{x} \qquad [1]$$

where y is the relative light availability at the measuring point, c (the intercept of the fitted curve with the y-axis) is the relative light availability at the lowest part of the tree crown, x (the exponent of the fitted curve) is the relative height in the crown and a (the basis of the fitted curve) expresses the slope of the light/height curve. The latter value describes the light distribution within the crown. The value of a should be higher in a scenario where a tree captures the majority of the available light in the top of the crown and low if the light interception is evenly distributed along the crown. We consider this value (i.e. the steepness of the light gradient) as an indicator for the light extinction coefficient of an individual tree. See Supporting information for visualisation of the light curves.

Leaf trait analysis

We analysed all leaves for SLA, LDMC, CN ratio, leaf C, leaf N, leaf Mg, leaf Ca and leaf K as these leaf traits are related to photosynthesis or leaf structure, which allows a ranking on the acquisitive-conservative axis of the LES. Leaf traits were analysed via NIRS using an ASD FieldSpec 4 WideRes Each leaf was scanned threefold using a contact probe The scans recorded relative reflectance values for each spectral region between 350 nm and 2500 nm. We selected a subset of 152 leaves for NIRS prediction model development and analysed them with conventional means (see Supporting information for reference methods). We created individual prediction models for each leaf trait using R (ver. 4.0.3; www.r-project.org) and a modified version of the 'plantspec' package (ver. 1.0; Griffith et al. (2019)). Our modification included a further optimization of the calibration process, which aimed at improving prediction model accuracy at the cost of longer calculation time. In particular, we added a loop that repeatedly re-iterated randomly selected combinations of spectral bands and mathematical pre-treatments until the most precise prediction model was found (Proß, 2023). We validated the prediction models via test-set validation using one-third of the samples (randomly drawn) as validation samples and two-thirds as calibration samples. The validation results indicate model accuracy (Supporting information). Subsequently, we applied the prediction models to all scans and averaged them at the leaf level to reduce instrument noise

Statistical analysis

All statistical analyses were conducted using R (ver. 4.0.3; www.r-project.org). All linear mixed effects models were fitted by using the 'lmer' function in the 'lmerTest' package (ver. 3.1-3; Kuznetsova et al. (2017)). These models were analysed using type three sum of squares in the analysis of variance with Satterthwaite approximation for degrees of freedom.

Growth as a function of tree species richness

We fitted two linear mixed effects models to assess the influence of tree species richness on plant growth at the plot level (H1a). The first model used the absolute increase in plot level woody biomass between the two surveys as response variable, and tree species richness as explanatory variable. The second model was fitted with the plot mean of the relative increase in woody biomass of each tree in a plot. Both models also contained the block and the species composition as nested random factors. Thereby, the species composition accounts for different species combinations that have been established at a given level of tree species richness.

To assess the influence of tree species richness on plant growth at the individual tree level (H1b), the relative increase in woody biomass was calculated for each tree. A linear mixed effects model was fitted that contained the relative increase in woody biomass of every tree as response variable, and a numeric value for the tree species richness as a fixed effect. The model also accounted for the identity of the tree species as a random effect crossed with another nested random effect which consisted of block, species composition and plot, orthogonal to the first random effect. In addition, the same model was fitted for a subset of the trees, excluding all coniferous trees.

Within-individual coordination of leaf traits

We conducted a principal component analysis (PCA) using all measured leaf level traits. As this PCA was strongly affected by the differences in species mean values (Supporting information), we calculated a second PCA by centring the leaf level traits, which was achieved by subtracting the species mean value from each observed value of that species and dividing the result by the trait's SD of each species. For broadleaved trees, both PCAs captured the LES on the first axis (results), and we used the scores for each leaf on the first PCA of the centred PCA axis as proxy for the position within the LES. To obtain trait values for the whole tree, all single leaf values were aggregated per tree using the arithmetic mean (hereafter 'mean trait scores'). The trait variation of each individual tree was calculated as the SD of the trait value of every leaf of the tree's mean. However, for the coniferous trees, the PCA axes did not capture the LES, which is why we were unable use an axis score as a proxy for the position within the LES, as well as its SD as proxy for the leaf trait variation. Consequently, we removed the conifers from the analyses that are based on these values.

Traits as a function of tree species richness and light extinction coefficient

To analyse the effect of tree species richness and the light extinction coefficient on mean trait scores and leaf trait variation, we fitted two separate linear mixed effects models, using either the mean values or the SD of the scores of leaf traits on the first PCA axis as response and both tree species richness and the light extinction coefficient as predictors. As above, both models included tree species identity as a random effect crossed with another nested random effect which consisted of block, species composition and plot. Both models were fitted without interactions to fully match the structure of the SEM (below). Furthermore, both models were calculated only with data from the four deciduous tree species, excluding the two coniferous species.

Influence of tree species richness, mean trait scores, leaf trait variation and the light extinction coefficient on individual tree productivity

To address the question whether individual tree productivity is dependent on tree species richness, the light extinction coefficient, mean trait scores or leaf trait variation, we fitted a linear mixed effects model that included tree growth as response variable and all four fixed effects simultaneously. In contrast to the model fitted for H1b, only broadleaved trees were included for which traits were measured. This model had the same random structure as the mixed models described above and also did not include interactions.

Mean trait scores and leaf trait variation as mediators and light as a covariate for the BPR

A SEM was fitted using the 'piecewiseSEM' package (ver. 2.1.2; Lefcheck and Freckleton (2015)). The model contained broadleaved trees with tree species richness as an exogenous variable, and light extinction coefficient, mean trait scores, leaf trait variation and the relative tree growth at the individual level as endogenous variables (see Supporting information for the path diagram and model description). Tree growth was explained by species richness, light extinction coefficient, mean trait scores and leaf trait variation; the leaf trait variation was explained by species richness, light extinction coefficient and mean trait scores; the mean trait scores were explained by species richness and light extinction coefficient; and finally, light extinction coefficient was explained by species richness. As in the models above, tree species identity as a random effect crossed with another nested random effect which consisted of block, species composition and plot. Additionally, separate SEMs were fitted for each species using the same model structure but omitting species identity as a random factor.

Results

Relationship of tree growth and tree species richness

The analysis of all trees of the Kreinitz experiment did not show any significant relationship between tree growth and tree species richness in the timeframe of three years. At the plot level, there was no relationship between tree species richness and tree growth, neither with respect to absolute (Fig. 1a), nor relative tree growth (Fig. 1b). Similarly, we found no significant relationships at the individual level, which however, in contrast to our expectation, showed a marginally significant negative slope (Fig. 1c). Removing the coniferous trees from the analysis (Fig. 1d), did not affect this relationship.

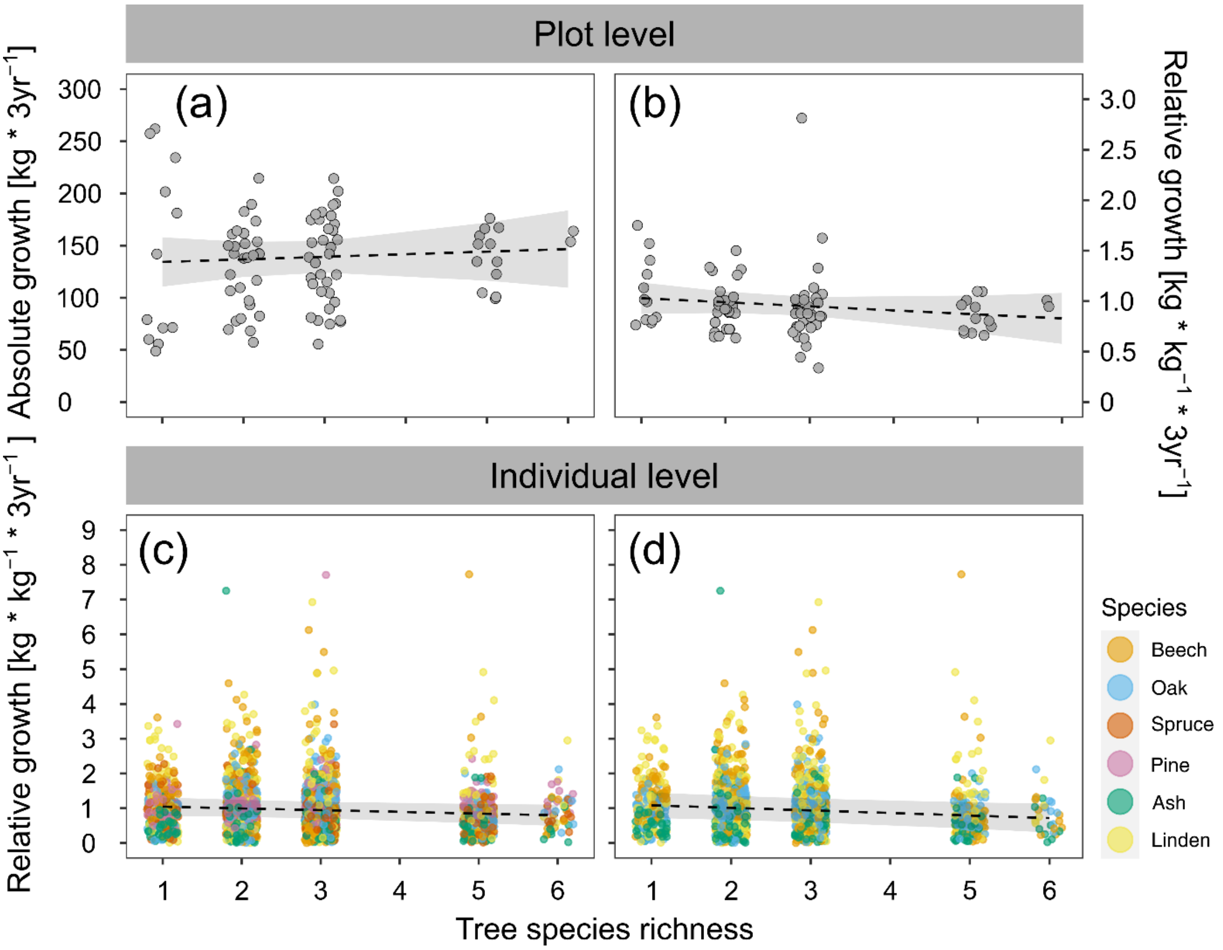

Figure 1: . Growth as a function of tree species richness, at the plot level (a–b) and at the level of individual trees (c–d). All plots share the same x-axis that indicates tree species richness. Grey dots indicate individual plots (a–b), coloured dots indicate individual trees (c–d). Dashed lines are based on the predictions of the underlying models (Table 1 for the results of the models), and the grey ribbon indicates the 95% confidence interval of these models. (a) Absolute increase in plot level woody biomass ($p = 0.955$). (b) Relative increase in plot level woody biomass ($p = 0.445$). (c) Relative growth at the individual level ($p = 0.099$). (d) Relative growth at the individual level excluding spruce and pine ($p = 0.055$).

