# COMPLEMENTARITY THROUGH LEAF TRAIT VARIATION:

## RESPONSES OF TREES TO SPECIES DIVERSITY AND SOIL CONDITIONS

Dissertation

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*If you listen carefully, you can hear the natural world talking to you. Can you hear it? It's saying:*

*"Shhh...don't worry"*

*"you don't matter"*

Joshua Barkman*, False knees*, 2018.

# Table of Contents

# SUMMARY

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To provide humanity with the tools for understanding and preserving ecosystems, an integral part of today's ecology focuses on the effects of biodiversity on ecosystem functioning (BEF). Plant functional traits have become an established way to gain insights into the physiology, structure and ecological strategy of plant individuals, and thereby capture the properties of an ecosystem. While most often used as reflection of a plant community's response, traits can also inform on the local processes behind BEF relationships. However, the processes occurring at small scales, at which individuals interact, are scarcely studied in the context of BEF research, despite the potential they offer for understanding what underlies the effects of biodiversity on ecosystem functions.

The aim of this thesis is to contribute to disentangling the influence of local tree species diversity on the adaptability and the resource allocation strategy of individual trees, and how it is modified by local soil conditions. Hence, I investigated the effect of species diversity of a focal tree's neighbours on within-tree leaf traits and trait variation, depending on belowground nutrients availability and microbiota. In both a field and a controlled experiment, I used optical spectroscopy methods to predict traits from several thousands of leaves collected *in situ* for each study, belonging to between eight and 16 tree species.

Specifically, in the subtropical tree diversity experiment BEF-China, I looked into (1) the effects of species diversity of the closest and the surrounding neighbours on a focal tree's resource allocation strategy, (2) the proportion of trait variability occurring within trees, and the drivers of within-tree trait variability, namely the species identity of the closest neighbour, the species diversity of the surrounding neighbours and the soil nutrient availability, as well as their interaction. Additionally, in a greenhouse experiment, (3) I investigated the differences of trees' leaf traits and trait variability in monocultures and 2-species mixtures, and studied how the effect of species diversity was modified by the soil biotic and abiotic properties for fast or slow growing species.

First, I found in the field experiment that species diversity tended to shift the individual trees' resource allocation strategy toward an acquisitive, fast growing strategy. In addition, the results indicated that more effects emerged from the closest neighbour of the focal tree compared to the surrounding neighbourhood. Also, further than the plateauing in BEF relationship reported in previous studies, I observed a threshold in species diversity after which positive effects of diversity seemed to be overtaken by competition, likely caused by the higher probability at higher diversity to encounter a strongly competitive species.

Second, I observed an unprecedented high amount of variation within tree individuals (on average over a quarter of the total variation) in comparison to variation between species or between individuals. I further showed that species diversity and soil nutrient availability independently had mixed effects on within-tree variation, but that more prominently these two drivers were strongly interlinked. Trait variation increased with soil nutrient availability when the species diversity of a tree's neighbourhood was moderate, but decreased at low or high species diversity.

Finally, investigating further the role of soil in the species-trait relationship uncovered in the field, I showed in the greenhouse experiment that the dependency of species diversity effects on soil conditions is different when considering the soil nutrient content or its micro-organisms community. Together, species diversity and phosphorus fertilization were associated with trait syndromes indicating a tendency for trees to go towards a slow growth strategy, and an increased within-tree variation. On the contrary, the interaction of species diversity and soil micro-organisms promoted a fast growth strategy, but decreased the within-tree variation.

Taken together, these results highlight that the individual scale, while rarely studied, is highly relevant for trait-based approaches used to better understand BEF relationships. Indeed, I found effects of diversity and soil at small scales, but also quantified the considerable relevance of the individual when considering trait variation, and hence the adaptability of trees to changing environments. In addition to emphasizing the interdependency of species diversity and soil conditions effects, I also uncovered a non-linear relationship between species diversity, soil conditions and trait variation, never previously reported in the literature. This relationship points to the interplay between complementary and competitive mechanisms dependent on species diversity and soil conditions, which trait variation reflects. Moreover, my results suggest different mechanisms behind the effects of biotic and abiotic soil conditions on individuals' resource allocation and variation. While the addition of limiting belowground resources tended to enhance individuals' plasticity, soil microbiota seemed to reduce plant competitive effects rather than to enable a greater resource uptake.

Overall, adopting an under-researched but promising perspective, this thesis demonstrates the importance of species complementary in tree-tree interactions. Based on this work, I advocate for including an individual aspect in trait-based approaches, as well as for considering the complex interactions between above and belowground processes at small scales. My results highlight the importance of maintaining species diversity locally, but also underline the conditions and limits within which this species diversity, together with the local environment, favours trees' growth and adaptability. Hence, this thesis contributes to a better understanding of the mechanisms behind BEF relationships, but has also broader implications for ultimately helping to build a sustainable future for forest ecosystems.

# ZUSAMMENFASSUNG

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Um der Menschheit zu ermöglichen, Ökosysteme zu verstehen und zu erhalten, beschäftigt sich ein wesentlicher Teil der modernen Ökologie mit der Frage wie Biodiversität Ökosystemfunktionen beeinflusst (BEF – Biodiversity-Ecosystem Functioning). Die Verwendung von funktionellen Merkmalen von Pflanzen hat sich dabei etabliert, da sie einen Einblick in die Physiologie, Struktur sowie die ökologische Strategie von Pflanzenindividuen erlauben, und damit Eigenschaften eines Ökosystems wiederspiegeln. Während funktionelle Merkmale von Pflanzen oft verwendet werden, um die Reaktionen von Pflanzengemeinschaften zu charakterisieren, können sie außerdem die lokalen Prozesse, die hinter BEF Beziehungen stecken, beschreiben. Ungeachtet des Potentials unser Verständnis von den Effekten, die Biodiversität auf Ökosystemfunktionen hat, zu verbessern, werden diese kleinräumigen Prozesse, bei denen Pflanzenindividuen interagieren, nur selten untersucht.

Das Ziel dieser Dissertation ist es, den Einfluss von lokaler Baumartendiversität auf die Anpassungsfähigkeit und Ressourcennutzungsstrategien einzelner Bäume, sowie den modifizierenden Einfluss lokaler Bodeneigenschaften zu verstehen. Dafür untersuche ich wie die lokale Diversität von Nachbarbäumen die funktionellen Blattmerkmale und deren Variation innerhalb eines Baumes beeinflusst, und wie dies von Nährstoffverfügbarkeit im Boden und dessen Mikrobiota abhängt. Ich nutze Methoden der optischen Spektroskopie um Blattmerkmale von mehreren tausend Blättern, die für jede Teilstudie *in situ* gesammelt wurden, vorherzusagen. Insgesamt wurden acht bis 16 Baumarten aus einem Feld- und einem Gewächshausexperiment untersucht.

Konkret habe ich in dem subtropischen Baumdiversitätsexperiment BEF China (1) die Effekte von Artenvielfalt des nächsten und der umgebenden Bäume auf die Ressourcennutzungsstrategien von Baumindividuen untersucht. Außerdem habe ich (2) den Anteil der Merkmalsvariabilität innerhalb einzelner Bäume quantifiziert und die treibenden Kräfte hinter dieser Variabilität, im Speziellen die Einzel- und Interaktionseffekte der Art des nächsten Baumes, der Diversität der umgebenden Bäume und der Nährstoffverfügbarkeit, untersucht. Des Weiteren habe ich (3) Blattmerkmale und deren Variabilität in Monokulturen

und 2-Arten Mischkulturen in einem Gewächshausexperiment verglichen und den Einfluss von biotischen und abiotischen Bodeneigenschaften auf schnell und langsam wachsende Arten betrachtet.

Meine Ergebnisse zeigen, dass Baumdiversität die Ressourcennutzung von Bäumen im Feldexperiment tendenziell hin zu schnell wachsenden Strategien verschiebt, bei denen Ressourcen schneller aufgenommen werden. Dieser Effekt war eher abhängig von dem nächsten Baum als von den umgebenden Bäumen. Im Gegensatz zu anderen Studien bei denen BEF Effekte abflachen, fand ich, dass die positiven Effekte von Diversität ab einem bestimmten Wert wieder abnehmen. Dies ist wahrscheinlich wegen dem erhöhten Konkurrenzdruck zwischen Nachbarbäumen, der einer höheren Wahrscheinlichkeit neben einer konkurrenzstarken Art zu wachsen geschuldet ist, der Fall.

Im Vergleich zur Variabilität von Blattmerkmalen zwischen und innerhalb der untersuchten Baumarten fand ich eine beispielslos große Variabilität innerhalb von Baumindividuen (im Mittel mehr als ein Viertel der Gesamtvariabilität). Baumdiversität und Bodennährstoffverfügbarkeit hatten unterschiedliche Effekte auf die Variabilität innerhalb von Baumindividuen, zeigten aber eine deutliche Wechselbeziehung. Die Variabilität von Blattmerkmalen ist demnach höher je mehr Bodennährstoffe verfügbar sind, jedoch nur bei einer mittleren Diversität. Bei hoher oder niedriger Diversität war der Effekt von Bodennährstoffe umgekehrt.

Im Gewächshausexperiment konnte ich den Einfluss der Bodeneigenschaften, den ich im Feldexperiment demonstrieren konnte, weiter spezifizieren. Meine Ergebnisse zeigen, dass sich die Einflüsse der Bodennährstoffverfügbarkeit und der Gemeinschaft der Bodenmikroorganismen auf den Effekt der Baumdiversität unterscheiden. Die Blattmerkmale von Bäumen deuteten demnach eine Tendenz von Bäumen an, langsamer zu wachsen, wenn die Diversität erhöht und mit Phosphor gedüngt wurde. Dies war gepaart mit einer erhöhten Variabilität der Blattmerkmale. Der Effekt von Diversität und dem Vorhandensein von Bodenmikroorganismen hatte einen umgekehrten Effekt, d.h. die Blattmerkmale der Bäume deuteten auf eine schnellere Wachstumsstrategie bei verringerter Variabilität hin.

Zusammenfassend zeigen meine Ergebnisse, dass das Individuum, obwohl selten Gegenstand von Untersuchungen, die funktionelle Pflanzenmerkmale nutzen, eine hohe Relevanz für ein besseres Verständnis von BEF Zusammenhängen besitzt. Ich konnte den Einfluss von lokaler Baumdiversität und Bodeneigenschaften zeigen, sowie die auffällig hohe

Variabilität von Blattmerkmalen innerhalb eines Baumes, was die Anpassungsfähigkeit von Bäumen an sich ändernde Umwelteinflüsse verdeutlicht. Zusätzlich zu der gegenseitigen Abhängigkeit von Diversität und Bodeneigenschaften fand ich außerdem einen bisher unbekannten, nichtlinearen Zusammenhang zwischen diesen mit der Variabilität von Blattmerkmalen. Dieser Zusammenhang verdeutlicht eine Wechselbeziehung von Komplementarität und Konkurrenz zwischen Bäumen, die von Diversität und Bodeneigenschaften abhängt und in der Variabilität von Blattmerkmalen ihren Ausdruck findet. Des Weiteren suggerieren meine Ergebnisse, dass die Effekten der biotischen und abiotischen Bodeneigenschaften auf Ressourcennutzung und Variation von Baumindividuen auf unterschiedliche Mechanismen beruhen. Während eine erhöhte Verfügbarkeit von limitierenden Nährstoffen die Plastizität von Baumindividuen erhöhte, hat das Vorhandensein von Bodenmikroorganismen scheinbar Konkurrenzeffekte reduziert anstatt die Nährstoffnutzung zu verbessern.

Diese Dissertation nimmt eine wenig untersuchte aber vielversprechende Perspektive ein und demonstriert dabei die Wichtigkeit vom Komplementarität in der Interaktion zwischen Bäumen. Basierend auf meiner Arbeit plädiere ich deshalb für eine Inklusion Individuen-basierter Ansätze bei der Verwendung funktioneller Merkmale, sowie für die Berücksichtigung der kleinräumigen, komplexen Interkationen von oberirdischen und unterirdischen Prozesse. Meine Ergebnisse zeigen, wie wichtig die Konservierung der lokalen Diversität ist. Außerdem betonen sie die Bedingungen und Grenzen unter welchen sie in Interaktion mit weitern Umweltbedingungen vorteilhaft für das Wachstum und die Anpassungsfähigkeit von Bäumen ist. Diese Dissertation leistet deshalb einen bedeutenden Beitrag zu einem besseren Verständnis der Mechanismen hinter BEF Zusammenhänge, hat aber auch generellere Implikationen, die uns erlauben werden die Zukunft von Walkökosysteme nachhaltig zu gestalten.

# CHAPTER 1

## General Introduction

### 1) Biodiversity and the functioning of ecosystems

Anthropogenic activities are affecting ecosystems globally. Since the beginning of the industrial era, ecosystem functions are being thereby disrupted at a consistently accelerating rate (IPCC 2021). However, human well-being depends on resources and functions provided by ecosystems in the form of ecosystem services. Ecosystem services have a variety of benefits, including holding cultural values, regulating air and water purification, biomass production and crop pollination. Because our survival relies on services provided by ecosystems, it is essential to preserve and thus to understand their functioning and how it is shaped and modified by environmental drivers.

Forest ecosystems in particular have a major importance in providing such services, both because of their global distribution, covering about a third of all emerged terrestrial surface, and their potential for climate mitigation (i.e., temperature and precipitation regulation, albedo modification, carbon sequestration; FAO 2022). In addition, forests foster a particularly important share of the world's biodiversity (Brockerhoff et al., 2017). Biodiversity, in turn, has been found to promote forest multifunctionality, that is, the simultaneous benefit of several ecosystem functions such as productivity and climate regulation (Gamfeldt et al., 2013; Schuldt et al., 2018).

Indeed, biodiversity is a crucial factor influencing ecosystem functioning. Over the last decades, this has motivated research aiming at identifying how biodiversity affects ecosystem functions. Early findings of positive biodiversity-ecosystem functioning (BEF) relationships in grasslands have been later accompanied by a large body of work that documents similarly enhanced ecosystem functioning in forests (Hooper et al., 2005; Tilman et al., 1997). Such studies often focuses on the effect of species richness on one critical ecosystem function: forest productivity (Duffy et al., 2017; Liang et al., 2016; Paquette & Messier, 2011). In particular, an increased tree species richness has been found to cause overyielding (Huang et al., 2018), that is, that species-rich forest mixtures were more productive than the average of their respective monocultures (Fichtner et al., 2018; Pretzsch & Schütze, 2009). These positive effects of biodiversity have been attributed to several processes, the most prominent one being niche complementarity, which includes resource use partitioning and interspecific facilitation (Tilman et al., 2001).

Resource use partitioning is a consequence of different species having different resource needs, resulting in a reduced competition for resources as well as a better total utilization of the available resource pool in species mixtures compared to monocultures. For example, as species have different crown architectures, trees of different species occupy different space aboveground, reducing the spatial overlap and thereby competition for incoming light when grown in a mixture (Kunz et al., 2019). When compared to monocultures, the total amount of intercepted light is therefore higher (Binkley et al., 2013). In addition, the difference between species can result in one modifying the environmental conditions in a way that benefits another. This so-called facilitation occurs for example when a species provides a buffer against extreme temperatures or a specific microclimate that is beneficial for another species (A. J. Wright et al., 2017).

While niche complementarity in particular has been dominating the literature as the mechanism behind positive diversity effects (Barry et al., 2019), in forests, a variety of other factors has been found to be involved. For example, increased litter diversity, litter abundance or decomposition (Beugnon et al., in prep.; Huang et al., 2017), increased diversity and activity of soil fungal and bacterial communities (Singavarapu et al., 2021), or reduced rates of pathogens and herbivores damages as the diversity of host tree species increases (Jactel et al., 2021; Rottstock et al., 2014) have been repeatedly associated with positive diversity effects. However, despite this diversity of mechanisms proposed as driving BEF relationships, their role and interactions remain largely unclear and are therefore often only speculative.

## 2) The functional approach: traits as tools for disentangling the BEF relationship

To face the complexity and difficulty of understanding the processes underlying BEF relationships, functional traits have emerged as a powerful and practical tool. Indeed, functional traits, plant characteristics measured at the individual level which affect their performance through growth, survival and reproduction (Violle et al., 2007), are widely used as summarizing and generalizing descriptors of plant physiology and as proxies of ecosystem functions. Relatively easy to measure, and correlating with multiple major ecosystem functions such as productivity and nutrient cycling, leaf traits in particular have become prominent for translating the effect of environmental changes on the ecosystem. For example, specific leaf area (SLA) or leaf nitrogen content are often used to infer on biomass production and growth, as they correlate with intercepted light energy and photosynthetic rates (Poorter et al., 2006).

While single traits can be related to specific functions, a combination of traits can describe more abstract plant characteristics which can be captured in trade-off axes. For example, the leaf economics spectrum (LES; I. J Wright et al. 2004) is based on a trade-off of the species' leaf durability and ability to exploit resources. Going from conservative, slow-growing species investing their resources in long-lasting leaves, to acquisitive, fast-growing species having a fast resource uptake and turnover, the LES therefore synthesizes species resource allocation strategies (Reich, 2014). According to the LES, species growing in an unfavourable environment (i.e., intense stresses, frequent disturbances, poor soil resource availability) tend to have a more conservative strategy, investing in structures that can withstand stressful conditions. In a more favourable environment, acquisitive species are more likely to thrive, producing biomass at a fast rate. Hence, traits, while partly inherent to a species' identity and strategy, can be heavily modified by biotic and abiotic environmental conditions.

As traits respond to different factors such as changing light conditions and herbivory rates, all of which change with plant biodiversity, traits are able to capture plants responses to varying species diversity. Indeed, species interactions, through competition and niche complementarity (namely resource-use partitioning and facilitation as described above), modify the plants growing conditions both aboveground (e.g., light availability gradient, space use, microclimatic variables) and belowground (e.g., nutrient availability and accessibility, interactions with the soil community). In addition, varying amounts of resources and interactions with soil biota and conditions directly affect traits. Indeed, plant growth depends on the quantities and forms of available nutrients, but also on the actors within the soil community that can modify both, and intervene in positive (mutualistic, commensalistic) or negative (competitive, pathogenic) interactions (reviewed by Eisenhauer, 2012). For example, while soil microorganisms compete with plants for nutrient uptake, they are themselves part of a so-called microbial loop in which they are consumed by other soil organisms, hence freeing nutrients, and consequently regulating their accessibility for plants (Bonkowski, 2004).

To quantify plants' resource allocation strategies and responses to changes in their environment, traits typically have been used as averaged values, most often describing species. However, as traits respond to changing biotic and abiotic conditions, they are not fixed, but vary, both intrinsically as part of the genetic differences between individuals, populations or species, and in the expression of their genotype (i.e., phenotype plasticity). This variation of traits has essential implications for the plant's potential to survive and persist in different environments, and to face changing environmental conditions. Using species' traits to explain and forecast ecological processes has been considered a 'Holy Grail' in ecology (Funk et al., 2017; Lavorel & Garnier, 2002). With species in focus, community ecology has scaled up trait compositions to explain the functioning of ecosystems (Dıá z & Cabido, 2001; McGill et al., 2006; Suding et al., 2008). Many established practices in trait-based approaches, such as the assumption of the highest proportion of variation being between species, or the wide use of community-weighted means as a general characterizer for environment-trait associations, are based upon the prominence of the species perspective. However, the acknowledgment of ecological subscales' importance has been growing in the last decade. In particular, trait variation within-species has challenged the classic species focus, as awareness of the subtleties regarding coexistence, functional diversity or response to environmental variation has been raising (Albert et al., 2012; Hart et al., 2016; Lepš et al., 2011).

Yet, the individual perspective has not benefitted from such resurgence of interest, and remains largely understudied. Indeed, while highlighted as one of the main knowledge gap for trait-based approaches (Münkemüller et al., 2020; Stump et al., 2021), studies integrating or focusing on the individual scale are scarce. Multiple aspects of functional traits, however, render this scale as highly relevant. Firstly, traits are defined at the level of the organism, capturing the basis of the response that ultimately results in the patterns observed at the level of the ecosystem. Secondly, the individual constitutes the smallest 'self-standing', indivisible ecological unit, and also embodies the link between the genotype and higher ecological scale, enabling to widen the use of evolutionary and genetic theories to the functioning of the ecosystem (Fontana et al., 2014). Moreover, biotic interactions occur at the scale of the individual, hence additionally highlighting the importance of local biotic and abiotic conditions, for example in the context of tree-tree interactions.

The individual scale is hence an untapped resource of information for improving our knowledge of what drives trees' ecological strategies, variability, and their role within interactions. However, investigating BEF relationship from the individual perspective comes with its specific challenges, ranging from the high resolution of data that it requires, to the lack of a general theoretical framework in which to embed empirical observations. To systematically study the effects of biodiversity on ecosystem functioning, tree diversity experiments provide an ideal environment, as they manipulate diversity, while controlling for tree density, ontogenic variation, and providing limited environmental heterogeneity (e.g., edaphic conditions, climatic variation; Jucker et al., 2016; Trogisch et al., 2021). Specifically, because trees are long-lived, larger in size, and interact in broader spatial and temporal scales (Scherer-Lorenzen et al., 2005), forest BEF experiments offer adequate conditions to investigate trait and trait variation insights at the individual level.

## 3) Outline of the thesis

This thesis aims at disentangling the effects of species diversity on tree-tree interactions at the local scale, using a trait-based approach. To address the pressing knowledge gap of the sub-specific scales, I adopted the individual perspective, an ecological scale particularly relevant for investigating local processes and pairwise interactions of trees. To do so, I used both mean traits, for inferring on trees' growth strategies, and trait variation, for assessing the adaptive capacity of individuals, in response to changes in their environment. I focused on two drivers: tree species diversity, and soil conditions, specifically nutrient availability and soil microorganisms. I investigated these effects in the BEF-China tree diversity experiment, in subtropical China. In addition, to tear apart the patterns observed in the field, I pushed my initial questions further in an experiment under controlled conditions in a greenhouse, partially mirroring the field setting. In order to tackle the large number of samples required to properly investigate intra-individual effects (several thousands of leaf samples in each study, encompassing eight to 16 tree species), I used optical spectroscopy, a high-throughput method enabling the prediction of trait values from a reduced number of measured samples.

In **Chapter 2**, *"Intra-specific leaf trait responses to species richness at two different local scales"*, I investigated the effect of the species identity of the closest neighbour and the species richness of the surrounding neighbourhood on individual trees' growth strategy. In Site A of the BEF-China experiment, I used systematic interactions of 16 tree species within 216 pairs of trees and surrounding neighbours of the pairs, and assessed means for each tree of nine leaf traits correlating with the leaf economics spectrum. I hypothesized that (I) increasing species richness, both of the closest neighbour from the focal tree and surrounding neighbours further away, results in a shift toward an acquisitive growth strategy, and that (II) this shift with increasing species richness of the surrounding neighbours is most pronounced when the closest neighbouring tree belongs to the same species than the focal tree.

In **Chapter 3**, *"High within-tree leaf trait variation and its response to species diversity and soil nutrients"*, I focused on the variability of leaf traits of over 400 trees from 14 species, in Site B of the BEF-China experiment. I first quantified the amount of variation within trees, compared to between trees and between species. Then, considering two local scales (our focal tree and its closest neighbour, as well as the ten neighbours surrounding this pair), I asked how species diversity affects individual trees' trait variation depending on the available belowground resources. In this specific location, edaphic conditions were notably different from average tropical and subtropical soils, with a high acidity, a low fertility and in particular a very low soil phosphorus content. Building up on the results of **Chapter 2**, I specifically tried to clarify how soil nutrient availability constrains or promotes positive diversity effects. I expected that (I) within-tree trait variation represents a considerable share of intraspecific variation, that (II) within-tree trait variation increases with increasing soil nutrient availability, that (III) within-tree trait variation is greater for trees with a closest neighbour from the same species, and increases with increasing diversity of the surrounding neighbours, and finally that (IV) positive effects of soil nutrient availability and species diversity both at the tree pair's and surrounding neighbourhood's scales amplify each other.

In **Chapter 4**, *"Species diversity effects on within-tree traits and variation depend on soil conditions"*, I decomposed soil conditions into two key aspects, soil microbiota presence and soil phosphorus availability for plants in order to understand the interactive effect of soil conditions and species diversity. Specifically, I asked how species diversity affects both individual trees' growth strategies and their variation depending on belowground resources and species' native microbiota. For looking into this complex interaction, I reduced potential environmental interference by using a greenhouse setting, in which soil conditions and diversity are systematically manipulated. Using a subset of the subtropical species studied in **Chapter 2** and **Chapter 3**, I focused again on pairwise tree interactions. Bringing together observations from the field, I hypothesized that (I) species diversity increases trees acquisitiveness, and this effect is enhanced by an increase in nutrients (phosphorus fertilization) as well as an increase in access to nutrients (soil inoculation with the species' native microbiota). In addition, I expected that (II) within-tree variation decreases with species diversity, but this relationship is inversed through an increase in nutrients (phosphorus fertilization) or a better access to nutrients (through soil inoculation with microbiota).

Finally, in **Chapter 5**, I propose a synthesis of the presented studies and their results, bringing together the effects of diversity at local scales for tree-tree interactions and how they depend on soil conditions. I expand on how my results, from trait syndromes and trait variation, enables to understand the implications of species diversity and belowground resources' effects on trees' resources allocation strategies and adaptability to biotic and abiotic modifications of their environment. With the basis of my findings, I discuss the integration of my work within functional ecology, and its implications for understanding and preserving forest ecosystems.

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# CHAPTER 2

## Intra-specific leaf traits responses to species richness at two different local scales

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# Intra-specific leaf trait responses to species richness at two different local scales

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## Abstract

Plant functional traits, especially leaf traits, are accepted proxies for ecosystem properties. Typically, they are measured at the species level, neglecting within-species variation. While there is extensive knowledge about functional trait changes (both within and across species) along abiotic gradients, little is known about biotic influences, in particular at local scales. Here, we used a large biodiversity-ecosystem functioning experiment in subtropical China to investigate intra-specific trait changes of 16 tree species as a response to species richness of the local neighbourhood. We hypothesized that because of positive complementarity effects, species shift their leaf traits towards a more acquisitive growth strategy, when species richness of the local neighbourhood is higher. The trait shift should be most pronounced, when a focal tree's closest neighbour is from a different species, but should still be detectable as a response to species richness of the directly surrounding tree community. Consequently, we expected that trees with a con-specific closest neighbour have the strongest response to species richness of the surrounding tree community, i.e., the steepest increase of acquisitive traits. Our results indicate that species diversity promoted reduced competition and complementarity in resource use at both spatial scales considered. In addition, the closest neighbour had considerably stronger effects than the surrounding tree community. As expected, trees with a con-specific nearest neighbour showed the strongest trait shifts. However, the predicted positive effect of local hetero-specificity disappeared at the highest diversity levels of the surrounding tree community, potentially resulting from a higher probability to meet a strong competitor in a diverse environment. Our findings show that leaf traits within the same species vary not only in response to changing abiotic conditions, but also in response to local species richness. This highlights the benefit of including within-species trait variation when analysing relationships between plant functional traits and ecosystem functions.

*Keywords:* Trait-based ecology; Plant functional traits; Intraspecific trait variability; BEF-China; Diversity effects; Complementarity; Subtropics

## Introduction

Functional ecology is based on the assumption that functional traits are related to ecosystem properties (Díaz & Cabido, 2001; Ebeling et al., 2014). A prominent example is that plants are more productive when possessing high values for

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traits related to efficient photosynthesis, such as high specific leaf area or high leaf nitrogen concentration (Reich, Ellsworth, & Walters, 1998; Reich, Walters, & Ellsworth, 1997). Since ecosystem functions are typically assessed at the plant community level, trait measures usually summarize individual species' trait values and thus also refer to this scale. For example, community weighted means (CWMs) are calculated by using average species' trait values and the species' abundances within the community to describe the mean trait value of the community (Lavorel et al., 2008).

This approach presumes that traits mainly vary across species, but ignores that traits also vary within species (Albert et al., 2010; de Bello, Carmona, Mason, Sebastià, & Lepš, 2013; Lemmen, Butler, Koffel, Rudman, & Symons, 2019). In fact, within-species trait variation has been estimated to represent up to 25% of the total amount of trait variation within communities (Siefert et al., 2015). However, trait differences within the same species are still less frequently addressed compared to trait differences across species, despite their importance being increasingly recognised (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; de Bello et al., 2011; Messier, McGill, & Lechowicz, 2010; Read, Henning, & Sanders, 2017; van Ruijven & Berendse, 2005). Trait differences within the same species might occur along environmental gradients (Anderson & Gezon, 2015; Fajardo & Siefert, 2018; Helsen et al., 2017; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013), for example in response to changing light (Derroire, Powers, Hulshof, Cárdenas Varela, & Healey, 2018; Williams, Cavender-Bares, Paquette, Messier, & Reich, 2020), temperature (Kühn, Ratier Backes, Römermann, Bruelheide, & Haider, 2021), humidity (Kessler, Siorak, Wunderlich, & Wegner, 2007), soil nutrients (Pérez-Ramos et al., 2012) or moisture (Cornwell & Ackerly, 2009). Additionally, but addressed only on rare occasions, traits can adjust to their biotic environment, for example to the plants in their direct surroundings (Le Bagousse-Pinguet et al., 2015; Proß et al., this issue).

Because all plant species need a common base of resources (light, water, nutrients), competition is the main type of plant-plant interaction (Connell, 1983; Gause, 1934; Wright, Schnitzer, & Reich, 2014). It is widely established that competition is strongest between individuals of the same species, as their needs and uptake pathways are identical (Adler et al., 2018; Barabás, J. Michalska-Smith, & Allesina, 2016; Metz et al., 2013; Uriarte, Condit, Canham, & Hubbell, 2004). Inversely, differences in the way various species exploit these resources (that is, resource use complementarity) might reduce the level of competition (Barabás et al., 2016; Cardinale et al., 2007; Loreau & Hector, 2001). Such niche partitioning might arise through functional differences, for example, in shade tolerance (del Río, Bravo-Oviedo, Ruiz-Peinado, & Condés, 2019; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Van de Peer, Verheyen, Ponette, Setiawan, & Muys, 2018). In addition, combinations of species are known to enable positive interactions (facilitation) between them, with certain species creating abiotic conditions beneficial for another species in the direct neighbourhood, for example by mitigating a stressful environment (Steudel et al., 2012).

The assumption that competition and facilitation happen within the local neighbourhood (Adler et al., 2018; Barabás et al., 2016; Trogisch et al., this issue) entails that local species richness should directly affect a plant's trait values. High competition from con-specific neighbours should lower the amount of a specific (form of a) resource available to an individual (Pornon, Escaravage, & Lamaze, 2007; Pretzsch, 2014). This resource limitation might result in slow growth and high carbon investment in leaves, and thus in an increase of traits related to a conservative growth strategy (e.g. high leaf dry matter content and high leaf carbon content; Reich, 2014). On the other hand, reduced competition between different neighbouring species might lead to faster growth and an increase of traits related to an acquisitive growth strategy (e.g. high specific leaf area and high leaf nutrient content; Díaz et al., 2004; I. J. Wright et al., 2004).

Because the resources available for a specific individual are located where the plant is growing, competition should be highest between the plant and its closest neighbour (Adler, HilleRisLambers, & Levine, 2007). Competition should be less strong, while still important, between the plant and neighbours that are further away (Chesson, 2000). The higher the number of species around a focal plant, the more we expect complementarity in resource use (Bastias et al., 2020; Ratcliffe et al., 2017), and thus a shift towards traits associated with an acquisitive growth strategy. Hence, with increasing species richness of the surrounding plant community, we expect the strongest trait responses for focal plants adjacent to a con-specific neighbour (Fig. 1).

