From trees to soil: microbial and spatial mediation of tree diversity effects on carbon cycling in subtropical Chinese forests

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Summary

The loss of biodiversity is affecting all ecosystems on Earth, one of the greatest threats to biodiversity being climate change. Forests have been highlighted for the potential to mitigate climate change by storing carbon above- and belowground in soils. In this thesis, I studied the effects of tree diversity on carbon cycling in subtropical Chinese forests. I aimed to explore the mechanisms behind tree diversity effects on carbon cycling by focusing on microbial-based processes and the consequences of tree diversity-induced spatial heterogeneity.

First, my colleagues and I tested the effects of tree diversity on litterfall spatial patterns and the consequences for litter decomposition and quantified the importance of microbial community in decomposition processes. Second, we explored the effects of tree diversity on relationships between soil microbial facets and soil microbial functions. Third, we tested the effects of tree diversity on soil microbial biomass and carbon concentrations, and their mediation by biotic and abiotic conditions. Finally, we explored the consequences of diversifying forests for re-/afforestation initiatives and plantations to reduce atmospheric carbon levels, and the benefits of diversity for mitigating the effects of climate change on ecosystems and human well-being.

We highlighted the positive effects of tree diversity on tree productivity. By increasing the amount and diversity of litterfall, tree diversity increased litter decomposition and subsequently the assimilation of tree products into the forest soils. Our investigation has shown the key role of microbial communities for forests carbon dynamics by carrying out litter decomposition, soil heterotrophic respiration, and soil carbon stabilization. Most notably, tree diversity effects on soil microbial respiration were mainly mediated by soil microbial biomass rather than soil microbial community taxonomic or functional diversity. The effects of tree diversity on microbial biomass were mediated by biotic and abiotic conditions. Taken together, we revealed the importance of considering space to understand biodiversity-ecosystem functioning relationships. Finally, we argued that tree diversity is a promising avenue to maximize the potential of re-/afforestation projects to mitigate increasing atmospheric carbon. Moreover, we highlighted that diversifying forests in re-/afforestation initiatives can help to reduce climate change effects on ecosystems: first, by increasing resistance and resilience to extreme climatic events, and second, by buffering microclimatic conditions in natural and urban areas.

My investigation highlighted that tree diversity effects on ecosystem functioning could be explained by both mass and diversity effects on higher trophic levels and their functions. In addition, I highlighted the key role of tree diversity-induced spatial heterogeneity and the need to consider space and time in further research. Moreover, these results need to be combined with practitioner constraints to enable feasible restoration projects.

Grab a coffee, you'll need it for the next four hundred pages

Summary table

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Glossary

Abiotic: non-living characteristic and/or parameter of the environment (e.g., climate).

Biota: All living organisms.

Buffering layer: physical layer reducing the exchanges of matter or energy between two compartments.

Carbon budget: sum of all carbon influxes and effluxes to a system.

Carbon cycle: whole of processes by which carbon is exchanged within a system.

Decomposition: fragmentation of organic mater, its incorporation into the environment, and its mineralization due to enzymatic activities.

Ecosystem: biotic and abiotic paramaters of an area and their interactions.

Ecosystem functioning: whole of biotic and abiotic processes within an ecosystem.

Ecosystem services: benefits human populations derive from ecosystems (e.g., goods, food, recreation area).

Ecosystem resilience: ability of an ecosystem to recover from an internal or external stress.

Ecosystem stability: temporal stability of ecosystem components and processes.

Erosion: loss of matter (or component) by the action of a mobile fluid (or agent), e.g., soil erosion by water flows.

Extreme climatic event: refers to climatic conditions out of the averaged climatic conditions of the location such as dough or flood.

Interdisciplinary (research): different academic disciplines working together to integrate disciplinary knowledge and methods, to develop and meet shared research goals achieving a real synthesis of approaches (Kelly *et al.* 2019).

Primary forest: a forest that has remained undisturbed by human activity.

Primary producers: species producing their biomass from inorganic components and energetic sources (e.g., plant fixing CO_2 by photosynthesis)