Coordination of leaf traits

The PCA of the leaf traits is shown in Fig. 2a. The trait space of the conifers pine P. sylvestris and spruce P. abies overlapped, but was mostly separated from broadleaved trees. The trait space of ash F. excelsior only partially overlapped with linden T. cordata, while there was hardly no overlap with oak Q. petraea and beech F. sylvatica. The strongest overlap showed oak and beech, partly overlapping with linden as well. Separate analyses for broadleaved trees (Fig. 2b) and conifers (Fig. 2c) revealed vastly different relationships between the leaf traits for these groups (see Supporting information for single species analyses). For the broadleaved trees (Fig. 2b) all cations, SLA and leaf P showed positive loadings with the first PCA axis, whereas LDMC, leaf N and leaf C had negative loadings. Leaf N and SLA were positively and CN ratio was negatively aligned with the second PCA axis. In contrast, for the conifers (Fig. 2c), leaf N, lLeaf C and leaf Mg showed negative loadings with the first PCA axis, whereas LDMC, SLA, CN ratio, leaf P, leaf Ca and leaf K had positive loadings. Regarding the second PCA axis, LDMC, leaf C, leaf Mg and leaf Ca were positively aligned while

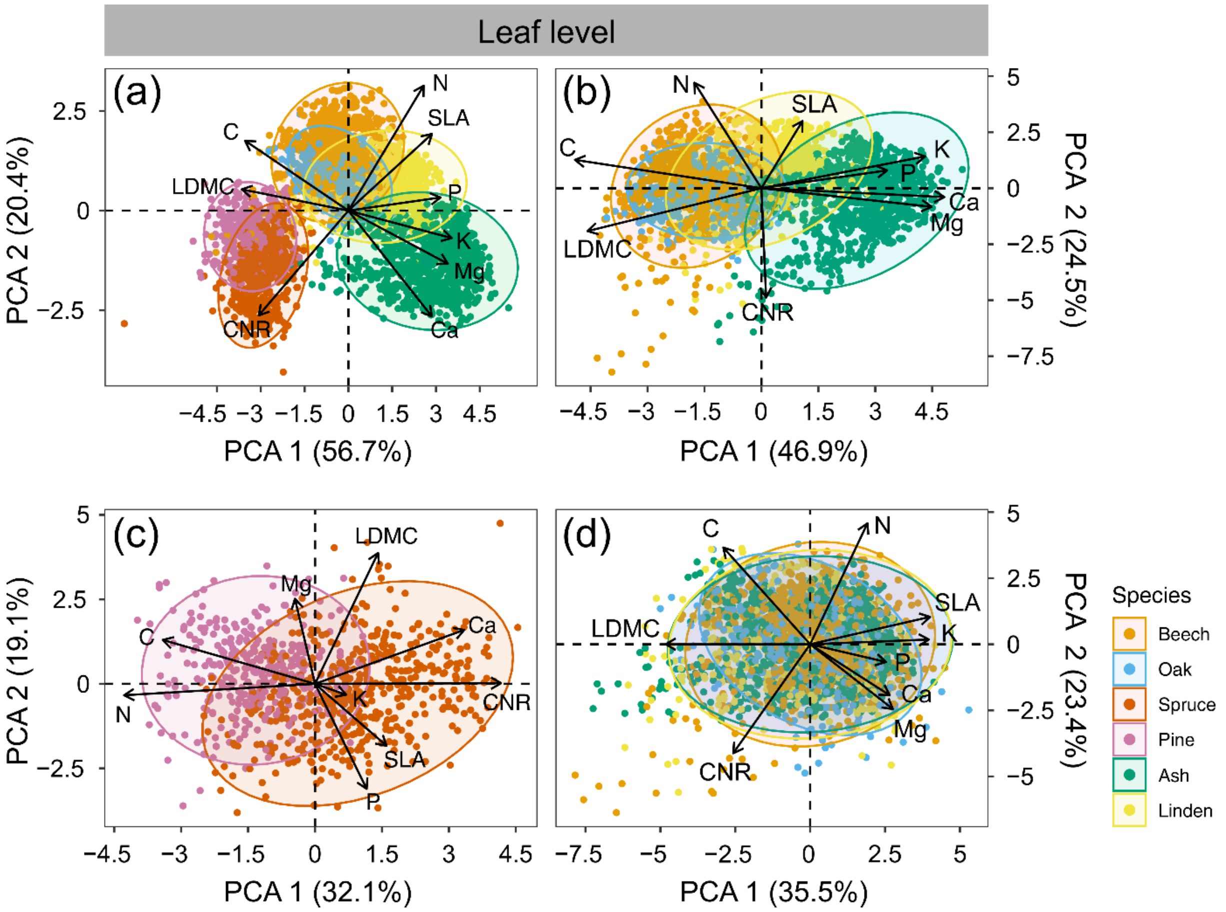

Figure 2: Principal component analysis (PCA). First versus second axes. Dots indicate individual leaves, coloured by species. Circles include 95% of the data points of each species. (a) Unscaled version including all species. (b) Unscaled version including only broadleaved species. (c) Unscaled version including only conifers. (d) Scaled version including only broadleaved species. Leaf traits were centred on the species mean trait values before conducting the PCA. LDMC, leaf dry matter content; SLA, specific leaf area; CNR, carbon-to-nitrogen ratio.

SLA, leaf P and leaf K were negatively aligned. When leaf traits of the broadleaved trees were centred on the species mean trait values (Fig. 2d), the amount of variation explained by axis 2 remained almost unchanged, while that of axis 1 decreased from 46.9 to 35.5%, i.e. by approximately one-quarter, which is the amount of variation only caused by species identity. The leaf traits still showed correlations with the first PCA axis which were similar to the previous PCA. The cations, SLA, leaf P and, leaf N showed positive loadings, and LDMC, leaf C and CN ratio showed negative loadings on the first PCA axis. The almost congruent ellipses indicated a comparable amount of variation within species, with the notable exception of oak (blue ellipse) with a slightly lower variation compared to that of the other species.

Light, Diversity and traits

We found that, with increasing tree species richness, mean leaf trait scores of the first axis of the centred PCA (Fig. 2b) increased. This indicated higher values on the LES,

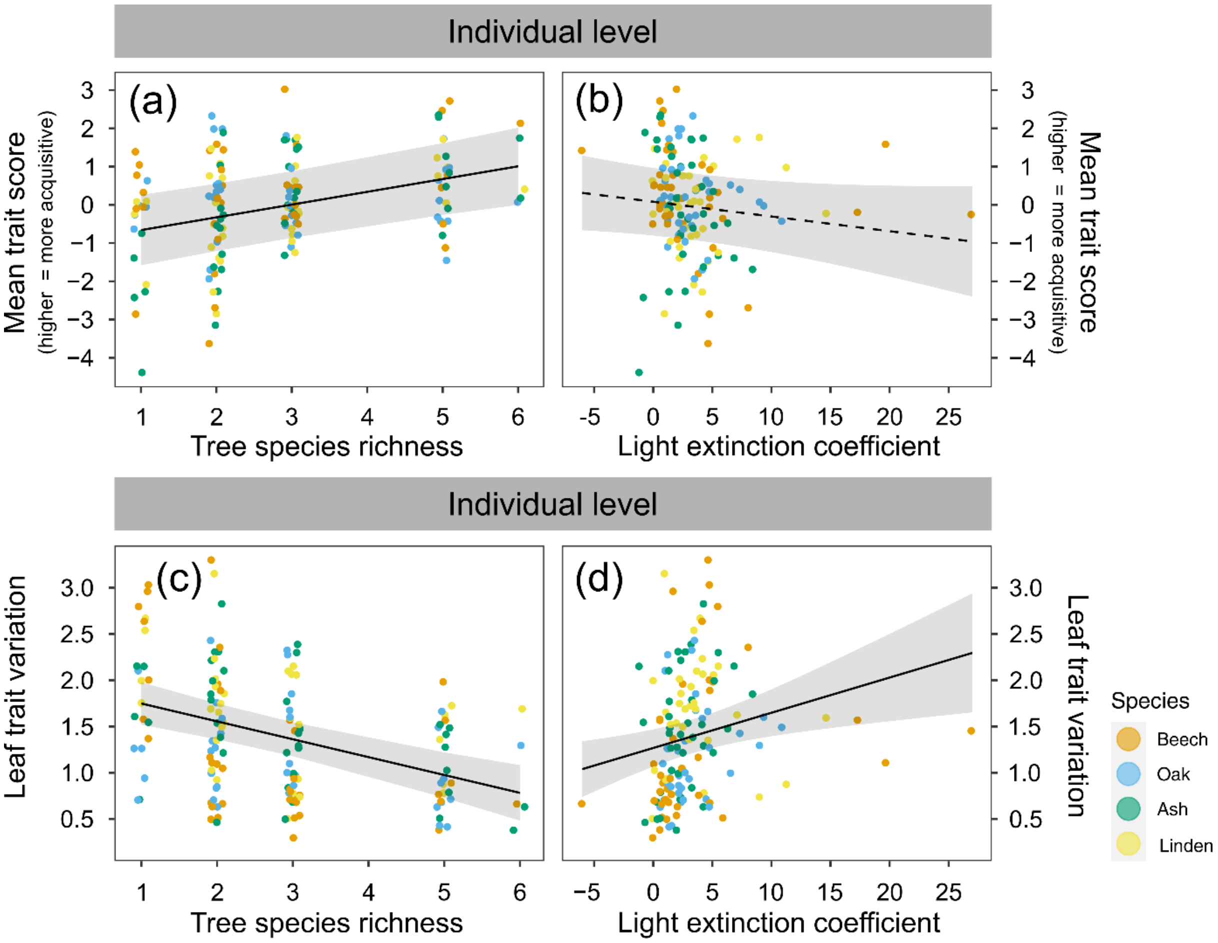

Figure 3: Effects of tree species richness and light extinction coefficient on mean trait scores of the first principal component analysis (PCA) axis and leaf trait variation expressed as the SD of these scores. Lines are based on the predictions of the underlying model, solid lines indicate significant effects and the dashed line indicates a non-significant effect (Table 1 for the results of the models). The grey ribbons indicate the 95% confidence interval of these models. Dots indicate individual trees, coloured by species. (a) Mean trait score versus tree species richness ($p < 0.001$). (b) Mean trait score versus light extinction coefficient ($p = 0.199$). (c) Leaf trait variation versus tree species richness ($p < 0.001$). (d) Leaf trait variation versus light extinction coefficient ($p = 0.004$)

and thus, more acquisitive leaves (Fig. 3a);, whereas the SD decreased, which indicated lower trait variation along this axis, and thus, less trait adjustments of leaves (Fig. 3b). The light extinction coefficient had no significant effect on the mean scores (Fig. 3c) but a positive influence on leaf trait variation (Fig. 3d).

Influence of mean trait scores, leaf trait variation, light extinction coefficient and tree species richness on tree growth

Figure 4 shows the model predictions of relative growth of the individual trees as responses to mean trait scores (Fig. 4a), leaf trait variation (Fig. 4b), tree species richness (Fig. 4c) and light extinction coefficient (Fig. 4d). Combining these four predictors in a single model revealed that an increase in tree growth was primarily driven by leaf trait variation along the LES.

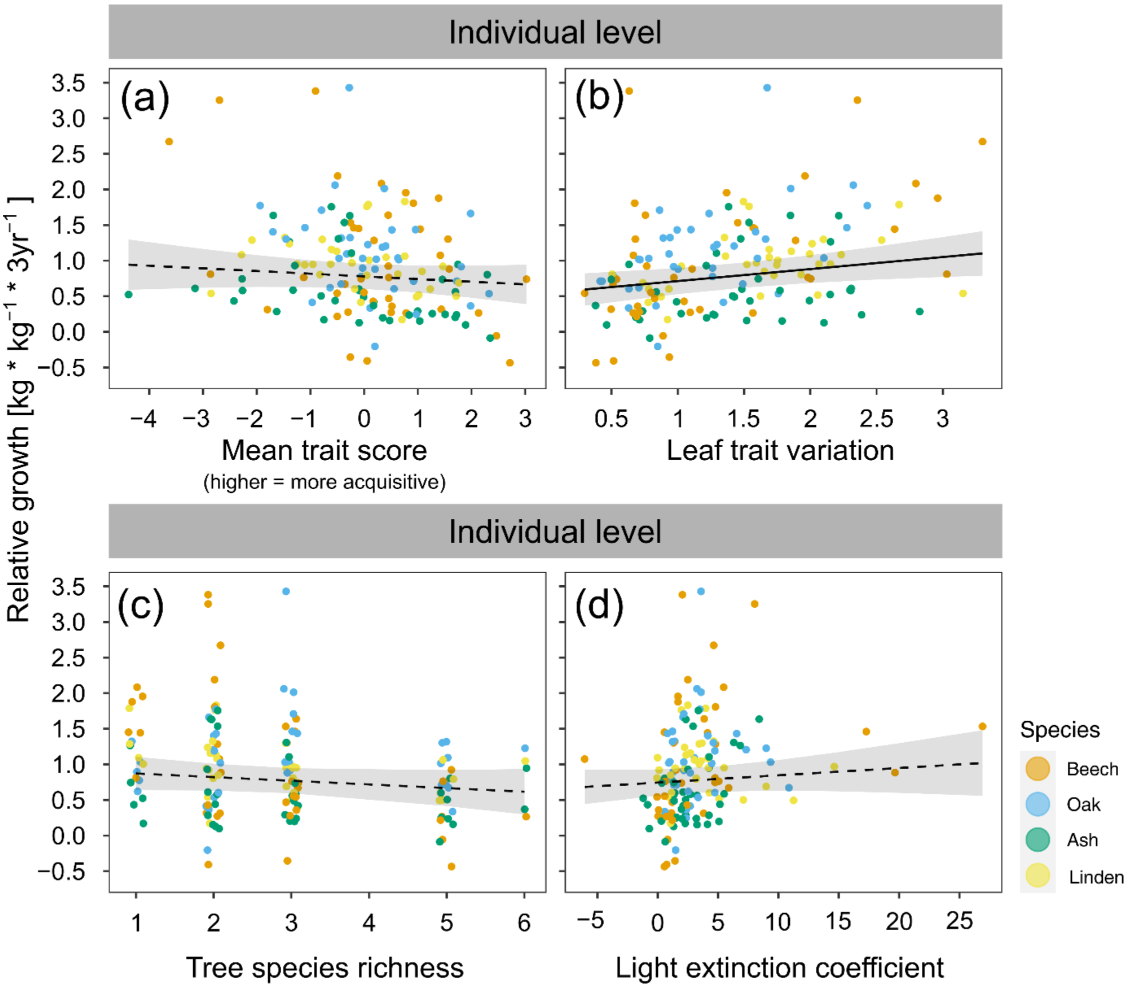

Figure 4: Relative growth as a function of mean trait scores, leaf trait variation, tree species richness and light interception efficiency, respectively. All plots share the same y-axis (relative growth of individual trees over 3 years). Lines are based on the predictions of the underlying model including all predictors (see Table 1 for the results of the models). The solid line indicates a significant effect (4b, p= 0.023), the dashed lines indicate non-significant effects (4a, p=0.212; 4c, p=0.287 4d, p=0.336). The grey ribbons indicate the 95% confidence interval of the predictions. Dots indicate individual trees, coloured by species.