Tree diversity experiments are a useful setting to study within-species changes of functional traits as a response to species richness of the local neighbourhood. Because trees are long-lived plants, it is specifically important for them to adjust to local conditions, as opposed to short-lived organisms, such as many forb and grass species, which could adjust through generation turnover. In addition, the target factor, species richness, is manipulated while all other conditions are kept as constant as possible. In particular, tree density and tree species richness are not confounded in tree diversity experiments, because trees are always planted at the same distance (Trogisch et al., 2017). Thus, it is possible to investigate the trait responses of the same species (here referred to as the intra-specific trait response) to different diversity levels of the local neighbourhood in a standardized way.

For this study, we used the largest tree biodiversity-ecosystem functioning (BEF) experiment worldwide, BEF-China (Bruelheide et al., 2014), to understand how tree species richness of a focal tree's local neighbourhood modifies the focal tree's functional leaf traits, and thus how species richness drives intra-specific trait responses. We hypothesized (Fig. 1):

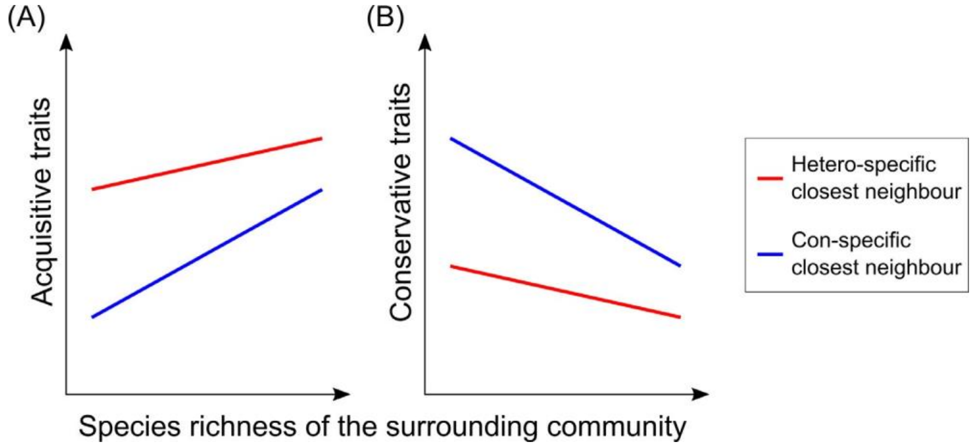

Fig. 1. Expected effects of species richness of the surrounding tree community on leaf functional traits related to (A) an acquisitive and (B) a conservative growth strategy. We hypothesize a stronger effect (steeper slope) for trees with a con-specific closest neighbour (blue lines) compared to trees having a hetero-specific closest neighbour (red lines).

i) Increasing species richness of the local neighbourhood leads to an increase in traits associated with an acquisitive growth strategy. This applies to the closest neighbouring tree as well as to the surrounding tree community.
ii) Trait shifts towards an acquisitive growth strategy with increasing species richness of the surrounding tree community are stronger if the closest and thus most impactful neighbour is a con-specific tree.

## Materials and methods

### Study site

Our study was conducted in the BEF-China tree diversity experiment located near Xingangshan, Jiangxi Province, Dexing County in southeast China (29°08$^0$–29°11$^0$N, 117°90$^0$–117°93$^0$E). This subtropical region has a mean annual temperature of 16.7°C and a mean precipitation of 1821 mm per year. The experiment consists of two distinct sites, established in 2009 (Site A) and 2010 (Site B), totalling 566 plots. In this study, we focused on Site A, spread over 26.6 ha with an elevation ranging from 105 to 275 m a.s.l. and a slope ranging from 8.5 to 40 degrees. We visited 69 plots of Site A, where each plot is a 25.8 m x 25.8 m square in which 400 trees are equally spaced 1.29 m apart, in a regular grid arrangement. We used trees belonging to 16 species native to the region (see Appendix: Table A.1), that were planted along a species richness gradient of 1, 2, 4, 8, and 16 species per plot. The species were arranged following a “broken-stick design”, in which the highest diversity level of 16 species is split into two equal groups at each of the following richness levels; that is, from the 16-species mixture down to the monoculture. Consequently, all species are equally represented at every species richness level (see Bruelheide et al., 2014; see Appendix A: Table A.2). Since species are randomly divided at every level of diversity bisection, the BEF-China experiment represents a random extinction scenario.

### Sampling design

Within the broken-stick design, we focused on four groups of four species each. For each group of four species we considered all ten possible combinations of two species, hereafter called ‘tree species pairs’ (TSPs): four con-specific TSPs (AA, BB, CC, DD) and six hetero-specific TSPs (AB, AC, AD, BC, BD, CD). These ten TSP combinations were sampled in the four-, eight- and 16-species mixtures (Fig. 2). In each of the two-species mixtures, we used all three possible TSP combinations (AA, BB, AB). Having eight different two-species mixtures, this resulted in a total of 24 different TSP combinations. Additionally, we sampled con-specific TSPs in all 16 monocultures (see Appendix A: Table A.2). To ensure a sufficient number of repetitions for each TSP combination, the pairs were replicated three times in the two-species mixtures and the monocultures, adding up to 240 TSPs included in the study.

At the time of leaf sample collection, height of the trees included in the study ranged from 1 m up to 12 m approximately, with 80% of the TSPs having overlapping or at least partially overlapping crowns. Because leaf samples for both TSP partners were collected along the vertical plane between the two trees, where their crowns were in contact or at least very close to each other (Fig. 2), we refer to the TSP partner of a focal tree as its 'closest neighbour', although all trees were planted in a grid and in the same distance to each other. We investigated leaf traits of a focal tree as a response to the tree’s TSP diversity, i.e. its closest neighbour (the TSP partner) being either con-specific or hetero-specific. Additionally, we determined the TSP’s local neighbourhood species richness, i.e., the number of different species within the

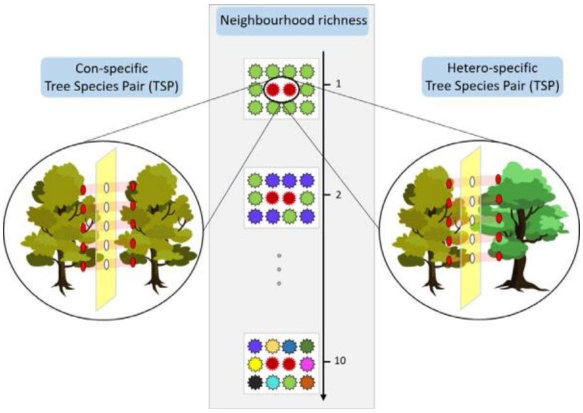

Fig. 2. Illustration of the sampling design. Sixty-nine plots were visited across Site A of the BEF-China experimental platform to collect leaves from selected Tree Species Pairs (TSPs). TSPs were surrounded by a gradient of neighbourhood species richness, theoretically ranging from one to ten species (star-shapes represent trees, red star-shapes represent TSP partners, other colours represent different species). For each neighbourhood richness level, con-specific and hetero-specific TSPs were sampled: at three to five sampling points (red dots) along the interaction plane between the trees, leaves were collected for each TSP partner and pooled as one sample for each tree.

group of the up to ten trees directly surrounding the TSP according to the grid plantation (Fig. 2). Due to mortality in the 16-species mixtures, the TSPs' local neighbourhood species richness reached at maximum eight different species for ten trees around the TSP.

Because of the random position of the tree species within the plots and the species' various survival rates depending on their environment, not all planned combinations were found in sufficient number. In addition, some tree crowns were too damaged (pathogen infestation, herbivory), too small to sample leaves without endangering the survival of the tree, or simply could not be reached by our means (over 12 m). As a result, the theoretical number of 240 TSPs was reduced to 216 TSPs. The exclusion of outlying samples from the laboratory processing led to a final number of TSPs between 209 and 216, depending on the trait considered.

## Leaf sample collection

Leaf sampling took place from late August to early October 2018. From each tree included in our study design, we collected leaves within the interaction plane between the focal tree and its TSP partner (the vertical plane where the two crowns of the TSP partners were in contact or at least close to each other). To ensure a representative mean trait value for each tree, we sampled at three to five different heights along the interaction plane (Fig. 2). At each height, we cut three fully developed leaves free from mechanical or pathogen damage. Immediately after collection, leaves were conserved in sealable plastic bags with tissues humidified with water. The samples were transported in an isothermal bag in which the temperature was kept cool with the help of ice blocks. In the laboratory, the samples were temporarily stored at +5°C.

In addition, we collected a so-called calibration set, in order to predict the regular samples' trait values (leaf samples from the TSPs) based on the relationship between reflectance spectra and measured trait values of the calibration set (see below for detailed use). The calibration set was composed of ten leaf samples per species across all plot species richness levels, collected at random heights and orientation within the crown (236 samples in total). Care was taken that the trees chosen for collecting these extra samples (referred to as "calibration samples") were not part of a TSP, and otherwise randomly chosen within the 400 trees of each plot. These calibration samples counted enough leaves to reach a minimum of 2 g of dry leaf powder per sample (between 10 and 25 leaves depending on the species). Calibration samples were transported and stored in the same way as described above for the regular samples.

## Leaf near-infrared reflectance spectroscopy

Because of the high number of leaf samples from the TSPs (>2000 samples) and because leaf material of each sample would not have been sufficient to conduct all chemical analyses in the laboratory, we used the high-throughput method of near-infrared reflectance spectroscopy to predict leaf trait values based on calibration models (Foley et al., 1998). For all leaves (regular samples and calibration samples), we acquired reflectance spectra with an ASD FieldSpec® 4 High Resolution Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom) between six to twelve hours after collection in the field. Reflectance was measured across the full range of solar irradiance (250-2500 nm), by taking three repeated measures on the adaxial side of each leaf while avoiding main veins. The equipment was optimized regularly with a calibration panel (Spectralon®, Labsphere, Durham, New Hampshire, USA). For each measurement, ten spectra were averaged internally to reduce the noise resulting from light scattering.

## Processing and laboratory analyses of calibration samples

The saturated fresh leaves of each calibration sample were weighed (DeltaRange Precision Balance PB303-S, Mettler-Toledo GmbH, Gießen, Germany) and scanned with a resolution of 300 dpi. From the resulting images, leaf area was analysed with the WinFOLIA software (Regent Instruments, Quebec, Canada). After drying for 72 hours at 80°C, leaves were weighed again. Leaf dry matter content (LDMC; leaf dry mass / leaf fresh mass) and specific leaf area (SLA; leaf area / leaf dry mass) were calculated (Pérez-Harguindeguy et al., 2013).

The dried leaves were then ground into fine powder (Mixer Mill 400, Retsch, Haan, Germany). From this powder, 200 mg were used for a nitric acid digestion. The resulting filtrate was analysed with atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany) for Mg, Ca and K content, and through a spectrophotometric assay using the acid molybdate technique for P content. Finally, 5 mg of leaf powder were used to determine C and N content with an elemental analyser (Vario EL Cube, Elementar, Langenselbold, Germany) from which the leaf C:N ratio was derived.

## Leaf spectra prediction model

Leaf spectra of the calibration samples were analysed in the Unscrambler X (version 10.1, CAMO Analytics, Oslo, Norway). In order to reduce noise and highlight relevant information from the spectra, different pre-treatments were applied to the original data. Spectra were then used to fit a Partial Least Square regression model (PLS) with the NIPALS algorithm (Dayal & Macgregor, 1997), where each PLS model was used to predict the regular samples' trait values. Models were selected based on their quality (higher $R^2$ value; lower Root Mean Square Error), parsimony (lower number of factors), and accuracy in predicting measured laboratory values of the calibration samples (higher $R^2$ predicted vs. reference value; Table 1). All models were kept for prediction despite some relatively low fit, as this approach does not increase the risk of getting false positive correlations.

## Statistical analyses

Statistical analyses were realised in R version 3.6.3 (R Core Team, 2020). For each trait, a linear mixed-effects model (R package 'lmerTest'; Kuznetsova, Brockhoff, & Christensen, 2017) was fitted with mean trait values for each tree as response variable. Each trait was explained by the following fixed effects: the TSP diversity (con- vs. hetero-specific TSP partner), the local neighbourhood species richness (i.e. number of species surrounding the TSP), and their interaction. Additionally, the height difference between the two TSP partners, expressed proportionally to the focal tree’s height, was included as a covariate. Negative values of height difference indicate that the focal tree was smaller than its TSP partner, positive values indicate that the focal tree was taller than its TSP partner. As random effect, TSP identity (i.e., the TSP identification code) was nested into plot identity (i.e., the plot identification code), and species identity of the focal tree was added separately as crossed random factor. All random effects were structured as random intercept with fixed mean. P-values were calculated from F-statistics of type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom. In addition, we assessed the initial difference in traits between con-specific and hetero-specific TSPs in their response to neighbourhood species richness. Therefore, the same linear mixed-effects models were fitted, but with neighbourhood species richness starting with one instead of zero (i.e., neighbourhood richness -1). In this model, the intercept represents the trait values for trees of hetero-specific TSPs at neighbourhood richness of one, with no difference in height to the TSP partner.

Table 1. Overview of the functional leaf traits analysed in this study and properties of the Partial Least Square regression models (PLS) used for the prediction of leaf traits based on near-infrared reflectance spectra. The last column indicates which pre-treatments were applied to the spectra before using them in the PLS models. Abbr.: trait abbreviation; $R^2$: coefficient of determination calculated from the explained variance of the validation set of the models (fit of the prediction model); $R^2$ pred. vs. ref.: coefficient of determination calculated from the explained variance when comparing predicted values from the model (pred.) and laboratory values (ref.) of the same samples; RMSE: Root Mean Square Error of the prediction model (lower values indicate a better quality of the model).

| Trait | Abbr. | Unit | Associated growth strategy | $R^2$ | Number of factors in the PLS model | RMSE | $R^2$ pred. vs. ref. | Pre-treatment of spectra |
|---|---|---|---|---|---|---|---|---|
| Specific leaf area | SLA | $mm^2/mg$ | acquisitive | 88.9 | 5 | 22.0 | 89.9 | Standard normal variate |
| Potassium content | K | mg/g | acquisitive | 24.2 | 4 | 0.2 | 27.1 | Normalisation |
| Phosphorus content | P | mg/g | acquisitive | 59.8 | 9 | 0.3 | 69.9 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |
| Nitrogen content | N | % | acquisitive | 83.7 | 9 | 0.2 | 83.7 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |
| Magnesium content | Mg | mg/g | acquisitive | 63.9 | 5 | 1.1 | 60.9 | Orthogonal signal correction |
| Calcium content | Ca | mg/g | acquisitive | 53.5 | 12 | 2.4 | 64.3 | Savitzky-Golay 2nd derivative |
| Leaf dry matter content | LDMC | mg/g | conservative | 81.7 | 8 | 37.8 | 84.4 | Savitzky-Golay 2nd derivative |
| Carbon content | C | % | conservative | 65.0 | 7 | 1.1 | 70.0 | Orthogonal signal correction |
| Carbon to nitrogen ratio | C:N | g/g | conservative | 81.8 | 8 | 3.3 | 84.2 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |

For each trait, we used the “calcVarPart” function within the “variancePartition” package (Hoffman & Schadt, 2016) on the results of the firstly described linear mixed-effects models to derive the amount of variance explained by each fixed and random effect and the covariate, and thus assess their relative importance. The fraction of explained variance by one of the variables corresponds to the correlation between the response trait and the respective predictor after correcting for all other variables included in the model.

## Results

SLA, leaf K, leaf P and leaf N contents were significantly higher (marginally significant for leaf N; Table 2) for hetero-specific TSPs compared to con-specific TSPs (Fig. 3B, D, F, H). In contrast, con-specific TSPs had significantly higher LDMC and leaf C content (Fig. 3J; see Appendix A: Fig. A.1F; marginally significant for leaf C content; Table 2). We found an overall increase of SLA and leaf K content, as well as a marginal increase of leaf Mg content with increasing neighbourhood species richness across all trees studied (Fig. 3A and C; see Appendix A: Fig. A.1A; Table 2).

Con-specific TSPs presented a stronger increase of SLA, leaf K, leaf P and leaf N content with increasing neighbourhood richness compared to hetero-specific TSPs (Fig. 3A, C, E, G). Similarly, for LDMC (and, to a marginal extent, for leaf C content), con-specific TSPs showed a decrease with neighbourhood richness more pronounced than hetero-specific TSPs (Fig. 3I; see Appendix A: Fig. A.1E). Leaf Ca content and leaf C:N showed no clear pattern regarding either the overall effect of neighbourhood species richness or the TSP diversity (see Appendix A: Fig. A.1 C-D and G-H).

Differences in height between the focal tree and its partner had a significant effect on the structural traits (SLA, LDMC) as well as on leaf K, leaf P and leaf Mg contents (Table 2). However, the effects of the TSP partner and neighbourhood species richness did not change whether the height difference was included in the models or not (results not shown).

The intercepts of con-specific TSPs were found significantly different or marginally significantly different from those of hetero-specific TSPs for all traits but leaf C:N, leaf Mg and leaf Ca content. For the acquisitive traits (SLA, leaf K, leaf P and leaf N contents), con-specific TSPs showed lower intercepts than hetero-specific TSPs, while for conservative traits (LDMC and leaf C) we observed the contrary (see Appendix A: Table A.3).

Table 2. Results of the linear mixed-effects models analysing the interacting effect of TSP diversity (hetero- or con-specific) and neighbourhood species richness (i.e., the ten trees surrounding the TSP) on each leaf trait. The height difference (Height diff.) between the focal tree and its TSP partner (relative to the height of the focal tree) was added as covariate. Significant effects at the 0.05 level are indicated in bold. Numerator degrees of freedom are all equal to one. For trait abbreviations, see Table 1. TSP div.: TSP diversity; N. rich.: neighbourhood species richness; DenDF: denominator degrees of freedom.

| Trait | Predictor | DenDF | F-value | p-value |
|---|---|---|---|---|
| SLA | Height diff. | 322.74 | 17.90 | <0.001 |
| | TSP div. | 186.25 | 5.69 | 0.018 |
| | N. rich. | 194.93 | 18.47 | <0.001 |
| | TSP div. : N. rich. | 179.52 | 7.91 | 0.005 |
| K | Height diff. | 327.56 | 10.95 | 0.001 |
| | TSP div. | 182.03 | 9.73 | 0.002 |
| | N. rich. | 197.20 | 11.90 | 0.001 |
| | TSP div. : N. rich. | 175.53 | 9.88 | 0.002 |
| P | Height diff. | 340.39 | 7.59 | 0.006 |
| | TSP div. | 195.47 | 7.62 | 0.006 |
| | N. rich. | 187.94 | 1.74 | 0.188 |
| | TSP div. : N. rich. | 188.64 | 9.55 | 0.002 |
| N | Height diff. | 375.62 | 0.81 | 0.370 |
| | TSP div. | 402.14 | 3.78 | 0.052 |
| | N. rich. | 327.89 | 1.16 | 0.282 |
| | TSP div. : N. rich. | 410.10 | 4.01 | 0.046 |
| Mg | Height diff. | 390.05 | 6.92 | 0.009 |
| | TSP div. | 361.45 | 0.95 | 0.330 |
| | N. rich. | 120.02 | 3.75 | 0.055 |
| | TSP div. : N. rich. | 383.00 | 1.64 | 0.201 |
| Ca | Height diff. | 328.61 | 0.00 | 0.987 |
| | TSP div. | 189.53 | 0.52 | 0.473 |
| | N. rich. | 175.18 | 0.00 | 0.986 |
| | TSP div. : N. rich. | 182.66 | 1.67 | 0.198 |
| LDMC | Height diff. | 325.62 | 9.32 | 0.002 |
| | TSP div. | 185.05 | 5.67 | 0.018 |
| | N. rich. | 197.94 | 3.54 | 0.061 |
| | TSP div. : N. rich. | 178.04 | 6.42 | 0.012 |
| C | Height diff. | 382.58 | 0.22 | 0.640 |
| | TSP div. | 385.89 | 3.83 | 0.051 |
| | N. rich. | 239.12 | 1.69 | 0.195 |
| | TSP div. : N. rich. | 402.64 | 3.37 | 0.067 |
| C:N | Height diff. | 331.35 | 0.04 | 0.836 |
| | TSP div. | 185.21 | 2.60 | 0.108 |
| | N. rich. | 194.59 | 1.36 | 0.245 |
| | TSP div. : N. rich. | 178.09 | 2.67 | 0.104 |

Having a closer look at how the trait variance divides between the different fixed and random effects involved in the model highlighted the predominant importance of tree species identity as well as the plot in which the TSP was located (Fig. 4A). TSP diversity, neighbourhood species richness, and their interaction explained together between 0.24% (leaf Ca content) and 6.40% (SLA) of the total trait variation (Fig. 4B). For all traits, the proportion of explained variance of the significant fixed effects (Table 2) increased from TSP diversity to the interaction between TSP diversity and neighbourhood richness and finally to the neighbourhood richness alone. These three variables had the highest effect on SLA and leaf K content (summing up to 6.40% and 6.30%, respectively) and the lowest effect on leaf C and leaf Ca content (summing up to 0.66% and 0.24%, respectively). Among the non-random effects, the height differences between the TSP partners explained the least variance,

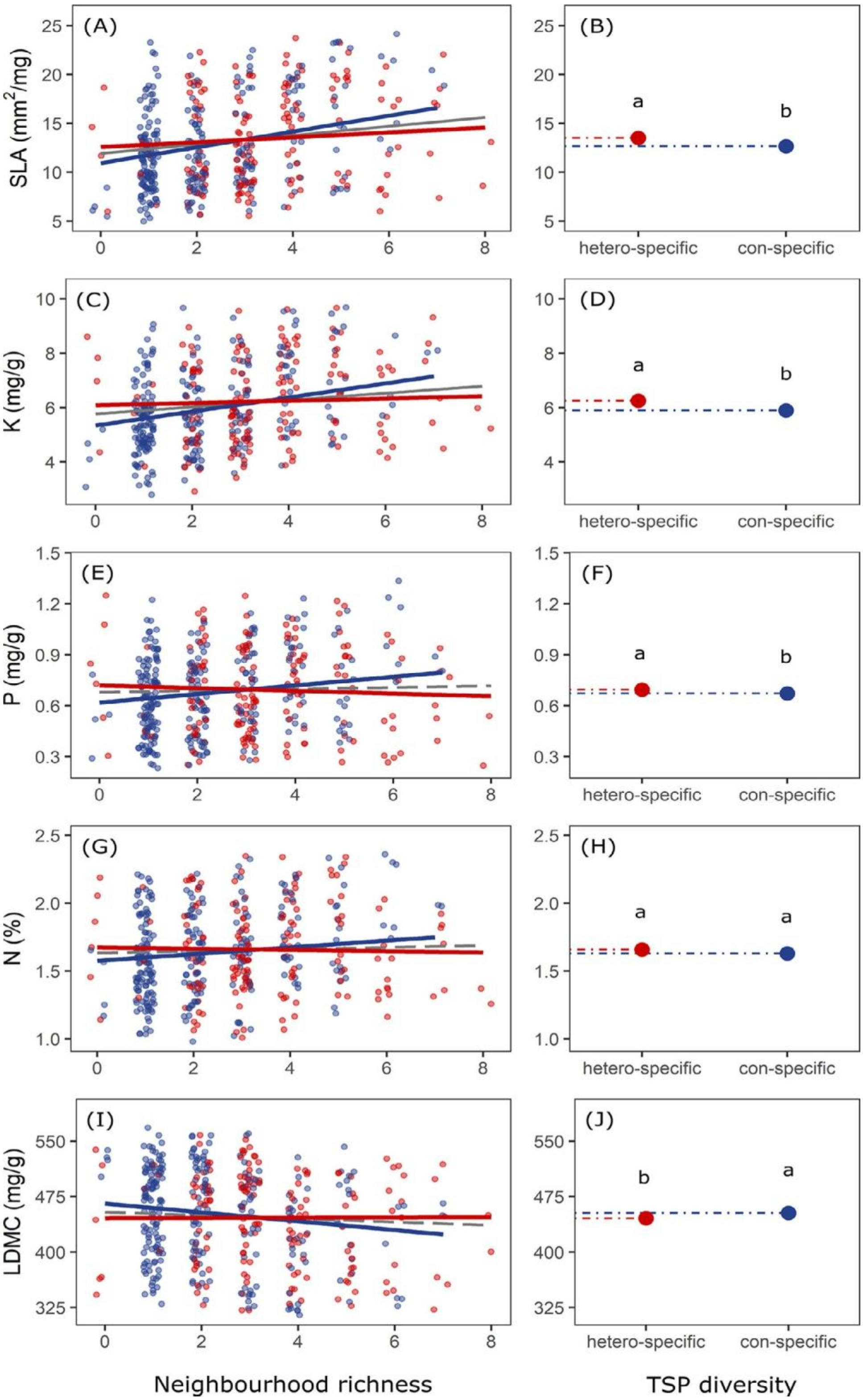

Fig. 3. Effect of the surrounding neighbourhood richness (i.e., the ten trees surrounding the TSP, see Fig. 2 for details) on acquisitive (A-H) and conservative (I-J) leaf traits. The traits displayed are those for which the interaction of TSP diversity and neighbourhood richness had a significant effect (for other traits see Appendix A: Fig. A.1). Solid lines indicate significant relationships at the 0.05 level, dashed lines represent non-significant relationships. Left: regression of the focal trees' trait values with neighbourhood richness, for TSPs in which the focal tree had a hetero-specific closest neighbour (red line and symbols), a con-specific closest neighbour (blue line and symbols), and for both TSP types together (grey line). Right: mean of the trait values depending on TSP diversity (i.e., whether the focal tree had a hetero- (red) or con-specific (blue) closest neighbour). Lowercase letters indicate a significant difference in the mean of each group (Table 2), 'a' being the higher mean.

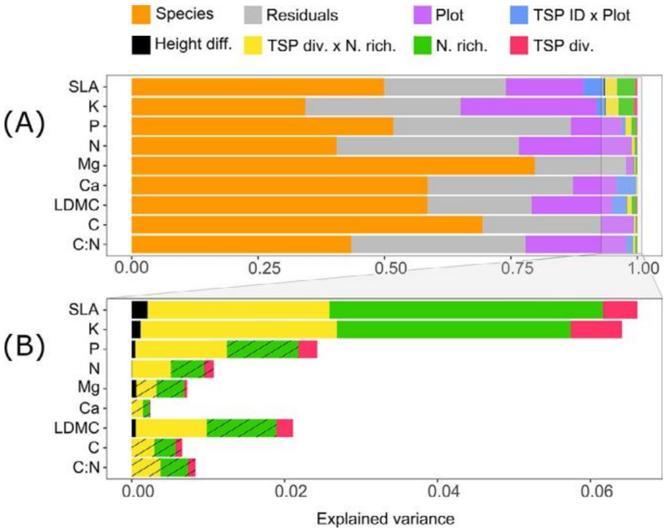

Fig. 4. Variance partitioning of the fixed and random factors of each trait's linear mixed-effects model. (A): Total variance partitioning between all variables. (B): Close-up on the variance explained by the three fixed factors of the model and the covariate. Dashed fill represents fixed factors which did not have a significant effect on the respective leaf trait (Table 2). Height diff.: height difference between the focal tree and its closest neighbour, relative to the height of the focal tree; TSP div.: TSP diversity (i.e., whether the closest neighbour within the TSP is a hetero- or con-specific individual); N. rich.: neighbourhood species richness; TSP ID: identity code of each TSP.

ranging from 0.00% (leaf Ca content, leaf C:N and leaf C) to 0.21% for SLA.

## Discussion

In this study, we investigated trait changes within 16 tree species as a response to species richness of the local neighbourhood. We consistently found that increasing species richness shifted the trait values towards a more acquisitive growth strategy, indicating that diversity leads to reduced competition among trees (Cardinale et al., 2007). We found this diversity effect both for the closest neighbouring tree (being from the same or a different species) and for the surrounding tree community. In addition, when the closest neighbouring tree was con-specific, we found a stronger shift in trait values towards an acquisitive growth strategy with increasing species richness of the surrounding tree community.

### Effects of the closest neighbour

Trees having a hetero-specific closest neighbour displayed on average higher SLA, and higher leaf P and leaf K contents, but lower LDMC. In agreement with our first hypothesis, these trait syndromes indicate that trees followed a more acquisitive growth strategy when neighbouring a different species. In particular, the increase of leaf K content, which is involved in many of the most essential physiological processes such as functioning of the photosynthetic apparatus (Tripler, Kaushal, Likens, & Walter, 2006) in combination with higher concentrations of leaf P content and (to a marginally significant extent) leaf N, indicate the potential for faster growth (I. J. Wright et al., 2005).

These findings might be explained by two different mechanisms. Firstly, hetero-specific tree species pairs might benefit from complementarity in belowground resource use (Loreau & Hector, 2001). For instance, Ashton et al. (2010) found that species grown in mixtures used different forms of nitrogen in the soil compared to the forms taken up in the respective monocultures. As a consequence of such more complete use of belowground resources, increased growth of species mixtures was observed in a plethora of studies (so called overyielding; e.g. Potvin & Gotelli, 2008; Williams, Paquette, Cavender-Bares, Messier, & Reich, 2017). The shift towards a more acquisitive growth strategy for trees with a hetero-specific neighbour might also result from aboveground spatial niche complementarity. For example, Kunz et al. (2019) showed that crown packing is denser in species mixtures compared to monocultures, and thus canopy space is used more completely. Especially in the upper part of mixed-species stands, denser crown packing can lead to a more complete use of the available light (Binkley, Campoe, Gspaltl, & Forrester, 2013). Combined with the complementary use of belowground resources as described above, this might further induce a shift towards more acquisitive traits in the whole tree, hence a higher SLA, as well as higher leaf nutrient concentrations. This can lead to increased biomass production in species mixtures as shown for example by Sapijanskas et al. (2014) in a tree diversity experiment. In addition, because of the denser crown packing in species mixtures, a greater proportion of light is captured in the upper part of the canopy, and consequently the vertical decrease of light is more pronounced and less light reaches the lower leaves. Such shade leaves are characterized by high SLA in order to maximise light capture and thus photosynthesis (Niinemets, Keenan, & Hallik, 2015). This effect might be especially important for smaller tree species for which the entirety of the crown is overshadowed by taller species, but it also applies to the bottom crown of taller species. Thus, the overall increase of SLA in species mixtures might be driven through stronger shading especially of smaller species, and an increase in above- and belowground resource use, especially through taller species.

Secondly, previous studies have also shown that species richness can provide a positive diversity effect on trees by means of facilitation, resulting in resource enrichment or abiotic buffering (reviewed by Wright, Wardle, Callaway, & Gaxiola 2017; Ammer, 2019). A reported case of facilitation is the indirect nutrient enrichment. For example, Pretzsch et al. (2010) observed that in Central European sites with low nutrient content, Norway spruce benefited from better litter decomposition and mineralization of European beech. Further, Fichtner et al. (2017) suggested that, in BEF-China, facilitation is mediated by a focal tree’s neighbours, via reduced excess irradiance, temperature buffering as well as limiting vapour pressure deficit.