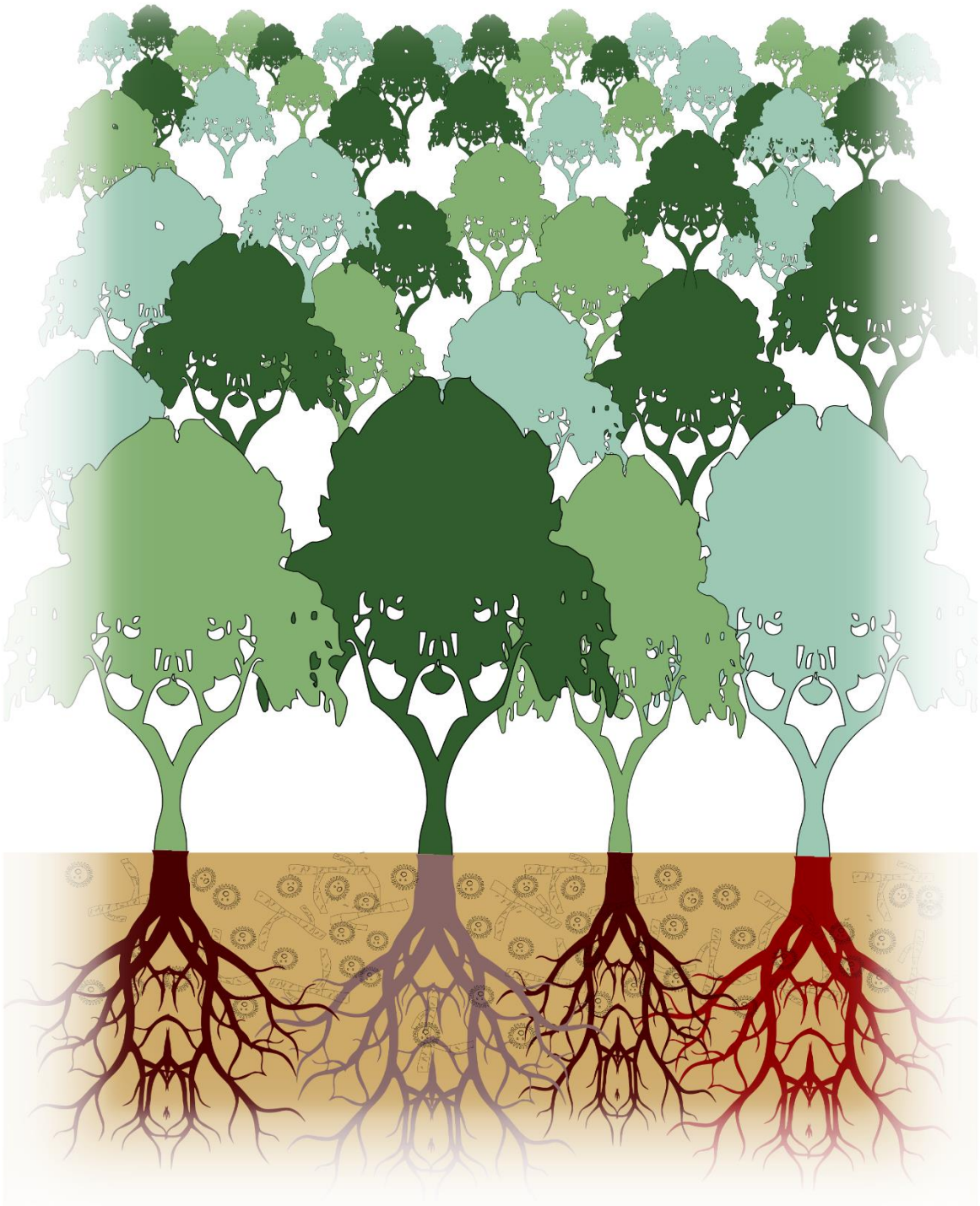
Primary productivity: biomass productivity of primary producers, informing about external inputs of energy to the ecosystem.

Residency time: average time spent by an element in a system (e.g., residency time of carbon in soil), calculated from the average influx and efflux.