Mediators and covariate for the BPR

The results of the SEM (Fig. 5) confirmed the key role of leaf trait variation as mediator in the BRP. Whereas leaf trait variation decreased with tree species richness, relative tree growth increased with leaf trait variation, which resulted in a zero net effect of tree species richness on tree growth. This relationship was further modified by the mean leaf trait scores of the first PCA axis, which increased with tree species richness (i.e. leaf traits shifted to more acquisitive values), and which themselves reduced leaf trait variation (i.e. trees with a more acquisitive trait scores showed less trait variation). As mean leaf trait scores had no significant direct effect on relative growth, the BPR remained unaffected by this indirect pathway. Finally, the light extinction coefficient did not depend on tree species richness, but a greater light extinction coefficient increased leaf trait variation, which also indirectly contributed to enhanced tree growth. Applying the same SEMs to the single species resulted in a loss of most of the observed significant relationships (Supporting information), which was probably a result of the much lower statistical power with using much fewer observations. An exception was the negative impact of mean leaf trait scores on leaf trait variation, which was consistent across all single species models.

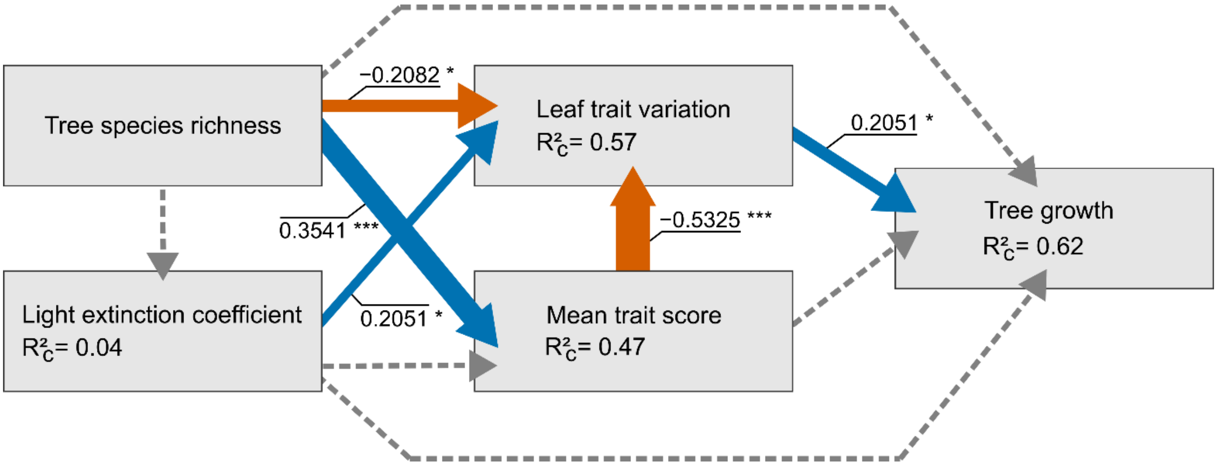

Figure 5: Path diagram derived from a structural equation model (SEM) describing the influence of plot tree species richness, light extinction coefficient, mean trait scores on the first PCA axis and, leaf trait variation (SD of the scores) on tree growth. Boxes represent measured variables, arrows represent directional relationships among variables. Solid arrows indicate significant relationships, dashed arrows indicate nonsignificant relationships (*** = $p < 0.001$, * = $p < 0.05$). Orange arrows indicate positive relationships, blue arrows indicate negative relationships. Width of the arrows is scaled according to the standardized regression coefficient, also indicated by the adjacent numbers. R^2c indicates the conditional coefficient of determination based on both the fixed and the random effects of the models. When removing all non-significant relationship, global goodness-of-fit was fulfilled ($C = 11.961$; 8 df; $p = 0.153$).

Table 1: Anova results on the different hypotheses. (A) Results of four separate models explaining tree growth as a function of tree species richness. (B) Results of two separate models explaining mean trait scores and leaf trait variation as functions of tree species richness and light extinction coefficient. (C) Results of a model explaining tree growth as a function of mean trait scores, leaf trait variation, tree species richness and light extinction coefficient jointly. All sums of squares (Sum. sq.), mean squares (Mean sq.), numerator degrees of freedom (numDF), denominator degrees of freedom (denDF), F-values and p-values refer to type III *A*nova results. Significant results ($p < 0.05$) are highlighted in bold font.

Table 1A

Response	Predictor	Sum sq.	Mean sq.	numDF	denDF	F-value	*p*-value
Absolute increase in plot level woody biomass	Tree species richness	10×10^{10}	10×10^{10}	1	45.39	0.003	0.955
Relative increase in plot level woody biomass	Tree species richness	0.024	0.024	1	39.77	0.592	0.445
Relative growth at individual level	Tree species richness	2.206	2.206	1	87.49	2.769	0.099
Relative growth at individual level (excl. conifers)	Tree species richness	4.057	4.057	1	84.63	3.780	0.055

Table 1B

Response	Predictor	Sum sq.	Mean sq.	numDF	denDF	F-value	*p*-value
Mean trait scores	Tree species richness	16.898	16.898	1	55.47	16.483	< 0.001
	Light interception efficiency	2.513	2.513	1	131.69	2.451	0.119
Leaf trait variation	Tree species richness	8.094	8.094	1	46.24	24.284	< 0.001
	Light interception efficiency	2.654	2.654	1	141.66	8.290	0.004

Table 1C

Response	Predictor	Sum sq.	Mean sq.	numDF	denDF	F-value	*p*-value
Relative growth at individual level	Leaf trait value	0.129	0.129	1	132.88	1.100	0.296
	Leaf trait variation	0.712	0.712	1	124.38	6.069	0.015
	Tree species richness	0.166	0.166	1	61.84	1.416	0.238
	Light interception efficiency	0.147	0.147	1	95.20	1.253	0.265

Discussion

Our study investigated the influence of tree species richness on tree growth in a biodiversity-ecosystem functioning experiment over a period of three years. Most strikingly, we were able to identify a connection between these two factors – albeit only for broadleaved trees and not for conifers. While we did not encounter a direct link between tree richness and productivity, we were able to identify leaf trait variation as the key mediating factor. An increase in biodiversity led to a decrease in leaf trait variation – but an increase in tree growth was caused by an increase in leaf trait variation (Fig. 5). Thus, the negative effect of tree richness on leaf trait variation cancelled out the positive effect of leaf trait variation on growth, which in summary resulted in the absence of a significant BPR.

Relationship between tree species richness and tree productivity

The experiment failed to confirm our hypothesis of a positive BPR in the particular study period, but nonetheless provided important insights on the mediators of this relationship. We did not encounter a significant BPR at the plot level nor at the level of individual trees, neither with including or excluding dead trees, nor when based on the full set of all six species, nor when conifers were excluded.

While a positive BPR has been largely confirmed for natural forest ecosystems (Liang et al. 2016), several studies in planted forest diversity experiments reported a non-significant BPR, as summarized by Kambach et al. (2019). A non-significant BPR might be brought about, for example, by strong differences in species-specific growth performances (Nguyen et al. 2012). Additionally, Tobner et al. (2016) argued that a high initial nutrient availability might reduce a potential biodiversity effect on growth. Finally, Guo and Ren (2014) also argued that a potential BPR might not be visible in the early stage of forest development. These mechanisms might also influence the Kreinitz experiment.

Regarding the differences in species performance, a potential factor in the Kreinitz experiment could be that here all ash trees showed signs of infection with *Hymenoscyphus fraxineus*, which is a fungus responsible for the large-scale ash dieback in central Europe. However, despite showing the lowest growth rate among all tree species, removing *F. excelsior* from the analysis had no effect on tree growth (Supporting information).

Similarly, a high soil nutrient availability could potentially play a role for the Kreinitz experiment, as it was established on former agricultural land which had obviously received large amounts of organic fertilizer (Landgraf 2001). A potential positive biodiversity effect on tree growth should be at least partially based on complementary usage of belowground resources (Houle et al. 2014, Teste et al. 2014). However, if soil nutrients are most likely not a limiting factor for tree growth, as might be the case for the Kreinitz experiment, nutrient-use niche partitioning as potential driver for a positive BPR could not come into play.

Finally, the Kreinitz experiment might have been in a too early stage of development to find a positive BPR. It was established in 2005 and the trees were at the time of the first and second measuring, at 8 and 11 years old. As BPR increase with time (Huang et al. 2018), it might be too early to detect significant effects. In addition, Guo and Ren (2014) pointed out that tree species differ in their speed of development, thus masking a potential BPR at this stage of the experiment. However, the fact that we did not find a direct link between biodiversity and productivity does not mean that diversity effects did not play a role. There were several important mediators for the BPR that were driven by tree richness.

Influence of the light extinction coefficient and tree species richness on leaf traits

Coordination of leaf traits at the within-individual level

The results of the PCA demonstrate a considerable amount of intraspecific trait variation (ITV), as proposed for example by Albert et al. (2012) and Siefert et al. (2015). In our case, all species show a comparable amount of ITV (Fig. 2), which is consistent with other studies in forest ecosystems (Fyllas et al. 2020, Schmitt et al. 2020). This also includes F. excelsior (Fig. 2d), despite its infection with *H. fraxineus*. As the infection does not appear to affect the ITV, we would assume that it also did not affect the role of ITV as mediator. In our case, the trait alignment with the first PCA axis also reflects the conservative/acquisitive nature of the leaf traits in broadleaved trees. The acquisitive traits SLA, leaf P and the cations aligned closely with the first PCA axis, which is consistent with previous studies showing similar relationships at the species level (Lin et al. 2020, Jiang et al. 2021). Furthermore, the conservative traits LDMC and leaf C were negatively aligned with the first PCA axis, which is also in agreement with previous studies (Lin et al. 2020, Jiang et al. 2021).

Influence of tree species richness on leaf traits

We observed that with increasing tree species richness, leaf trait variation decreased and leaf traits shifted to more acquisitive values, which provides strong support for the first part of our second hypothesis (H2a). The decrease of leaf trait variation with increasing tree species richness is in agreement with Proß et al. (2021) who reported a similar relationship. Thus, mixing different species allows leaves to stay more closely at the tree's mean values. In contrast, leaves of trees growing in monocultures show higher variation further away from the mean to increase light capture.

Furthermore, our results also confirm those of Davrinche and Haider (2021), who found a shift towards more acquisitive leaf traits in more diverse forest communities. A possible explanation for this observation is, that more diverse communities have a vastly different light regime compared to that of monocultures (Sapijanskas et al. 2014), and leaf traits might shift to more acquisitive values in response to inner canopy light conditions (Iio et al. 2005). However, a tree species richness effect on leaf traits can also occur independently of the diversity-light interaction (Benomar et al. 2011), for example as a response to differences in belowground resource use (Richards et al. 2010).