## Effects of the surrounding neighbourhood species richness

The mechanisms described above apply to our findings regarding a tree’s response to its closest neighbour as well as to its response to species richness of the surrounding tree community. However, we observed fewer significant effects of the surrounding tree community compared to the effects of the closest neighbour (Table 2). This finding indicates that tree-tree interactions happen at very small scales and that competition fades over short distances (Chesson, 2000). SLA increased with increasing species richness of the surrounding tree community, which, as explained above, strengthens the role of denser crown packing and the diminished amount of light reaching the lower leaves (Sapijanskas et al., 2014). Except for leaf K content, we did not find a general response of leaf nutrient contents to species richness of the surrounding tree community. However, we observed a shift towards a more acquisitive strategy with increasing species richness of the surrounding tree community for con-specific, but not for hetero-specific tree species pairs. These findings were also displayed in the variance partitioning (Fig. 4): for SLA and leaf K content only, the explained variance was visibly larger for species richness of the surrounding tree community compared to each of the other fixed explanatory variables. In opposition, for LDMC, leaf N and leaf P content, it was the closest neighbour that determined the effect of the surrounding tree community on the traits, leading to a larger part of the variation being explained by the interaction term (TSP div. x N. rich.) rather than by the species richness of the surrounding tree community alone. We thus conclude that the closest neighbouring tree has the strongest effect on functional leaf traits, because of its direct influence and its additional impact on the further species richness effect. This emphasizes the importance of studies at smaller scales than plot level to capture these interacting effects (Messier, McGill, Enquist, & Lechowicz, 2017; Potvin & Dutilleul, 2009). Differences in the height of the two trees of a TSP did not change the strength or direction of the trait responses to species richness of both the TSP and the surrounding tree community. However, interestingly, height difference significantly affected the same traits which responded to the TSP diversity (SLA, leaf K, leaf P contents and LDMC), as well as leaf Mg content. This supports our interpretation that light plays a crucial role, since SLA significantly increased when a tree was smaller than its TSP partner and thus more shaded.

## Reversed effects at high neighbourhood richness

As expected, trait shifts towards an acquisitive growth strategy with increasing species richness of the surrounding tree community were stronger for trees with a con-specific TSP partner. The positive diversity effects described above – complementarity in resource use and through facilitation – are maximized, leading to the strongest trait responses for con-specific TSP. Since trees with a con-specific TSP partner had on average and also at the lowest neighbourhood richness level more conservative trait syndromes (Fig. 3; see Appendix A: Table A.3), we conclude that in our study the magnitude of intra-specific trait responses was not limited by species’ mean trait values. In contrast to our findings, other studies found conservative species to express less trait variability compared to acquisitive species (e.g. Böhnke & Bruelheide, 2013).

However, for trees with a hetero-specific closest neighbour we did not only predict less pronounced intra-specific trait changes along the neighbourhood species richness gradient, but in our second hypothesis we also expected that these TSPs display more acquisitive traits compared to trees with a con-specific closest neighbour at all neighbourhood species richness levels. Yet, we found this pattern only in the first half of the species richness gradient, while at the highest levels of neighbourhood species richness the situation flipped over, and trees with a con-specific closest neighbour had the more acquisitive traits. A possible explanation for this result is the effect of species number, amplified by strong species identity effects. Indeed, more species in the surrounding community involves a higher probability to meet a strong competitor among them. In addition, the imbalance in competitive strength due to differences in traits is also stronger at high diversity levels, which is supported by species identity explaining the largest proportion of variation in trait values. For weak competitors, having a hetero-specific TSP partner might then be an additional disadvantage. Similarly, another plant-plant interaction based on distance and competitive strength has been reported in the literature: intra-specific facilitation (also called intra-specific cooperation), has been studied mostly along stress gradients (Fajardo & McIntire, 2010), but also in the context of species coexistence: for example, Stoll and Prati (2001) have shown through different aggregation intensities of annual plants that weaker competitors benefit from the proximity of con-specific individuals. Even though extrapolated from different study systems, spatial aggregation effects could potentially occur at the scale of a TSP and offset intra-specific competition by intra-specific facilitation when a TSP species is poorly competitive in a high diversity environment. A mechanism suggested behind this positive effect is habitat amelioration (Fajardo & McIntire, 2010), but overall, intra-specific plant facilitation remains mostly unexplored.

## Conclusions

Previous studies have barely addressed species richness effects at the local neighbourhood scale (but see e.g. Fichtner et al., 2017), and details of the one-to-one relationship of the individual trees have not been taken into account specifically. In this context, our approach offers a new way to investigate the effects of diversity systematically along a neighbourhood richness gradient, and getting more insight from the single tree effect. In this study, we found support for both our hypotheses: our findings reveal the importance of the closest neighbour’s positive diversity effect on within-species trait changes towards a more acquisitive growth strategy, which was also found at the local neighbourhood level. However, these effects are neither linear nor converging with the increasing surrounding diversity, and underline the necessity to consider the threshold for which high diversity leads to a shift towards a slower growth strategy at the local scale.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.04.011.

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Supporting information to the paper Davrinche, A. and Haider, S.: Intra-specific leaf trait responses to species richness at two different local scales. Basic and Applied Ecology.

## Appendix A

**Table A.1**: Tree species included in the study. Species names and families are taken from The Flora of China (http://flora.huh.harvard.edu/china). Abb.: abbreviated species names. Simple line separator: species combinations of two-species mixtures; double lines separator: species combination of four-species mixtures. Species of the first two four-species mixtures grow together in an eight-species mixture, as do the species of the following two four-species mixtures (see Table A.2).

| Species name | Author | Abb. | Family |
|---|---|---|---|
| *Castanea henryi* | Rehder & E.H.Wilson | Che | Fagaceae |
| *Nyssa sinensis* | Oliver | Nsi | Nyssaceae |
| *Liquidambar formosana* | Hance | Lfo | Hamamelidaceae |
| *Sapindus mukorossi* | Gaertner | Smu | Sapindaceae |
| *Quercus serrata* | Thunberg | Qse | Fagaceae |
| *Castanopsis sclerophylla* | Schottky | Csc | Fagaceae |
| *Choerospondias axillaris* | (Roxb.) B.L.Burtt & A.W.Hill | Cax | Anacardiaceae |
| *Sapium sebiferum* | (L.) Roxb. | Sse | Euphorbiaceae |
| *Quercus fabri* | Hance | Qfa | Fagaceae |
| *Cyclobalanopsis glauca* | (Thunberg) Oersted | Cgl | Fagaceae |
| *Schima superba* | Gardn. & Champion | Ssu | Theaceae |
| *Rhus chinensis* | Mill | Rch | Anacardiaceae |

| | | | |
|---|---|---|---|
| *Lithocarpus glaber* | (Thunberg) Nakai | Lgl | Fagaceae |
| *Koelreuteria bipinnata* | Franch. | Kbi | Sapindaceae |
| *Cyclobalanopsis myrsinifolia* | Oersted | Cmy | Fagaceae |
| *Castanopsis eyrei* | (Champion ex Benth.) Hutch. | Cey | Fagaceae |

**Table A.2**: Tree species pairs combinations within the broken-stick design of the BEF experiment (Bruelheide et al., 2014). Letter code refers to the abbreviations of species names (see Table A.1). Each cell of the grid in the left half of the table represents a group of species (including 1, 2, 4, 8 or 16 species). Each species is present at every plot species richness level, and studied in a combination, that is, in a pair with itself or with a different species belonging to the same group (e.g. *Castanea henryi* (Che) and *Sapindus mukorossi* (Smu) can build a species pair in a four-species mixture, but not in a two-species mixture). For the eight- and 16-species mixtures, the same groups of four species than in the four-species mixtures were considered, in order to keep a feasible number of combinations to study. According to all the possible combinations within groups of one, two or four species and their respective replication, the total number of combinations sums up to 240 tree species pairs (TSPs). Adapted from Bruelheide et al. (2014).

<table>
<tr><th>Plot species richness</th><th colspan="16">Broken-stick design of species diversity levels in BEF-China</th><th>Realised TSP combinations for one group</th><th>Realised TSP combinations for all groups</th><th>Number of replicates</th><th>Total number of TSPs</th></tr>
<tr><td>16</td><td colspan="16">Che Nsi Lfo Smu Qse Csc Cax Sse Qfa Cgl Ssu Rch Lgl Kbi Cmy Cey</td><td>10</td><td>40</td><td>1</td><td>40</td></tr>
<tr><td>8</td><td colspan="8">Che Nsi Lfo Smu Qse Csc Cax Sse</td><td colspan="8">Qfa Cgl Ssu Rch Lgl Kbi Cmy Cey</td><td>10</td><td>40</td><td>1</td><td>40</td></tr>
<tr><td>4</td><td colspan="4">Che Nsi Lfo Smu</td><td colspan="4">Qse Csc Cax Sse</td><td colspan="4">Qfa Cgl Ssu Rch</td><td colspan="4">Lgl Kbi Cmy Cey</td><td>10</td><td>40</td><td>1</td><td>40</td></tr>
<tr><td>2</td><td colspan="2">Che Nsi</td><td colspan="2">Lfo Smu</td><td colspan="2">Qse Csc</td><td colspan="2">Cax Sse</td><td colspan="2">Qfa Cgl</td><td colspan="2">Ssu Rch</td><td colspan="2">Lgl Kbi</td><td colspan="2">Cmy Cey</td><td>3</td><td>24</td><td>3</td><td>72</td></tr>
<tr><td>1</td><td>Che</td><td>Nsi</td><td>Lfo</td><td>Smu</td><td>Qse</td><td>Csc</td><td>Cax</td><td>Sse</td><td>Qfa</td><td>Cgl</td><td>Ssu</td><td>Rch</td><td>Lgl</td><td>Kbi</td><td>Cmy</td><td>Cey</td><td>1</td><td>16</td><td>3</td><td>48</td></tr>
</table>

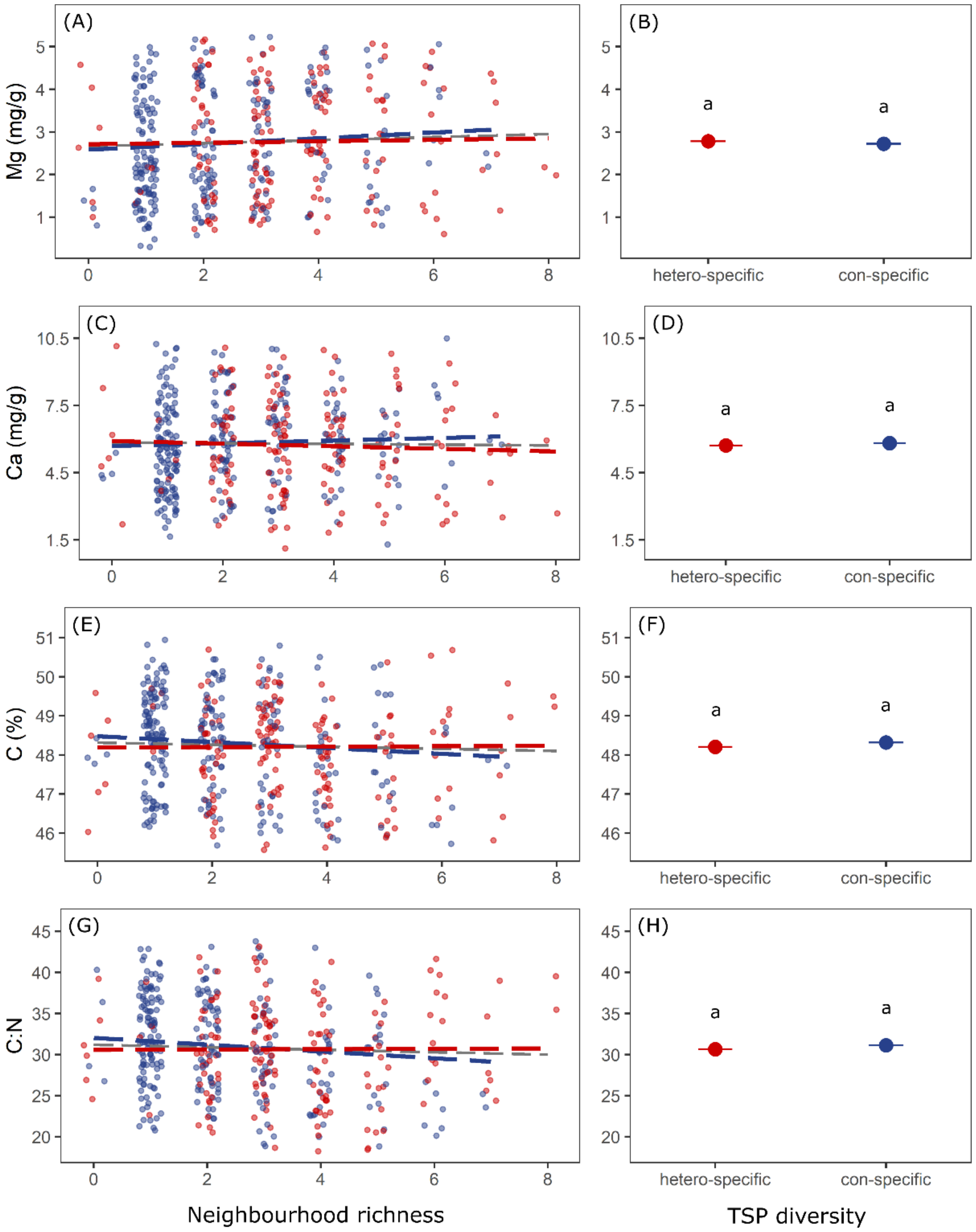

**Fig. A.1**: Effect of the surrounding neighbourhood species richness on acquisitive (A-D) and conservative (E-H) leaf traits of the tree species pairs (TSPs). The traits displayed are those without significant response to the TSP diversity, neighbourhood richness or their interaction according to Table 3. Dashed lines indicate the absence of significant relationships at the 0.05 level. Left: regression of the focal trees' trait values with neighbourhood richness, for hetero-specific (red), con-specific TSPs (blue), or both TSP types together (grey). Right: mean of the trait values depending on the TSP diversity (i.e., whether the focal tree had a hetero- (red) or con-specific (blue) partner. Lower-case letters indicate the significant difference in the mean of each group (see Table 2). Regression lines and trait means are based on model predictions.

**Table A.3**: Summary output of linear mixed-effects models analysing the interacting effect of TSP diversity (hetero- or con-specific tree species pair) and neighbourhood species richness (i.e., the ten trees surrounding the TSP) on each leaf trait. The proportion of the TSP partners' height difference for the focal tree was added to the model as covariate (Height diff.). In contrast to the models described in the main text, we used here neighbourhood richness minus 1 (N. rich. -1), in order to compare the intercepts of hetero- and con-specific TSPs at neighbourhood richness of one and not of zero. The predictor of interest (TSP div) is highlighted in white on black. Significant differences at the 0.05 level are indicated in bold. TSP div was coded with mix (=hetero-specific) and mono (=con-specific), meaning that positive estimates for TSP div reflect a higher intercept for con-specific TSPs and negative estimates higher intercept for hetero-specific TSPs. Abbreviations: SLA: specific leaf area; LDMC: leaf dry matter content; C:N: carbon:nitrogen ratio; C: carbon content; N: nitrogen content; P: phosphorus content; Mg: magnesium content; Ca: calcium content; K: potassium content; Std. Error: standard error; Df: degrees of freedom, Signif.: significance, '***': p-value < 0.001, '**' : p-value < 0.01, '*' : p-value < 0.05, '.' : p-value < 0.1, ' ' : p-value < 1.

| Trait | Predictor | Estimate | Std. Error | Df | t-value | p-value | Signif. |
|---|---|---|---|---|---|---|---|
| SLA | Intercept | 127.234 | 9.429 | 25.060 | 13.494 | 0.000 | *** |
| | Height diff. | -0.081 | 0.019 | 322.741 | -4.231 | 0.000 | *** |
| | (N. rich. -1) | 2.499 | 1.502 | 158.371 | 1.663 | 0.098 | . |
| | TSP div. cons. | -10.807 | 5.183 | 185.607 | -2.085 | **0.038** | ***** |
| | TSP div. cons. : (N. rich. -1) | 5.587 | 1.987 | 179.525 | 2.812 | 0.005 | ** |
| K | Intercept | 6.097 | 0.277 | 34.117 | 22.035 | 0.000 | *** |
| | Height diff. | -0.002 | 0.001 | 327.557 | -3.309 | 0.001 | ** |
| | (N. rich. -1) | 0.042 | 0.050 | 151.652 | 0.828 | 0.409 | |
| | TSP div. cons. | -0.526 | 0.179 | 181.289 | -2.944 | **0.004** | ****** |
| | TSP div. cons. : (N. rich. -1) | 0.217 | 0.069 | 175.532 | 3.143 | 0.002 | ** |
| P | Intercept | 0.707 | 0.051 | 24.211 | 13.803 | 0.000 | *** |
| | Height diff. | 0.000 | 0.000 | 340.388 | -2.756 | 0.006 | ** |
| | (N. rich. -1) | -0.008 | 0.008 | 176.719 | -0.975 | 0.331 | |
| | TSP div. cons. | -0.068 | 0.028 | 194.920 | -2.459 | **0.015** | ***** |
| | TSP div. cons. : (N. rich. -1) | 0.033 | 0.011 | 188.643 | 3.090 | 0.002 | ** |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| N | Intercept | 1.667 | 0.063 | 30.143 | 26.496 | 0.000 | *** |
| | Height diff. | 0.000 | 0.000 | 375.620 | -0.897 | 0.370 | |
| | (N. rich. -1) | -0.005 | 0.011 | 396.381 | -0.416 | 0.678 | |
| | TSP div. cons. | -0.069 | 0.038 | 402.967 | -1.812 | 0.071 | . |
| | TSP div. cons. : (N. rich. -1) | 0.029 | 0.015 | 410.101 | 2.002 | 0.046 | * |
| Mg | Intercept | 2.712 | 0.310 | 17.250 | 8.757 | 0.000 | *** |
| | Height diff. | -0.001 | 0.000 | 390.055 | -2.630 | 0.009 | ** |
| | (N. rich. -1) | 0.017 | 0.030 | 359.786 | 0.582 | 0.561 | |
| | TSP div. cons. | -0.078 | 0.098 | 367.234 | -0.790 | 0.430 | |
| | TSP div. cons. : (N. rich. -1) | 0.050 | 0.039 | 383.004 | 1.282 | 0.201 | |
| Ca | Intercept | 5.858 | 0.462 | 22.649 | 12.667 | 0.000 | *** |
| | Height diff. | 0.000 | 0.001 | 328.610 | 0.016 | 0.987 | |
| | (N. rich. -1) | -0.059 | 0.071 | 172.185 | -0.832 | 0.406 | |
| | TSP div. cons. | -0.106 | 0.236 | 188.914 | -0.448 | 0.655 | |
| | TSP div. cons. : (N. rich. -1) | 0.120 | 0.092 | 182.662 | 1.293 | 0.198 | |
| LDMC | Intercept | 446.920 | 13.302 | 21.875 | 33.597 | 0.000 | *** |
| | Height diff. | 0.072 | 0.023 | 325.624 | 3.053 | 0.002 | ** |
| | (N. rich. -1) | 0.147 | 1.814 | 160.371 | 0.081 | 0.935 | |
| | TSP div. cons. | 13.656 | 6.244 | 184.380 | 2.187 | **0.030** | ***** |
| | TSP div. cons. : (N. rich. -1) | -6.119 | 2.415 | 178.043 | -2.533 | 0.012 | * |
| C | Intercept | 48.196 | 0.280 | 19.176 | 172.333 | 0.000 | *** |
| | Height diff. | 0.000 | 0.000 | 382.577 | 0.469 | 0.640 | |
| | (N. rich. -1) | 0.006 | 0.033 | 408.080 | 0.167 | 0.867 | |
| | TSP div. cons. | 0.211 | 0.112 | 388.380 | 1.882 | 0.061 | . |
| | TSP div. cons. : (N. rich. -1) | -0.080 | 0.044 | 402.641 | -1.835 | 0.067 | . |
| C:N | Intercept | 30.601 | 1.153 | 28.653 | 26.538 | 0.000 | *** |
| | Height diff. | 0.001 | 0.003 | 331.353 | 0.208 | 0.836 | |
| | (N. rich. -1) | 0.020 | 0.199 | 159.852 | 0.101 | 0.919 | |
| | TSP div. cons. | 1.035 | 0.684 | 184.504 | 1.513 | 0.132 | |
| | TSP div. cons. : (N. rich. -1) | -0.434 | 0.266 | 178.086 | -1.633 | 0.104 | |

# CHAPTER 3

## High within-tree leaf trait variation and its response to species diversity and soil nutrients

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Davrinche, A., Bittner, A., Harpole, W. S., Albert, G., Bruelheide, H., & Haider, S.

**Abstract**

1. Leaf functional traits provide important insights into plants' responses to different environments. Leaf traits have been increasingly studied within-species in the last decade, following the growing realisation that neglecting the intra-specific scale can result in misreading plants' response to environmental change. However, while likely to lead to similar pitfalls, within-individual leaf traits are under-researched despite being the scale at which elementary biotic and abiotic interactions shape local to global ecosystem processes.
2. To address this critical lack of understanding at the local scale, we assessed leaf trait variation in a large biodiversity-ecosystem functioning experiment in subtropical China. We used optical spectroscopy to determine nine morphological and biochemical traits of over 5800 leaves from 414 trees representing 14 species. We evaluated the relative importance of the intra-individual level for total leaf trait variation, and the interacting effect of two trait variation's drivers, soil nutrient availability, and a gradient of local species richness.
3. Comparing the amount of trait variation at the between-species, between-individuals and intra-individual levels, we found that intra-individual variation accounted on average for over 25% of total trait variation. Additionally, intra-individual variation was the most prominent component of intra-specific variation, consistently exceeding between-individual variation, and even between-species variation for specific leaf area and leaf carbon to nitrogen ratio.
4. We also found partial support for positive effects of soil nutrient availability and species diversity on intra-individual trait variation, and a strong interdependence of both factors. Contrary to the amplifying effects we expected, we found that trait variation increases with soil nutrient availability at intermediate diversity but decreases at low and high diversity. This suggests two mechanisms driving trait variation, involving competition and complementarity at both ends of the species diversity gradient.
5. Our findings quantify the relevance of the intra-individual level for leaf trait variation, and expose a complex interaction between its drivers. Our results indicate that effects of soil nutrient availability on trait variation can range from alleviating competition to enhancing complementarity, depending on local species diversity. Taken together, our work highlights the importance of integrating an intra-individual

perspective to understand trait-based mechanisms in biodiversity-ecosystem functioning relationships.

**Keywords**

Local neighbourhood ; species richness ; within-individual ; leaf functional traits ; plant-plant interactions ; spectroscopy ; belowground resources ; BEF-China.

## Introduction

Plant functional traits in general (Reich *et al.* 1997; Liu *et al.* 2016; Cadotte 2017) and leaf functional traits specifically (Wright *et al.* 2004) can provide essential insights into ecosystem processes. Traits can, for example, inform how species interact with each other (Kraft *et al.* 2015; Bastias *et al.* 2020), and how species contribute to ecosystem functioning (Mokany *et al.* 2008a; Ratcliffe *et al.* 2017). In particular, analysing how traits vary with biotic and abiotic environmental conditions can help to understand those factors' effects on the ecosystem (Trugman *et al.* 2019; Joswig *et al.* 2022).

It is generally assumed that plant traits vary the most between species, as opposed to within species (Garnier *et al.* 2001; McGill *et al.* 2006; Shipley *et al.* 2016). Hence, most studies have focused on between-species trait variation and described species by their mean trait values (Lavorel *et al.* 2008; Weiher *et al.* 2011), implying that trait variation within the same species (intra-specific trait variation) is negligible. However, such assumptions were critically challenged in the last decade (e.g. Albert et al., 2010; Fajardo & Piper, 2011; Hulshof & Swenson, 2010; Messier, McGill, & Lechowicz, 2010), and multiple studies argued to broaden this view (Violle *et al.* 2012; Des Roches *et al.* 2018; Westerband *et al.* 2021). In particular, recent work has raised awareness of the limitations resulting from ignoring intra-specific trait variation, such as underestimating functional diversity (Albert *et al.* 2012) or overlooking mechanisms affecting species coexistence (Hart *et al.* 2016). For example, Lepš *et al.* (2011) showed that intra-specific variability explained the main part of community variation for some traits in response to different environmental conditions combinations, and thus be dominant compared to, for example, species turnover alone. Ignoring intra-specific trait variation might therefore lead to an underestimation of the effects of environmental variation. As a result, interest in intra-specific trait variation gained considerable momentum, revealing that, on average, about a quarter of total variation can be explained by differences within species (Siefert *et al.* 2015), this proportion even reaching up to 40 % (Kattge *et al.* 2011).

In addition to substantial variation within species, traits can also vary greatly within an individual (i.e., intra-individual variation). So far, only few studies have zoomed in from intra-specific trait variation to intra-individual trait variation (Messier *et al.* 2010; Auger and Shipley 2013; Kang *et al.* 2014; Umaña *et al.* 2018), suggesting that intra-individual trait variation can even be greater than between-individuals trait variation (Herrera *et al.* 2015; Kafuti *et al.* 2020). Ignoring the intra-individual scale of variation means neglecting an essential aspect of the answer to understanding the structure and functioning of plant communities. As similarly described by Messier et al. (2010) for intra-specific variation, trait variation of the individual is subject to assumptions on its importance that are the basis of approaches aiming at clarifying how and why species coexist and interact with each other and their environment. Hence, it is essential to identify the scales at which a large share of the trait variation occurs in order to apply ecological theories realistically but also to study ecological processes at the very scale where they have a defining importance for the ecosystem – that is, where individuals interact. For example, Valdés-Correcher *et al.* (2021) showed that in natural forest stands, accounting for the intra-individual scale when explaining variation of leaf defence and herbivory related traits enables a better assessment of trees' genetic relatedness as a explaining factor. As a result, ignoring intra-individual variation would occult the importance of genetic signals when explaining trees' response to herbivory. However, in practice, studying leaf traits at the intra-individual level involves a high workload and associated costs, in addition to limitations due to small amounts of leaf biomass available for analysis. Because of these limitations, spectroscopy, a fast and non-destructive high-throughput method (Serbin *et al.* 2014; Burnett *et al.* 2021), has emerged as an advantageous tool for determining leaf traits, allowing the inclusion of thousands of samples to quantify intra-individual leaf trait variation (Davrinche and Haider 2021; Proß *et al.* 2021). Because of the low number of studies addressing intra-individual leaf trait variation, little is known about its drivers. However, trait variation at the intra-specific scale was found to be influenced by the abiotic environment (Lemke *et al.* 2015; Souza *et al.* 2018; Proß *et al.* 2021). For example, several experimental studies showed that high soil nutrient availability enhanced intra-specific trait variation (Lemke *et al.* 2012; Helsen *et al.* 2017). In contrast, the relationship between resource availability and intra-individual trait variation has hardly been studied so far. Therefore, the question arises whether the results found at the intra-specific level are transferable to the intra-individual level.

In addition to abiotic drivers, biotic factors likely influence intra-individual trait variation. In particular, competition, a dominant driver of plant interactions (Connell 1983; Wright *et al.* 2014), imposes strong interactions between individuals of the same species that share comparable needs for resources, with similar uptake pathways (Grime 1973; Tilman 1982; Barabás *et al.* 2016). This can result in less resources available for each individual either aboveground (e.g., light; Pretzsch, 2014) or belowground (e.g., nutrients; Pornon, Escaravage, & Lamaze, 2007). Inversely, diversity of co-existing species can decrease competition and promote the availability of resources through resource-use complementarity (Loreau and Hector 2001; Cardinale *et al.* 2007; Barabás *et al.* 2016). Additionally, in forests, increased species richness increased litter diversity, abundance (Huang *et al.* 2017) and decomposition (Beugnon *et al.* 2022), thus increasing the incorporation of organic matter in the soil and contributing to enriching it with nutrients (Gartner and Cardon 2004). Aboveground, species richness has been positively linked to the spatial complementarity of tree crowns (or "canopy packing", Jucker, Bouriaud, & Coomes, 2015), that is, a more complete use of available space for the canopies resulting in an improved interception of incoming light. Such possible effects on a tree individual's trait variation resulting from plant interactions should be greatest from directly neighbouring plants, and fade for more distant neighbours (Mokany *et al.* 2008b; Vogt *et al.* 2010). For example, a study carried out in subtropical China quantifying leaf biochemical and morphological traits found effects of the directly adjacent tree to be more frequent than those of surrounding trees further away (Davrinche and Haider 2021). Few studies have so far attempted to look specifically at the effects of the neighbouring species richness on intra-specific trait variation (but see Benavides, Valladares, Wirth, Müller, & Scherer-Lorenzen, 2019; Le Bagousse-Pinguet et al., 2015) and even less addressed its effect on intra-individual trait variation (but see Proß et al., 2021), preventing any general conclusion.

To investigate changes in functional traits in response to soil resource availability and species richness of the local neighbourhood, tree diversity experiments are an ideal framework, as species richness is manipulated while other macro-ecological conditions, as well as plant density, are constant. In addition, trees are long-lived organisms for which trait variation and adaptation to varying environmental conditions is particularly critical. In this study, carried out in a subtropical tree diversity experiment, we aimed at determining the shares of different levels of trait variation (between species, between individuals, within individuals) to the overall trait variation. In addition, focusing specifically on intra-individual trait variation, we investigated the influences of soil nutrient availability, a tree's directly adjacent (i.e., 'direct') neighbour, as well as the surrounding neighbourhood.

We hypothesized that (I) the largest proportion of total leaf trait variation is explained by differences between species, but intra-individual variation represents a considerable share of the remaining intra-specific part (which includes both variation between and within individuals). Further, we expected intra-individual leaf trait variation (II) to be positively related to soil nutrient availability and (III) to be larger for trees that have a different tree species as their direct neighbour (hetero-specific direct neighbouring tree), and to increase with increasing species diversity of the surrounding neighbourhood. Thereby, we assumed the effect of the direct neighbour to be more important than the surrounding neighbourhood. Finally, we hypothesized that (IV) the positive effects of soil nutrient availability, a hetero-specific direct neighbouring tree and the surrounding neighbourhood diversity amplify each other, that is, that the positive effect resulting from their interaction is greater than the sum of their respective positive effect.

## Materials and Methods

### 1. Study site

Our study was conducted in the BEF-China tree diversity experiment, which was set up in subtropical China near Xingangshan in the Jiangxi Province (29.08–29.11 N, 117.90-117.93 E) in 2009 (Site A) and 2010 (Site B). The mean annual temperature in Xingangshan is 16.7 °C and the mean annual precipitation is 1821 mm (Yang *et al.* 2013). BEF-China covers 38.4 ha, composed of 566 plots with a size of 25.81 m x 25.81 m. Each plot comprises 400 trees planted in a regular grid 1.29 m apart. The plots vary in their species richness, ranging from monocultures to mixtures of two, four, eight, or 16 native tree species (Bruelheide *et al.* 2014). Our study took place in Site B, a 20 ha part of the main experiment.

### 2. Experimental design

The BEF-China experiment follows a so-called "broken-stick" design (*sensu* Bruelheide et al., 2014), in which all species are equally represented at each plot diversity level: the total pool of 16 species at the highest diversity level is divided into halves at each following diversity level, ending up with 16 monocultures. To represent a random extinction scenario, the sequence and division of the 16 species is random.

With the basis of the broken-stick design, four groups of four species each were defined, corresponding to the four different species combinations in the plots comprising four-species mixtures. Within each group, we used all possible combinations of two tree species, referred to as Tree Species Pairs (TSPs), that is, two directly adjacent trees of either the same (mono-specific TSP) or different species (hetero-specific TSP). For each group of four species, there are four possible mono-specific TSPs (AA, BB, CC, DD) and six hetero-specific TSPs (AB, AC, AD, BC, BD, CD). These ten TSP combinations were sampled not only in the four-, but also in the eight- and 16-species mixtures. In addition, in the two-species mixtures, we sampled all three possible TSP combinations (AA, BB, AB) as well as mono-specific TSPs in all monocultures. To have sufficient replication, TSP combinations were repeated three times in two-species mixtures and monocultures.