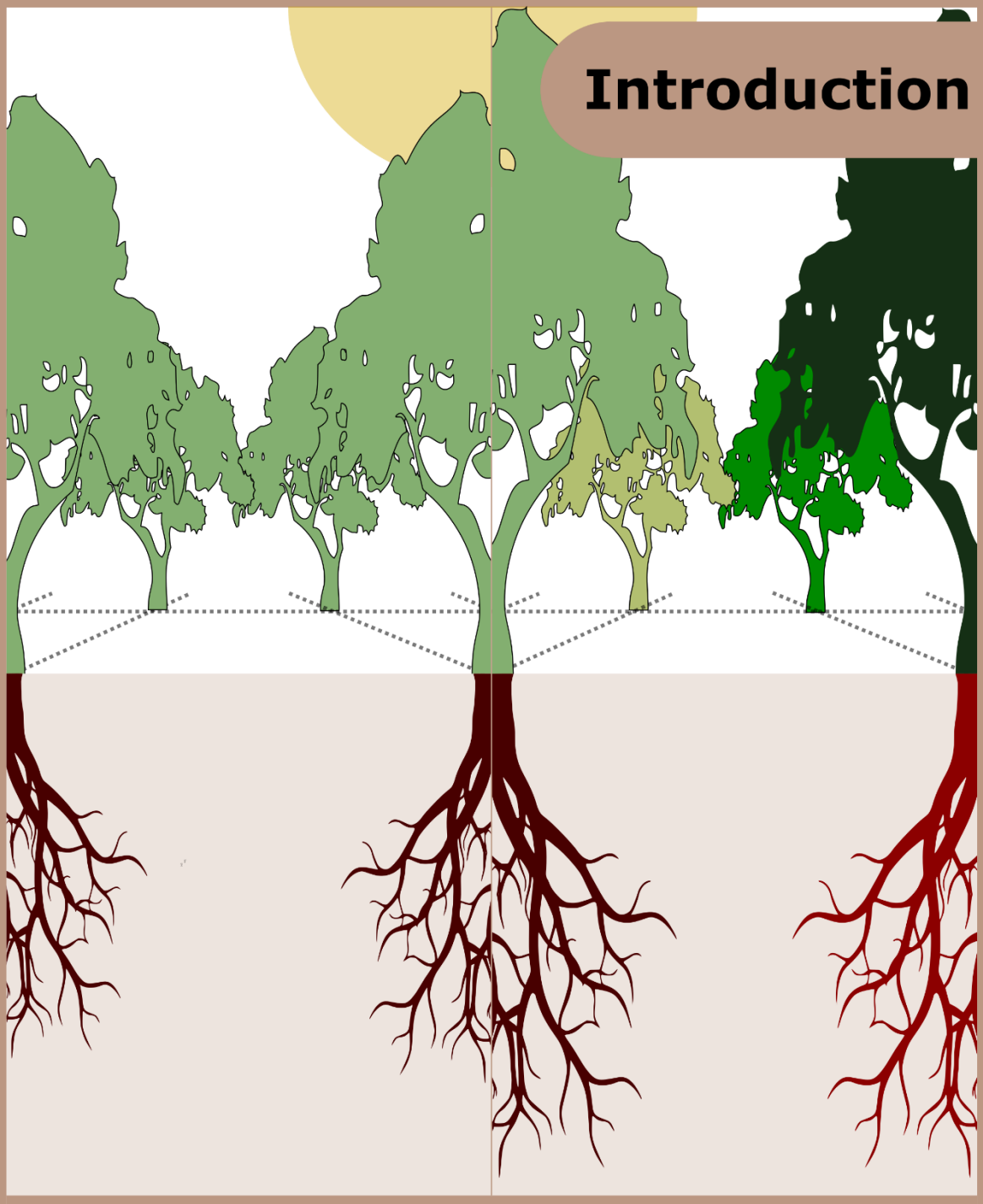
Sessile: species trait describing if lack of self-locomotion means

Stressor: “external force or factor, or stimulus that causes changes in the ecosystem” (Rapport *et al.* 1985).

Transdisciplinary (research): Different academic disciplines working together with non-academic collaborators to integrate knowledge and methods, to develop and meet shared research goals achieving a real synthesis of approaches (Kelly *et al.* 2019).



Introduction



Tree diversity and carbon cycling: from tree productivity to soil carbon storage

Introduction

Citation

"*Climate change is the single greatest challenge of our time,*

Of this, you're certainly aware.
It's saddening, but I cannot spare you
From knowing an inconvenient fact, because
It's getting the facts straight that gets us to act and not to wait.

So I tell you this not to scare you,
But to prepare you, to dare you
To dream a different reality,

Where despite disparities
We all care to protect this world,
This riddled blue marble, this little true marvel"

from *Earthrise* by Amanda Gorman

Prologue

Anthropic activities have a disastrous effect on climate; however, climate change is not the "*single greatest challenge*"; our impact on Earth is even broader. We have entered the sixth major species loss crisis the world has ever experienced, and we are causing it. Earth will survive with or without these species, but will we? If this "*scares us*", we need to understand the impact of species loss on Earth's ecosystems and the functions they provide for us in order to "*prepare ourselves*", protect our future and this "*little true marvel*" that are our ecosystems. Understanding the impact of species loss on ecosystems is one of the most important research questions of the last century. The relationships between species and their ecosystem is even the core of ecology: "*the relationships between air, land, water, animals, plants, etc., usually of a particular area, or the scientific study of it*" (Cambridge Dictionary). One way to explore these questions and understand the consequences of species loss is to simulate their loss in designed diversity experiments: the so-called biodiversity-ecosystem functioning (BEF) experiments. For decades, scientists have been building BEF experiments across biomes worldwide (Bruelheide *et al.* 2014; Givnish 1994; Lepš 2004; Wardle 2016; Eisenhauer *et al.* 2016). In this work, my colleagues and I investigated how the loss of tree species affects carbon cycling in subtropical Chinese forests, as this biome accounts for the highest average net ecosystem productivity among Asian forests (Yu *et al.* 2014).

Background

Human activities increase the worldwide biodiversity loss

Humanity is changing its environment worldwide (Crutzen 2006; IPBES 2019; IPCC 2013, 2021). Numerous studies are pointing out the effects of human activities; such as urbanization, farming, or industrial productions; on environmental *abiotic*[1] conditions (Fig. 1): climate (IPCC 2013, 2021), air (Akimoto 2003) and water quality (Baker 2006), and soils (FAO *et al.* 2020). In addition, human effects on the environmental *abiotic* conditions (e.g., temperature, water quality) have negative consequences on *biota* (Fig. 1, IPBES 2019). For example, increasing atmospheric CO_2 and its effects on climate change are responsible for species extinctions (IPBES 2019). Likewise, increasing atmospheric CO_2 is increasing seawater acidity and leads to species extinctions in marine ecosystems (Bindoff *et al.* 2019). Moreover, human activities are the main direct stressors of environmental biotic parameters (Fig. 1) by increasing species extinctions (FAO *et al.* 2020; Fenoglio *et al.* 2020; IPBES 2019) or biotic invasions (Bellard *et al.* 2016; Domenech *et al.* 2005; IPBES 2019). For example, increasing land-use intensity reduces the abundance and diversity of birds (Jetz *et al.* 2007), mammals (Brehm *et al.* 2019; Gallego-Zamorano *et al.* 2020), and arthropods (Attwood *et al.* 2008;