Influence of light on leaf traits

We could only partly confirm our second hypothesis that a higher light extinction coefficient results in shifts in mean trait scores and a higher leaf trait variation (H2b). While we encountered support for the latter (Fig. 5), we have to reject the former part of the hypothesis. Our finding that a higher light extinction coefficient results in a stronger leaf trait variation is also supported by reports in the literature (Niinemets et al. 2015). The different responses of mean trait scores and leaf trait variation are consistent with results from Herrera et al. (2015) who demonstrated that, for the herb *Helleborus foetidus*, within-individual leaf trait variation was largely independent of plant mean trait scores. Our findings suggest that individual trees broaden their trait space by diversifying their leaf traits, rather than shifting it to more acquisitive trait scores as a response to changes in light availability.

In the densely planted Kreinitz experiment, crown space could be the most limiting factor for tree growth. The strong competition for light might facilitate the optimisation of crown space for all individuals (Pretzsch 2014). For an individual tree, a densely packed, narrow crown would result in a steep light interception curve and consequently a steep gradient in leaf traits. A tree with flexible leaf traits would have the benefit of a larger potential crown length that can be used for light capture. Across the whole tree, a directional shift of the leaf trait might not occur if the light conditions for the average leaf remained the same, but leaves expanded a steeper light gradient in both directions, either becoming more acquisitive at one end and/or more conservative at the other end of the light gradient

Influence of mean trait scores, leaf trait variation, tree species richness and light extinction coefficient on tree growth

When we analysed the effects of the leaf's position on the LES axis, leaf trait variation, tree species richness and the light extinction coefficient on tree growth, we found that leaf trait variation was the only significant driver of tree growth (Fig. 5). The causal explanation for this finding would be that an increased variability of LES traits allows the tree to more effectively exploit the light gradient. We are not aware of any other study that was able to demonstrate this direct link between increased leaf trait variation and tree growth. However, it is equally remarkable that a shift of the mean trait scores towards higher acquisitiveness did not have a similar effect on tree growth, as such a relationship was demonstrated before (Poorter and Bongers 2006, Chaturvedi et al. 2011, Li et al. 2017). A possible explanation could be that a shift towards higher acquisitiveness comes at the cost of lower leaf longevity at the within-individual level and higher susceptibility to herbivore and pathogen attack. However, evidence for this assumption is lacking so far. Anderegg et al. (2018) reported that leaf longevity and SLA are positively correlated within species but it is unclear to which degree this is brought about by genetic differentiation within species or by phenotypic plasticity. In particular, the relationship between leaf longevity and SLA within individuals is unknown. If such trade-offs exist, they might offset any positive effects of leaf trait shifts on growth.

Leaf trait variation is a mediator and light is a covariate for the BPR

We observed that the leaf trait variation mediates the influence of tree species richness on tree growth. In addition, the light extinction coefficient modified this interaction by increasing the leaf trait variation. In contrast, the leaf position on the LES axis did not influence tree growth, which is why we can only partially confirm our fourth hypothesis. We interpret these observations as a mechanism to adjust to changes in the available trait space, based on the limiting similarity theory (MacArthur and Levins 1967). In monocultures, the similarity between individuals could be a limiting factor for tree growth, as individuals of the same species occupy the same trait space (Violle et al. 2012). However, it seems that trees partially compensate for this negative effect of limiting similarity on growth by diversifying their leaf traits. In plots with higher tree species richness, the different species might be already sufficiently diverse regarding their leaf traits to show optimal growth. This would be compatible with observations by Benavides et al. (2019), who observed a reduction in species level trait space as a reaction to increased tree species richness. However, in order to reach the upper canopy faster, trees might shift their traits towards more acquisitive values (Pellis 2004). In this scenario, the majority of the trees might actually grow close to their optimal growth rate, which would explain the absence of a clear diversity effect on growth.

In conclusion, the absence of a positive BPR in forests does not mean that there is no relationship between tree richness and tree growth. It seems that tree richness operates both through increased acquisitive trait scores and leaf trait variation, two processes that can cancel out each other and result in the absence of a significant effect of tree richness on productivity. These two opposing mechanisms might be the reason for the absence of positive BPRs in the literature. However, unless we have more data on the within-tree trait variation, we can only speculate whether these findings only apply to the unique situation of the Kreinitz experiment in Germany or whether they offer a general explanation for the negative (Firn et al. 2007) or non-significant BPR (Nguyen et al. 2012, Staples et al. 2019) described in the literature. A plausible mechanism would be that the direction of the BPR depends on which factor is more strongly influenced by the tree species richness. A scenario where the tree species richness effect dominates the leaf trait variation could result in a negative BPR. Conversely, if the species richness effect on leaf traits predominates, a positive BPR would be more likely. Which of these factors is more strongly influenced by tree species richness might be dependent on several other factors. In any case, our results point to the importance of within-individual leaf trait variation as one important moderator in BPRs.

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Data availability statement

Data are available from the Zenodo Digital Repository:
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Supporting information

Tested path diagram

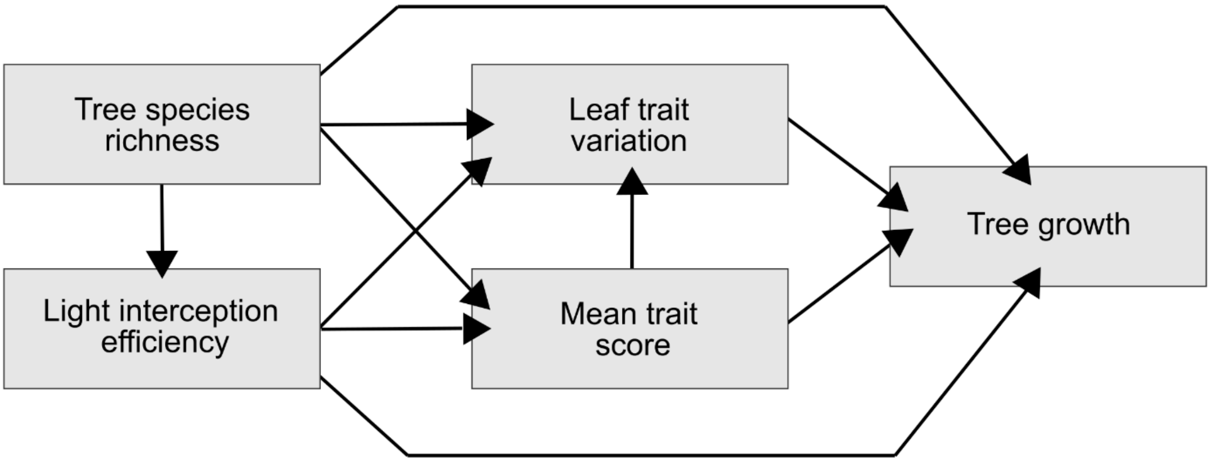


Figure S1: tested path diagram of the structural equation model. Tree growth is explained by species richness, light interception efficiency, mean trait scores and leaf trait variation, the leaf trait variation is explained by species richness, light interception efficiency and mean trait scores, mean trait scores are explained by species richness and light interception efficiency, light interception efficiency is explained by species richness.

The SEM is fitted in R (version 4.0.3; The R core Team, 2020) using the packages 'piecewiseSEM' (Version 2.1.2; Lefcheck and Freckleton, 2015) and lmerTest (Version 3.1-3; Kuznetsova et al. (2017) using the following equations.

```
psem(
lmer(Growth      ~ TSR + Light + Trait value + Trait SD + (1 | Block / Comp / Plot) + (1 | Species)),
lmer(Trait SD    ~ TSR + Light + Trait value            + (1 | Block / Comp / Plot) + (1 | Species)),
lmer(Trait value ~ TSR + Light                          + (1 | Block / Comp / Plot) + (1 | Species)),
lmer(Light       ~ TSR                                  + (1 | Block / Comp / Plot) + (1 | Species)))
```

Thereby 'Growth' refers to the increase in woody biomass, 'TSR' refers to the tree species richness of the plot, 'Light' refers to the light extinction coefficient, 'Trait value' refers to the trait score of the first PCA axis, 'Trait SD' refers to the standard deviation of the trait value. Furthermore, the models contain the block, species composition (Comp), plot and species as random factors

Design of the Kreinitz experiment

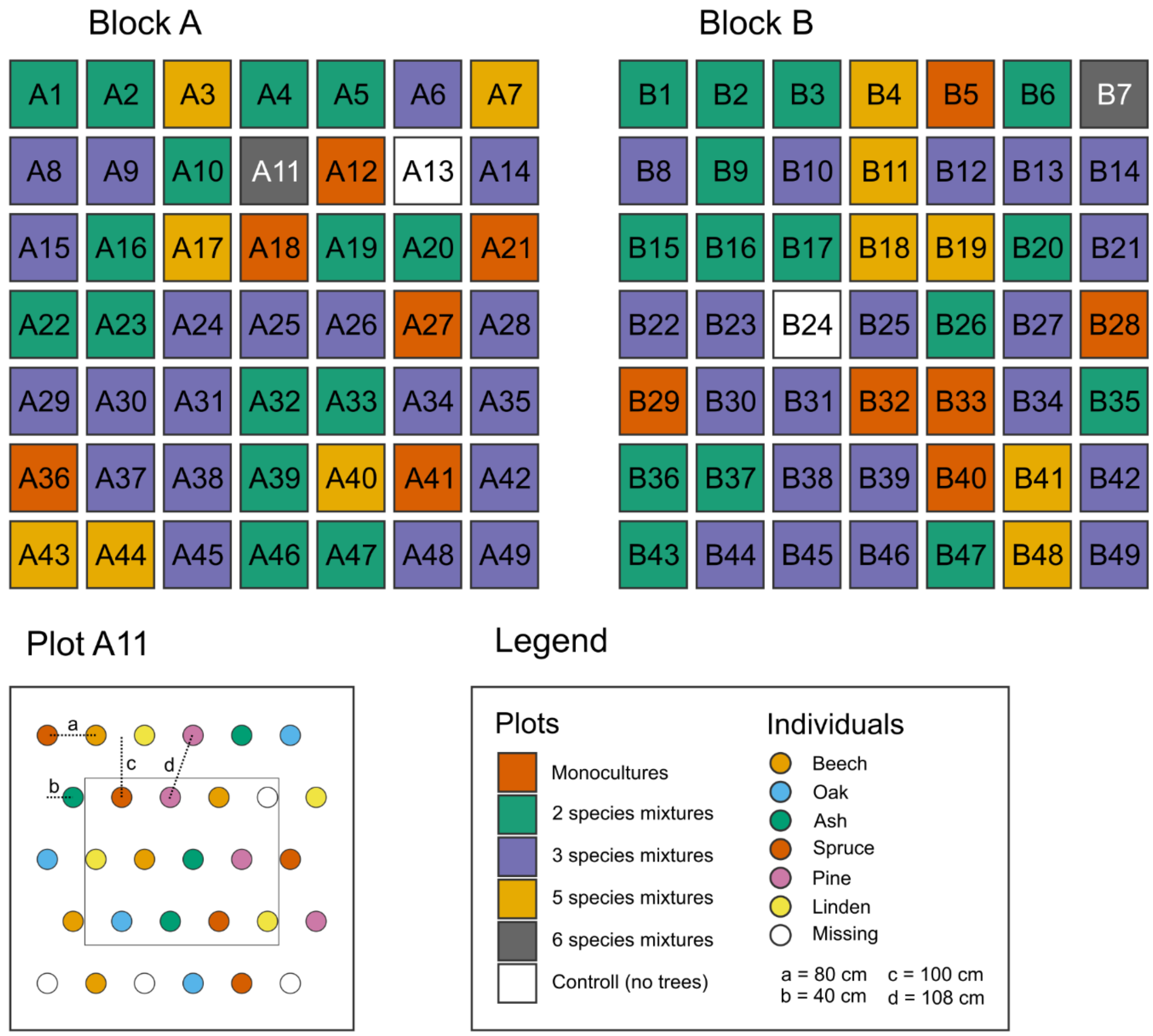


Figure S2: Design of the Kreinitz experiment. The Kreinitz experiment consists of two blocks (block A and block B) which contain 49 Plots each (A1 to A49 and B1 to B49). The Plots are monocultures, two-, three-, five- or six species mixtures as well as control plots without trees. Both blocks contain the same number of each plot but plots are randomly arranged within the blocks. All plots contained originally 30 trees that were planted in a hexagonal pattern. Within the plots, species were randomly arranged in the planting pattern. Plot A11 is shown as representative example: a = horizontal distance between individuals, b = horizontal offset between rows, c = vertical offset between rows, d = diagonal distance between trees. The core area of the plot is marked with an additional rectangle. Only individuals within the core area were sampled.