It must be noted that in Site B, low germination reduced the species pool to a total of 14 species instead of 16 (Supp. Table S1), and as a result, two species occur twice within the broken-stick design (in two different four-species groups; Supp. Table S2). In total, the study design encompassed 222 TSPs.

We focused on the leaf traits of each tree within a TSP, and how they vary depending on the number of different species within the ten trees directly surrounding the TSP (i.e., the TSP's local neighbourhood diversity), which ranged between zero and six when accounting for tree mortality. In addition, we looked at the effect of a tree's direct neighbour (i.e., the TSP partner) being mono-specific or hetero-specific (i.e., the TSP diversity). Although all trees are planted at equal distance from each other, we considered the TSP partner the 'direct neighbour', as leaf traits were measured at the side of the crown in contact to the crown of the TSP partner (Supp. Fig S1).

## 3. Field methods

### *Leaf sampling*

Distributed over 57 plots, a total of 220 TSPs (440 trees) were sampled between mid-August and mid-September 2019. For each tree of a TSP, we sampled three leaves at two to five heights along the area where the crowns of the two TSP trees met or were closest to each other (i.e., their interaction plane; Supp. Fig S1). In addition, for each tree species, we collected calibration samples from non-TSP trees, in order to predict trait values of the TSP samples via optical spectroscopy (see below for details). Calibration samples were composed of about 15 leaves from one sampling point each, with sampling points distributed at multiple heights and positions within the crown of randomly selected trees, totalling 252 samples representative of all species across all plot diversity levels. After leaf collection, TSP and calibration samples were transported in a water saturated and cooled atmosphere to the laboratory facilities, to be stored at 6-8 °C until being processed.

### *Leaf spectral data acquisition*

Because of the high number of leaf samples (over 5800) and because leaf material of each TSP sample (i.e., three leaves from the same height within a tree's crown) would be insufficient to conduct all chemical analyses for some species, we used reflectance spectroscopy including near-infrared wavelengths (NIRS), a fast and cost-effective method (Serbin *et al.* 2014; Trogisch *et al.* 2017; Burnett *et al.* 2021) to predict leaf trait values. For doing so, spectral data of all leaves (i.e., TSP samples and calibration samples) was acquired on the sampling day using an ASD FieldSpec4 Wide Resolution Field Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom) with the RS$^3$-Software, over a 350 nm to 2500 nm wavelength range. The device was regularly calibrated with a diffuse reflectance target (Spectralon, Labsphere, Durham, New Hampshire, USA) as white reference. Three repeated spectral measures of each fresh leaf were taken on its upper surface, with every spectral measurement consisting of ten internally averaged recordings of the device.

### *Soil sampling*

For each of the 220 TSPs, one bulk soil sample was taken at equal distance from both trees of a TSP, and one meter away from the interaction plane (Supp. Fig A1). About 30 g of fresh soil were collected from the mineral layer, between 5 and 10 cm depth. We ensured that there was as little organic material in the sample as possible (e.g., root parts, litter, etc.). Samples were kept cool at 4 °C until being processed.

## 4. Laboratory analyses

### *Leaf calibration samples*

Nine leaf traits were measured from the calibration samples: specific leaf area (SLA), leaf dry matter content (LDMC), leaf carbon (C) and leaf nitrogen (N) contents, leaf carbon to nitrogen ratio (C:N), leaf calcium (Ca), leaf potassium (K), leaf magnesium (Mg) and leaf phosphorus (P) contents.

Fresh leaves were first weighed before spectral data acquisition with the FieldSpec (see above). Then, leaf area was measured with a flatbed scanner and the WinFolia software (Regent Instruments, Quebec, Canada). Afterwards, leaves were dried at 80 °C for 72 h before being weighed again, and SLA (leaf area / leaf dry mass) and LDMC (leaf dry mass / leaf fresh mass) were calculated (Pérez-Harguindeguy *et al.* 2013).

The dry leaves were ground in a ball mill (MM 400, Retsch, Germany) and the resulting leaf powder divided for the different analyses. Total C and N content, from which C:N was calculated, were determined gas-chromatographically with an elemental analyser (vario EL cube, Elementar, Hanau, Germany). Following an $HNO_3$ digestion, the filtrate was used to measure leaf Mg, Ca and K content by atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany), and leaf P content with an acid molybdate spectrophotometric assay.

*Soil samples*

To characterise soil nutrient availability, we measured soil P content, soil C:N and soil cation exchange capacity (CEC). The fresh soil samples were sieved to 2 mm. Soil P was measured photometrically using the Olsen method (Olsen 1954). To determine CEC, we performed a percolation with barium chloride. In the resulting percolate, the concentrations of Ca, Mg and K were analysed by atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany), and by measuring the pH of the percolate we calculated the hydrogen concentration. Cation exchange capacity was then calculated as the sum of the ion equivalents of all cations (Ca, Mg, K and H). To determine total C and total N contents, the sieved soil was dried at 105 °C and milled to fine powder. The C and N contents were obtained by gas chromatography performed with an elemental analyser (vario EL cube, Elementar, Hanau, Germany), from which soil C:N was calculated afterwards.

## 5. Leaf trait prediction models

All spectral data analyses were performed using the Unscrambler X software (Version 10.5.1, CAMO Analytics, Oslo, Norway). Trait data of the leaf calibration samples were matched with their leaf spectral data. Since the calibration samples consisted of ca. 15 leaves each, and for each individual leaf we acquired spectral data, but laboratory analyses were done together for all leaves of a sample (i.e., resulting in only one trait values per sample), the spectral data of the different leaves of the same sample had to be averaged. Based on the averaged spectral data and the measured trait values of each calibration sample, we fitted models to predict trait values of the TSP leaf samples’ spectral data. For doing so, different mathematical pre-treatments were applied to the averaged calibration samples’ spectra in order to highlight their most relevant features, and informative wavelength ranges were selected (Supp. Table S3). The averaged spectra and measured leaf trait value of each calibration sample were then used together to fit a Partial Least Square Regression (PLSR) for each trait, which was then applied to each of the three repeated spectral measure of each TSP leaves to predict their trait values. The three predictions per leaf where then averaged, resulting in one predicted trait value for each leaf. The R-Square ($R^2$), root mean square error (RMSE) and number of factors of the PLSR were used to estimate robustness and performance of the models (Supp. Table S3).

## 6. Data analysis

All statistical analyses were carried out with R, version 4.0.4 (R Core Team 2021). After excluding outlying predicted trait values (i.e., negative values, values exceeding a 5 % deviation from the range limits of calibration data, and values outside a 95 % confidence interval), we included 195 to 207 TSPs in the analyses, depending on the trait. Care was taken that leaf trait values originated from at least two different sampling heights within a tree. In addition, only complete TSP pairs were included, that is, trees with a TSP partner having only outlying trait values or all trait values coming from one sampling height were also excluded. In order to determine the proportion of total trait variation explained by differences between species, between individuals within a species, and within individuals (hypothesis I), linear mixed-effects models were fitted for each trait (“lme” function in the “nlme” package, Pinheiro et al., 2017). The response variable consisted of the predicted trait values for each repeated leaf spectral measure (i.e. three values for each leaf of each sample), and as fixed effect, only the intercept was included. The random term consisted of the leaf nested in sampling height (as intra-specific, intra-individual trait variation; ITVI) nested in tree identity (as intra-specific, between-individuals trait variation; ITVB) nested in species identity (as between-species trait variation; BTV). The function “varcomp” from the R package “ape” (Paradis and Schliep 2019) was used to obtain the variances.

For hypothesis II, III and IV, we used Rao’s quadratic entropy (Rao’s Q; Botta-Dukát, 2005) to quantify intra-individual trait variation (ITVI). Considering the design of our study, abundance or weights of each sample within a tree individual were not relevant, and were all set to one. Rao’s Q was calculated with the “dbFD” function from the package “FD” (Laliberté *et al.* 2014) for each trait for each tree, using trait values averaged at the leaf level. This way, Rao’s Q gives the average Euclidian distance between the traits values of all leaves within one individual, as a measure of within-tree variation.

To exclude bias arising from differences in sample size per tree, we first fitted linear mixed-effects models (“lmer” function from package “lmerTest”; Kuznetsova, Brockhoff, & Christensen, 2017) with Rao´s Q (i.e., ITVI) as response to the number of values used to calculate Rao’s Q. As random factors, TSP identity was nested in plot identity, and as a crossed random factor, species identity of the tree were added in the models. We extracted the residual variance of these models, and in a second step, used simple linear models to explain the residual variance with soil nutrient availability (CEC, soil C:N ratio, soil P content), TSP diversity (i.e., mono- or hetero-specific TSP partner) and neighbourhood diversity (i.e., Shannon Diversity Index of the trees directly surrounding the TSP) as fixed effects. The interactions of all fixed effects were added, except for interactions between soil variables. The Shannon Diversity Index, quantifying the species richness and evenness within a community, was calculated using the “vegan” package (Oksanen *et al.* 2020), and used as a measure of diversity of the local neighbourhood.

Model assumptions were checked with the R package “performance” (Lüdecke *et al.* 2021). To correct for non-normality of the residuals, Rao´s Q values were log-transformed in all models. The full models were then simplified by stepwise removal of model terms based on Akaike’s information criterion (AIC, function “stepAIC” from package “MASS”; Venables & Ripley, 2002).

## Results

### 1. Distribution of trait variation

Averaged across all traits, intra-specific trait variation ($\text{ITV}_\text{I}$ and ITVB taken together) represented the largest share of the total variation (43%; Fig 1). Specifically, for five out of the nine traits studied (SLA, leaf C:N, leaf N, leaf Mg and leaf Ca), the proportion of ITV was greater than that of BTV. Within ITV, intra-individual trait variation ($\text{ITV}_\text{I}$) accounted on average for more than a quarter of the total variation (27%), and between-individual trait variation (ITVB) for around 16%. In particular, $\text{ITV}_\text{I}$ exceeded 25% for four traits (SLA, leaf

C:N, leaf N, leaf K), driven by differences between heights. For SLA and leaf C:N, ITV$_I$ was also greater than BTV (49 % vs. 38 % and 39 % vs. 28 % respectively).

Differences between traits were pronounced for BTV, with values ranging from 11 % (leaf Mg) to 64 % (LDMC) of the total variation, as well as for ITV$_I$, reaching between 9 % and 49 % (resp. leaf Mg and SLA). Also ITVB differed between traits, ranging from 6 % to 28 % (resp. leaf Mg and leaf C:N). For most traits, the proportion of the total variation which could not be explained by the scales studied (BTV, ITVB or ITV$_I$) was small (10% or less), except for leaf Ca (32%), leaf C (33%) and leaf Mg (74%).

## 2. Effects of chemical soil properties on intra-individual leaf trait variation

For three out of the nine leaf traits studied (SLA, leaf C:N, and leaf K), we found partly an increase of ITV$_I$ with higher nutrient availability in the soil, i.e. higher soil P content or lower soil C:N (Fig 2).

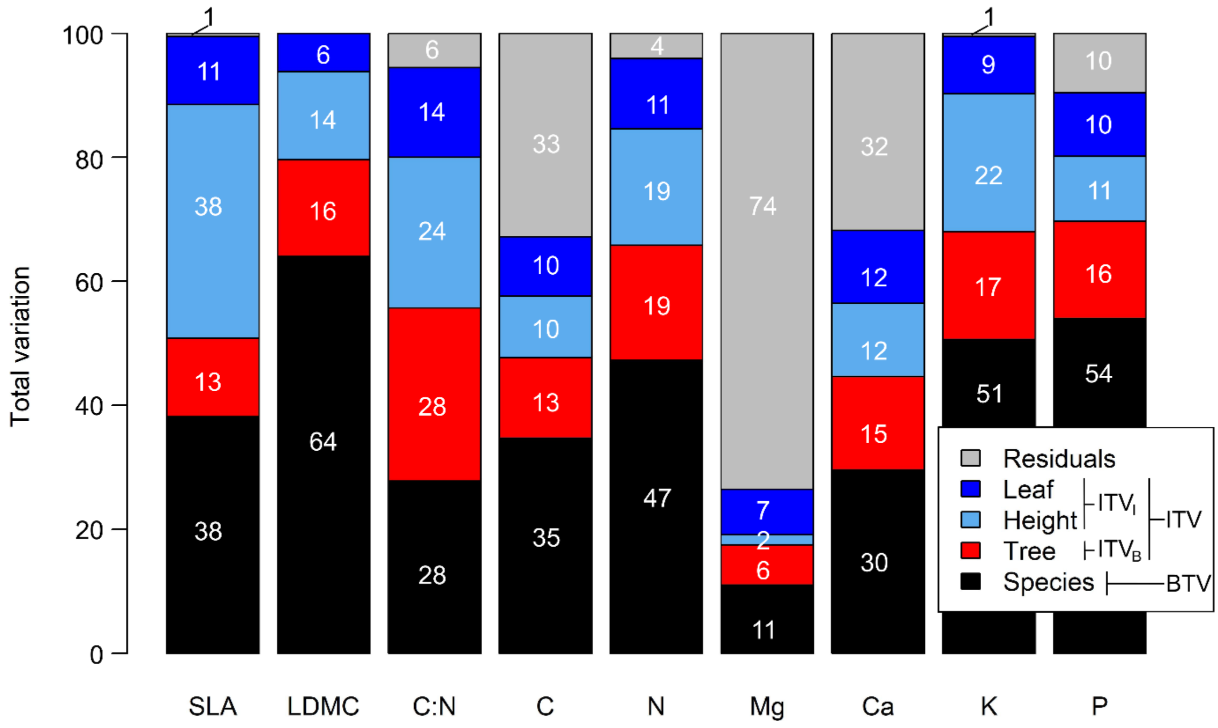

**Fig 1:** Partitioning of the variation in leaf traits at different scales: between species (BTV – between species trait variation) and within species (ITV – intra-specific trait variation). The latter separates into between trees trait variation (ITV$_B$) and within tree trait variation (ITV$_I$ – intra-individual variation including between heights and between leaves variation). Amount of variation is indicated in percent (%). Residual variation includes variation between repeated collection of leaf spectra (within-leaf variation) and error.

Overall, leaf C:N variation increased with increasing soil P content, which was mainly driven by the steep increase of leaf C:N variation in hetero-specific TSPs, while leaf C:N variation in mono-specific TSPs decreased with increasing soil P content (Table 1; Fig. 2a). Similarly, leaf K of trees with a hetero-specific neighbour showed an increase in variation with increasing soil nutrient, while variation of trees within mono-specific TSPs decreased. However, mono- and hetero-specific TSPs were most similar in leaf K variation at highest nutrient availability, while leaf C:N variation was most similar for mono- and hetero-specific TSPs at the lowest nutrient availability (Table 1; Fig. 2a, with increasing soil P, and 2b, with decreasing soil C:N). The described contrasting effect of soil C:N on leaf K variation in mono- and hetero-specific TSPs was not consistent across neighbourhood diversity levels. Rather, for the variation of leaf K as well as SLA, the effect of higher soil nutrients (that is, lower soil C:N) on variation was positive at null and low neighbourhood diversity, slightly positive or negative at medium neighbourhood diversity, and negative at high neighbourhood diversity for hetero-specific TSPs. For mono-specific TSPs, we found the opposite pattern, with increasing soil nutrient having a negative effect at null and low neighbourhood diversity and a positive effect at high neighbourhood diversity (Fig. 2c and d).

### 3. Diversity effects on intra-individual leaf trait variation

The results showed evidence of both TSP diversity and neighbourhood diversity effects on ITV$_{I}$. Trees in mono-specific TSPs displayed a larger variation of leaf P and leaf C:N than those growing in hetero-specific ones (Table 1; Fig. 3a and b).

While these effects seem to illustrate a negative relationship between diversity and trait variation, interaction between TSP and neighbourhood diversity showed that LDMC and leaf K variation decreased with neighbourhood diversity only for mono-specific TSPs, but increased for hetero-specific TSPs (Fig. 3c and d). For leaf C:N, we also found an overall slight increase of variation with neighbourhood diversity (Table 1). For four out of the nine leaf traits studied (leaf C, leaf N, leaf Mg and leaf Ca), no significant effects of soil nutrient availability and/or neighbourhood diversity on trait variation were found (Table 1).

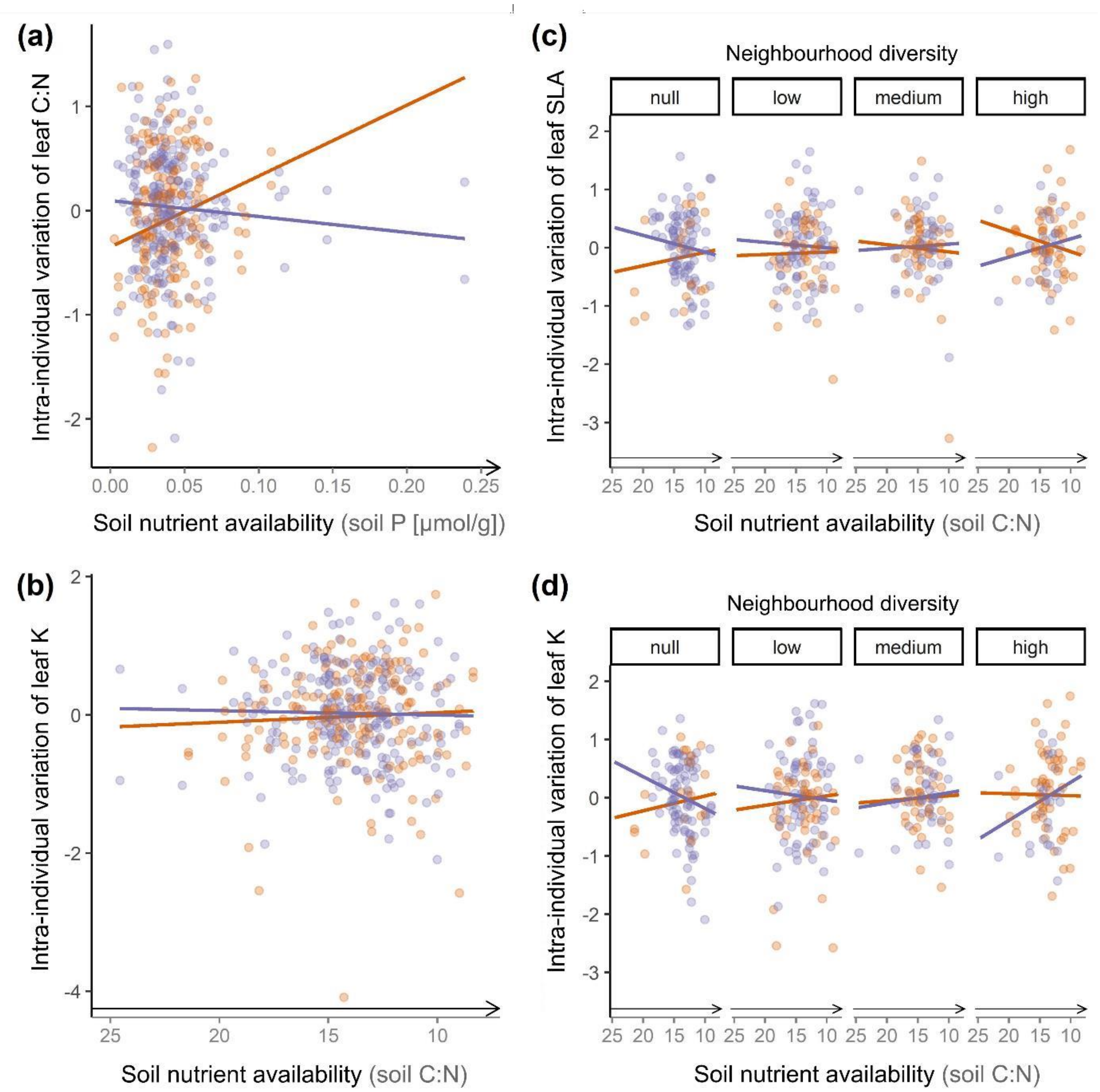

**Fig 2:** Interacting effects of soil nutrient content and species diversity on intra-individual leaf trait variation. Diversity of the tree species pair (orange line: hetero-specific direct neighbour; purple line: mono-specific direct neighbour) interact with the soil nutrient availability (soil P; soil C:N) and modify the intra-individual variation of leaf C:N **(a)** and leaf K **(b)**. Specific leaf area (SLA) **(c)** and leaf K **(d)** also vary depending on TSP diversity interacting with soil nutrient content, but also local neighbourhood diversity (Shannon Diversity Index of the ten trees surrounding a pair; null: SDI=0, low: 0<SDI≤0.8, medium: 0.8<SDI≤1.1, high: 1.1<SDI≤1.8). Intra-individual trait variation is calculated as logarithm-transformed Rao's Q value of each tree; therefore the scale of variation ranges from negative to positive values. Increasing soil nutrient availability corresponds to increasing soil P content or decreasing soil C:N, hence, soil C:N axis is shown in reverse order.

**Table 1**: Model results analysing the interacting effects of neighbourhood diversity (Shannon Diversity Index of the ten trees surrounding a TSP), TSP diversity (mono- or hetero-specific direct neighbour) and soil nutrient variables (either soil C:N, soil P or Cation Exchange Capacity) on the intra-individual variation of nine leaf traits (calculated as the log-transformed Rao's Q value of each studied tree). Full models were specified to include all possible interactions, except for the interaction between several soil nutrient variables, and simplified by stepwise removal of terms based on model AIC. Significant effects ($p<0.05$) of the most parsimonious models are indicated in bold. Abbreviations: SLA: specific leaf area; LDMC: leaf dry matter content; C:N: leaf carbon to nitrogen ratio; C: carbon leaf content; N: leaf nitrogen content; Mg: leaf magnesium content; Ca: leaf calcium content; K: leaf potassium content; P: leaf phosphorus content; Neigh. div.: local neighbourhood diversity; TSP div.: diversity of the tree species pair; CEC: cation exchange capacity; soil C/N: soil carbon to nitrogen ratio; soil P: soil phosphorus content.

| Intra-individual leaf trait variation | Predictor | Estimate | Std. Error | F-value | p-value |
|---|---|---|---|---|---|
| SLA | Neigh. div. | -0.462 | 0.467 | 0.979 | 0.323 |
| | TSP div. | -0.737 | 0.598 | 1.520 | 0.218 |
| | Soil C/N | -0.032 | 0.033 | 0.982 | 0.322 |
| | Neigh. div. : TSP div. | 1.124 | 0.663 | 2.876 | 0.091 |
| | Neigh. div. : Soil C/N | 0.047 | 0.033 | 1.989 | 0.159 |
| | TSP div. : Soil C/N | 0.071 | 0.043 | 2.733 | 0.099 |
| | Neigh. div. : TSP div. : Soil C/N | -0.095 | 0.047 | 4.040 | **0.045** |
| LDMC | Neigh. div. | 0.247 | 0.131 | 3.536 | 0.061 |
| | TSP div. | -0.005 | 0.243 | 0.000 | 0.985 |
| | CEC | -0.048 | 0.028 | 2.953 | 0.086 |
| | Neigh. div. : TSP div. | -0.330 | 0.163 | 4.122 | **0.043** |
| | TSP div. : CEC | 0.057 | 0.032 | 3.168 | 0.076 |

| | | | | | |
|---|---|---|---|---|---|
| C:N | Neigh. div. | 0.526 | 0.266 | 3.926 | **0.048** |
| | TSP div. | 0.853 | 0.300 | 8.061 | **0.005** |
| | Soil P | 15.686 | 6.915 | 5.145 | **0.024** |
| | Neigh. div. : TSP div. | -0.584 | 0.305 | 3.675 | 0.056 |
| | Neigh. div. : Soil P | -12.740 | 6.610 | 3.715 | 0.055 |
| | TSP div. : Soil P | -16.864 | 7.104 | 5.635 | **0.018** |
| | Neigh. div. : TSP div. : Soil P | 12.237 | 7.362 | 2.763 | 0.097 |
| C | TSP div. | 0.083 | 0.043 | 3.715 | 0.055 |
| N | TSP div. | 0.209 | 0.136 | 2.339 | 0.127 |
| | CEC | 0.016 | 0.020 | 0.640 | 0.424 |
| | TSP div. : CEC | -0.029 | 0.023 | 1.644 | 0.200 |
| Mg | Neigh. div. | -0.470 | 0.320 | 2.156 | 0.143 |
| | TSP div. | -0.315 | 0.408 | 0.594 | 0.441 |
| | Soil C/N | -0.011 | 0.022 | 0.256 | 0.613 |
| | Neigh. div. : TSP div. | 0.804 | 0.455 | 3.123 | 0.078 |
| | Neigh. div. : Soil C/N | 0.026 | 0.023 | 1.296 | 0.256 |
| | TSP div. : Soil C/N | 0.012 | 0.029 | 0.174 | 0.677 |
| | Neigh. div. : TSP div. : Soil C/N | -0.047 | 0.032 | 2.108 | 0.147 |
| Ca | Neigh. div. | 0.054 | 0.080 | 0.446 | 0.505 |
| | TSP div. | 0.046 | 0.094 | 0.239 | 0.625 |
| | Neigh. div. : TSP div. | -0.087 | 0.099 | 0.771 | 0.381 |
| K | Neigh. div. | -0.227 | 0.549 | 0.171 | 0.680 |
| | TSP div. | -1.322 | 0.704 | 3.532 | 0.061 |
| | Soil C/N | -0.030 | 0.038 | 0.623 | 0.430 |
| | Neigh. div. : TSP div. | 1.546 | 0.783 | 3.901 | **0.049** |
| | Neigh. div. : Soil C/N | 0.023 | 0.039 | 0.344 | 0.558 |
| | TSP div. : Soil C/N | 0.104 | 0.050 | 4.266 | **0.040** |
| | Neigh. div. : TSP div. : Soil C/N | -0.119 | 0.056 | 4.542 | **0.034** |
| P | TSP div. | 0.670 | 0.326 | 4.237 | **0.040** |
| | Soil C/N | 0.025 | 0.017 | 2.166 | 0.142 |
| | TSP div. : Soil C/N | -0.042 | 0.023 | 3.305 | 0.070 |

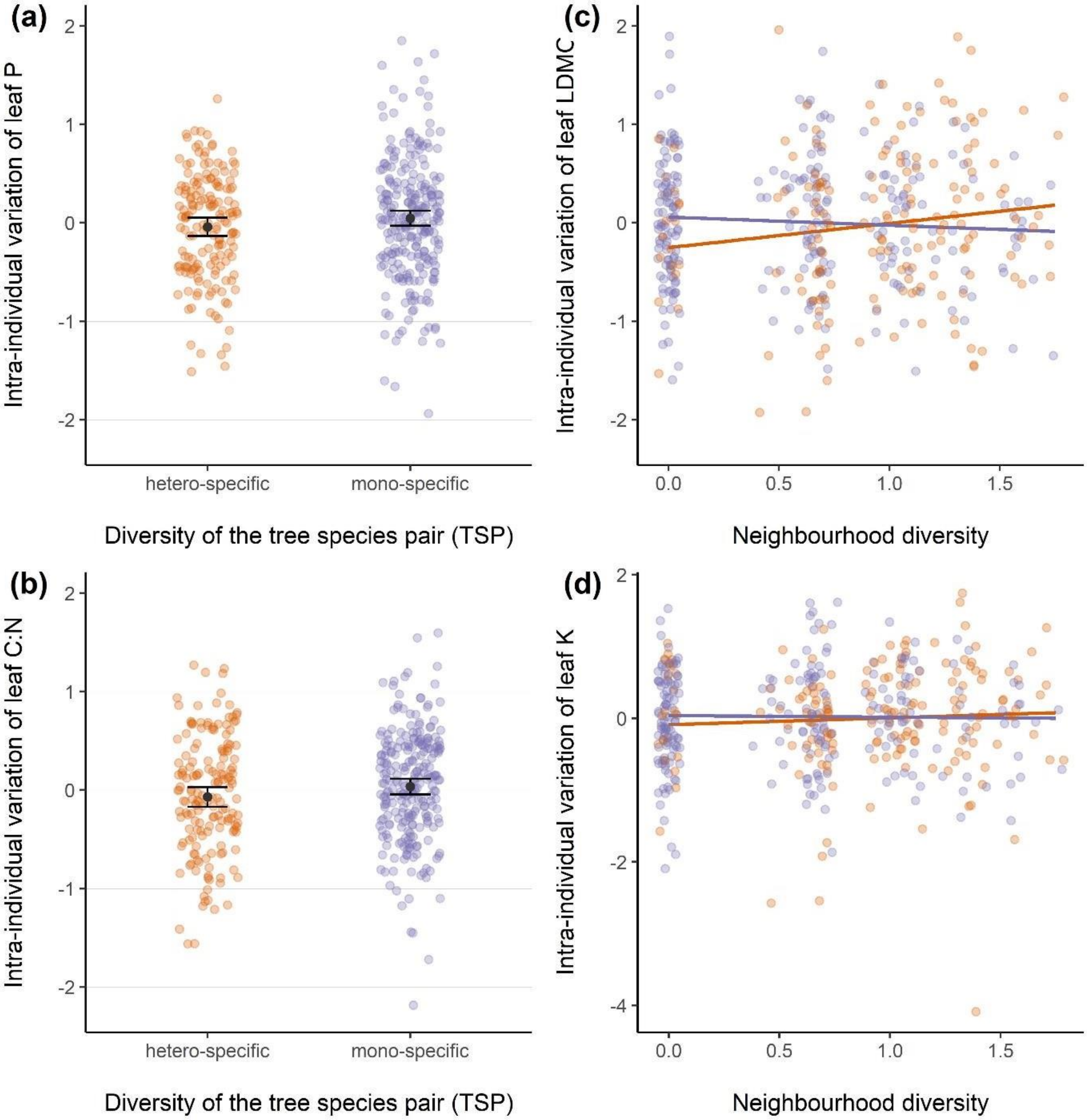

**Fig 3:** Effects of diversity on the intra-individual leaf trait variation. **(a)** and **(b)**: effect of the diversity of the tree species pair – mono- or hetero-specific direct neighbour – on leaf P and leaf C:N variation, respectively. Black dots indicate the mean of each group, and error bars two standard errors around the mean. The diversity of the tree species pair's interaction with local neighbourhood diversity (calculated as the Shannon Diversity Index of the ten trees surrounding the TSP) modifies **(c)** leaf dry matter content (LDMC) variation, and **(d)** leaf C:N variation. Intra-individual trait variation is the logarithm-transformed Rao's Q value of each tree; therefore the scale of variation ranges from negative to positive values.

## Discussion

Using an extensive dataset with over 5800 leaf trait values collected in a large tree diversity experiment, our study is the first to consistently find, across a range of morphological and biochemical leaf traits, that the contribution of intra-specific trait variation to total trait variation amounts to a similar or even higher magnitude than the contribution of variation between species. Moreover, our results demonstrate that, within intra-specific trait variation, trait variation within individual trees holds a substantial share beside trait variation between individuals of the same species. Focusing on the intra-individual level, we could further show positive effects of soil nutrient conditions on trait variation. However, these were contingent on local species diversity.