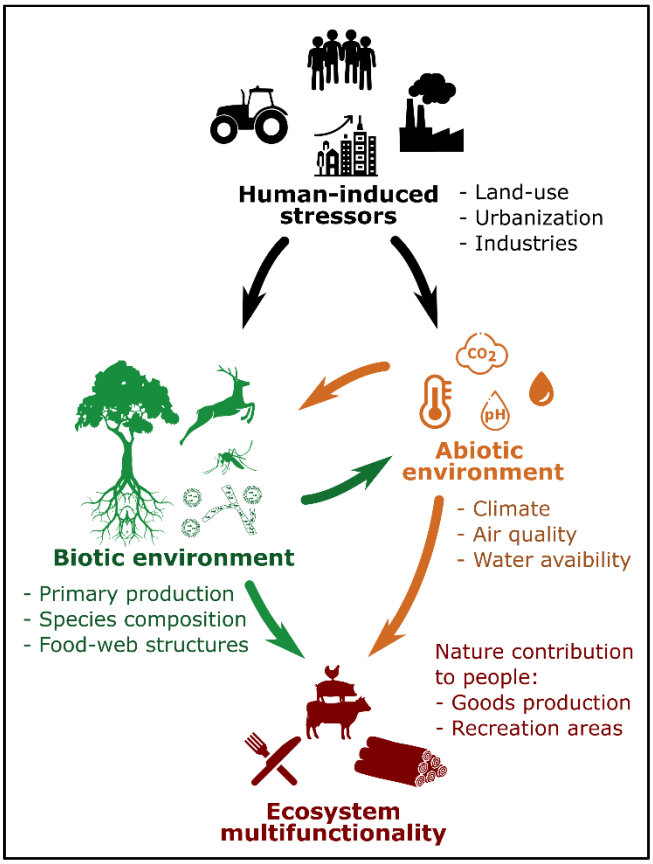


Fig. 1: Human-induced stressors of abiotic and biotic environmental conditions and consequences for ecosystem multifunctionality, adapted from Giling *et al.* (2019).

[1] words in *italics* are defined in the Glossary section page 2

Birkhofer *et al.* 2015; Hendrickx *et al.* 2007; Toussaint *et al.* 2021). Likewise, industrial pollutions can get rid of entire ecosystems (Beaumelle *et al.* 2021; Rodríguez-Eugenio *et al.* 2018).

Together, human activities directly and indirectly (e.g., through human-induced climate change) affect all *biota* on Earth, resulting in the worldwide loss of species (IPBES 2019; Pörtner *et al.* 2021), from the most charismatic ones (e.g., white bears and dodo) to the most ignored ones (e.g., soil biodiversity loss, FAO *et al.* 2020). For example, a recent report shows that 15% of the species are declining in the UK, and about 2% are threatened of extinction (JNCC 2019). The actual species loss is so intense and fast that we are even losing species we have not discovered yet (Ceballos *et al.* 2015).

Species loss affects ecosystem functioning

The consequences of species loss for ecosystems has been a hot topic in science for the past decades (Elton 1958; Tilman 1997; Yachi and Loreau 1999). Studies suggested that diversity maintains higher *ecosystem functioning* (Midgley 2012; Schuldt *et al.* 2018), and thus, the *ecosystem services* provided to human populations (Bennett *et al.* 2015; Brockerhoff *et al.* 2017; Cardinale *et al.* 2012). Biodiversity maintains ecosystem services such as wood for human production (Brockerhoff *et al.* 2017; FAO and UNEP 2020), arable lands, food for livestock and humans (FAO *et al.* 2020; FAO and UNEP 2020), and recreational areas (Bolund and Hunhammar 1999). Together, the human-driven *stressors* of ecosystems and the loss of species increase the risks of ecosystem collapse (MacDougall *et al.* 2013), and thereafter, the loss of all the *ecosystem services* they provide (Pörtner *et al.* 2021; IPBES 2019). However, a holistic and mechanistic understanding of species loss consequences for ecosystem functioning remains to be further explored (Eisenhauer 2019; Eisenhauer *et al.* 2020).