Estimation of above ground woody biomass

Woody biomass was estimated according to Annighöfer et al. (2016) by first calculating the root collar diameter (RCD) according to

$$RCD = T_{10}D_{10}$$

Whereas D_{10} refers to the tree diameter, measured 10 cm above ground and T_{10} represents the transformation factor for this measurement ($T_{10} = 1.16$). Afterwards, above ground woody biomass (AGB) was calculated according to

$$AGB = \beta 1 \, (RCD^2 \, H)^{\beta 2}$$

Whereas beta 1 and beta 2 refer to species specific correction factors (see below) and H refers to the measured height of the tree.

Table 1: Species specific correction factors according to Annighöfer et al. (2016)

Species	*Beta 1*	*Beta 2*
F. sylvatica	0.62342	0.87409
Q. petreae	0.5274	0.81213
F. excelsior	0.07555	1.07047
P. abies	2.24952	0.76318
P. sylvestris	0.75897	0.85012
T. cordata	0.10615	1.02416

Visualisation of the light/height curves

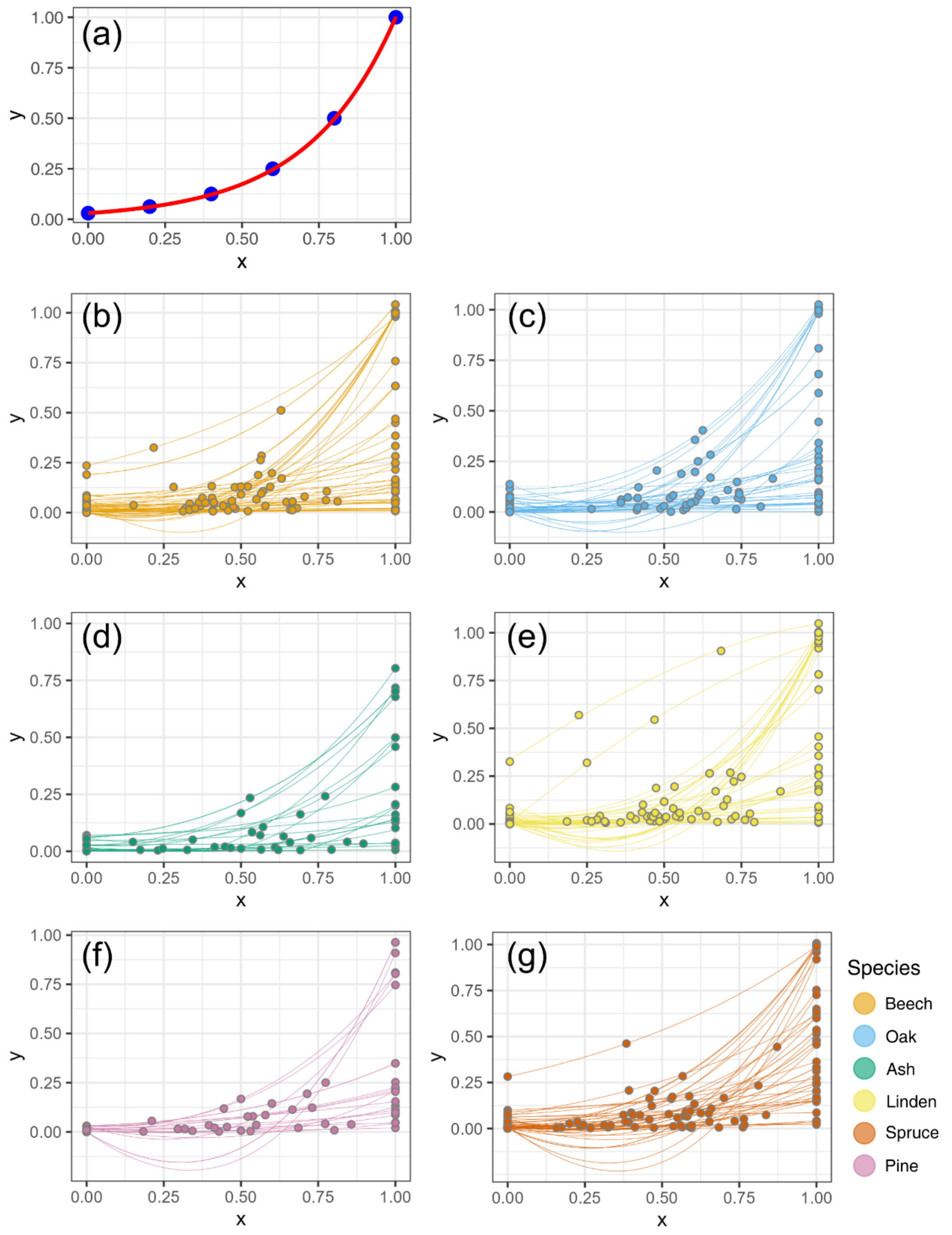


Figure S3: (a): assumed light distribution in a trees' crown following an exponential light increase with increasing height. Blue points indicate example measurements, red line indicates the fitted curve according to the equation:

$$y = c \cdot a^x$$

Where y is the relative light availability at the measuring point, c is the relative light availability at the lowest part of the tree crown, x is the relative height in the crown and a expresses the slope of the light/height curve. (b-g): Lines indicate actual fitted curves for all trees using the same formula. Points indicate measurements, coloured by species.

Reference methods leaf traits

After harvesting, leaves were weighed for leaf fresh mass and scanned for leaf area using a flatbed scanner. Subsequently, all leaf samples were dried for 72 hours at 60°C and weighed again for leaf dry mass. Leaf dry matter content (LDMC) specific leaf area (SLA) were calculated as:

$$\text{LDMC} = \text{leaf dry mass in mg} \,/\, \text{leaf fresh mass in g}$$

$$\text{SLA} = \text{leaf area in mm}^2 \,/\, \text{leaf dry mass in mg}$$

For all subsequent analysis, leaf samples were ground to a fine powder using a Retsch MM400 ball mill (Retsch GmbH, Haan, Germany). To analyse leaf C, leaf N and the CN ratio, a subsample of approximately 5 mg plant material was analysed using a vario EL cube (Elementar Analysentechnik GmbH, Langenselbold, Germany). For further analysis, a subsample of approximately 200 mg ground plant material was cooked for eight hours at 160 °C in 70% nitric acid (nitric acid digestion) and afterwards diluted to 100 ml with an solution of water and 0.2 % caesium and lanthanum. The digested samples were analysed for calcium, magnesium and potassium using a contrAA 300 atomic absorption spectrometer (Analytik Jena GmbH, Jena, Germany). Separate aliquots of the digested samples were analysed for phosphate by measuring their extinction at 712 nm using a UV/Vis Spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA).

NIRS calibration results

Table 2: Model details of the NIRS prediction models for each trait. 'R^2' indicates the Coefficient of determination between the reference data and the predicted values for model calibration (R^2 Cal) and model validation (R^2 Val). 'RSMEP' is the root mean square error of prediction. 'Rank' refers to the number of main factors in the calibration model. 'Variables' refers to the selected wavelength regions of the model. 'Preproc' indicates the selected mathematical pretreatment that was applied to the spectral data: MSC = multiplicative scatter correction, D1f = first derivative, D2f = second derivative, SNV = vector normalisation, SLS = single line subtraction. 'Mean Ref' refers to the mean value of reference data for comparison with the RMSEP value. Unit of the trait is valid for RMSEP and trait mean value.

Trait	R^2 Cal	R^2 Val	RMSEP	Rank	Variables [nm]	Preproc	Mean Ref	Unit
LDMC	0.98	0.98	7.87	11	434-597; 1692-2220; 2311-2500	MSC	383.9	mg/g
SLA	0.96	0.99	1.21	10	350-468; 1203-1395; 2356-2500	D1f & SNV	20.3	mm^2/mg
Leaf C	0.95	0.95	0.49	11	801-1348; 1603-2072; 2241-2500	D2f	44.9	%
Leaf N	0.97	0.98	0.09	8	522-640; 1829-2202	D1f & MSC	2.2	%
CN ratio	0.97	0.98	1.57	8	1273-1624; 1991-2200	D1f & MSC	22.6	mg/mg
Leaf P	0.89	0.72	0.35	19	505-682; 1960-2320	MSC	2.7	mg/g
Leaf Ca	0.91	0.91	2.26	12	1115-1755; 1855-2500	D1f & MSC	15.5	mg/g
Leaf Mg	0.86	0.92	0.48	11	571-651; 1147-1838; 2265-2500	D1f	2.7	mg/g
Leaf K	0.85	0.91	1.95	12	1207-1286; 1811-2119	SLS	13.1	mg/g

NIRS prediction models

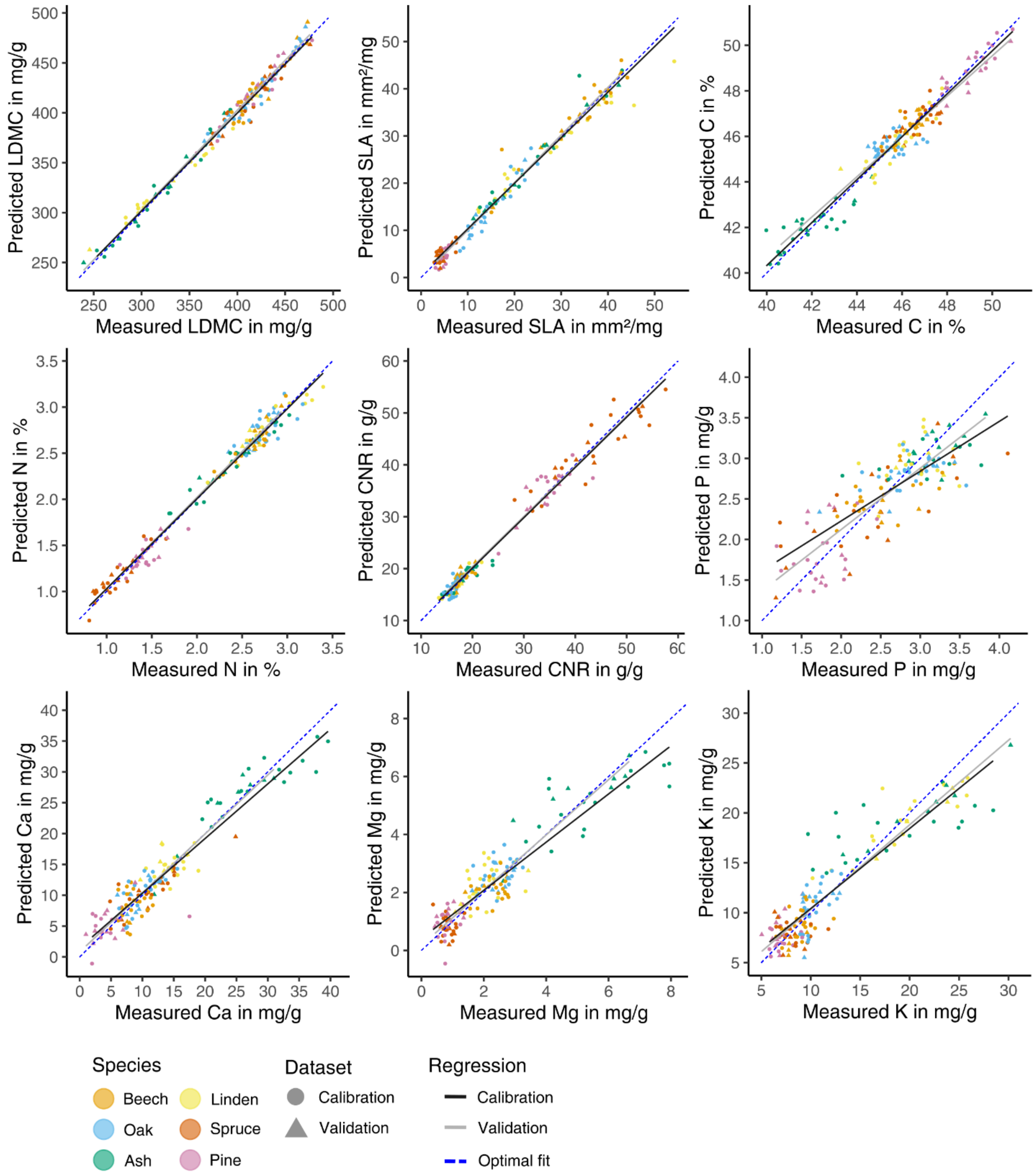


Figure 4: Graphical overview on the calibration and validation results for each prediction model. X-axes indicate leaf traits measured by reference methods; Y-axes indicate predictions by the models. Each datapoint thereby visualises the difference between reference measurement and model prediction (colour by species, shape by dataset). Lines indicate a linear regression between measured and predicted values, coloured by dataset (optimal fit indicates a linear regression between all data points with a R^2 of 1). For the R^2 and RMSE of the regressions, see also table 2.