### Intra-individual level: a substantial share of the total trait variation

Confirming our first hypothesis, we found that intra-individual variation ($\mathrm{ITV}_\mathrm{I}$) represented on average over a quarter of the total variation, and was especially important in SLA and leaf C:N, where it exceeded the variation between species. Intra-specific variation, divided into variation between trees ($\mathrm{ITV}_\mathrm{B}$) and within tree individuals ($\mathrm{ITV}_\mathrm{I}$), was most often dominated by $\mathrm{ITV}_\mathrm{I}$ or in similar proportions. This is in contrast to most of the few studies that included $\mathrm{ITV}_\mathrm{I}$ in the comparison to higher levels of variation (e.g., Auger & Shipley, 2013; Hulshof & Swenson, 2010; Messier, McGill, & Lechowicz, 2010), as $\mathrm{ITV}_\mathrm{I}$ was mostly found to explain the least amount of variation (but see Herrera, Medrano, & Bazaga, 2015). Between-species trait variation (BTV) displayed the largest share of variation, confirming findings of previous studies (Albert *et al.* 2010; de Bello *et al.* 2011; Siefert *et al.* 2015), but only when compared to the other sources of variation considered in isolation. In contrast, the total ITV added up to the largest proportion of variation, suggesting that overlooking the partition of variance into lower ecological levels (i.e. between and within-individual) could lead to underestimating the share of intra-specific variation.

Even though largely consistent with the overall trend, the partition of variation showed different patterns for some traits. For example, SLA had an outstandingly large $\mathrm{ITV}_\mathrm{I}$. Specific leaf area is known to respond strongly to local light conditions and hence to vary substantially in response to the light gradient of individual tree canopies (Niinemets *et al.* 2015). By adjusting the values of SLA, plants are able to optimise their light capture and thus their photosynthesis to adapt to light heterogeneity at the crown scale.

While most of the traits presented a considerably larger share of ITV compared to BTV, the opposite occurred for LDMC, leaf K and leaf P. In particular, we found the largest proportion of BTV for LDMC, which can be related to the larger scale conditions of the study site. Considering the limited spatial extent of the study, we can assume that the environmental variables, including the location's water conditions, are relatively homogeneous across the site. As LDMC is primarily dependent on water availability (Niinemets 2001), this could explain a lesser importance of $ITV_B$ and $ITV_I$. In addition, contrary to other abiotic conditions (e.g., light), water availability does not present such strong variability within the tree crown, therefore contributing to a lower $ITV_I$.

Hence, differences in the variation distribution among the traits could not be assigned, for example, to the trait type (morphological or chemical) or the leaf economics spectrum (i.e. acquisitive or conservative growth strategy; Reich 2014), but seem to arise from the spatial variability of the respective trait's most important environmental driver (e.g., light, water availability etc.).

### Effects of soil nutrient availability on intra-individual trait variation

For three out of the nine leaf traits studied (SLA, leaf C:N and leaf K), we partially found an increase of $ITV_I$ with higher nutrient availability in the soil, in line with our expectations (hypothesis II). Previous works showed that trait variation can be favoured by better soil conditions at the intra-specific level (Lemke *et al.* 2015; Helsen *et al.* 2017). For example, Lemke et al. (2012) reported for five herbaceous species in Germany an overall increase of intra-specific trait variation of both vegetative and reproductive traits with increasing soil P and soil N concentration. Our results suggest that better soil nutrient availability can promote trait variation not only at the intra-specific level, but also at the intra-individual level. However, apart from the positive effect of soil P concentration on leaf C:N variation, none of the soil effects was consistent across neighbourhood diversity levels, and no soil effect was independent of TSP diversity.

Previous studies already reported cases of higher soil nutrient availability and plant nutrient concentrations in more diverse neighbourhoods compared to less diverse ones (Zak *et al.* 2003; Fargione *et al.* 2007; Dybzinski *et al.* 2008). This pattern has been suggested to result primarily from a) resource-use complementarity, b) increased litter diversity, abundance and decomposability, and c) increased nutrient uptake arising from of higher microbial diversity. Resource-use complementarity is based on the capacity of different species to absorb different forms of nutrients from the soil (McKane *et al.* 2002; Ashton *et al.* 2010), or to have different nutrient uptake pathways, needs and dynamics (Uriarte *et al.* 2004; Barabás *et al.* 2016). For example, several studies showed higher total phosphorus supply from the soil in species mixtures, because a greater number of different forms of soil P were used compared to those present in monocultures (Zou *et al.* 1995; Bu *et al.* 2020).

In addition to resource-use complementarity, species mixtures may benefit from improved soil nutrient supply through increased litter production (Huang *et al.* 2017; Beugnon *et al.* 2022), or species-specific differences in litter inputs (Richards and Schmidt 2010). Furthermore, a greater diversity of fungi and bacteria has been shown to improve ecosystem soil functions, for example by increasing plant nutrient uptake and litter decomposition (Wagg *et al.* 2019). This was also observed for our study site in BEF-China, where Singavarapu et al. (2021) found that in species mixtures, fungal and bacterial communities exhibited higher species richness.

However, in the results of the present study, these positive effects of diversity on soil nutrients were not consistently reflected by intra-individual trait variation. Instead, we found a decrease of intra-individual trait variation with increasing soil nutrient availability, depending on the leaf trait either generally for trees in mono-specific TSPs, or in particular for trees in mono-specific TSPs at null or low neighbourhood diversity and for trees in hetero-specific TSPs at medium and high neighbourhood diversity.

Indeed, the slope of the soil-trait variation relationship described a hump-shape in response to increasing diversity (i.e., taking in account both TSP and neighbourhood diversity together; Fig. 4), peaking at medium diversity. Hence, at both ends of the diversity gradient, a low diversity environment (null or low neighbourhood diversity for mono-specific TSPs) and a highly diverse environment (medium or high neighbourhood diversity for hetero-specific TSPs) had a similarly negative effect on the soil-trait variation relationship. Inversely, the greatest increase of variation with soil nutrients occurred at in moderately diverse environments, that is, at low neighbourhood diversity for hetero-specific TSPs and at medium neighbourhood diversity for mono-specific TSPs.

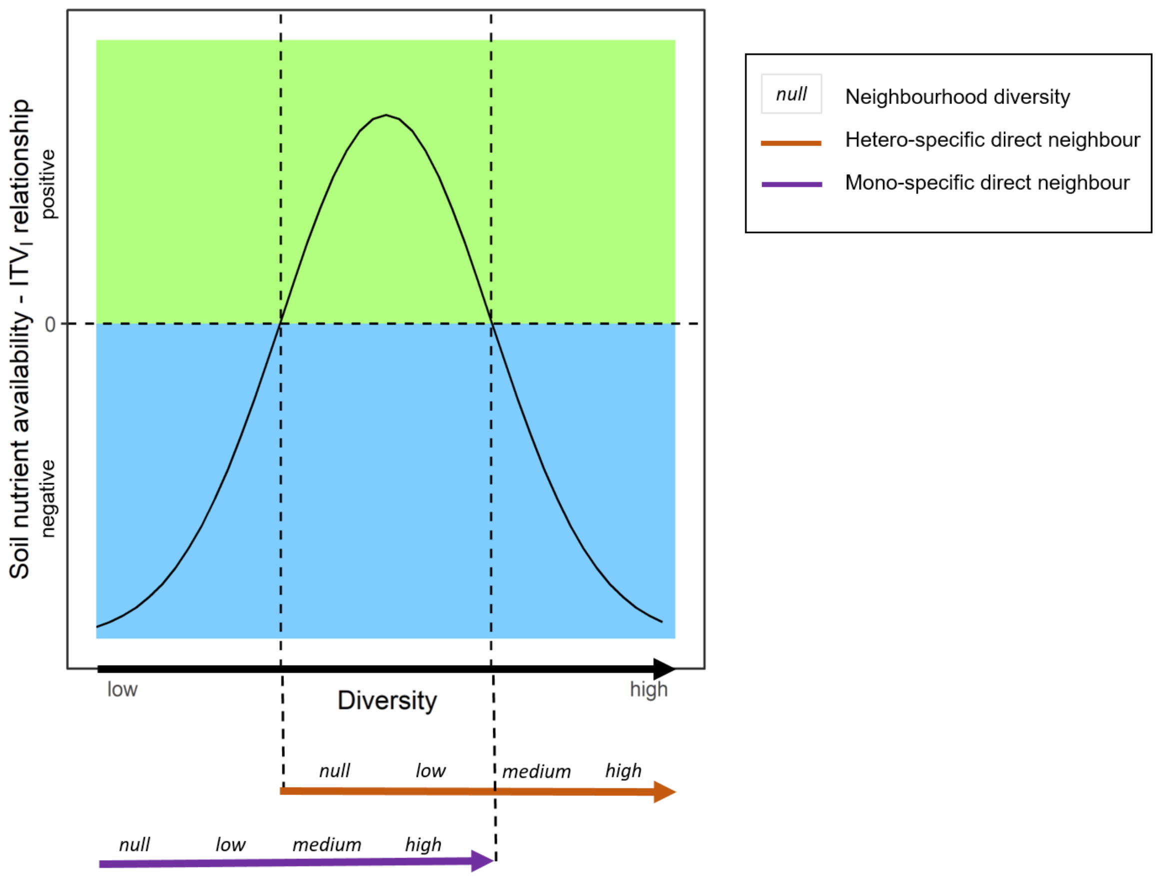

**Fig 4**: Conceptual representation of the effect of combined diversity on the soil nutrient availability relationship with intra-individual trait variation (slope of the regression). Combined diversity considers jointly both the diversity of the tree species pairs (TSP), that is, having a mono or hetero-specific direct neighbour, and the local neighbourhood diversity, calculated as the Shannon Diversity Index of the ten trees surrounding a TSP. Green area represents an increase in variation with higher soil nutrient availability and blue area, a decrease. Coloured arrows indicate the breaking down of diversity into TSP (orange or purple) and neighbourhood (italic font levels) components.

The fact that we find negative relationships between soil nutrient availability and intra-individual trait variation at both ends of the diversity gradient suggests that there are different mechanisms involved. A possible explanation is that in conditions with very low diversity, intra-specific competition from either the mono-specific direct neighbour or surrounding neighbours is the main mechanism at play, making trait variation a mean to avoid competition. With soil nutrient availability increasing in such low-diversity environments, the opportunity for better nutrient uptake might alleviate the necessity to vary (Forrester 2014). Similarly, high diversity might result in comparably negative effects for soil-trait variation relationship. Indeed, species richness, which drives the diversity gradient in our study, has been shown to reach a threshold after which positive diversity effects seem to be overtaken by inter-specific competition, as the chance to encounter a strong competitor increases with the number of neighbouring species (Davrinche and Haider 2021). As well as for low diversity conditions, a greater soil nutrient availability in highly diverse environments might improve the growing conditions of hetero-specific TSPs, and hence reduce the need for variation as a way to mitigate competition. Finally, in moderately diverse conditions, species richness might reach a balance that results in the beneficial effects of diversity (i.e., resource-use complementarity; litter diversity, abundance and decomposability; microbial diversity). Consequently, these positive diversity effects would enable exploitation of increased available soil nutrients for more trait variation, and hence the possibility to maximise a tree's local adaptation to changing environmental conditions.

### Effects of diversity on intra-individual trait variation

Additionally, we found effects of diversity independent of soil conditions: for leaf P and leaf C:N, mono-specific TSPs varied on average more than hetero-specific TSPs, contrary to our expectation (hypothesis III). While the overall response of leaf C:N variation was an increase with neighbourhood diversity, the TSP and neighbourhood diversity interaction resulted in an increase in variation with neighbourhood richness for hetero-specific TSPs but a decrease for mono-specifics for LDMC and leaf K.

This increase in trait variation at higher TSP and neighbourhood diversity, as expected in hypothesis III, can be explained by the effect of diversity improving the use of belowground resources (i.e., resource-use complementarity, as described above), increasing resource uptake and hence enabling for more variation in trait values. In addition to the belowground partition of resource, aboveground spatial niche complementarity might also occur with increasing neighbourhood diversity. In a study also conducted within trees' local neighbourhoods in the BEF-China experiment, Kunz et al. (2019) found crown packing to be denser in mixtures compared to monocultures, that is, that canopy space was used more efficiently. This might increase the gradient of light within a tree crown and, consequently, the variation of leaf traits.

In contrast, the decrease of intra-individual variation for LDMC and leaf K with increasing neighbourhood diversity for trees within mono-specific TSPs could be related to the greatest influence of the direct neighbour in comparison to more distant neighbours, in line with our assumption (hypothesis III). Indeed, having a direct neighbour from the same species implies a strong effect of intra-specific competition for trees in mono-specific TSPs. Hence, while increasing neighbourhood diversity might enable trees in hetero-specific TSPs to vary more by increasing the resource uptake and consequently the possibility to vary, it might also reduce their need for variation by alleviating the intra-specific competition for trees within mono-specific TSPs.

### Effects of interacting soil nutrient availability and diversity on intra-individual trait variation

Considering the observed interdependency of diversity and soil nutrient availability, we could not unequivocally refute or confirm our hypotheses II and III, assuming general positive effects of soil nutrient conditions and species diversity, on intra-individual trait variation.

However, we found partial support for our fourth hypothesis: although there was no amplification of soil and diversity effects, intermediate species diversity ensured positive soil effects. Unexpectedly, both high and low extremes of species diversity reversed these effects, potentially revealing different processes behind what drives intra-individual trait variation. This emphasizes that the drivers of trait variation should not be considered in isolation, but are environment-dependent. Such an interplay is well-known, for example, from diversity-productivity relationships, which depends on environmental harshness (Mulder, Uliassi, & Doak, 2001), but has not been demonstrated for trait variation, and in particular not at the intra-individual scale.

Overall, our results strongly support the pledge for the inclusion of trait information below the species scale, when associating traits with ecosystem functions (Albert *et al.* 2010; Hulshof and Swenson 2010; Messier *et al.* 2010; de Bello *et al.* 2011; Siefert *et al.* 2015; Kafuti *et al.* 2020). In particular, we could demonstrate for multiple traits the great share of intra-individual trait variation, which has not been found in such a consistent way and in a comparable extent so far. Regarding the abiotic and biotic drivers of intra-individual trait variation, our study is just a starting point. Even though the systematic exploration of multiple environmental drivers' interacting effects on individual's traits variation may be a challenge, knowledge about what drives and limits intra-individual trait variation will be crucial to understand local adaptations of plants to their complex environments. This will enable us to understand the potential of trees' response to changing environments due to, for example, global change, ultimately providing guidance for the conservation and rebuilding of sustainable forests.

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## Authors' contributions

SH, WSH, HB and AD conceived the ideas and designed methodology; AD and AB collected the data; AD and AB analysed the data, with support from SH, WSH, GA and HB; AD, AB and SH led the writing of the manuscript. All authors contributed critically to the drafts.

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# SUPPLEMENTARY MATERIAL

## High within-tree leaf trait variation and its response to species diversity and soil nutrients

Davrinche, A., Bittner, A., Harpole, W. S., Albert, G., Bruelheide, H., & Haider, S.

**Table S1:** List of tree species included in the study. Nomenclature according to The Flora of China (http://flora.huh.harvard.edu/china).

| Species name | Abbreviation | Author | Family |
|---|---|---|---|
| *Ailanthus altissima* | Aalt | (Miller) Swingle | Simaroubaceae |
| *Alniphyllum fortunei* | Afor | (Hemsley) Makino | Styracaceae |
| *Betula luminifera* | Blum | Winkler | Betulaceae |
| *Castanopsis fargesii* | Cfar | Franchet | Fagaceae |
| *Castanopsis sclerophylla* | Cscl | (Lindley & Paxton) Schottky | Fagaceae |
| *Cinnamomum camphora* | Ccam | (Linnaeus) Presl | Lauraceae |
| *Cyclobalanopsis glauca* | Cgla | (Thunberg) Oersted | Fagaceae |
| *Daphniphyllum oldhamii* | Dold | (Hemsley) Rosenthal | Daphniphyllaceae |
| *Elaeocarpus chinensis* | Echi | (Gardner & Champion) Hooker ex Bentham | Elaeocarpaceae |
| *Machillus leptophylla* | Mlep | Handel-Mazzetti | Lauraceae |
| *Machillus thunbergii* | Mthu | Siebold & Zuccarini | Lauraceae |
| *Manglietia fordiana* | Mfor | Oliver | Magnoliaceae |
| *Quercus phillyreoides* | Qphi | Gray | Fagaceae |
| *Schima superba* | Ssup | Gardner & Champion | Theaceae |

**Table S2:** Tree species pairs (TSPs) combinations within the broken-stick design of the BEF-China experiment (*sensu* Bruelheide et al., 2014). Abbreviations refer to species names in Table A1. Each cell of the ‘Species combination’ column represents a group of species (including 1, 2, 4, 8 or 14 species). While the design originally counted 16 species, two of them did not have sufficient individuals surviving to establish the required number of TSP, and were hence replaced by the repetition of two other species (*Alniphillum fortunei* (Afor) and *Castanopsis fargesii* (Cfar)).
Each species occurs at each plot species richness level, and is studied in a combination with itself (mono-specific TSP) or another species from the same four-species group (hetero-specific TSP). For example, *Machilus leptophylla* (Mlep) and *Machilus thunbergii* (Mthu) can form a pair in a four-species mixture, but not in a two-species mixture. In order to keep the number of TSPs manageable, for eight- and 14-species mixtures, we used the same groups of species as in the four-species mixtures. According to all the possible combinations within groups of one, two or four species and their respective replication, the total number of tree species pairs (TSPs) sums up to 222 from which 220 were possible to sample for this study. Adapted from Bruelheide et al. (2014).

<table>
<tr><th>Plot species richness</th><th colspan="16">Species combinations within the BEF-China broken-stick design (Site B)</th><th>Theoretical number of combinations</th><th>Theoretical number of replication</th><th>Realised number of combinations</th><th>Total number of realised TSPs</th></tr>
<tr><td>14</td><td colspan="16">Afor Mlep Mthu Echi Blum Cfar Mfor Qphi Cgla Ssup Ccam Dold Cfar Cscl Aalt Afor</td><td>38</td><td>1</td><td>37</td><td>40</td></tr>
<tr><td>8</td><td colspan="8">Afor Mlep Mthu Echi Blum Cfar Mfor Qphi</td><td colspan="8">Cgla Ssup Ccam Dold Cfar Cscl Aalt Afor</td><td>38</td><td>1</td><td>32</td><td>33</td></tr>
<tr><td>4</td><td colspan="4">Afor Mlep Mthu Echi</td><td colspan="4">Blum Cfar Mfor Qphi</td><td colspan="4">Cgla Ssup Ccam Dold</td><td colspan="4">Cfar Cscl Aalt Afor</td><td>38</td><td>1</td><td>36</td><td>38</td></tr>
<tr><td>2</td><td colspan="2">Afor Mlep</td><td colspan="2">Mthu Echi</td><td colspan="2">Blum Cfar</td><td colspan="2">Mfor Qphi</td><td colspan="2">Cgla Ssup</td><td colspan="2">Ccam Dold</td><td colspan="2">Cfar Cscl</td><td colspan="2">Aalt Afor</td><td>22</td><td>3</td><td>22</td><td>68</td></tr>
<tr><td>1</td><td>Afor</td><td>Mlep</td><td>Mthu</td><td>Echi</td><td>Blum</td><td>Cfar</td><td>Mfor</td><td>Qphi</td><td>Cgla</td><td>Ssup</td><td>Ccam</td><td>Dold</td><td>Cfar</td><td>Cscl</td><td>Aalt</td><td>Afor</td><td>14</td><td>3</td><td>14</td><td>41</td></tr>
<tr><td></td><td colspan="16"></td><td></td><td></td><td></td><td>220</td></tr>
</table>

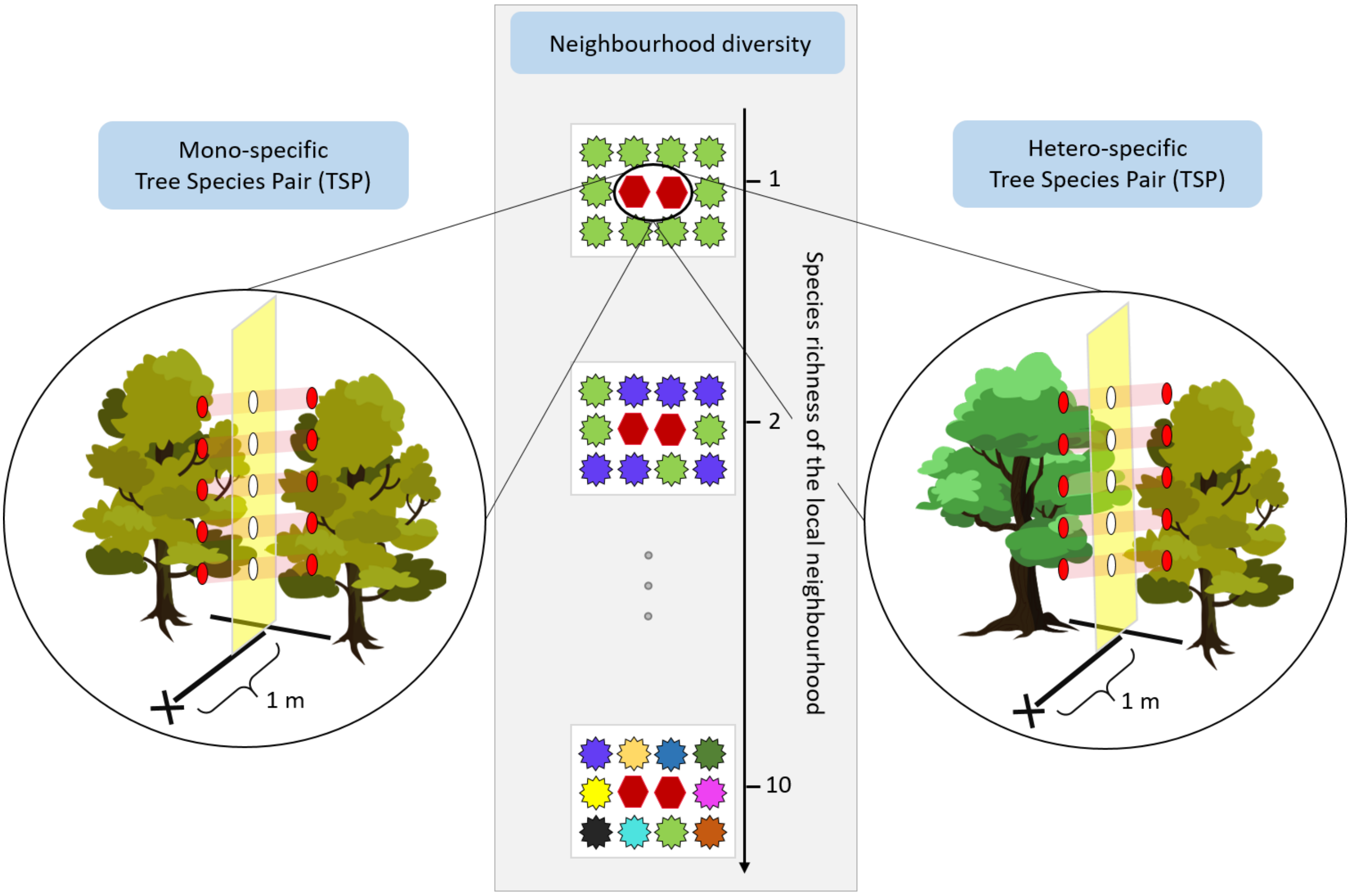

**Fig. S1:** Leaf and soil sampling design. Across Site B of the BEF-China experiment, we visited 220 Tree Species Pairs (TSP) from 57 plots. Around the TSP, the ten neighbouring trees belong to a gradient from one to ten different species (however, when accounting for tree mortality, this gradient is reduced to a maximum of six different species surrounding the TSP). Toothed shapes represent trees, red hexagons represent TSP partners and other colours represent different species. For each TSP, a soil sample was collected one meter away from the interaction plane of the two trees (black cross). For each tree, two to five samples (red dots) composed of three leaves each were taken along the crown, on the interaction plane between the two TSP partners.

**Table S3**: Functional leaf traits used and their Partial Least Square regression models (PLS) characteristics, with accuracy of the models evaluated by their Root Mean Square Error (RMSE) and coefficient of determination ($R^2$). Mathematical transformations applied to the spectra before fitting the PLS models are indicated as pre-treatments.

| Leaf trait | Abbr. | Growth strategy | Unit | $R^2$ | Number of factors in the PLS model | RMSE | Pre-treatment of spectra |
|---|---|---|---|---|---|---|---|
| Specific leaf area | SLA | acquisitive | $mm^2/mg$ | 89.88 | 7 | 9.35 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |
| Leaf dry matter content | LDMC | conservative | mg/g | 88.99 | 5 | 22.67 | Normalisation |
| Carbon to nitrogen ratio | C:N | conservative | g/g | 78.62 | 9 | 2.86 | Normalisation;<br>Savitzky-Golay 2nd derivative |
| Carbon content | C | conservative | % | 78.62 | 8 | 0.69 | Normalisation;<br>Savitzky-Golay 2nd derivative |
| Nitrogen content | N | acquisitive | % | 75.97 | 8 | 0.13 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |
| Magnesium content | Mg | acquisitive | mg/g | 60.46 | 8 | 0.65 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |
| Calcium content | Ca | acquisitive | mg/g | 58.84 | 8 | 1.71 | Savitzky-Golay 2nd derivative |
| Potassium content | K | acquisitive | mg/g | 75.97 | 2 | 2.08 | Normalisation |
| Phosphorus content | P | acquisitive | mg/g | 64.06 | 8 | 0.16 | Standard normal variate;<br>Savitzky-Golay 2nd derivative |

## REFERENCE

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# CHAPTER 4

# Complementarity behind tree-level trait expression and variation: soil conditions modify species diversity effects

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Davrinche, A., & Haider, S.

## ABSTRACT

Examples of positive effects of biodiversity on ecosystem functions have kept adding-up in the last two decades. While mechanisms such as niche complementarity have often been invoked as underlying these effects, their functioning and the conditions they are subordinate to remain elusive. For a better understanding of these mechanisms, functional traits can be used as an approachable reflection of plants' responses to diversity. However, they are rarely studied at the scale where complementarity mechanisms are likely to originate, that is, between two interacting individuals.

Here, we investigated in a greenhouse experiment how the effect of species diversity is modified by soil conditions, namely the amount of resources and their accessibility. For this, we looked into the effect of phosphorus fertilization and inoculation of the species' soil native microbiota on the leaf traits and trait variation of trees planted in monospecific or heterospecific pairs. Using optical spectroscopy methods, we analysed nine structural and biochemical traits of more than 400 trees from eight subtropical species, and inferred from trait values the fast or slow growing strategy of trees according to the leaf economics spectrum, and from their variation, the variety of tree's phenotypic responses to changes in their growing environment.

Our results highlight that species diversity effects on both traits and trait variation depend on soil conditions. In addition, the two soil treatments differed in their effects when interacting with species diversity. We found that the interaction of soil microbiota and species diversity decreased trait variation, reversing their independent respective effects. Soil microbiota showed no consistent pattern in its interaction with diversity regarding trees' growth strategy. On the contrary, phosphorus fertilization seemed to favour the effects of diversity, namely increasing trait variation, and suggested a biomass dilution of leaf nutrients through an overall decrease in leaf nutrient contents independently from the growth strategy they reflect.

Overall, our study showed that the effect of species diversity on trees' adaptability and growth strategy needs to be taken into consideration together with the soil biotic and abiotic aspects. More than just providing nutrients, interaction of plants with the belowground compartment can help us clarify the mechanisms behind complementarity at the individual level, and ultimately at larger scales.

## KEYWORDS

Functional traits; within individual variation; soil nutrients; phosphorus fertilization; microorganisms; spectroscopy; controlled experiment; complementarity.

## INTRODUCTION

In the last decades, numerous studies have pointed out the prominent role of biodiversity as a main driver of ecosystem functioning and its associated services. Among the multitude of functions species-rich forests provide (i.e., multifunctionality; Schuldt et al., 2018), the relationship probably most often studied is the effect of plant diversity on productivity (e.g. Bongers et al., 2020; Cardinale et al., 2007; Huang et al., 2018). For exploring the link between biodiversity and ecosystem functioning, inferring ecosystem's responses from plant functional traits has emerged as an efficient approach to characterize ecosystem processes, and shed light on the mechanisms behind its relationship with biodiversity.

Some traits can stand directly as proxy for ecosystem functions, as for example plant height, for estimating aboveground biomass and hence productivity, or specific leaf area (SLA) for photosynthetic capacity (L. Poorter et al., 2006). In addition, traits and their correlations also reflect plants' ecological strategies. Aboveground, leaf traits are indicators of the plant species position within the leaf economics spectrum (LES; I.J. Wright et al., 2004), a gradient capturing species growth strategies from acquisitive to conservative resource use. On the one hand, plants from species with an acquisitive growth strategy, characterised by a fast growth, invest resources into 'cheap' structures with a high turnover. On the other hand of the spectrum, slow growing conservative species have a slow resource uptake and invest into costly, long-lasting structures. Typically, the acquisitive strategy translates into high values in leaf traits related to resource acquisition and use (e.g., SLA, leaf nitrogen, leaf cations), whereas the conservative strategy is reflected into leaf traits related to structural and defensive functions (e.g., leaf dry matter content, leaf carbon).

Depending on the position of the species within the LES, leaf traits can have more or less potential to vary. Indeed, species with a short lifespan and hence a fast turnover (i.e., acquisitive species) have been found to build new leaves phenotypically adjusted to their local environment, compared to conservative species (Böhnke & Bruelheide, 2013; Valladares et al., 2000). Hence, the acquisitive strategy is more likely to enable species, and the individuals within them, to keep pace with changing growing conditions.

Traits and their variation have received much attention at the species', and more recently the within-species' level, but have rarely been investigated at the individual one. Yet, the individual level is the scale at which traits are defined (Violle et al., 2007), and where local biotic interactions first occur before to shape higher scales' processes.

Interactions between plant individuals are known to be driven by competition for resources (Barabás et al., 2016; Tilman, 1982) as individuals share the needs for similar resources, *a fortiori* when they belong to the same species. Consequently, increased species diversity is thought to reduce the overlap in common needs, and thus lessen the strength of competition through complementarity in resource-use. Indeed, because individuals from different species require different forms and amounts of resources, species diversity can enable an increased use of the total resource pool (Cardinale et al., 2007; Loreau & Hector, 2001).

In addition to reducing competition, diversity has also been shown to modify the environment through positive effects of one species benefitting another (i.e., facilitation). By alleviating abiotic pressures (e.g., enabling a hydraulic lift increasing belowground water availability through different rooting lengths) or influencing biotic variables (e.g., diluting species-specific soil pathogen loads), species diversity can foster direct and indirect positive interactions between individuals. For example, in a subtropical BEF experiment, species diversity has been suggested to lead to an increase in available nutrients for plant growth in mixtures when compared to monocultures, through higher microbial diversity (Singavarapu et al., 2021), higher litter abundance (Huang et al., 2017) and decomposition (Beugnon et al., in prep.). Hence, species diversity can not only increase the amount of potentially accessible resources, but also support the nutrient cycle and the resources availability in plant-usable forms by enhancing soil biota diversity and activity.

These positive effects of diversity, mitigating unfavourable environments and increasing resource availability, have translated into traits shifting towards more acquisitive values (faster growth strategy) as opposed to more conservative values in non-diverse environments (slower growth strategy; Davrinche & Haider, 2021; Kafuti et al., 2020). Regarding trait variation, the very few reported effects of diversity at the individual scale have shown that trait variation can increase, as the higher resources availability allow for a wider range of trait values (Davrinche et al., Chapter 3), but can also decrease in response to reduced competition and thus a lesser need for variation (Proß et al., 2021, Davrinche et al., Chapter 3). However, as the individual scale is still scarcely studied, individuals' traits responses can mostly be inferred from studies addressing a higher ecological scale (that is, intraspecific patterns). Therefore, the lack of previous research at the individual scale calls for more focus on tree-tree interactions.