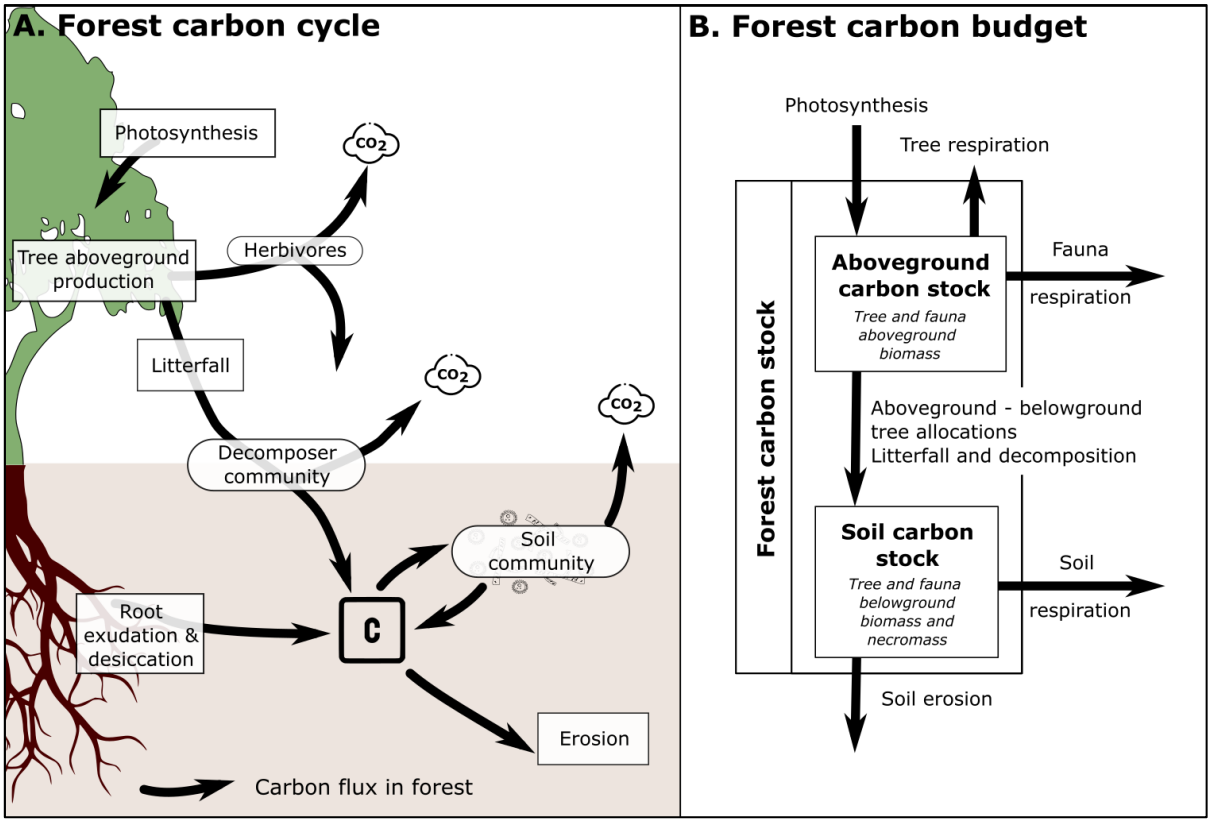


Fig. 2: Forest carbon cycle (A) and its associated carbon budget (B). Black arrows represent carbon fluxes in forest.

Forests are an essential ecosystem on Earth

Reducing *primary producer* diversity (e.g., plants and phytoplankton) has negative consequences for *primary productivity* (Cardinale *et al.* 2012; Duffy *et al.* 2017; Huang *et al.* 2018; Liang *et al.* 2016), *ecosystem resilience* and *stability* to major events such as droughts (Vogel *et al.* 2012; Kreyling *et al.* 2017; Rodriguez-Ramirez *et al.* 2017). Thus, by limiting carbon fixation and organic input, the lost *primary productivity* is a critical loss of *ecosystem services* for human populations and the ecosystem. Especially, forests are crucial *primary producers* (Bastin *et al.* 2019; FAO and UNEP 2020); indeed, among biomes, forests represent more than 30% of the Earth's surface, account for 75% of the global primary production, and contain 80% of the Earth plant production (FAO and UNEP 2020; Pan *et al.* 2013). Primary forests are irreplaceable for sustaining biodiversity (Gibson *et al.* 2011); however, global tree plantation initiatives show the potential of reforestation programs to mitigate climate change

(Bastin *et al.* 2019; Cook-Patton *et al.* 2020; Lewis *et al.* 2019) by fixing carbon aboveground and enhancing carbon storage belowground (Domke *et al.* 2020; Shao *et al.* 2019; Walker *et al.* 2020; Fig. 2).

Tree diversity affects carbon budget in forests

Worldwide, tree diversity increases forests productivity (Forrester and Bauhus 2016; Liang *et al.* 2016; Zhang *et al.* 2012), and thus, increases forest aboveground carbon storage (Castro-Izaguirre *et al.* 2016; Huang *et al.* 2018). Moreover, tree diversity increases soil carbon storage (Li *et al.* 2019; Liu *et al.* 2018; Xu *et al.* 2020). Consequently, tree diversity increases aboveground and belowground carbon pools, thereby, the overall forest carbon content (Liu *et al.* 2018; Fig. 2).