Principal component analyses

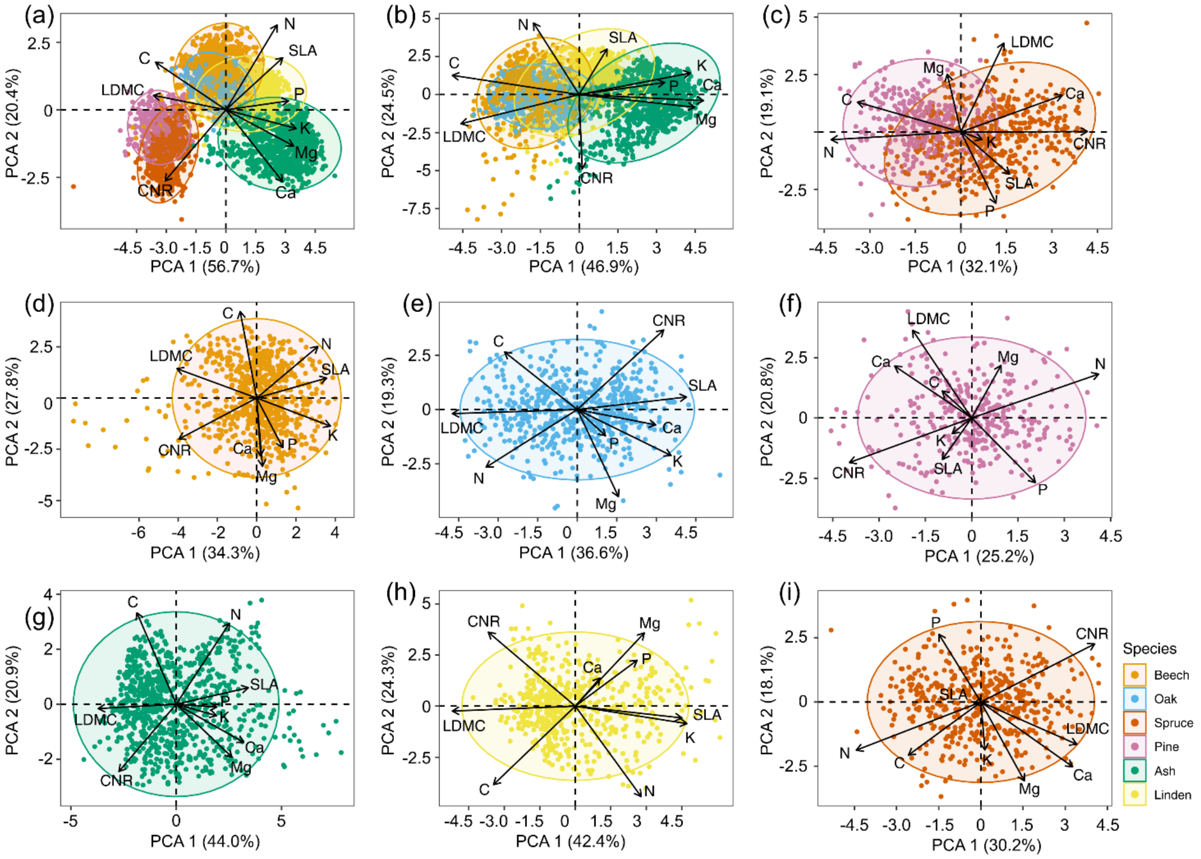
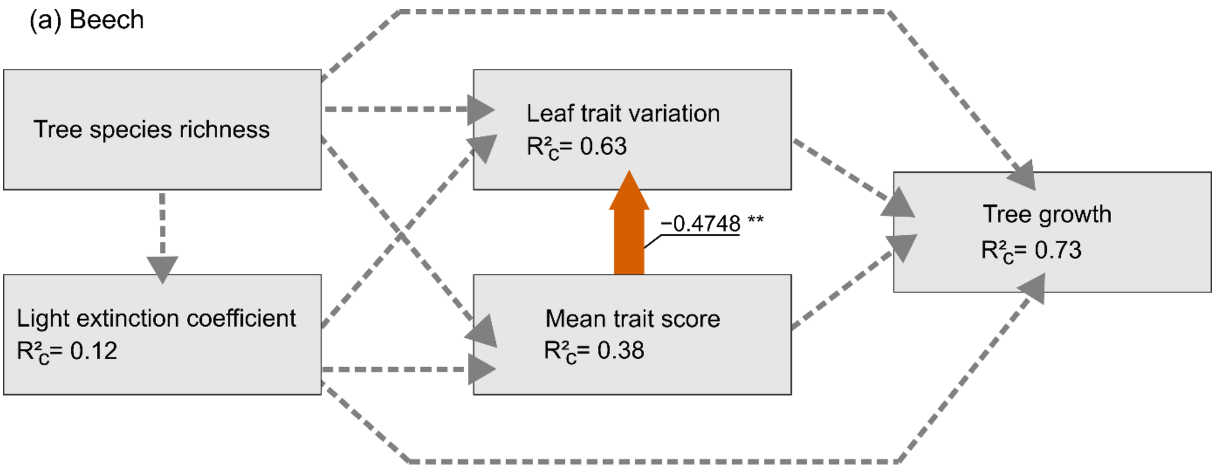
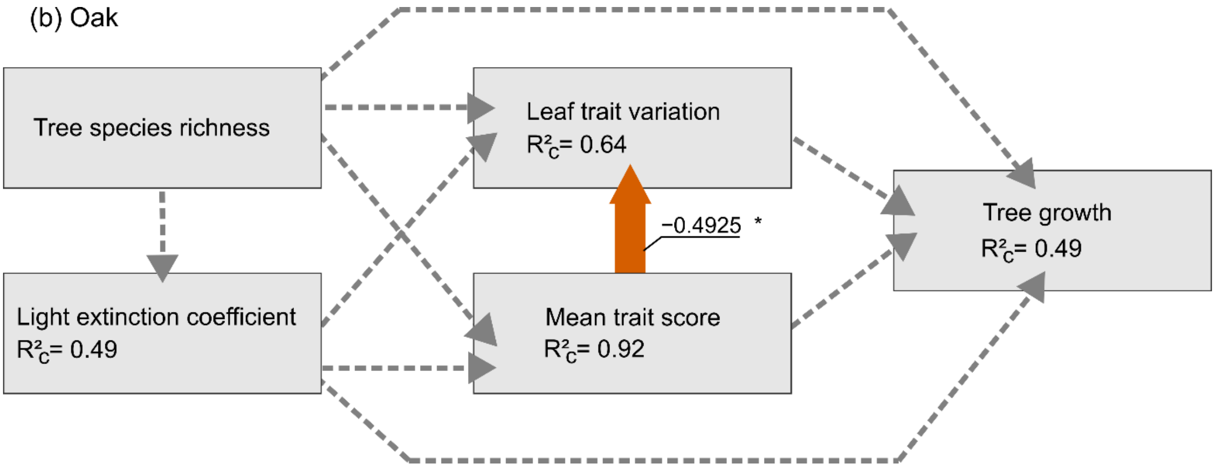


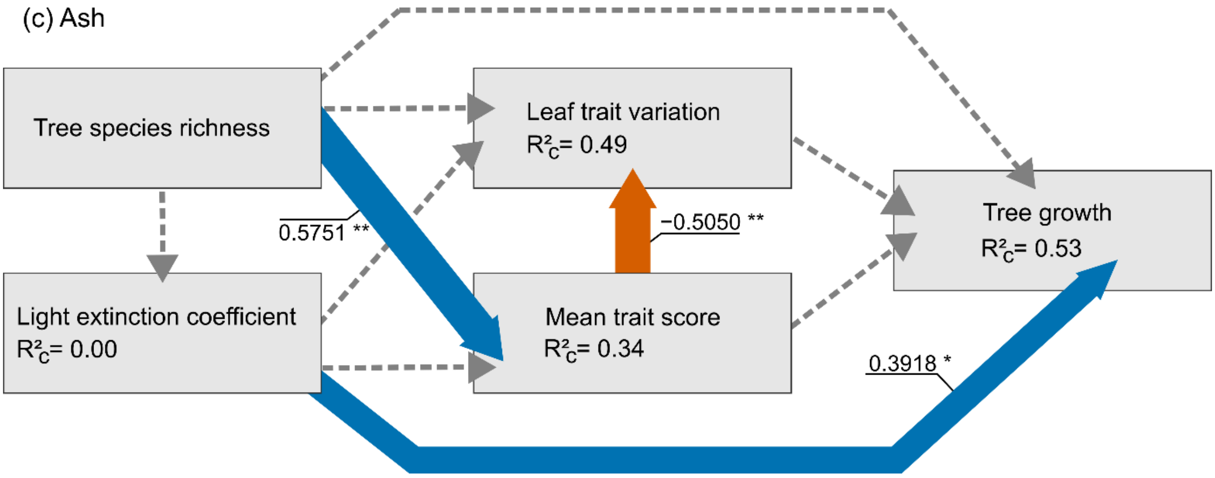
Figure 5: Principal component analysis. First vs. second axes. Dots indicate individual leaves, coloured by species. Circles include 95% of the data points of each species. (a): All species. (b): Only deciduous species. (c): Only conifers. (d-i): individual species.

Path diagrams for individual species





(c) Ash



(d) Linden

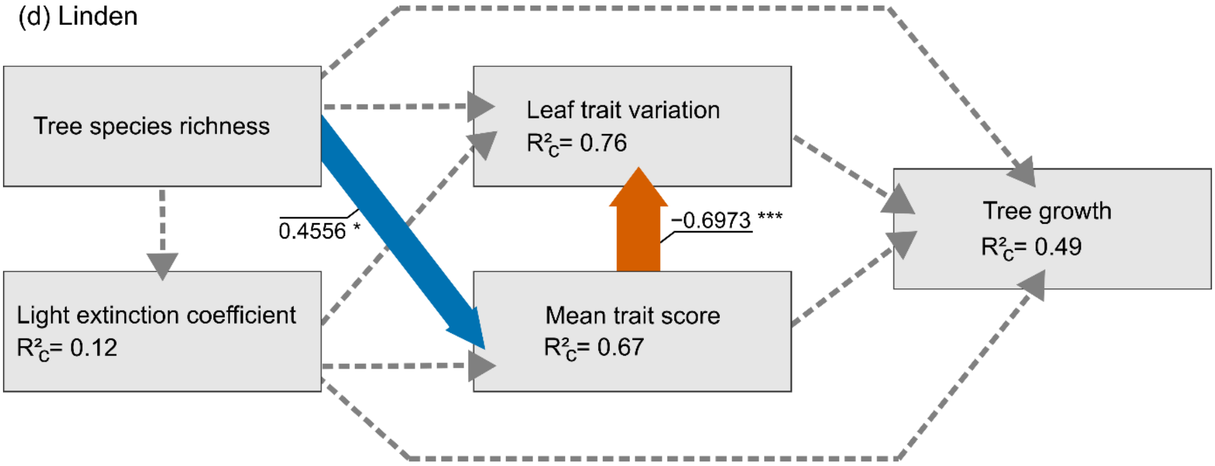


Figure 5: Separate path diagrams for each species, derived from SEMs describing the influence of tree species richness, light extinction coefficient, mean traits scores of the first PCA axis, leaf trait variation (standard deviation of these scores) on tree growth. Boxes represent measured variables, arrows represent directional relationships among variables. Solid arrows indicate significant relationships, dashed arrows indicate nonsignificant relationships (***=$p<0.001$, **=$p<0.01$, *=$p<0.05$). Blue arrows indicate positive relationships, orange arrows indicate negative relationships. Width of the arrows is scaled according to the standardized regression coefficient, also indicated by the adjacent numbers. R^2c indicates the conditional coefficient of determination based on both the fixed and the random effects of the models.