As described above, diversity influences the availability of resources for individual trees and consequently affects functional traits and trait variation. Hence, environmental variation itself, and in particular variation in soil properties, may also directly act upon traits and ultimately, ecosystem functions.

Similarly as for diversity effects, the resources themselves (that is, the amount of nutrients) but also their availability, resulting from interactions with the soil biota, can affect traits and their variation. Indeed, higher nutrients amounts have been found to increase traits reflecting a more acquisitive growth strategy (Báez & Homeier, 2018; Ordoñez et al., 2009), as well as trait variation (Lemke et al., 2012). Further, a field study conducted with the same species as used in this work found opposite effects of soil nutrient availability depending on the species diversity of a tree's neighbours. These results suggested that belowground resources could reduce competition, and hence decrease the need to vary for trees surrounded by a low diversity. Inversely, increasing resources could increase variation for trees benefiting from higher surrounding diversity and its associated positive effects, as it enables the maximization of a tree's adaptability to changing environmental conditions (Davrinche et al., Chapter 3).

While plants needs several nutrients, phosphorus in particular has been shown to be a major determinant for plant metabolism, and one of the most limiting nutrients for plant growth (Chapin, 1980). Indeed, phosphorus plays a role not only as a direct input in in the mineral nutrition of the plant, but also in lifting co-limitations with other nutrients (for example, nitrogen; Ostertag & DiManno, 2016) related to generally low availability of phosphorus present in forest soils (Fox et al., 2011) including the one on which the species used in this study naturally grow (Bittner & Haider, unpublished results; Han et al., 2005). Moreover, as the soil microorganisms participate in an improved access and/or absorption of resources though mutualistic or commensalistic plant-microorganism relationship, their presence is expected to have comparable effects on plant's traits to a direct input of plant-usable nutrients (Jacoby et al., 2017).

In this study, we aimed at understanding the effect of tree species diversity on leaf functional traits and their variation. In particular, focusing on trees with either a monospecific or a heterospecific neighbour, we propose to disentangle how soil nutrient availability (here, manipulated through phosphorus fertilization) and soil biota (through inoculation of the tree species' natural soil) modify diversity effects at the individual tree level. While diversity and soil nutrient amount and availability are expected to have an additive effect on the shift towards a more acquisitive growth strategy, the positive effect of soil resources on trait variation are thought to depend on the amount of diversity. Therefore, we hypothesize that:

H1. The acquisitiveness of trees increases with tree species diversity. The increase in nutrients (phosphorus fertilization) or in access to nutrients (through soil microbiota added with soil inoculation) enhances the effect of diversity. As the soil microbiota from the inoculum can facilitate the uptake of added phosphorus, the synergy of treatments results in a stronger effect of their interaction with diversity on trait values. The increase in trees acquisitiveness with soil treatments at higher diversity is stronger than at lower diversity (Fig. 1a).

H2. Trait variation decreases with species diversity, but this relationship is inversed with an increase in nutrients (phosphorus fertilization) or a better access to nutrients (through soil microbiota added with soil inoculation). Specifically, soil treatments independently, and *a fortiori* combined, decrease variation for trees at low diversity, while increasing variation at higher diversity (Fig. 1b).

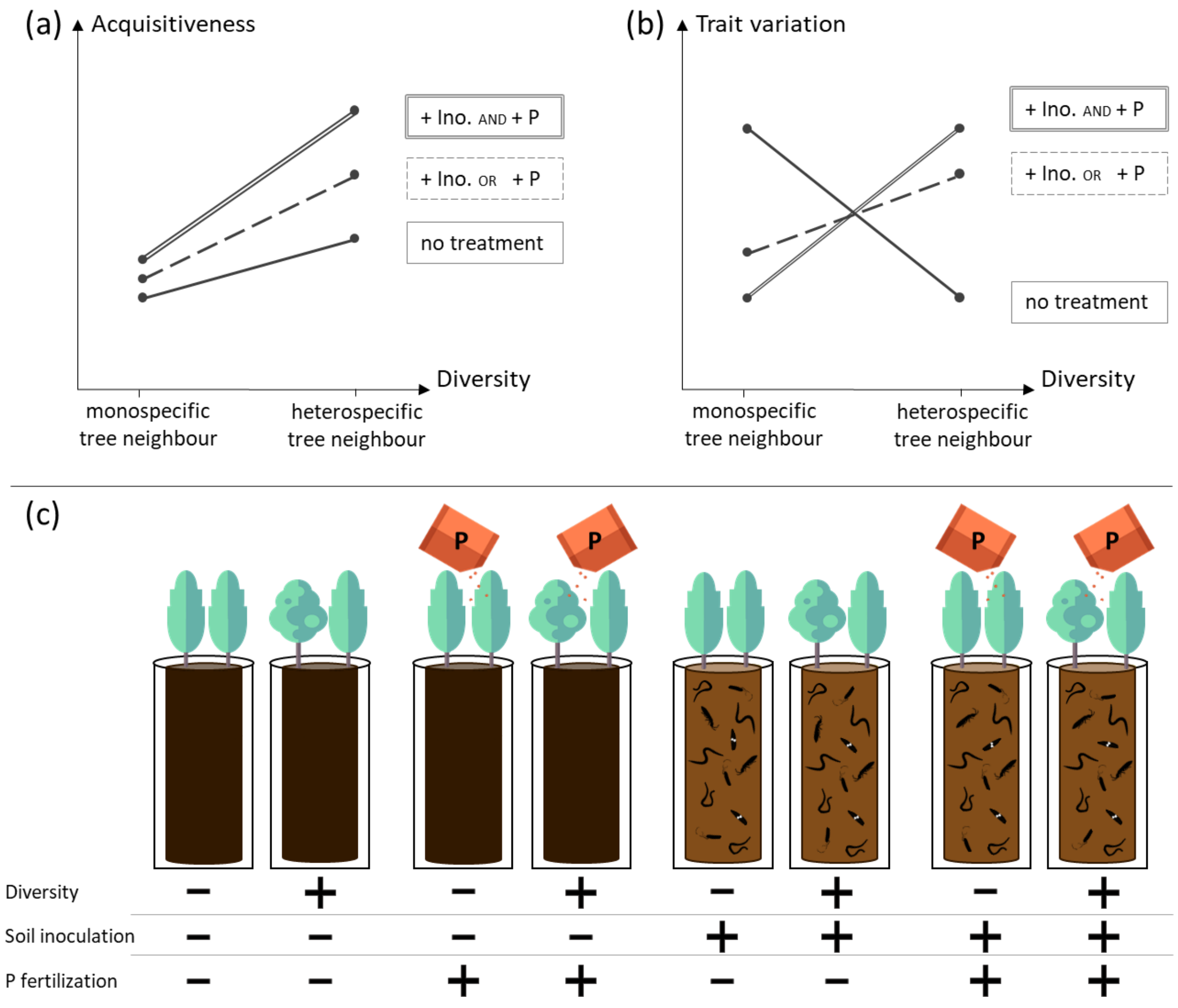

**Fig. 1:** Expected trait acquisitiveness **(a)** and trait variation **(b)** of a focal tree in response to increasing species diversity (from mono to heterospecific tree neighbour; solid line), with inoculation of the native soil microbiota (+ Ino; dashed line), phosphorus fertilization (+ P; dashed line), or both soil treatments together (+ Ino and + P; double line). **(c)** Experiment design. Trees are planted in mono- or heterospecific pairs (diversity) in soil either sterilized or inoculated with microbiota (soil inoculation) with addition or not or phosphorus (P fertilization). Each association of treatments represented (diversity, soil inoculation, P fertilization) is repeated for 20 species combinations (2 groups of 4 species, each forming 4 monospecific and 6 heterospecific pairs) and replicated three times, amounting to 480 planted trees (a maximum of 412 trees was used for the analyses).

## METHODS

### Species combinations

Seeds from eight native species from subtropical China were collected from the Gutianshan Nature Reserve (Jiangxi, China; Supp. Table S1). After germination and growth of the seedlings for nine to 18 months, individuals were planted in 30 L tubes filled with a mix of sterilised German forest soil and sand.

The eight species were separated in two sets of four (Supp. Table S1). Trees were planted at a rate of two individuals per tube, according to all possible species combination within each set of four species, totalling 20 different combinations (six hetero-specific and 4 mono-specific tree species pairs for each set, referred to as TSPs).

### Native soil inoculation

For each species combination, the upper 5% of the tube soil volume was mixed before planting with soil from the native region of the studied species (Jiangxi, China). This native soil was collected in each species respective monoculture (BEF-China, Site A) and blended. The mixture of native soil was used either with its microbiota kept alive as an inoculum (+Ino), or sterilised, to provide a control (-Ino; Fig. 1c).The tubes where then covered with a 2 cm layer of sand to prevent external pathogens.

### Phosphorus fertilization

After planting, each species combination received every three weeks 20 ml of a fertilizer solution consisting of equal proportions of calcium, magnesium, nitrogen, potassium and either phosphorus (+P) or water (-P; Fig. 1c).

### Data collection

Overall, the experiment consisted of 20 species combinations treated with soil inoculum, 20 without inoculum, 20 with phosphorus fertilization, and 20 without. Each soil treatment and species combination association was replicated three times, amounting to 240 tubes. Tubes were randomly distributed across six greenhouse chambers kept in subtropical conditions (25 °C, 70-80 RH).

After one year of growth, we collected for each tree between two and eight leaves along the crown, on the side where the two trees of a pair were the closest. Leaves were then immediately measured with the ASD FieldSpec4 Wide Resolution Field Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom) to acquire leaf reflectance spectral data, over a 350 to 2 500 nm wavelength range. A white diffuse reflectance target (Spectralon, Labsphere, Durham, New Hampshire, USA) was used as reference on which the device was regularly calibrated in parallel to the measurements. To minimize measurement errors, each individual spectral measurement was repeated three times for each leaf.

### Data processing

In order to predict trait values from leaf spectra, we used Partial Least Square regression models linking spectral data and laboratory measured values of each trait from the same species. These models were fitted on data collected in the BEF-China Site A (Jiangxi, China) during August to October 2018, including the species of interest for this study (see (Davrinche & Haider, 2021 for details). A trait value was predicted for each repeated spectral measurement of each leaf, for both traits related to an acquisitive strategy (SLA, leaf N, leaf Mg, leaf K, leaf Ca, leaf P) or a conservative strategy (LDMC, leaf C, leaf CN).

### Statistical analysis

Outlying predicted trait values were excluded for each trait on the base of a 99% confidence interval applied species-wise, in addition to negative values and values with a standard error exceeding five time the mean standard error. Trait values from the repeated measurements were then averaged, resulting in one value per leaf. Individuals with less than two sampled leaves, as well as individuals with no neighbour in the same tube (incomplete pairs) were then excluded from the analyses, totalling between 404 and 412 trees (3030 and 3198 leaves), depending on the trait. We used the predicted traits values for two separate analyses as described below.

*Species classification*

In order to capture treatments and diversity effects on traits that would be dependent on strong species identities in early stages of growth, we grouped species according to their growth strategy. We performed a principal component analysis on all traits averaged for each treatment combinations of each species and used the two resulting clusters as proxy for acquisitive and conservative species (Supp. Fig. S1, Table S1). This approach was favoured over using species identity directly in order to account for species effects, while conserving the general purpose of traits to characterise interaction without describing hardly generalizable species-specific behaviour.

*Leaves' trait values*

We used the trait values of each individual tree averaged at the leaf level as response variable in linear mixed model for each of the nine studied traits. Leaf level trait values were explained by the species diversity of the TSP (i.e., Div, either monospecific or heterospecific), the presence of soil inoculum instead of sterilized soil (Ino), fertilization with phosphorus (P), and the growth strategy of the species to which the tree belonged (i.e., Sp. group, either acquisitive or conservative) and all their interactions. The species identity, possible species combination, as well as the tree identifier nested in the growing tube identifier, itself nested in the greenhouse chamber's identifier, were added as crossed random factors (Supp. Table S2). To correct for heteroscedasticity and non-normality of the residuals, trait values were log-transformed for four out of nine traits (leaf C:N, leaf Mg, leaf Ca and leaf K) and model predicted values back transformed for plotting purposes.

*Within-tree trait variation*

In parallel, trait values of each individual tree averaged at the leaf level were used to calculate Rao's quadratic entropy as a measure of trait variation within-tree. With setting weights and abundance to one as all leaves within each tree were considered equal, we used the FD package to determine Rao's Q for each trait for each tree, that is, the mean Euclidian distance between trait values of all sampled leaves within an individual.

We then fitted a linear mixed model for each of the nine studied traits, with all trees Rao's Q explained by the same factors than for trait values models (species diversity of the TSP, presence of soil inoculum, fertilization with phosphorus, species growth strategy  and all their interactions). The random structure was also the same as for trait values models, except for the absence of the tree identifier. To fulfil linear model requirements, Rao's Q of all traits were log-transformed to correct for heteroscedasticity and non-normality of the model residuals.

Both trait variation and trait values full models were simplified by stepwise removal of model terms based on significance at p=0.05. P-values were extracted from F-statistics of type III sum of squares with Satterthwaite approximation for estimating the denominator degrees of freedom (Supp. Table S2 & S3). All statistical analyses were performed in R, version 4.0.4.

## RESULTS

### Species growth strategy

Based on a principal component analysis, two clusters were distinguished along the first axis which corresponded to the acquisitive- (SLA, leaf N, leaf P) conservative (LDMC, leaf CN) spectrum (Supp. Fig. S1). Driven by acquisitive-related traits, *Quercus serrata* (*Qs*), *Choerospondias axillaris* (*Ca*), *Sapium sebiferum* (*Ss*), *Koelreuteria bipinnata* (*Kb*), and *Quercus fabri* (*Qf*), were separated from conservative *Cyclobalanopsis glauca* (*Cg*), *Schima superba* (*Ssu*), and *Rhus chinensis* (*Rc*).

### Leaves' trait responses

While the species classification was based on all nine leaf traits, it was  also reflected in single traits values, with for example leaf P and leaf N (Fig. S2a & b) having higher values in trees belonging to acquisitive species, and oppositely for leaf C:N (Fig. S2c; Supp. Table S2). As for the effect of the soil treatments on trait values, traits related to an acquisitive growth strategy responded predominantly, with the exception of leaf C (Fig. 2d, Fig. 3c). Soil inoculation increased leaf P, leaf Mg (Fig. 2a & b), and leaf K, however, for the latter only when P was added as well (Fig. 2e). The addition of P lowered both acquisitive and conservative-related trait values, specifically leaf P, leaf K (only with sterile soil), and leaf C for trees from conservative species (Fig. 2c, d and e).

Regarding the effects of diversity, trees belonging to monospecific TSPs displayed a higher SLA than heterospecifics, but only for trees from acquisitive species (Fig. 3a). For leaf K, increasing diversity (from monospecific to heterospecific TSPs) had a consistently negative effect on trait values in both inoculated and sterile soil, and for both species' growth strategy. Soil inoculation seemed however to amplify this negative effect in trees from conservative species.

The addition of P yielded opposite results for conservative- (leaf C; Fig. 3c) and acquisitive-related traits (leaf Mg; Fig. 3d), regarding the effect of diversity. Without added P, leaf C decreased with increasing diversity, and inversely increased with diversity when P was added. We found the opposite for leaf Mg, which decreased with increasing diversity when P was added, but increased with increasing diversity without P addition. While trees in heterospecific TSPs had a slightly negative response to P addition for both traits, trees in monospecific TSPs showed a strong decrease in leaf C (resp. increase in leaf Mg) with added P.

Without soil treatments, the increase in diversity had a positive effect on leaf Ca (Fig. 3e). Both soil treatments seemed to buffer or reverse the effect of diversity (steepest positive slope for trees without P or inoculum), resulting in a moderate increase in leaf Ca with soil inoculation (both with and without P addition), and a decrease when only P was added. Compared to the baseline situation (no addition of P or soil inoculation; black line), leaf Ca was higher for trees in monospecific TSPs, but lower for trees in heterospecific ones with each treatment independently. The joint effect of soil treatments resulted in the highest values of Ca for trees in both monospecific and heterospecific TSPs, also increasing with increasing diversity.

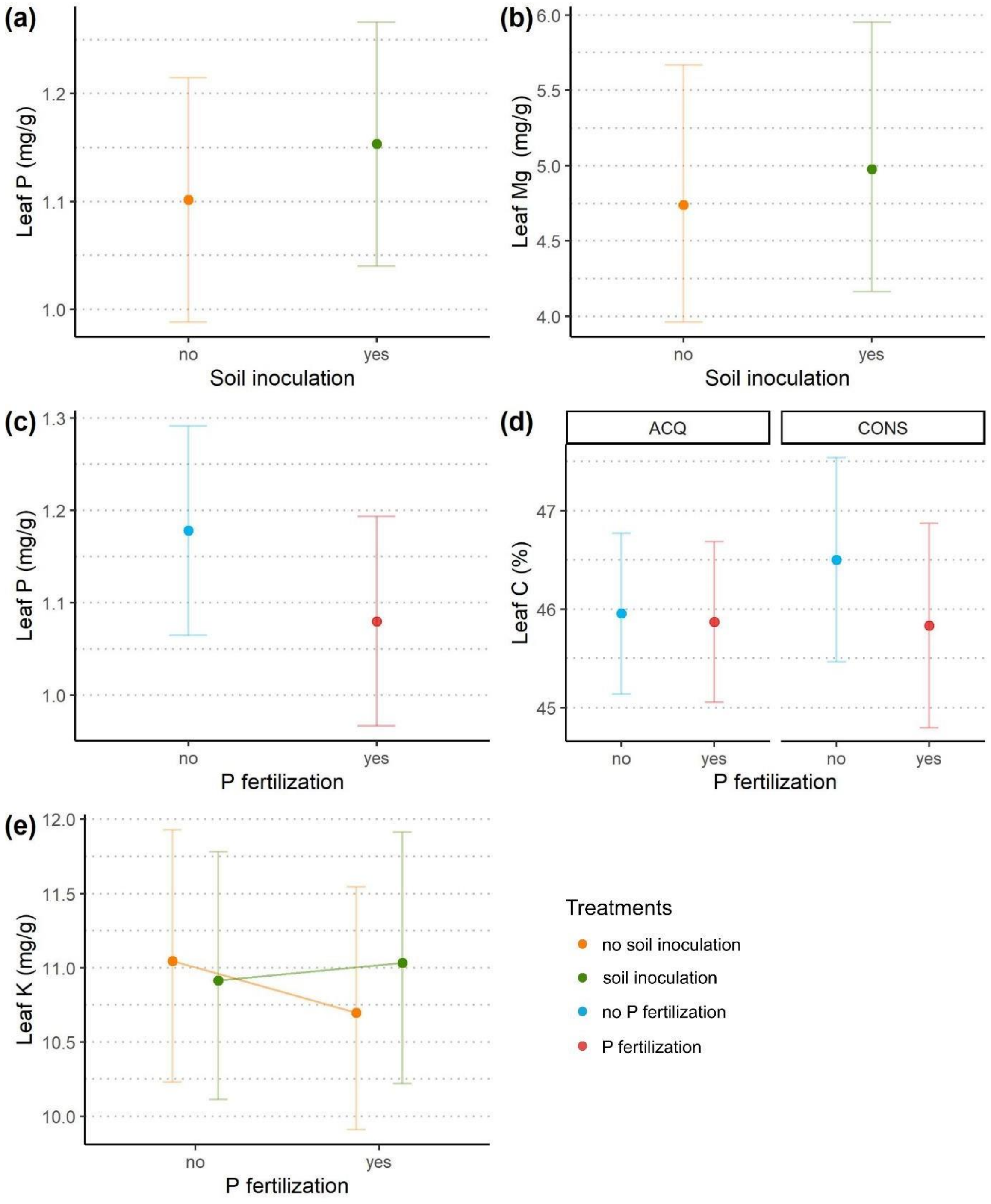

**Fig. 2:** Effect of soil inoculation with microbiota (a, b), phosphorus fertilization (c; d) and the interaction of both soil treatments (e) on leaf traits. The effect of phosphorus fertilization on leaf C (d) also depends on the tree's species growth strategy, either acquisitive (ACQ) or conservative (CONS; see Supp. Table S1 & Fig. S1). Dots indicate trait values averaged at the leaf level predicted from significant effects of the respective trait linear mixed model (see Supp. Table S2). Leaf Mg (b) and leaf K (e) values were log-transformed for the analysis and back-transformed for illustration purpose. Error bars represent two standard errors around the mean.

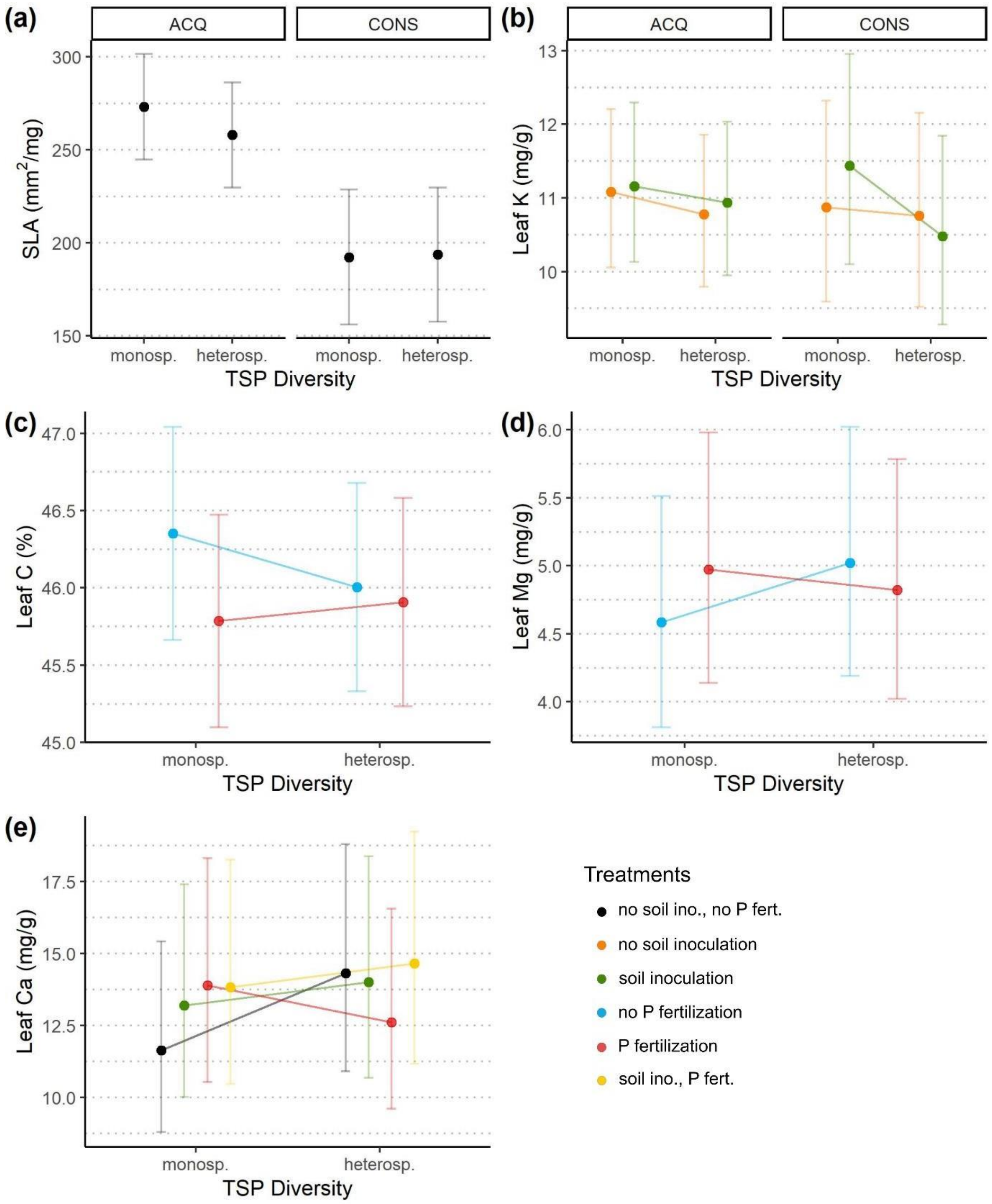

**Fig. 3:** Effect of the tree species pair diversity (mono or heterospecific TSP; a) and its interaction with soil inoculation with microbiota (b), phosphorus fertilization (c, d) and both soil treatments (e) on leaf traits. Effects of diversity (a) and diversity's interaction with soil inoculum (b) on SLA and leaf K respectively also depends on the tree's species growth strategy, either acquisitive (ACQ) or conservative (CONS; see Supp. Table S1 & Fig. S1). Dots indicate trait values averaged at the leaf level predicted from significant effects of the respective trait linear mixed model (see Supp. Table S2). Leaf K (b), leaf Mg (d) and leaf Ca (e) values were log-transformed for the analysis and back-transformed for illustration purpose. Error bars represent two standard errors around the mean.

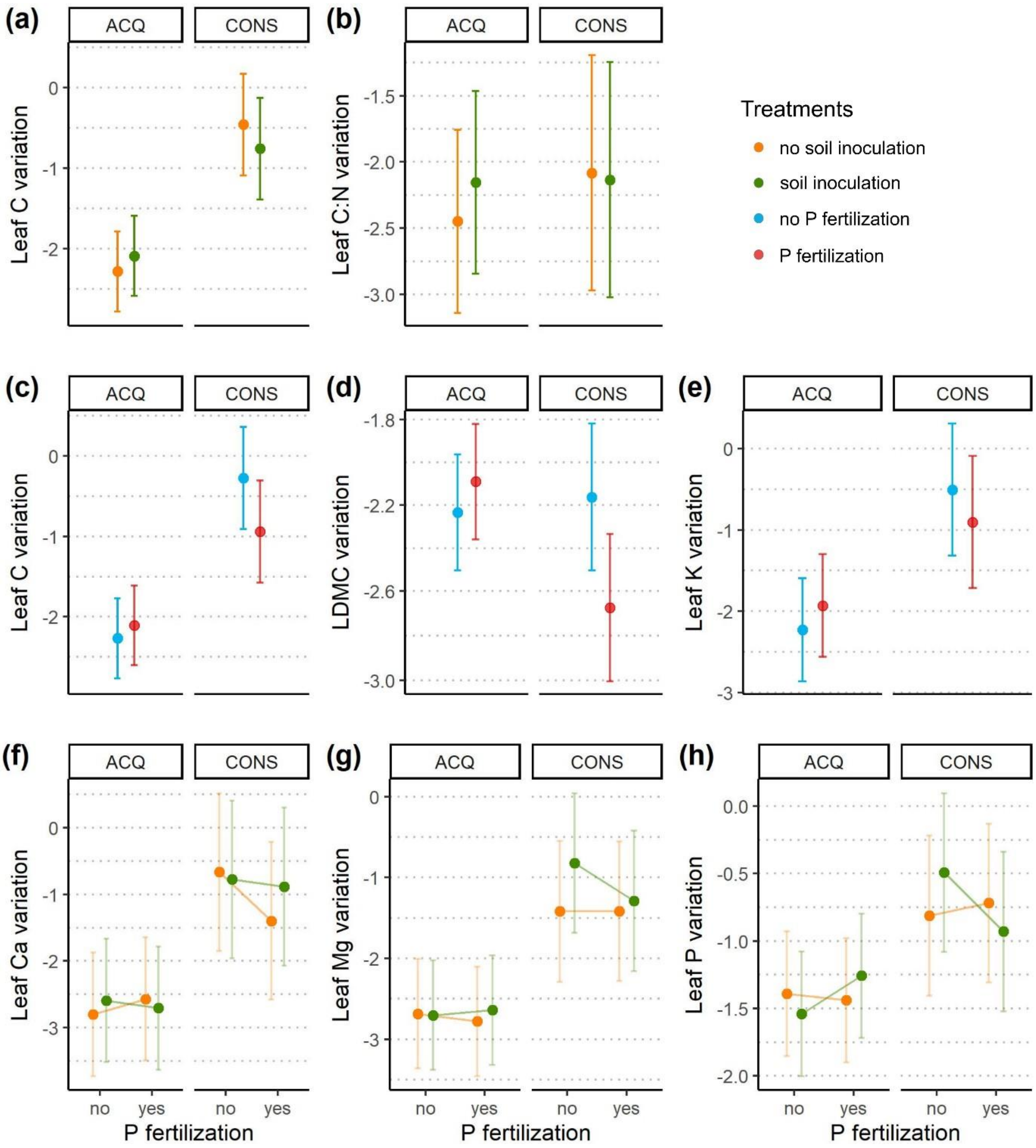

**Fig. 4:** Effect of soil inoculation with microbiota (a, b), phosphorus fertilization (c, d, e) and the interaction of both soil treatments (f, g, h) on leaf trait variation. All effects also depend on the tree's species growth strategy, either acquisitive (ACQ) or conservative (CONS; see Supp. Table S1 & Fig. S1). Dots indicate trait variation within each individual, calculated as log-transformed within-tree Rao's Q, predicted from significant effects of the respective trait linear mixed model (see Supp. Table S3). Error bars represent two standard errors around the mean.

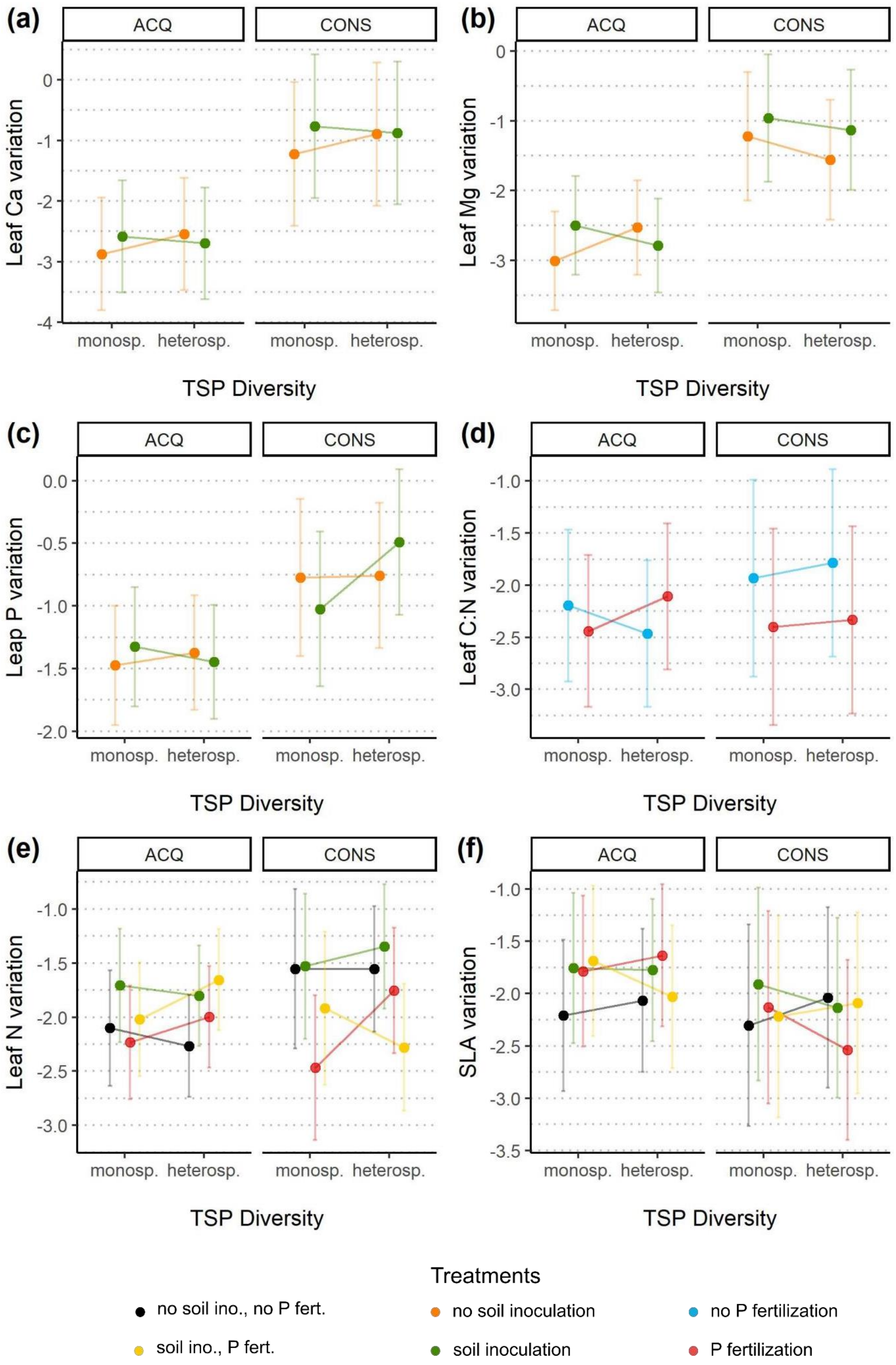

**Fig. 5:** Effect of the tree species pair diversity (mono or heterospecific TSP) interaction with soil inoculation with microbiota (a, b, c), phosphorus fertilization (d) and both soil treatments (e, f) on

leaf trait variation. All effects also depend on the tree's species growth strategy, either acquisitive (ACQ) or conservative (CONS; see Supp. Table S1 & Fig. S1). Dots indicate trait variation within each individual, calculated as log-transformed within-tree Rao's Q, predicted from significant effects of the respective trait linear mixed model (see Supp. Table S3). Error bars represent two standard errors around the mean.