In addition, tree diversity reduces carbon efflux (Fig. 2.B), such as erosion (Schuldt *et al.* 2018; Song *et al.* 2019), while maintaining a high level of carbon flux between forest carbon compartments (e.g., trees, consumers, soil, Fig. 2.B). For example, tree diversity enhances the amount of litterfall (Huang *et al.* 2017) and litter decomposition (Scherer-Lorenzen *et al.* 2007; Kou *et al.* 2020); thus, the release of aboveground products to soils. Altogether, by increasing carbon inputs and reducing carbon outputs, tree diversity increases carbon *residency time* in forests (Fig. 2.B); therefore, tree diversity could play a major role in carbon mitigation. In the following sections, I reviewed the mechanisms behind tree diversity effects on carbon cycling in forests explaining tree diversity positive effects on carbon storage.

Tree diversity increases forest productivity

In forests, trees are the main *primary producers* fixing inorganic carbon (CO_2) by photosynthesis in their leaves. The mechanisms behind diversity-productivity relationships are manifold and were reviewed by Forrester and Bauhus (2016). In short, tree diversity increases forest productivity by increasing complementarity between species, thus allowing for better nutrient, water, and light uptakes. For example, tree diversity increases light interception by

increasing crown structural complementarity (Williams *et al.* 2017); likewise, tree diversity increases water and nutrient uptakes by sharing nutrients through the tree associated mycorrhizal network (Simard *et al.* 2012) or by increasing root foraging (Brassard *et al.* 2013). Forrester and Bauhus (2016) highlighted two types of complementarity: the complementarity of structures (e.g., canopy structure, root foraging strategies) and the complementarity of processes (e.g., differences of mycorrhizal symbiosis strategies). The complementarity of structures and processes for light, nutrients, and water can take place at three levels (Barry *et al.* 2019): (i) by using complementary substrates (e.g., using different chemical forms of a given nutrient), (ii) by increasing spatial complementarity (e.g., increasing crown complementarity or root foraging strategies Cheng *et al.* 2016; Williams *et al.* 2017), and (iii) by increasing temporal complementarity (e.g., increasing the differences in trees phenology, Sapijanskas *et al.* 2014). In addition, tree diversity stabilizes forest productivity (Fichtner *et al.* 2020; Morin *et al.* 2014) by enhancing the asynchronous responses of tree species to environmental variability and extreme climatic events (Goodman 1975; Schnabel *et al.* 2019).

Further, understory plant communities are related to the tree community composition and diversity (Germany *et al.* 2017). Therefore, one could expect tree species richness to affect the understory plant community; indeed, tree diversity was shown to increase the cover of forbs (Vockenhuber *et al.* 2011). These positive effects of tree diversity on understory productivity would increase the overall forest productivity. However, neither herb layer productivity nor diversity is affected by tree layer diversity (Both *et al.* 2011; Germany *et al.* 2017).

Tree diversity controls aboveground fauna

Tree primary production is the basis of the food web in forests; this is especially true for primary consumers such as herbivores (Fig. 2.B). Herbivory is a major threat to forest productivity (Flower and Gonzalez-Meler 2015; Visakorpi *et al.* 2021); meanwhile, herbivore faeces and necromass are a significant flux of organic carbon from the tree to the forest floor

(Kenis *et al.* 2017; Metcalfe *et al.* 2014). Moreover, the conversion of plant material into faeces is now known to increase litter decomposition and stimulate litter carbon dynamic (Joly *et al.* 2018; Joly *et al.* 2020). Overall, herbivory is critical for carbon cycling in forests by transferring tree products to the forest floor and stimulating organic matter recycling (Metcalfe *et al.* 2014; Schmitz and Leroux 2020).

By increasing tree productivity, tree diversity should enhance herbivory and thus carbon release to the forest floor. However, a recent review of tree diversity effects on herbivory by Jactel *et al.* (2021) showed the negative effect of tree diversity on herbivory (Schuldt *et al.* 2018; Vehviläinen *et al.* 2007). In this meta-analysis, Jactel *et al.* (2021) review the different mechanisms behind diversity effects on herbivorous species. Tree diversity is expected to increase herbivore diversity by increasing specialist herbivores. However tree diversity reduces the abundance of herbivore by reducing the abundance of host tree species for specialist herbivores (i.e., Ressouce Concentration hypothesis, Root 1973; Castagneyrol *et al.* 2014) and/or increasing the pressure of predators and parasitoids by providing a higher diversity of diets/hosts and micro-habitats to the predators/parasitoids (i.e., Enemies hypothesis, Russell 1989; Castagneyrol and Jactel 2012). Therefore, we would expect tree diversity to reduce herbivory stimulation of the carbon cycle (Metcalfe *et al.* 2014; Schmitz and Leroux 2020); however, such causal relations have not yet been tested in forests.