Path diagrams excluding ash

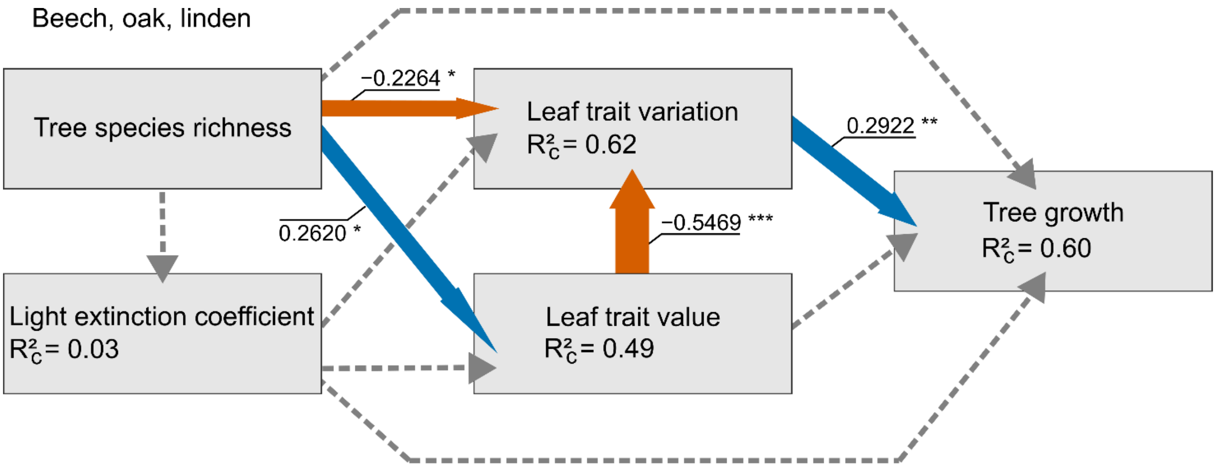


Figure 6: path diagram excluding ash, describing the influence of tree species richness, light extinction coefficient, mean traits scores of the first PCA axis, leaf trait variation (standard deviation of these scores) on tree growth. Boxes represent measured variables, arrows represent directional relationships among variables. Solid arrows indicate significant relationships, dashed arrows indicate nonsignificant relationships (***=$p<0.001$, **=$p<0.01$, *=$p<0.05$). Blue arrows indicate positive relationships, orange arrows indicate negative relationships. Width of the arrows is scaled according to the standardized regression coefficient, also indicated by the adjacent numbers. R^2c indicates the conditional coefficient of determination based on both the fixed and the random effects of the models.

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Chapter 5

Synthesis

5.1 Summary of results

This thesis investigated the response of leaf traits to environmental conditions and the effect of leaf traits on EF in forest ecosystems. The studies described in chapters 2, 3 and 4 took place in biodiversity experiments in the tropical, subtropical and temperate biomes. These chapters focused on the questions of how leaf traits and their variation respond to tree species richness, how they react to changes in light availability and how they influence tree growth. Figure 5.1 illustrates the main results of the thesis.

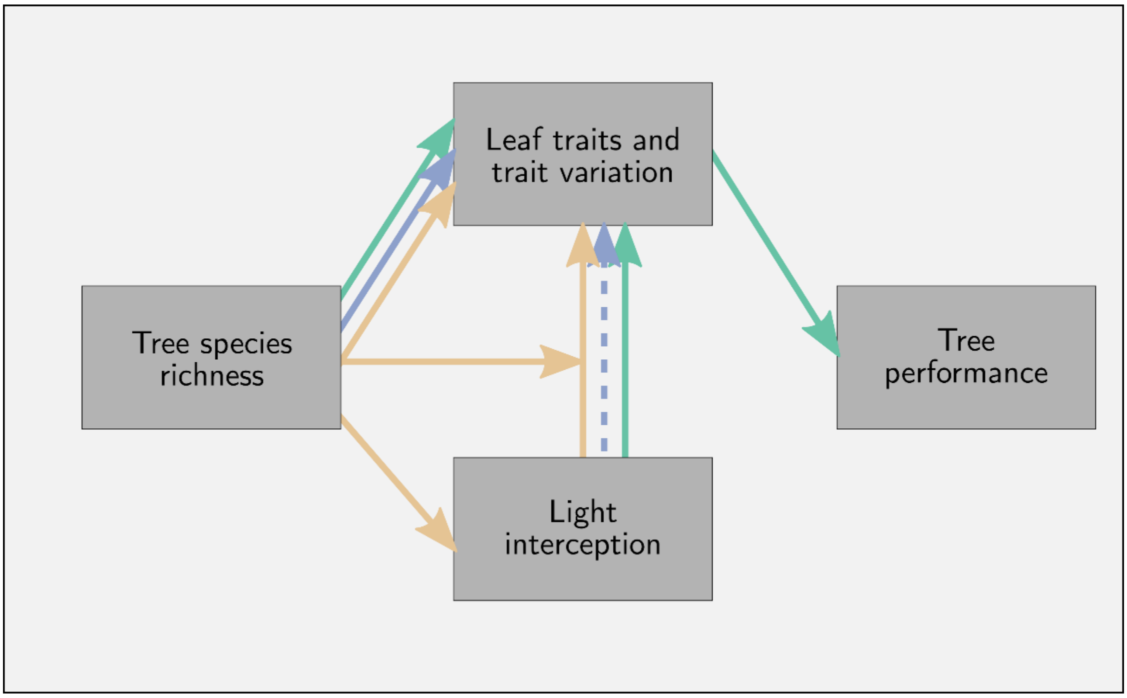

Figure 5.1: Main results of the thesis. This graphical overview visualises the different findings of this thesis. The arrows indicate significant relationships between the factors. Different chapters are indicated by different arrow colours: blue for chapter 2, brown for chapter 3, green for chapter 4. Solid lines indicate relationships based on direct measurement of the factors, the dashed line indicates a relationship based on an indirect measurement (in chapter 2, light is considered to be a function of height). The direction of the arrows indicates the direction of causality.

In chapter 2, I demonstrated that tree species richness can be a source of leaf trait variation and that the sampling height is the axis along which this variation can be measured. The leaf trait variation within individuals and within species decreased with increasing tree species richness. However, the mean trait values both at the species level and at the individual level remained unaffected. Furthermore, there was evidence that the surrounding tree species richness influences the trait-height relationship (demonstrated for LDMC in *Cedrela odorata*).

In chapter 3, I showed that most leaf traits are strongly influenced by local light availability. Yet, leaf trait values remain largely unaffected by tree species richness (with the single exception of leaf P in deciduous trees). The main conclusion of this chapter is that leaf traits are modified by the *interaction* between light and the surrounding biodiversity. The tree species richness of a plot and the closest neighbour of a tree modify the relationship between light availability and leaf traits, with the closest neighbour being more relevant in many cases. Additionally, this chapter also highlights the differences between evergreen and deciduous trees.

In chapter 4, I demonstrated that the relationships between tree species richness, leaf traits and light availability, that were observed in chapters 2 and 3 are connected to each other and are further connected to the individual tree performance. In particular, an increase in tree species richness results in a decrease in within-individual leaf trait variation. In contrast, within-individual leaf trait variation positively influences individual tree growth, which means that at the ecosystem level, both relationships balance each other out. The mean trait value and the light availability further modify the indirect association of tree species richness and tree growth, as they both directly affect within-individual leaf trait variation.

Using the method of optical spectroscopy, I was able to analyse leaf traits via highly accurate prediction models. The method's high sample throughput allowed me to process the high amount of samples that is required for a within-individual analysis. At the same time, the comprehensive and non-destructive data collection made it possible to analyse each leaf for multiple leaf traits, which would have been impossible with conventional methods.

5.2 General discussion

Leaf trait variation at the within-individual level

Chapters 2, 3 and 4 of this thesis demonstrate that leaf traits vary strongly at the within-individual level. This was observed across different biomes and leaf habits. These observations are consistent with previous studies (Sack et al. 2006, Escribano-Rocafort et al. 2016), adding further evidence that it is an intrinsic characteristic of broadleaved forests. However, despite the general understanding of the existence of within-individual leaf trait variation, the underlying mechanisms are not fully understood and the ecological consequences remain largely unexplored.

In this thesis, I could demonstrate that leaf traits respond to multiple factors including local light availability and sampling height. In chapter 2, I observed an increase in LDMC and a decrease in SLA with increasing sampling height. Chapter 3 showed the same leaf trait reaction as response to increasing light availability. These observations are further consistent with the results of chapter 4, where an increase in light availability results in a decrease of leaf acquisitiveness (which is strongly influenced by LDMC and SLA). The local light availability and sampling height are considered to be strongly corelated (Valladares 2003, Niinemets 2007). In particular, the light availability is thought to be a function of sampling height (Matsuo et al. 2021), which could imply that the leaf traits only respond to light availability and the correlation with sampling height is merely secondary. In this case, trait response to light and height should be identical. The previous observations regarding LDMC and SLA are consistent with this conjecture. However, there are some discrepancies regarding other traits. For example, the response of lignin and cellulose to sampling height demonstrated in chapter 2 does not have an equivalent response to light in chapter 3. In contrast, leaf N responds to light (chapter 3) but not to sampling height (chapter 2), which implies that other mechanisms might be in place. Indeed, it has been argued before that leaf traits can respond to sampling height independently of light availability, but there is no consensus on which leaf traits are affected by this (Niinemets and Kull 1997, Niinemets and Tenhunen 1997, Niinemets et al. 1998, Rijkers et al. 2000, Ishii et al. 2007, Coble and Cavaleri 2015). One possible explanation is that the trait-height relationship (chapter 2) and the trait-light relationship (chapter 3) are both linear, but the light-height relationship is not linear (chapter 4). In the lower regions of the crown, a height difference in several meters only results in a minimal change in light availability. Here, leaf trait adaptation to height might be more important, possibly as a result of branch hydraulics, water potential or turgor pressure constraining leaf traits (Ambrose et al. 2009, Cavaleri et al. 2010). At the top of the crown, a height difference in one meter might result in a drastic change in light availability. Here, the potential effects caused by height differences are less relevant compared to the effects caused by change in light availability, and light should be the dominating factor affecting leaf traits (Coble and Cavaleri 2015). Interestingly, there was little indication that a change in light availability results in a shift in mean leaf traits at the individual level. Interestingly, there was little indication that leaf trait variation along the light or height gradient would result in a shift in mean leaf traits of the individual trees.

The influence of tree species richness on mean leaf traits

In contrast to the previously mentioned lack of light and height effects on mean leaf traits, the surrounding tree species richness does influence the mean leaf traits at the individual level. However, this could not be demonstrated universally across all chapters. In chapter 4, I showed that an increase in tree species richness results in a mean trait shift towards more acquisitive trait values. While there was no indication for this in chapter 2, there was a single case in chapter 3 that is consistent with the previous observation (increase in leaf P in species-rich environments). These results are further consistent with Davrinche and Haider (2021), who found similar results in the BEF-China experiment. Most notably, this type of response is fully visible in the most densely planted Kreinitz experiment (12’000 trees per hectare), only partially visible in the intermediate-density BEF-China experiment (6’000 trees per hectare) and not visible in the low-density Sardinilla experiment (1'000 trees per hectare). Hence the mean trait shift towards acquisitive values in species rich environments might be density-dependent. This could be interpreted as a response to light competition. Increased density and tree species richness are known to increase light utilisation (Pretzsch 2014, Jucker et al. 2015, Kunz et al. 2019). However, the combination of high species richness and high planting density could result in less light being available for each individual tree. This light scarcity is known to shift leaf traits to more acquisitive values (Kitajima 1994, Valladares et al. 2000), which would explain the observations.

The influence of tree species richness on within-individual leaf trait variation

Besides its effect on mean leaf traits, the tree species richness influences also the within-individual variation of leaf traits. I could demonstrate across chapters 2, 3 and 4, that an increase in tree species richness results in a decrease in within-individual leaf trait variation. Indeed, the within-individual leaf trait variation might be equally relevant for individual trees as their mean trait values. This consideration is referred to as the "Haldane-Roy conjecture" (Herrera 2009) which is based on the works of Haldane (1957, 1959) and Roy (1959, 1963). It postulates that the leaf traits standard deviation of an individual might vary independently of its mean value. Indeed, I was able to demonstrate this for example in chapter 2, where I could show that the within-individual standard deviation of leaf N decreases with increasing tree species richness, yet its mean value remains unchanged.