**Within-tree trait variation**

Overall, the responses observed for trait variation were less consistent than those of trait values. The interaction of soil treatments (P, soil inoculation) as well as the interaction of treatments with species diversity mostly affected the variation of traits related to an acquisitive growth strategy, but not of traits related to a conservative strategy (Fig. 4, Fig. 5; Supp. Table S3). For the latter, the direction of treatment effects on trait variation mostly depended on the species' growth strategy (Fig. 4).

Either the addition of phosphorus (for LDMC) or the presence of inoculum (for leaf C and CN) resulted in an overall increase of within-tree variation for individuals of acquisitive species, while we observed the opposite for conservative species (Fig. 4).

When looking at the joint effect of the treatments, we found that for individuals belonging to acquisitive species, any combination of the treatments yielded little effects, except for an increase of variation of leaf P when phosphorus was added to inoculated soil (Fig. 4h). In contrast, for conservative species, effects of P addition led to a decrease of variation of some traits (Fig.2). This response was found either for inoculated (leaf Mg and leaf P; Fig. 4g & h) or sterile soil (leaf Ca; Fig. 4f).

Regarding the effect of diversity on trait variation, we could see opposite patterns for individuals of acquisitive species, depending on soil inoculation (Fig. 5a). Increasing diversity was associated with an increase of variation in sterile soil, but a decrease of variation in inoculated soil (leaf Ca, Mg, P; Fig. 5a, b & c). Moreover, for acquisitive species in inoculated soil, variation of trees in monospecific TSPs was higher than in sterile soil, but lower for trees in heterospecific TSPs. Contrarily, individuals of conservative species showed higher trait variation in inoculated soil for trees in both monospecific and heterospecific TSPs (Fig. 5a, b & c). However, for conservative species, the diversity effect on variation was not consistent across traits and soil inoculation treatments.

The P fertilization modified the effect of diversity on variation for individuals from acquisitive species, reversing a decrease in variation without P to an increase with P (leaf CN; Fig. 5d). Variation of acquisitive trees in monospecific TSPs was lower with P addition than without, contrary to heterospecifics. For conservatives, the effect of increased diversity tended to increase trait variation, but did not depend on P addition. Moreover, the addition of P decreased variation of conservative TSPs, independently of their diversity status.

For the variation of SLA and leaf N, we found positive, negative and no diversity effects, strongly depending on the combination of soil treatments and species' strategies (acquisitive and conservative) and differing between the two traits (Fig. 5e & f). However, we found rather consistent responses to the soil treatments. The effect of soil inoculation on variation was most often positive for the two traits, and this for both diversity levels (partly no effect, but never a reversed effect). The addition of P mostly decreased trait variation for conservative species, but led to mixed responses for acquisitive species, including positive, negative and no effects.

## DISCUSSION

In a controlled environment, we investigated species diversity effects on trait values and trait variation and how they are modulated by manipulated soil phosphorus (P) and species' native microbiota. Without soil treatments, most trait values showed strikingly little response to species diversity, with only a few shifts towards an overall acquisitiveness of trees (leaf Mg & leaf C, leaf Ca). The soil treatments' interaction with the effect of species diversity were complex, and often led to results contrary to those hypothesized. Namely, increased diversity resulted most often in less acquisitive trait syndromes, in particular with P fertilization.

Diversity had also little influence on trait variation independently from soil conditions, as we observed no main effect, but tended to increase trait variation of trees on sterile soil contrary as hypothesized, while increasing variation in absence of fertilization. When phosphorus was added, diversity tended to increase trait variation in accordance with our hypothesis. Increased diversity on inoculated soil, however, displayed generally the opposite pattern, contrary to our expectation of a similar effect from the two soil treatments. Finally, the joint effect of both soil treatments with diversity showed little consistent patterns. We found that acquisitive-related trait and their variations generally responded stronger to diversity and soil treatments. Taken together, our findings demonstrate the dependency of plant interactions to their local growth conditions, suggesting a high level of individual plants' adaptability in response to a changing biotic and abiotic environment.

## General effect of diversity

The effects of diversity on both trait variation and trait values were strongly dependent on the two soil treatments and differed between acquisitive and conservative species. The only effect independent from soil conditions was a decrease of SLA with increasing diversity. Considering that SLA is mainly driven by light (H. Poorter et al., 2019), this result is likely to reflect the contrasting crown architecture of trees in heterospecific pairs, compared to more similarly shaped crowns in monospecific ones. Because of this spatial occupancy, competition for light is expected to be stronger intra- than interspecifically, resulting in trees in monospecific pairs having higher SLA values in average, in order to maximise their light capture. Together with the sensitivity of SLA to light conditions, the shift towards conservative growth strategy in response to an increasing diversity is likely in response to a dominance of competitive interactions.

## Diversity's effect on trait values is modified by phosphorus fertilization and soil microbiota (H1)

Except when grown on sterile soil, increased species diversity increased trees acquisitiveness when no soil treatments were applied, supporting H1 (leaf C, leaf Mg, leaf Ca). It is consistent with the idea that positive diversity effects (i.e., complementarity in resource-use, facilitation) enhance resource availability, therefore fostering an acquisitive growth strategy.

However, on sterile soil, increased diversity had no or little effect on leaf K, with a tendency to shift toward acquisitive values. This result is surprising, considering leaf K involvement in several fast growth mechanisms such as photosynthesis and sugar production, as well as the high mobility and the higher concentration of this nutrient in young leaves – also more likely to occur in trees with an acquisitive strategy. The absence of positive effect of diversity on leaf K seems nonetheless not to be conditional to soil inoculation.

The two soil treatments, independently from diversity, seemed to have opposite effects on tree's acquisitiveness. Soil inoculation tended to increase acquisitiveness, independently or in association with P fertilization (leaf P, leaf Mg, leaf K, leaf Ca). This is consistent with the assumption that an increased availability of resources tends to promote a tree's fast growth strategy (Ordoñez et al., 2009), which is reflected in higher acquisitive-related and lower conservative-related trait values. In contrast, P fertilization alone tended to lower both trait values related to an acquisitive or conservative strategy. As a limiting nutrient, adding phosphorus not only increases its availability but also fosters the uptake of other nutrients (Turner, 2008). Therefore, the resulting decrease in trait values when adding phosphorus could be due to an increased tree biomass in response to more available nutrients, and hence a lower amount of nutrients (leaf P, leaf K) per unit of leaf material (Smith et al., 1994). This would explain lower values in conservative trait (leaf C), as P fertilization would still favour an investment of resources in fast growth rather than strong structures.

Consequently, the joint effect of P fertilization or soil inoculation and increased diversity yielded different results, contrary to our expectation of these two aspects of soil conditions having comparable outcomes. Specifically, increased diversity with P fertilization resulted in a decrease in traits related to an acquisitive growth strategy (leaf Mg, leaf Ca), potentially as a result from nutrient dilution due to increased biomass. In addition, trees in heterospecific pairs also displayed decreased trait values (leaf C, leaf Mg) in presence of P fertilization. However, we also observed single notable exceptions to this pattern, such as an increase in leaf C with increasing diversity and P fertilization, and an increase in leaf Mg in monospecific tree pairs with P fertilization. These mixed results reflect the variety of responses found in previous studies focusing on P fertilization, including the recurring finding that the response to P fertilization can be highly species specific, in particular for species adapted to low P soils in their natural habitat (Zalamea et al., 2016).

The effect on trait values of diversity in inoculated soil contrasted with the higher acquisitiveness observed on inoculated soil, independently from diversity (leaf P, leaf Mg), or in monospecific pairs (leaf K, leaf Ca). With increasing diversity and in heterospecific pairs on inoculated soil, trees' traits values seemed to be idiosyncratic, buffering diversity effects (leaf Ca), tending to more conservative values or showing no effect (leaf K).

### Diversity's effect on trait variation is modified by phosphorus fertilization and soil microbiota (H2)

We found few evidence supporting the hypothesis that beneficial effects of diversity (complementarity in resource use, facilitation) reduce competition and thus the need for variation (leaf CN and leaf N for acquisitive species, leaf Mg for conservative ones). On the contrary, increasing species diversity tended to increase variation for trees from both acquisitive and conservative species (SLA, leaf Ca, leaf P, leaf Mg, leaf CN). The scarcity of main effects of diversity on trait variation suggests, as for the growth strategy reflected by traits (see above), a strong dependency of diversity effects on the soil nutrients and microbiota.

Both P fertilization and soil inoculation had independently positive effects on trait variation of trees from acquisitive species and negative effects on trees from conservative species, respectively (LDMC, leaf C and leaf K with P fertilization; leaf C and leaf CN with soil inoculum). While the treatments did not show amplifying effects, their interaction with diversity led to opposite patterns.

Specifically, when increasing diversity under phosphorus fertilization, trait variation showed a tendency to increase (leaf CN, leaf N, SLA). This supports H2 and indicates that increased resource availability enables more variation in a more favourable environment. In addition, when adding phosphorus, we found higher variation in heterospecific tree pairs and lower variation in monospecific ones for trees from acquisitive species, and inversely for those from conservative species. It is likely that because of strong competition within monospecific pairs and the associated necessity to vary for mitigating competition, the addition of resources reduces the need for variation by providing a more favourable environment to the competitors. Inversely, while already benefiting from reduced competition, trees within heterospecific pairs can use this excess of resources to optimize their variation and maximise their potential for adapting to a changing environment. Taken together, the effects of P fertilization associated to diversity were positive and indicated synergistic effects on trait variation.

In contrast, the joint effect of diversity and soil inoculation mostly yielded a decrease of trait variation (leaf Ca, leaf Mg, leaf P, leaf N, SLA). In addition, soil inoculation also resulted in generally higher variation in monospecific tree pairs (leaf Ca, leaf Mg, leaf P, leaf N, leaf SLA), and lower variation in heterospecific ones (leaf Ca, leaf Mg, leaf P).

This could indicate that a more diverse pair would be more efficient in mobilizing the microbiota, as different actors from the soil community would be solicited by the presence of different species. Hence, higher species diversity would tend to reduce the trees competition for interaction with beneficial soil microorganisms. Inversely, at low diversity, the interaction of the soil biota with multiple individuals from the same species, soliciting similar belowground partners, would reinforce the trees competitive interactions. In addition, these results reinforce the idea of different roles of the two soil treatments in their interaction with diversity. Specifically, soil inoculation, together with diversity and contrary to our expectation, did not seem to enhance nutrient uptake, therefore increasing the potential for variation. Instead, their combined effect reduced variation, suggesting a reduction in competition, lessening the need to vary for trees in diverse settings.

### Responsivity of individuals from acquisitive vs conservative growth strategy

When considering the trees' response to diversity and soil treatments, we observed more dependency to the species growth strategy in their variation than in their trait values. This suggested that while the modified conditions enabled flexibility in the individuals' response, the individual shift towards a growth strategy was not strongly constrained by the species strategy itself. For both trait values and variation, conservative species mostly displayed opposite patterns to acquisitive ones (Fichtner et al., 2017), with however less consistent responses than acquisitive species. In addition, independently from the tree species' growth strategy, the traits related to an acquisitive growth strategy were the most responsive to the diversity and soil treatments for both trait values and variation. While acquisitive-related traits, measured at the individual level, were the most variables,  acquisitive species were not necessarily more variable than conservative ones in the setting of our study. Hence, assumption about a baseline potential for trait variation might benefit from being considered at the level of the individual, and inform at the local scale about an effective use of increased resources and beneficial effects of diversity as trees adapt to changing environmental conditions.

In addition, the difference in the two growth strategies responses' consistency might also affect the dependency of diversity effects on soil conditions. Indeed, the growth strategy of the neighbours could reinforce competitive interactions, for example when conservative and acquisitive species compose a pair, with likely the acquisitive species being dominant.

### Conclusion

In this study, we make a first step towards disentangling how soil conditions alter diversity effects on both trait values and trait variation of individual trees. Taken together, our results highlight that the effects of diversity can hardly be considered in isolation from the soil conditions. While phosphorus fertilization seemed to consolidate positive effects of diversity on tree acquisitiveness and enhance their variation, the presence or absence of the species' native microbiota yielded unexpected responses, likely inherent to the complexity of its composition and functioning. Finally, individuals with a fast growing strategy seemed to benefit more from improved soil and diversity conditions, emphasizing the importance of considering not only traits and trait combinations of individuals but also the interaction of strategies when looking at the effect of species diversity. Our results show that identifying which mechanism behind diversity effects is driving the biodiversity ecosystem functioning relationship might require us to embrace the multiple facets of the plant-soil interaction.

### ACKNOWLEDGMENTS

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# SUPPLEMENTARY MATERIAL

## Complementarity behind tree-level trait expression and variation: soil conditions modify species diversity effects

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**Table S1:** List of tree species included in the study. Nomenclature according to The Flora of China (http://flora.huh.harvard.edu/china). Species were planted two by two in all possible combinations within each set. Abb.: abbreviated name; Acq.: acquisitive; Cons.: conservative.

| Species name | Abb. | Author | Family | Growth strategy | Set |
|---|---|---|---|---|---|
| *Choerospondias axillaris* | Ca | (Roxb.) B.L.Burtt & A.W.Hill | Anacardiaceae | Acq. | A |
| *Koelreuteria bipinnata* | Kb | Franch. | Sapindaceae | Acq. | A |
| *Quercus fabri* | Qf | Hance | Fagaceae | Acq. | B |
| *Quercus serrata* | Qs | Thunberg | Fagaceae | Acq. | A |
| *Sapium sebiferum* | Ss | (L.) Roxb. | Euphorbiaceae | Acq. | A |
| *Cyclobalanopsis glauca* | Cg | (Thunberg) Oersted | Fagaceae | Cons. | B |
| *Rhus chinensis* | Rc | Mill. | Anacardiaceae | Cons. | B |
| *Schima superba* | Ssu | Gardn. & Champion | Theaceae | Cons. | B |

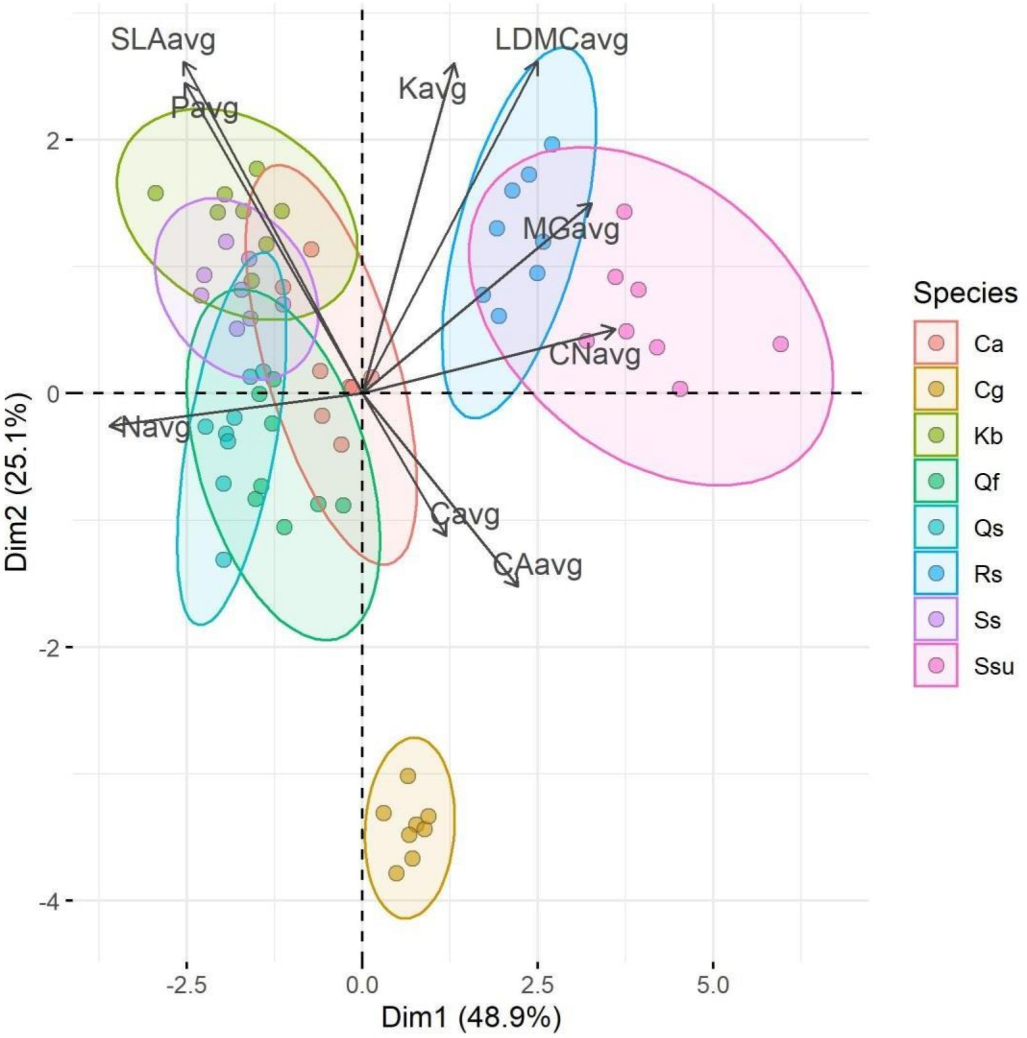

**Fig. S1:** Principal component analysis performed on all trait values, averaged for each treatment combinations of each species. The two groups delimited by the first dimension was used as separation between acquisitive (Ca, Kb, Qf, Qs and Ss) and conservative species (Cg, Rc, Ssu). Species abbreviations are detailed in Table S1.

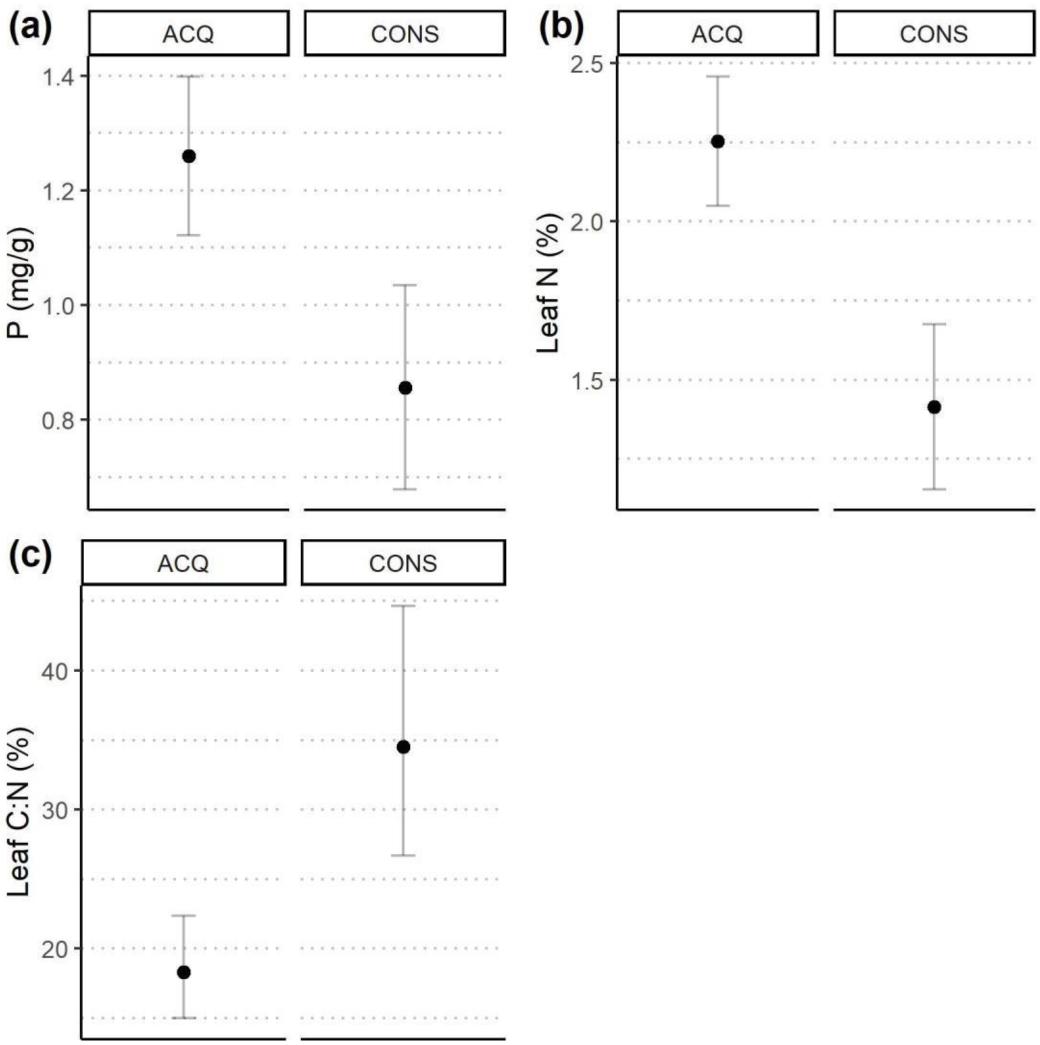

**Fig. S2:** Effect of trees species growth strategy on leaf traits (ACQ: acquisitive, CONS: conservative; see also Supp. Table S1 & Fig. S1). Dots indicate trait values averaged at the leaf level predicted from significant effects of the respective trait linear mixed model (see Supp. Table S2). Error bars represent two standard errors around the mean.

**Table S2**: Mixed-effects models (anova, type III sum of squares) for effects of Diversity (i.e., monospecific or heterospecific tree species pair), Ino. (soil inoculation with species' native microbiota), P fert. (phosphorus fertilization), Strategy (species growth strategy, see Table S1 and Fig S1) and their interaction on the different leaf traits. Leaf trait values for C:N, Mg, Ca and K are log-transformed.

| Leaf trait values | Predictor | NumDf | DenDF | F-value | p-value |
|---|---|---|---|---|---|
| SLA | Diversity | 1 | 192.53 | 4.66 | **0.032** |
| | Strategy | 1 | 7.36 | 10.23 | **0.014** |
| | Diversity * Strategy | 1 | 237.85 | 7.36 | **0.007** |
| C:N | Strategy | 1 | 6.55 | 14.85 | **0.007** |
| C | Diversity | 1 | 11.71 | 0.59 | 0.459 |
| | Strategy | 1 | 7.55 | 0.11 | 0.747 |
| | P fert. | 1 | 181.82 | 15.23 | **<0.001** |
| | Diversity * P fert. | 1 | 175.24 | 5.58 | **0.019** |
| | Strategy * P fert. | 1 | 291.44 | 8.56 | **0.004** |
| N | Strategy | 1 | 7.05 | 25.57 | **0.001** |
| Mg | Diversity | 1 | 14.25 | 1.00 | 0.335 |
| | P fert. | 1 | 178.41 | 0.72 | 0.396 |
| | Ino. | 1 | 179.39 | 4.23 | **0.041** |
| | Diversity * P fert. | 1 | 177.91 | 6.40 | **0.012** |
| Ca | Diversity | 1 | 191.00 | 2.45 | 0.119 |
| | Ino. | 1 | 190.98 | 2.90 | 0.090 |
| | P fert. | 1 | 190.83 | 0.94 | 0.333 |
| | Diversity * Ino. | 1 | 190.82 | 0.00 | 0.959 |
| | Diversity * P fert. | 1 | 190.74 | 4.36 | **0.038** |
| | Ino. * P fert. | 1 | 191.30 | 0.08 | 0.776 |
| | Diversity * Ino. * P fert. | 1 | 191.13 | 4.28 | **0.040** |
| K | Ino. | 1 | 180.83 | 1.08 | 0.299 |
| | Diversity | 1 | 9.66 | 7.65 | **0.021** |
| | Strategy | 1 | 6.89 | 0.02 | 0.903 |
| | P fert. | 1 | 176.04 | 1.06 | 0.305 |
| | Diversity * Strategy | 1 | 11.87 | 0.99 | 0.340 |
| | Ino. * Diversity | 1 | 179.98 | 2.46 | 0.119 |
| | Ino. * Strategy | 1 | 239.79 | 0.00 | 0.952 |
| | Ino. * P fert. | 1 | 177.08 | 4.24 | **0.041** |
| | Ino. * Diversity * Strategy | 1 | 237.40 | 3.94 | **0.048** |
| P | Ino. | 1 | 186.50 | 3.93 | **0.049** |
| | P fert. | 1 | 185.42 | 14.15 | **<0.001** |
| | Strategy | 1 | 6.51 | 12.58 | **0.011** |

**Table S3**: Mixed-effects models (anova, type III sum of squares) for effects of Diversity (i.e., monospecific or heterospecific tree species pair), Ino. (soil inoculation with species' native microbiota), P fert. (phosphorus fertilization), Strategy (species growth strategy, see Table S1 and Fig S1) and their interaction on the different leaf traits within-tree variation. All trait variation, calculated as within-tree Rao's Q values, were log-transformed.

| Within-tree trait variation | Predictor | NumDf | DenDF | F-value | p-value |
|---|---|---|---|---|---|
| SLA | Diversity | 1 | 15.17 | 0.10 | 0.759 |
| | Ino. | 1 | 168.44 | 2.56 | 0.112 |
| | P fert. | 1 | 167.93 | 0.01 | 0.911 |
| | Strategy | 1 | 6.76 | 0.32 | 0.590 |
| | Diversity * Ino. | 1 | 167.36 | 0.78 | 0.379 |
| | Diversity * P fert. | 1 | 167.27 | 0.85 | 0.357 |
| | Ino. * P fert. | 1 | 168.87 | 2.00 | 0.160 |
| | Diversity * Strategy | 1 | 15.43 | 0.04 | 0.847 |
| | Ino. * Strategy | 1 | 201.79 | 0.14 | 0.713 |
| | P fert. * Strategy | 1 | 201.12 | 4.94 | **0.027** |
| | Diversity * Ino. * P fert. | 1 | 169.13 | 1.02 | 0.315 |
| | Diversity * Ino. * Strategy | 1 | 200.74 | 1.54 | 0.216 |
| | Diversity * P fert. * Strategy | 1 | 200.66 | 0.00 | 0.996 |
| | Ino. * P fert. * Strategy | 1 | 203.23 | 3.75 | 0.054 |
| | Diversity * Ino. * P fert. * Strategy | 1 | 203.36 | 5.72 | **0.018** |
| LDMC | P fert. | 1 | 200.59 | 5.97 | **0.015** |
| | Strategy | 1 | 6.80 | 1.49 | 0.263 |
| | P fert. * Strategy | 1 | 2137.33 | 64.08 | **<0.001** |
| C:N | Diversity | 1 | 15.09 | 0.28 | 0.602 |
| | P fert. | 1 | 177.20 | 6.52 | **0.012** |
| | Ino. | 1 | 181.66 | 1.97 | 0.162 |
| | Strategy | 1 | 6.46 | 0.11 | 0.746 |
| | Diversity * P fert. | 1 | 175.05 | 2.20 | 0.140 |
| | Diversity * Strategy | 1 | 15.22 | 0.11 | 0.743 |
| | P fert. * Strategy | 1 | 216.29 | 15.17 | **<0.001** |
| | Ino. * Strategy | 1 | 1970.39 | 13.58 | **<0.001** |
| | Diversity * P fert. * Strategy | 1 | 215.50 | 5.59 | 0.019 |
| C | Ino. | 1 | 184.57 | 0.26 | 0.610 |
| | P fert. | 1 | 183.27 | 6.09 | **0.015** |
| | Strategy | 1 | 6.81 | 15.84 | **0.006** |
| | Ino. * Strategy | 1 | 2907.98 | 36.07 | **<0.001** |
| | P fert. * Strategy | 1 | 2904.05 | 101.94 | **<0.001** |
| N | Diversity | 1 | 15.29 | 1.04 | 0.323 |
| | Ino. | 1 | 174.77 | 4.78 | **0.030** |
| | P fert. | 1 | 174.41 | 10.41 | **0.001** |
| | Strategy | 1 | 6.90 | 0.26 | 0.627 |

| | | | | | |
|---|---|---|---|---|---|
| | Diversity * Ino. | 1 | 172.82 | 0.83 | 0.363 |
| | Diversity * P fert. | 1 | 172.95 | 1.83 | 0.178 |
| | Ino. * P fert. | 1 | 177.01 | 0.44 | 0.508 |
| | Diversity * Strategy | 1 | 15.45 | 0.06 | 0.804 |
| | Ino. * Strategy | 1 | 202.85 | 3.52 | 0.062 |
| | P fert. * Strategy | 1 | 202.38 | 15.18 | **<0.001** |
| | Diversity * Ino. * P fert. | 1 | 177.08 | 2.46 | 0.118 |
| | Diversity * Ino. * Strategy | 1 | 202.18 | 3.10 | 0.080 |
| | Diversity * P fert. * Strategy | 1 | 202.01 | 1.28 | 0.260 |
| | Ino. * P fert. * Strategy | 1 | 208.14 | 0.02 | 0.877 |
| | Diversity * Ino. * P fert. * Strategy | 1 | 208.08 | 4.55 | **0.034** |
| Mg | Diversity | 1 | 15.56 | 0.33 | 0.575 |
| | P fert. | 1 | 179.31 | 1.91 | 0.168 |
| | Ino. | 1 | 176.64 | 6.43 | **0.012** |
| | Strategy | 1 | 6.80 | 7.54 | **0.030** |
| | Diversity * Ino. | 1 | 174.00 | 2.61 | 0.108 |
| | P fert. * Ino. | 1 | 179.39 | 0.75 | 0.388 |
| | Diversity * Strategy | 1 | 15.79 | 2.02 | 0.175 |
| | P fert. * Strategy | 1 | 2278.70 | 5.81 | **0.016** |
| | Ino. * Strategy | 1 | 209.89 | 2.21 | 0.139 |
| | Diversity * Ino. * Strategy | 1 | 207.37 | 9.47 | **0.002** |
| | P fert. * Ino. * Strategy | 1 | 2280.15 | 11.98 | **0.001** |
| Ca | Ino. | 1 | 198.44 | 2.12 | 0.147 |
| | Diversity | 1 | 192.62 | 1.09 | 0.298 |
| | P fert. | 1 | 197.74 | 3.00 | 0.085 |
| | Strategy | 1 | 6.16 | 5.36 | 0.059 |
| | P fert. * Strategy | 1 | 2719.88 | 25.81 | **<0.001** |
| | Ino. * Diversity | 1 | 192.48 | 4.46 | **0.036** |
| | Ino. * P fert. | 1 | 197.39 | 0.46 | 0.499 |
| | Ino. * Strategy | 1 | 2734.55 | 3.19 | 0.074 |
| | Ino. * P fert. * Strategy | 1 | 2716.33 | 26.71 | **<0.001** |
| P | Diversity | 1 | 183.94 | 2.55 | 0.112 |
| | P fert. | 1 | 188.55 | 0.12 | 0.733 |
| | Ino. | 1 | 184.54 | 0.08 | 0.774 |
| | Strategy | 1 | 6.34 | 3.15 | 0.124 |
| | Diversity * Ino. | 1 | 184.74 | 0.77 | 0.380 |
| | P fert. * Ino. | 1 | 188.80 | 0.38 | 0.536 |
| | Diversity * Strategy | 1 | 196.31 | 3.67 | 0.057 |
| | P fert. * Strategy | 1 | 2289.43 | 12.73 | **<0.001** |
| | Ino. * Strategy | 1 | 221.29 | 0.02 | 0.877 |
| | Diversity * Ino. * Strategy | 1 | 221.29 | 7.43 | **0.007** |
| | P fert. * Ino. * Strategy | 1 | 2295.95 | 28.61 | **<0.001** |

# CHAPTER 5

## Synthesis

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Despite being extensively studied, the biodiversity-ecosystem functioning relationship still holds many unresolved aspects, especially with regard to the identity of its drivers. In particular, processes occurring at small scales are often disregarded while having the potential to provide valuable insights. Since trait-based approaches are useful to unravel the mechanisms behind BEF relationships at the scale of plant communities, they can also be adapted to investigate processes at smaller scales at which plants interact directly. In this thesis, using leaf traits, I looked into the effects of species diversity on trees' adaptability and growth strategies at a local scale, and how these effects are modified by soil conditions. In this chapter, I summarize my findings and expand on their meaning and implications in a broader context, to contribute to a better understanding of processes underlying BEF relationships and a more sustainable management of forests.