Tree diversity increases the release of organic carbon on forest floors

The carbon newly fixed by photosynthesis is released on the forest floor through litterfall (Fig. 2.A). The increase of tree productivity increases the amount of litterfall released (Huang *et al.* 2017; Sonkoly *et al.* 2019), and thus tree organic carbon releases. Therefore, litterfall becomes a critical process to understand tree diversity effects on carbon fluxes between the trees and soil compartments, and thus carbon cycling in forests. Moreover, tree diversity increases the diversity of tree carbon products (e.g., leaf litter, exudates). For example, increasing tree

diversity increases litter diversity (Huang *et al.* 2017), thus increasing the diversity of substrates offered to consumer communities such as decomposers. Therefore, in diverse forests accounting for higher productivity, recycling this high input of diverse organic compounds is crucial for carbon cycling.

Tree diversity increases the assimilation of forest aboveground products in soils

Litter *decomposition* – including the fragmentation of litter, its incorporation into the soil, and its mineralization due to enzymatic activities – is the main recycling process in forests controlling for the release of nutrients (e.g., nitrogen and phosphorus) into soils (Coûteaux *et al.* 1995; Hättenschwiler *et al.* 2005; Wardle *et al.* 2002). Increasing tree diversity enhances litter *decomposition* in forests (Garnier *et al.* 2004; Gessner *et al.* 2010; Joly *et al.* 2017; Handa *et al.* 2014). Thus, tree diversity effects on litter *decomposition* are mediated by (i) litter quality, (ii) decomposer activity, and (iii) environmental conditions (Hättenschwiler *et al.* 2005).

(i) Effects of tree diversity on litter quality: the litter quality effect on *decomposition* can be characterized by the litter decomposability (i.e., ability of the litter to decompose measured in controlled environment, Freschet *et al.* 2012). Litter decomposability is strongly influenced by the litter chemical and physical traits (Lin and Zeng 2018; Lin *et al.* 2021). For example, increasing nitrogen and phosphorus litter content increases litter decomposability by reducing stoichiometric limitations for the decomposer community (Fanin *et al.* 2012; Patoine *et al.* 2020). In addition, increasing litter diversity increases litter decomposability (Zhou *et al.* 2020; Lin and Zeng 2018). The positive effect of litter diversity on litter decomposability was reported as resulting from the enhancement of slow-decomposing species by fast-decomposing species (Lin and Zeng 2018). The positive effect of fast decomposing species over slow-decomposing species was explained by the complementarity of species litter chemical composition (Hättenschwiler 2005). For instance, the nitrogen-rich litter will provide nitrogen

to nitrogen-poor litter; this nutrient transfer between species is expected to be carried out by decomposer communities, especially through the fungal network (Schimel and Hättenschwiler 2007). However, the effects of litter diversity on litter *decomposition* strongly depend on the environmental conditions (Madritch and Cardinale 2007) and decomposer community adaptation (Barantal *et al.* 2011; Fanin *et al.* 2021; Zhou *et al.* 2020).

Furthermore, litter addition is known to enhance remaining litter and soil organic matter *decomposition* by providing new nutrient-rich litter to decompose (Xu *et al.* 2018). Therefore, positive effects of tree diversity on tree litterfall asynchrony (Huang *et al.* 2017) would be expected to have a positive effect on litter *decomposition* by providing several litter inputs during the year. However, such mechanisms remain to be tested.

(ii) Effects of tree diversity on the decomposer community: tree species diversity is expected to enhance decomposer community biomass and diversity (Wardle *et al.* 2006). Several mechanisms are expected to play a role there: first, the positive effect of tree diversity on tree productivity has a positive effect on decomposer biomass by increasing the abundance of substrates, thus reducing competition for resources; however, such a mechanism may only play a significant role in resource-limited environments (see Enrichment paradox, Rosenzweig 1971; Roy and Chattopadhyay 2007). Second, increasing tree diversity increases litter diversity, which is expected to increase the number of niches offered to the decomposer community, and thus the decomposer community biomass and diversity (Gessner *et al.* 2010). Maintaining a higher abundance and diversity of decomposers would enhance their activity, and thereafter, litter decomposition (Ebeling *et al.* 2014; Nielsen *et al.* 2011). For example, a high complementarity of microbial physiological pathways enhances carbon use efficiency and decomposition (Loreau *et al.* 2001). Taken together, tree diversity should enhance decomposer community abundance, functioning, and stability (Nielsen *et al.* 2011).

(iii) Effects of tree diversity on the micro-climatic conditions: tree diversity effects on micro-climatic conditions is gaining attention in ecology studies. First, the increase of sensors increases the data availability worldwide; for example, with the creation of worldwide databases of soil temperature (Lembrechts *et al.* 2020). Then, the predicted increase of worldwide temperatures and *extreme climatic events* (e.g., drought and flood, IPCC 2013, 2021) is expected to have consequences for ecosystem functions such as *decomposition* (Aerts 1997; Wall *et al.* 2008) and forest productivity (Ciais *et al.* 2005). Tree diversity is expected to increase litter *decomposition* by optimizing the micro-climatic conditions such as temperature and humidity (Gottschall *et al.* 2019; Hättenschwiler *et al.* 2005). For example, a recent study suggests that increasing tree diversity would increase litter *decomposition* in European temperate forests by reducing night cooling and favoring decomposer activity at night (Gottschall *et al.* 2019). This tree diversity effect on temperature could result from a higher canopy cover in species-rich forests (Williams *et al.* 2017), which acts as a buffering layer (Frenne *et al.* 2021). Therefore, tree diversity buffering of soil temperature is the consequence of higher aboveground crown structural complementarity and productivity in species-rich forests, however, only few studies explored these mechanisms.