The observation that the individuals in monocultures have a higher within-individual leaf trait variation than the individuals in species mixtures could be explained as the individuals' response to within-species competition. For each individual, a strong similarity regarding the leaf traits could be disadvantageous in terms of resource acquisition. In that case, it would be advantageous for each individual in a monoculture to diversify its leaf traits in order to cover a greater trait space, thereby avoiding within-species competition at the individual level. However, this would not necessarily occur in complex species mixtures where each neighbouring tree of an individual is of a different species and thereby already covers a slightly different trait space. The concept, that a high variability of traits is beneficial – or low variability is disadvantageous – has been established at higher levels of organisation. At the between-species level, the concept of 'limiting similarity' (MacArthur and Levins 1967) suggests that different species cannot coexist if they are too similar regarding their resource requirements. Furthermore, at the within-species level, Benavides et al. (2019) observed a reduction in within-species level trait space as a response to increased tree species richness, which can be interpreted as a response to reduced competition. The observations of this thesis expands this concept to the within-individual level. A higher within-individual leaf trait variation might be advantageous for each individual plant in terms of tree growth.

Within-individual leaf trait variation is the mediator between tree species richness and tree growth

In forest ecosystems, tree species richness and tree growth are often positively corelated (Pretzsch et al. 2015, Liang et al. 2016, Huang et al. 2018, Zeller et al. 2018). However, in this thesis, as in several other studies (Nguyen et al. 2012, Staples et al. 2019), a direct link between these factors was not found. One factor that should be considered when analysing the relationship between tree species richness and biodiversity is the age of the forest ecosystems. Guo and Ren (2014) argued, that a potential positive relationship between these factors might not be visible in the early stage of forest development. This is further confirmed by the observation that a positive biodiversity-productivity relationship can increase over time (Huang et al. 2018). However, in chapter 4 I demonstrated that also a comparably young biodiversity experiment (Kreinitz experiment, twelve years old at the time of sampling) can show a positive tree growth, albeit only as an indirect response to tree species richness. Kreinitz experiment is also the experiment that is most densely planted. It is possible that in this case, a high planting density could have a similar effect than a higher stand age. As trees in a plantation grow older, their interaction plane with neighbouring individuals increases as their crowns grow bigger. Higher initial planting density could have a similar effect, as here younger trees have initially higher interaction with their neighbours. Indeed, a positive biodiversity-productivity relationship due to increased density was demonstrated in a grassland experiment (Marquard et al. 2009), and the results of my thesis suggest that it could be similar in forest ecosystems. It appears that the relationship between tree species richness and tree growth is complex and might further depend on other factors. To fully understand the relationship between tree species richness and tree growth, it is therefore important to investigate it jointly with its cofactors. Indeed, including the cofactors leaf traits, light availability as well as their interaction and variation on the individual level, I was able to demonstrate in chapter 4 that the tree growth indirectly depends on the tree species richness. A decrease in tree species richness causes an increase in within-individual leaf trait variation and individuals with higher leaf trait variation show stronger growth. That means for example that monocultures – that might have a lower growth rate due to lower resource utilisation – can compensate this disadvantage by trees diversifying their leaf traits. These factors balance each other out, which is why this effect is visible at the individual level but not at higher levels of organisation.

Leaf traits align with the leaf economics spectrum at the within-individual level

Another important observation of this study is, that the relationships between leaf traits at the within-individual level are remarkably similar among all leaf samples taken in the chapters 2, 3 and 4. All leaves appear to be subject to the same trade-off between conservative and acquisitive trait values – even at the smallest scale. This pattern of leaf trait coordination has been established as the LES at the species level (Wright et al. 2004, Reich 2014). Here, it indicates the trade-off between resource acquisition and structure to which plant species are constrained. While the LES describes the between-species coordination of leaf traits, there are several studies that indicate that the same pattern of coordination might be also present at the within-species level (Fajardo and Siefert 2018, Gorne et al. 2022). Yet, even though the leaf trait coordination of the LES is visible across multiple scales, its causes and effects at different scales might be different (Derroire et al. 2018). Regarding the within-individual scale, it could be, that the light availability drives the conservative-acquisitive trade-off (Chen et al. 2020), while on other scales other environmental factors, such as climate and local resource availability, might dominate or even overturn this relationship (Anderegg et al. 2018, Liu et al. 2019). Regardless, this thesis demonstrates that the leaf traits show good alignment with the LES at the within-individual level. Overall, this indicates that the trade-off between conservative and acquisitive leaf traits resembles a form of evolutionary convergence of leaf trait relationships.

Limitations and future perspectives

The results of this thesis are limited to forest ecosystems of the temperate, tropical and subtropical biome. While evergreen and deciduous trees are considered in this thesis, its scope extends only to broadleaved trees. Consequently, a potential future study could focus on the leaf trait response to tree species richness in conifers. A possible location for such a study would be the Sault-Ste-Marie biodiversity experiment (Canada). This site includes (among other species) two evergreen conifer species (*Picea glauca* and *Pinus strobus*) and one deciduous conifer species (*Larix laricina*), which means that besides focusing on conifers, a further distinction between evergreen and deciduous species could be made.

Another crucial factor is that this thesis was conducted in large scale forest biodiversity experiments (chapter 2 in the tropical Sardinilla experiment, chapter 3 in the subtropical BEF-China experiment and chapter 4 in the temperate Kreinitz experiment). The main advantage of this approach is that, in contrast to natural ecosystems, the work in biodiversity experiments allows causal inference between the biodiversity of the ecosystem and ecosystem processes. However, it is unclear to which degree the results from biodiversity experiments can be applied to natural ecosystems.

Follow-up studies could, for example, utilize the comparative study plots in Barro Colorado Island (Panama) for the tropical biome, the Hainich Forest (Germany) for the temperate biome and the Gutianshan Forest (China) in the subtropical biome.

Concluding remarks

This thesis gives a comprehensive overview of the role of leaf traits in forest ecosystems at the within-individual level. Using the method of optical spectroscopy, I was able to process the high number of samples necessary for this analysis. The ability to analyse each single leaf for all relevant traits thereby also demonstrates the viability of this method. Leaf traits respond to biotic and abiotic factors at the within-individual level. Especially within-individual leaf trait variation is a key factor in forest ecosystems, as it responds to changes in tree species richness and influences tree growth, thereby acting as a mediating factor. The individuals' adaptation via within-individual leaf trait variation could be interpreted as their mechanism to optimise trait space – in particular to avoid within-species competition in monocultures. Yet besides these adaptations, leaf traits remain coordinated on the conservative-acquisitive axis of the leaf economic spectrum, even at the within-individual level. By balancing the trait values of its single organs, each individual is able to adapt to its local environment and optimise its performance. In ecological research, it is therefore crucial to include within-individual analyses in order to fully understand the individuals' responses to their environment.

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Appendices

Author contributions

Chapter 2

HB, SH and ST conceived and designed the experiment. HB, MS, ST and TP conducted the field work. TP analysed the data and wrote the first draft of the manuscript under the supervision of SH. All authors contributed to the interpretation of the results and the revision and final version of the manuscript. My overall contribution was 70%.

Chapter 3

HB and SH conceived and designed the experiment. TP conducted the field work and analysed the data. TP wrote the first draft of the manuscript under the supervision of SH. All authors contributed to the interpretation of the results and the revision of the final version of the manuscript. My overall contribution was 75%.

Chapter 4

HB, SH and TP conceived and designed the experiment. TP conducted the filed work and wrote the first draft of the manuscript under the supervision of HB. All authors contributed to the interpretation of the results and the revision and final version of the manuscript. My overall contribution was 85%.

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Curriculum Vitae

Personal information

Scientific employment

2022 – present	Research associate for the ‘MultiTroph’ project *Martin Luther University Halle-Wittenberg* Curation and development of the BEF-China database
2017 – 2022	Research associate for the ‘Dr. Forest’ project *Martin Luther University Halle-Wittenberg* Administrative support and logistic coordination
2016 – 2017	Research assistant *Martin Luther University Halle-Wittenberg* Lab work including method development, method implementation and technical support.
2015 – 2016	Research assistant *Senckenberg Gesellschaft für Naturforschung* Field work in Schwäbische Alb biodiversity exploratories Lab work including equipment maintenance
2014 – 2015	Research assistant *Martin Luther University Halle-Wittenberg* Field work in Schorfheide-Chorin and Hainich national park, Lab work including soil and leaf analysis

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Teaching experience

2016 – 2018	Tutor for master's students research internship Utilization of near-infrared spectroscopy for lignin measurement as an alternative for conventional gravimetric measurement
2016 – 2018	Teaching assistant for bachelor's students lab course Teaching methods of elemental analysis including atomic absorption spectroscopy and near-infrared spectroscopy

Education

2017 – present	Doctoral researcher *Martin Luther University Halle-Wittenberg* Research focus: The role of within-individual leaf trait variation in forest ecosystems. Leaf traits as responses to biotic and abiotic environmental conditions and predictors for ecosystem functions
2012 – 2016	Master of Science in Biology *Martin Luther University Halle-Wittenberg* Thesis title: “The application of field spectroscopy as a method of fast and differentiated analysis of Chinese woody species leaf traits”
2008 – 2012	Bachelor of Science in Biology *Martin Luther University Halle-Wittenberg* Thesis title: "Near-infrared spectroscopy as a method of fast and non-destructive prediction of the phenol and tannin content of Chinese woody species"

Scientific memberships and activities

Since 2023	British Ecological Society (BES)
Since 2023	Reviewer for Journal of Plant Ecology
Since 2020	Gesellschaft für Ökologie (GfÖ)
Since 2017	International Research Training Group TreeDì
Since 2017	yDiv Graduate School of iDiv Elected PhD representative as chair of the PhD meetings
Since 2017	Graduate scholarship program of the federal state Saxony-Anhalt

Halle (Saale), 01.11.2023

Tobias Proß

List of publications

Journal articles

Proß, T., Bruelheide, H., Potvin, H., Sporbert, M., Trogisch, S. & Haider, S. (2021) “Drivers of within-tree leaf trait variation in a tropical planted forest varying in tree species richness”. *Basic and Applied Ecology 50 (3): pp. 203-216. http://doi.org/10.1016/j.baae.2020.11.001*

Proß, T., Bruelheide, H., Auge, H. & Haider, S. (2024) “Leaf trait variation within individuals mediates the relationship between tree species richness and productivity“. *OIKOS* e10255. https://doi.org/10.1111/oik.10255.

Proß, T., Bruelheide, H., & Haider, S. (2025) “Within-individual leaf trait response to local light availability and biodiversity in a subtropical forest experiment“. *Ecology* 106 (7) https://doi.org/10.1002/ecy.70160

Trogisch, S., ... *Proß, T.*, ... Bruelheide, H., (2017) Toward a methodical framework for comprehensively assessing forest multifunctionality. *Ecology and Evolution 7 (24): pp. 10652-10674.*

Conference contributions and invited talks

Proß, T., Bruelheide, H., Potvin, H., Sporbert, M., Trogisch, S. und Haider, S. (12. Sep 2019): “Drivers of within-tree leaf trait variation in a tropical forest varying in tree species richness“ *Talk* at the GfÖ annual meeting (Münster, Germany)

Proß, T., Bruelheide, H., Potvin, H., Sporbert, M., Trogisch, S. und Haider, S. (23. Mar 2019): “Intra- and intercrown leaf trait variation in tropical lowland forests – influence of local biodiversity“ *Talk* at the Hainan University (Haikou, China)

Proß, T., Bruelheide, H., Potvin, H., Sporbert, M., Trogisch, S. & Haider, S. (11. Dec 2018): “Neighbourhood species richness and canopy height influence leaf trait variation in a tropical forest“ *Poster* at the annual meeting of the German centre for integrative biodiversity research, iDiv (Leipzig, Germany)

Proß, T., Haider, S. & Bruelheide H. (12.Dec 2017): “The application of near-infrared field spectroscopy as a method of fast and detailed analysis of leaf traits” *Poster* at the BES joint annual meeting (ICC Ghent, Belgium)

Proß, T. (12. Mar 2017): ” Leaf near-infrared spectra as predictors for forest ecosystem functions: The role of species richness, nutrient availability and complementarity in leaf traits in forest ecosystem functions: explanation of complementarity effects in forest ecosystems via near-infrared spectra” *Talk* at the TreeDi Conference (Leipzig, Germany)

Proß, T. (24. Aug 2016): “Using field spectroscopy to predict leaf traits for Chinese subtropical tree species” *Talk* at the institute of botany of the Chinese academy of sciences (Beijing, China)

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „The role of leaf traits in forest ecosystems: mediators in the relationship between biodiversity and ecosystem functions“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Tobias Proß, Halle (Saale) 01.11.2023

“I may not have gone where I intended to go,
but I think I have ended up where I needed to be.”

— Douglas Adams, The Long Dark Tea-Time of the Soul