### Summary of the results

In **Chapter 2**, across a systematic gradient of species richness surrounding pairs of trees, I looked into the effects of local species diversity on tree growth strategies. I found that trait syndromes of individual trees shifted towards a more acquisitive growth strategy in response to increasing species diversity of the local neighbours. This effect was visible both for the closest neighbour of the focal tree (con- or heterospecific to the focal tree) and for neighbours further away. Trees with a conspecific closest neighbour showed a steeper response to species richness of the surrounding neighbourhood, compared to those with a heterospecific closest neighbour. Furthermore, at low and up to intermediate species richness of the surrounding neighbourhood, trees with a heterospecific closest neighbour showed more acquisitive trait syndromes than those with a conspecific closest neighbour. However, this effect was reversed at high species richness, suggesting positive effects of closely neighbouring a conspecific tree in a highly diverse environment.

Within a similar field setting, in **Chapter 3**, I showed that trait variation within-tree represents a considerable amount of the variation occurring at the sub-species level. Beyond the observed partial positive effects of species diversity and soil nutrient availability on trait variation within trees, I showed that the influence of these two drivers strongly depended on each other. Together, they showed a nonlinear relationship with trait variation, which highlights the influence of environmental favourability on how diversity affects trait variation. In particular, depending on the local species diversity, the availability of belowground resources seemed to reduce or enhance within-tree trait variation. This pattern suggests a role of trait variation as a response to the balance between competition, at high and low species diversity, and complementary effects at intermediate species diversity, modulated by belowground resources. This highlights variation as a mechanism both increasing organisms' adaptability to environmental changes and their competitive tolerance, depending on the favourability of their environment determined by biotic interactions and resource availability.

In **Chapter 4**, I analysed the relationships addressed in **Chapter 2** (diversity effects on trees' growth strategy) and **Chapter 3** (diversity and soil effects on within-tree trait variation) simultaneously. Under controlled conditions, using pairs of trees grown together in a shared pot, I investigated the effect of manipulated con or heterospecificity of the neighbour and two aspects of soil nutrient availability (i.e., phosphorus amounts and presence of the soil microbial community) on the growth strategy and trait variation of individual trees. Specifically, I showed that the effects of diversity on both the growth strategy and trait variation were strongly contingent on soil conditions. In addition, the effects of nutrient addition and soil microorganisms' presence differed in their interaction with diversity. Together with increased species diversity, fertilization with phosphorus decreased individuals' traits, potentially indicating a biomass dilution due to increased nutrient uptake. The interaction between phosphorus and diversity also increased within-tree trait variation, suggesting that enough resources were present and available for the trees to maximize their plasticity. In contrast, soil microorganisms' interaction with species diversity increased individuals' acquisitiveness, but decreased their trait variation. These results points towards soil microorganisms playing a greater role in reducing competition than in enhancing resource uptake, compared to phosphorus addition.

## 1) Effects of biodiversity

In this thesis, I have shown considerable responses of leaf traits to species diversity. However, results of the different Chapters also emphasize that biodiversity effects on traits are not straightforward, as it is often the case when considering them in the context of BEF relationships (Funk et al., 2017). I showed that species diversity affects the variability of leaf traits, as well as the trees' growth strategy, suggesting overall beneficial effects for trees' adaptability and productivity. In particular, results of the three Chapters indicate that trees in species-rich forest use more complementary niches. The role of soil conditions in modulating diversity effects, as suggested in **Chapter 2** and stressed in particular in **Chapter 3** and **Chapter 4**, is an especially prominent finding, pointing at resource-use complementarity as a key mechanism behind the observed patterns in each chapter. Additionally, and despite overall positive effects of local species diversity on traits syndromes and variation, I exposed limits of these effects in **Chapter 2** and **Chapter 3**, which instead of displaying a saturating relationship known from many BEF relationships assessed at the community scale (e.g. Duffy et al., 2017; Huang et al., 2018), weaken after a threshold in species diversity. This discrepancy between local and larger scales suggests that, despite local interactions being the source of the fundamental processes behind the positive effects of diversity, the intricacies of such interactions are blurred when studying BEF relationships at the ecosystem scale.

## 2) The individual perspective and importance of the local scale

In addition to focusing on individual tree's growth strategy (**Chapter 2 & 4**) and within-tree variability (**Chapter 3 & 4**) responses to species diversity, I quantified the substantially large extent of leaf trait variation explained by the individual level, amounting to over a quarter of the total variation averaged across all traits (**Chapter 3**). Overall, I showed a considerable response of leaf traits to their environment at the tree level, indicating the individuals' potential to adjust to their local conditions. However, the individual perspective remains seldom addressed: many ecological concepts that try to explain interactions are defined at the species level, assuming that the individual level is irrelevant, whereas in reality it is individuals interacting (Messier et al., 2010). This stands in stark contrast to findings that highlight the effects of genetic diversity, which is expressed in individual plants, on several key ecosystem functions (Crutsinger et al., 2006; Hughes et al., 2008; Tang et al., 2022). When comparing models predicting tree growth from individual or species average trait values, Yang et al. (2021) found a clear loss of information and poor predictive power with models built on species averages, as traditionally used. Instead, the authors show that the use of tree level trait data improves their growth models, and apply methods borrowed from quantitative genetics to model individual growth from individual trait data.

The individual level is an adequate organisational level for understanding mechanisms behind ecosystem functioning systematically, as it constitutes the smallest self-standing and indivisible ecological unit. Moreover, the individual is also the link between genetic and physiological scales (divisions within the individual), and species' populations (set of individuals). Detaching ourselves from the historically species-centred view in ecology would therefore allow for scaling up not only implications of observations made at small organisational levels, but also to apply theories built at those scales on wider ones, to ultimately practice an integrative trait ecology (Fontana et al., 2016, 2021; Swenson et al., 2020).

While trait-based studies addressing the individual level are still rare, this specific perspective has already been identified as a critical knowledge gap in functional ecology. Indeed, already in the 2010s, a raising awareness of the importance of processes below the species level evolved, aiming at improving the understanding in community ecology, and hence the question of the plant individual scale had been approached (Bolnick et al., 2011; Clark, 2010; Jung et al., 2010; Lepš et al., 2011; Messier et al., 2010). Today, as the gain from investigating intraspecific processes is becoming more and more obvious, a renewed interest in going further in this direction and including the individual scale is emerging (March-Salas et al., 2021; Stump et al., 2021; Swenson et al., 2020; Worthy et al., 2020). The relevance of the individual scale might be particularly important for the study of trait variation and its consequences. For example, to better understand the role of individuals in BEF relationships, Proß et al. (2021) took an individual perspective on the niche concept and its consequences for coexistence. In this study, the authors investigated the response of tree individuals' trait variation to local species richness and showed that niche theory applies to individuals as well as to species independently. Hence, the information held at the individual scale is likely to have far-reaching implications for ecosystem properties such as stability and coexistence.

In this thesis, when looking at the response of within-tree variation to soil nutrient availability and species diversity (**Chapter 3**), I found partial increases in trait variation with each driver independently. However, the interactive effects of soil conditions and diversity resulted in a non-linear relationship with trait variation. Specifically, the soil nutrient availability-trait relationship was positive only at intermediate species diversity, suggesting that positive effects of resource complementarity peak at intermediate values of local species diversity. Hence, my results not only indicated the multidimensionality of individuals' niche space, but also the importance of the interaction between its niche axes. Despite trait-based approaches being an essential part of ecological research and the recognition of its intraspecific aspects' importance continuously growing, a general framework bringing together the drivers and ecological outcomes of trait variation is still missing, and a fortiori one including an individual component (Westerband et al., 2021). This task is complicated by the wide diversity of responses found to abiotic and biotic environmental conditions and their interaction, likely resulting from the spatio-temporal structure of variation, often hard to account for (Girard-Tercieux et al., 2022). Consequently, at the level of the individual, there is little consensus about expected responses of trait variation to a set of environmental conditions, and the results of this thesis reflect this complexity. However, taking interactive effects of the drivers of variation into account, as in **Chapter 3**, and systematically investigating trait variation in competition experiments could clarify the mechanisms behind the observed patterns.

Together with the individual perspective itself comes the importance of the local scale to which it is associated. Indeed, in addition to tree-level trait information, the local scale entails considering its related biotic and abiotic specificities. In **Chapter 2** and **Chapter 3**, the neighbour the closest to the focal tree showed more influence on its leaf traits than neighbours further away. Despite small differences when comparing the distance between the interaction plane of a focal tree's crown and its closest neighbour with its surrounding neighbours, a distinction between the neighbours' effect was visible in the results. For example, in **Chapter 2**, the effect of a tree's closest neighbour was found more frequently than the effect of its surrounding neighbourhood. Together, the greater influence of the closest neighbour over the surrounding community, as well as the effects found within the surrounding community, emphasize the importance of the local scale when looking into traits' response to diversity.

These results raise the question of the importance of distance and planting patterns when considering the effects of species diversity. In a meta-study, X. Yang et al. (2022) look into net interactions between plants, and compare plants in isolation or with neighbours. In addition to competitive interactions, the results show a tendency towards facilitative ones. Therefore, local composition and distance has important implications for the nature of plant interactions, as suggested by the present thesis' results. While already commonly integrated aspects in ecology and in forestry, the output of classic spatially explicit theories applied to forests are most often applied to the management of forest on larger scales. Distance-dependent models have attracted moderate attention in a BEF research context, with results often not primarily aimed at clarifying processes underlying complementarity (but see (Pretzsch, 2022; Uriarte et al., 2004). For example, in individual-based models, individual processes are used to infer on outcomes at the population-level (often structural or growth-focused) while interactions between neighbours are often simplified to additive competition, with little consideration of the adaptive nature of traits, other types of tree-tree interactions or response specificity of the different plant organs (Grimm & Railsback, 2005). However, with the evolution of simulation models (including individual-based ones) and the generalisation of their use in community ecology, the identification of the challenges related to their applications for addressing BEF questions is rapidly improving (Maréchaux et al., 2021). A study using individual-based modelling to look into the effects of species richness and functional composition in a tropical forest also highlight the effect of local processes on species coexistence and ecosystem functions such as productivity and aboveground biomass (Maréchaux & Chave, 2017). The authors advocate for the inclusion in the model of more aspects potentially underlying complementarity and selection, such as limiting nutrients and belowground resource sharing, in order to improve the realism of such studies. In this thesis, I add to these approaches as my results show the intricacies of local interactions, contributing to the improvement of the empirical knowledge on which simulations can be based and validated.

Finally, in addition of the trees themselves, environmental conditions are heterogeneous at local scales (Baraloto & Couteron, 2010). Such micro-environments determine the availability of resources and the local conditions in which tree individuals can survive and interact, and has strong implications for coexistence in larger scale communities.

For example, Girard-Tercieux et al. (2022) argue that a large trait variability within species could be due to the many fine scale dimensions of environmental heterogeneity that are usually ignored. When considering local processes, the authors found a greater similarity in the response to spatial heterogeneity of conspecific compared to heterospecific trees, with consequences for competitive strength locally, and coexistence stability globally. The conclusions of Girard-Tercieux et al. (2022) concur with the results presented in this thesis in that they point at the importance of the individual tree's perspective for trait-based approaches.

### 3) Growth strategies as both a response and a constraint to diversity effects

The leaf economics spectrum (LES) is a classic, broadly studied trait spectrum that finds widespread use along latitudinal and environmental gradients as well as across biomes (Wright et al., 2004). The LES describes a gradient going from conservative slow-growing species, allocating resources to durable, long lasting structures, to fast-growing acquisitive species, allocating resources to 'cheap' structures with a high turnover. It is reflected in single or sets of traits associated with a rather acquisitive (e.g. SLA, leaf cations, leaf nitrogen) or conservative (e.g. LDMC, leaf carbon, tannins and phenolics) growth strategy (Reich, 2014). This spectrum is hence highly dependent on the resources available to the plants, with fertile environments or nutrient poor ones being associated with acquisitive or conservative strategy, respectively. In **Chapter 2**, the increase in resources available to individual trees, attributed to complementary effects of surrounding species diversity, confirmed this expectation derived from the LES, with trees displaying more acquisitive (and respectively less conservative) trait values. In **Chapter 4**, although overall less systematic and depending on soil conditions, increased species diversity together with soil microorganisms also resulted in more acquisitive trait syndromes among individual trees. Regarding variation, although patterns were generally less consistent between traits,

I found that traits related to an acquisitive strategy predominantly responded to species diversity and soil conditions (**Chapter 4**), compared to traits associated with a conservative growth strategy. In addition, individuals belonging to species with an acquisitive strategy seemed to display more consistent responses to these drivers. These results bring us to a recurrent issue in functional ecology, which is to identify under which conditions the LES is present and discernible (Anderegg et al., 2018; Gorné et al., 2022; Messier et al., 2017). As investigated by Messier et al. (2017), the LES is not necessarily expected to be visible at small scales, because environmental heterogeneity is greater than at larger ones. Thus, as the LES is applied to species, trait-trait correlations part of the LES do not entail that they independently respond similarly to a same environmental driver at the subspecies scale. I agree with the authors that the strength of the correlation between LES traits does not systematically determine how similarly they respond to a driver, but only constrains how much they can differ in their response. However, in this thesis, I found that correlated LES traits tend to have a similar response frequency to those drivers. Although correlated traits did not vary in the same direction or amplitude, their tendency to respond significantly or not to soil and diversity drivers seemed to be linked to the growth strategy they are associated with. The LES might hold importance at the local scale as it might be reflected in the trait variation responsivity (that is, the susceptibility to responding significantly), in addition to the trait responses themselves, for which I also found evidence (**Chapter 2, Chapter 4**). My findings highlight the importance of considering the growth strategy of an individual, and the growth strategy a specific trait reflects, when considering trait variation – even at local scales.

### 4) Limits of complementary effects & interactions with soil conditions

Using individual level trait data efficiently, for example for an accurate estimation of mechanisms behind ecosystem functioning, requires adequate contextual information from the local scale (Swenson et al., 2020). This context dependency also applies to the environmental conditions in which the individual grows (Liu et al., 2016). Belowground variables, in particular, play a key role in BEF research, as they not only directly modify the growth and survival of the tree, but also influence the effect of diversity on such parameters (Bardgett et al., 2014; Cheng et al., 2020; Yuan et al., 2019). Indeed, since resource use partitioning is linked to belowground resource availability, soil conditions can favour or limit mechanisms underlying diversity effects in local tree-tree interactions.

In this thesis, **Chapter 3** underlines the interactive effect of soil resources and species diversity on trait variation. While they tended to independently increase trait variation, as expected from a greater availability of resources, soil nutrients and species diversity showed together a non-linear relationship with trait variation. In particular, low or high species diversity correlated with a decrease in trait variation with increasing soil nutrient availability. To understand such limits of diversity effects, it is necessary to gain a deeper understanding of the plant-soil interactions in diverse plant communities.

It is a difficult task to integrate soil processes when considering aboveground traits, given the complexity of the plant-soil relationship. While the effects of soil conditions are reflected in trees’ leaf traits (Ordoñez et al., 2009), the diversity of plant-soil interactions can blur the link between below- and aboveground processes, in particular when looking at the response to environmental changes (Asefa et al., 2022). In addition, when considered from an aboveground perspective, the belowground compartment is often simplified into a pool of resources (Richards et al., 2010). In **Chapter 4**, I incorporate aspects of the plant-soil relationship complexity by considering both a biotic and an abiotic element of the soil, that is, a limiting nutrient (phosphorus) and the soil microbiota present in the BEF-China experiment’s soil on which the studied tree species grow. The results highlight the importance of soil resources modifying the effect of diversity on trait variation. More importantly, I uncover opposite patterns for different aspects of soil resources. Increased nutrients, through phosphorus fertilization, tended to increase within-tree variation when associated with a reduced competition from increased diversity, enabling the trees to respond plastically to environmental changes. On the contrary, inoculation of the soil microorganisms seemed to enhance the reduction of competition as well as the decrease of trait variation with greater species diversity, rather than to promote a greater plasticity enabled by more available resources. Contrary to our expectations based on **Chapter 3**, the soil microbiota yielded different effect to an addition of resources, showing that its biotic interaction with tree species diversity had more impact than its contribution to nutrient uptake.

Overall, the unexpected inconsistencies in the results observed in **Chapter 4** hint at more intricate interactions between species diversity and soil microbiota than the hypothesized positive or negative effects. As trait variation is intrinsically highly responsive to many aspects of very local conditions, considering the complexity of the above- and belowground interaction at the individual scale is essential. Doing so, for example with the help of a synthesizing framework at the interface of the interaction such as the root economics spectrum, might increase the realism of experiments and help making sense of the observed patterns behind BEF processes.

## Conclusion and future perspectives

The concept and use of functional traits, including as predictors for ecosystem functioning, keeps being challenged since its broader adoption in ecology, be it about its relevance, consistency or predictive potential (Dawson et al., 2021; Moles, 2018; van der Plas et al., 2020). Thanks to a frequent reassessment, functional traits have become a major part of today's ecology, continuously evolving into an approach that enables grasping complexity without compromising accuracy and realism. This thesis, embedded into functional ecology, participates more specifically to disentangling the mechanisms behind the BEF at the local scale. Looking into tree-tree interactions and focusing on the individual tree perspective, it proposes multiple considerations for future research.

First, this thesis highlights how and to which extent tree-tree interactions and the individual perspective can be relevant and contribute to better understand the effects of diversity, both in term of the plant traits themselves, but also the (micro)environmental factors that influence them. Generally, it emphasizes the importance of the right scale for the right question, and the recurrent question of how to transfer knowledge between scales. While this is not a new issue in ecology (Carmona et al., 2016; Enquist et al., 2015; He et al., 2019), the fast-pace technological advancement, together with the need of finding solutions to climate change, is facing us with the urgency of communicating and generalizing findings across scales and biogeographic regions. Indeed, growing possibilities, from expanded resolution of remote sensing (Chen et al., 2022; Jetz et al., 2016; Zellweger et al., 2019) to new applications of genetic and molecular methods for trait-based ecology (McGale et al., 2020; Walker et al., 2022; Wuest & Niklaus, 2018), by way of increased availability of trait data (Schiller et al., 2021; Vasseur et al., 2022), are enabling us to look into an unprecedented large range of scales. Hence, the multiplication of possibilities reinforces the need for an efficient identification of the scale(s) that will hold the most relevant information for a given research question. Within this framework, the individual scale is an important player to link the genetic, evolutionary and ecological fields, which, despite recurrent efforts, are still often not actively benefitting from each other (Fontana et al., 2021).

For addressing scaling issues, as well as the complexity of the patterns I uncover within the local scale, theoretical approaches could be a considerable help. Putting this complexity into a theoretical framework could guide the conceptual understanding of these issues. For example, regarding variation, despite a large body of theory around the idea of the niche and its response to diversity at the species and subspecies level, a translation of expected outcomes and implication of the individual scale for coexistence has been lacking and is coming to existence only recently (Proß et al., 2021; Stump et al., 2021). Beyond concepts, theory can have a wide range of concrete applications even in the experimental sense. The idea of a virtual ecologist (sensu Zurell et al., 2010), based on *in silico* simulation experiments, enables the exploration of a multiplicity of experimental scenarios, a systematic exploration of the addressed questions, and a consistent reduction of noise. This latter aspect might be particularly important in the context of the local scale, as it might have a higher sensitivity to external factors. Hence, paired with empirical approaches, theoretical ones offer numerous avenues for supporting the understanding of BEF at all scales.

This thesis also contributes to providing elements for improving future sustainable forest management. First, my results highlight the importance of maintaining or planting diverse forests, as higher species diversity tend to fosters higher variability, which promotes a better adaptability and resilience of trees to changing environmental conditions (Fichtner et al., 2020; Schnabel et al., 2019). Second, while I find that diversity is overall beneficial for proxies of a fast growth and for variability, I also underline the limits between which species diversity has a positive effect on these variables. I have shown in particular that relatively ‘too low’ or ‘too high’ diversity, at the local scale, can hamper adaptability and productivity. Finally, in addition to the limits of species diversity itself, my results describe the dependency of its effects on the local soil conditions. Specifically, available nutrients and soil microorganisms influence both the growth and the adaptability of trees in a diverse environment, resulting for example into a higher variability in nutrient-rich conditions, but a lower one with the presence of soil microorganisms.

Overall, my results point out the complexity of the mechanisms underpinning diversity effects and their reflection in functional traits. For example, while plasticity is a valuable property for the trees to face future stresses, it rather underlies consequences of interactions between trees and between soil and trees, which can be positive or negative for growth. While the focus on the mechanisms with traits as proxies contributes considerably to shedding light on diversity effects within tree-tree interactions, the question remains as for the predictive power of functional traits. With this in mind, one limitation of the present thesis is the absence of testing the link between the trait patterns I observed and the ecosystem functions they reflect, which remains the Holy Grail of ecology (Laughlin et al., 2020). Hence, a natural follow-up of this work is to directly correlate this response to a function, such as tree productivity. Doing so will not only help clarifying the outcome of the complex processes I described, but also be an opportunity for increasing the tangibility of the effects to consider for forest management applications.

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# APPENDICES

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## Authors’ contributions

### Chapter 2

SH and AD conceived the ideas and designed methodology; AD collected the data; AD analysed the data, with support from SH. AD led the writing of the manuscript, supported by SH. Both authors contributed critically to the drafts. My overall contribution was 75%.

### Chapter 3

SH, WSH, HB and AD conceived the ideas and designed methodology; AD and AB collected the data; AD and AB analysed the data, with support from SH, WSH, GA and HB; AD, AB and SH led the writing of the manuscript. All authors contributed critically to the drafts. My overall contribution was 70%.

### Chapter 4

SH and AD conceived the ideas and designed methodology; AD and SH collected the data; AD and SH analysed the data. AD led the writing of the manuscript, supported by SH. Both authors contributed critically to the drafts. My overall contribution was 75 %.

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I also thank Helge Bruelheide, for the scientific help, but also the legendary curiosity, interesting conversations and the good mood. Thank you for always be up for some explanations and opinions, whatever the subject. Being part of this group has been a very pleasant an insightful experience.

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In particular, I thank, as an office team, Tobias Proß, Amanda Ratier Backes and Lina Lüttgert for always patiently hearing me vent, and provide the best sweets. Tobi, thank you for your kindness since day one, for introducing me to the world of spectral data and sharing your passion for everything technical, as well as many of the German mysteries. Amanda, on top of being a great flatmate, I am grateful to have explored with you the quest for a slow science balance. Thank you for being what made Halle home for me when I arrived. Sharing the PhD adventure with you has significantly reduced the gravity of it all, while providing a healthy distance for reflexion. Special thanks to my mental and physical sanity colleagues: Lina, for dragging me into some kind of physical activity and being an ideal (although fierce) fighting opponent, and Carolin Plos, for the always insightful and on point conversations, self-reflection and kindness. Thank you for caring!

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***Name:*** Andréa DAVRINCHE
***Nationality:*** French
***Birth:*** 23rd May 1993 in Saint-Denis, Réunion

## CURRENT POSITION

**2018 - present**
**Doctoral Researcher in the Sino-German Research Training Group TreeDi**
*Martin Luther Halle-Wittenberg University (MLU) - (Halle/Saale, Germany) & German Center of Integrative Biodiversity Research (iDiv) – (Halle-Jena-Leipzig, Germany)*
Thesis: Complementarity through leaf traits: responses of trees to species diversity and soil conditions
Supervisors: Dr. Sylvia Haider, Prof. Stan Harpole

## EDUCATION

**2014 -2016**
**MSc in Science of the Environment & Ecology**
**Specialization in Ecophysiology and Ecotoxicology**
*Université Pierre et Marie Curie - UPMC (Paris, France)*
Thesis: Thermoregulation and carbon gain of oak leaves in a semi-natural woodland - a pilot study
Supervisor: Dr. Benjamin Blonder, Prof. Yadvinder Malhi (U. of Oxford)

**2011 – 2014**
**BSc in Life Sciences**
*Université Pierre et Marie Curie - UPMC (Paris, France)*
*and Université de Montréal (Montréal, Canada) International program*

## PROFESSIONAL EXPERIENCE

**2018-2021**
***Teaching Assistant & Co-supervisor – Martin Luther Halle Wittenberg University***
Teaching assistance for the MSc course "Field Ecology", BSc practical "Population & Vegetation Ecology", co-supervision of MSc internships and MSc thesis

**2017**
**(1 month)**
***Visiting Researcher - Environmental Change Institute, University of Oxford (UK)***
Collaborative writing research stay: Thermoregulation and carbon gain of oak leaves

**2015**
**(3 months)**
***Intern in the Forest Ecology and Ecophysiology team, Université de Lorraine & French National Institute for Agricultural Research (INRA, France)***
Study of the sensitivity and tolerance to $O_3$ of several poplar genotypes for short rotation coppice : a three-scale study for the key characters of acclimation to Ozone

**2016**
**(6 months)**
***Coworking project with the startup ZéBU - Zone-AH! for eco-innovation as member of the GreenLab - UPMC Fab Lab, (France)***
Experimental design, project management and realization of prototypes for Drêch'oponik : aquaponics systems valorizing spent grain from local breweries

**2014**
**(7 months)**
***Research Assistant at the Plant Biology Research Institute of Montréal (Canada)***
Study of genotyping strategies applied to reproductive preferences of *Solanum chacoense*; speciation boundaries upholding in the sympatric Solanacea from South America.

**2014**
**(1 month)**
***Teaching Assistant –Université de Montréal (Canada)***
Preparation, lab work and filming of «Molecular biology : practical work project» for online course videos

**2013**
**(2 months)**
***Intern at the Cellular and Molecular Plant Physiology Lab – UPMC (Paris, France)***
Study of the genotype and phenotype of cold-stressed mutants: physiological response; estimation of the effects of NO on *Arabidopsis thaliana* seeds.

**2012 - 2013**
***University student staff/ Freshmen tutor, UPMC (Paris, France)***
Promotion of the University in official events, scientific vulgarization and communication, technical support for conferences and cultural occasions, new students support.

# PUBLICATIONS

## PUBLISHED

**Davrinche A.** & Haider S. (2021). Intra-specific leaf trait responses to species richness at two different local scales. Basic and Applied Ecology, 55, 20-32.

Gandin A.*, **Davrinche A.***, & Jolivet Y. (2019). Deciphering the main determinants of $O_3$ tolerance in Euramerican poplar genotypes. Science of the Total Environment, 656, 681–690. *Co-first authors.

## SUBMITTED, IN REVISION, IN PREPARATION

Beugnon R., …, **Davrinche A.**, …, Eisenhauer N. (in revision). Abiotic and biotic drivers of scale-dependent tree trait effects on soil microbial biomass and soil carbon concentrations. Ecological monograph.

Beugnon R., …, **Davrinche A.**, …, Cesarz S. (submitted). Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes. Oikos.

Anttonen P., …, **Davrinche A.**, …, Schuldt A. (submitted). Leaf nutritional content, tree richness, and season shape the caterpillar functional trait composition experienced by trees. Ecology and Evolution.

**Davrinche A.**, Bittner A., Harpole S., Albert G., Bruelheide H. & Haider S. (in prep). Large within-tree leaf trait variation: response to local species richness and soil nutrient availability.

**Davrinche A.** & Haider S. (in prep). Species diversity effects on tree-level traits values and variation depends on soil conditions.

Castro Sánchez-Bermejo P., **Davrinche A.**, Matesanzc S., Harpole S. & Haider S. (in prep). Within-individual leaf trait variation increases with phenotypic integration in a subtropical tree diversity experiment.

# CONFERENCE CONTRIBUTIONS

**World Biodiversity Forum 2022, Davos (Switzerland)**
Oral contribution: *Intra-individual leaf trait variation response to local tree diversity and soil nutrients*

**iDiv conference 2022 (online)**
Oral contribution: *Large within-tree leaf trait variation: responses to diversity and edaphic factors*

**TreeDì-BEF China Seminar Series 2020 (online)**
Oral contribution: *Species richness increases intraspecific trait variation at two local scales*

**Annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfO) 2019, Münster (Germany)**
Oral contribution: *Neighborhood diversity affects leaf trait variation at inter-specific and intra-specific scales*

**TreeDì Doctoral Conference 2019, Beijing (China)**
Oral contribution: *Complementarity through trait variation, a story of individuals*

**iDiv conference 2018, Leipzig (Germany)**
Demonstration session of optical spectroscopy techniques for ecological questions

# GRANTS

**TreeDì startup funding (iDiv, Germany)**
Short term postdoctoral project support grant, awarded for 5 months

**Selective scholarship for the International Bachelor in Life Science (UPMC & UdeM, France-Canada)**
Exchange program for scientific excellence and cooperation with Canada, awarded for 6 months

# RELEVANT SKILLS

- Experienced with both fieldwork, in temperate and subtropical settings, and lab work from the molecular to the ecosystem scale
- Proficient in optical spectroscopy approaches for multivariate analyses
- Familiar with R for statistical methods (e.g, random effect models) and data wrangling
- Basic knowledge of GIS methods
- Fluent in French; Advanced knowledge of English; Basic knowledge of German and Spanish

# REFERENCES

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# Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Complementarity through leaf traits: responses of trees to species diversity and soil conditions“ 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.

Andréa Davrinche, Halle (Saale), 20.10.2022