Tree diversity increases soil carbon storage

Tree diversity increases soil carbon storage (Li *et al.* 2019; Liu *et al.* 2018; Xu *et al.* 2020), which is the result of carbon influx from the vegetation to the soil and carbon efflux from the soil to the atmosphere or by erosion (Fig. 2.B). As mentioned earlier, increasing tree diversity increases tree productivity, and thereafter tree organic matter released into the system, for example, by increasing the amount of litterfall (Huang *et al.* 2017) and its *decomposition* (Handa *et al.* 2014), or by increasing root desiccation and exudation as suggested in grassland systems (Eisenhauer *et al.* 2017). However, tree diversity was shown to reduce the root to shoot ratio (Guillemot *et al.* 2020), as tree diversity is expected to increase aboveground productivity

(Kunz *et al.* 2019) while reducing root productivity (Madsen *et al.* 2020). The reduction in root productivity is explained by a lower investment of trees in root foraging with increasing root structural complementarity in species-rich forests. Therefore, we could expect a lower amount of exudation in forests due to a lower amount of fine roots, but such evidence remains scarce. Moreover, until recently, dead fauna biomass (e.g., herbivores, detritivores, and higher food web levels) was expected to have a neglectable impact on soil carbon cycle due to the pyramidal structure of the food web biomass (Odum and Barrett 2005). However, a recent literature review shows the strong significance of the consumer food web in controlling the soil carbon cycle by providing recalcitrant organic material to the system (Schmitz and Leroux 2020). Thereafter, positive effects of tree diversity consumers communities should enhance inputs of recalcitrant organic matter and thus enhance soil carbon storage.

Tree diversity is expected to reduce soil erosion (Song *et al.* 2019). For example, increasing litter coverage reduces the impact of raindrops on soil (Seitz *et al.* 2015). Likewise, tree diversity was shown to increase root filling of the soil volume (Madsen *et al.* 2020), and thus reduce soil erosion (Reubens *et al.* 2007; Burylo *et al.* 2012). However, these mechanisms remain weakly studied in forest systems, but additional support for these mechanisms can be found in grasslands (Berendse *et al.* 2015; Durán Zuazo and Rodríguez Pleguezuelo 2008; Hou *et al.* 2016; Pérès *et al.* 2013).

In addition to a physical stabilization of soil carbon by tree diversity effects on soil erosion, tree diversity is expected to promote the biochemical stabilization of the soil organic matter (Xu *et al.* 2020). Plant organic compounds integrate the soil organic matter pool and are consumed by soil decomposers, especially soil microfauna. Therefore, the stability of soil organic matter and its *residency time* highly depend on the performance of soil microbial communities (Bastida *et al.* 2021; Maron *et al.* 2018; Crowther *et al.* 2019). Recent studies suggest a positive effect of microbial activity on soil carbon storage by enhancing the

transformation of soil organic matter to stable microbial necromass (Buckeridge *et al.* 2020; Lange *et al.* 2015; Miltner *et al.* 2012; Schmidt *et al.* 2011). Therefore, the success of soil carbon sequestration is highly limited by our understanding of tree diversity ~ soil microbial community functioning relationships.

Microbial communities are determined by aboveground vegetation type and its diversity (Durán and Delgado-Baquerizo 2020; Pei *et al.* 2016). For instance, tree diversity enhances soil microbial biomass (Pei *et al.* 2017; Gillespie *et al.* 2020), diversity (Singavarapu *et al.* 2021) and functioning (Gillespie *et al.* 2020; Gillespie *et al.* 2021), thus tree diversity should increase soil carbon storage. Together, tree diversity control over soil carbon storage is physical by reducing soil erosion and leaching, and biochemical by increasing soil organic carbon inputs and microbial stabilization of soil carbon.

A handful of mechanisms can explain tree diversity effects on the carbon cycle

Tree diversity effects on forest carbon cycling are manifold; however, a few mechanisms can explain these effects: the increase of complementarity between species, modification of consumer communities and their functions, and the stabilization of biological processes (Fig. 3). Primary producers (e.g., trees) complementarity effects on ecosystem functioning have been reviewed by Barry and colleagues (2018) and categorized as follows: (i) resource partitioning, (ii) abiotic facilitation, and (iii) biotic feedbacks from other trophic levels. At the food web level, trophic complementarity has been defined as the combined effect of exploitative processes and competition in the food web (Poisot *et al.* 2013); in other words, the combined effect of resource partitioning of the different trophic levels. For example, at the plant level, the trophic complementarity is the combined effect of plant resource partitioning and complementarity of herbivores (or "negative biotic feedback", Barry *et al.* 2019). Increasing trophic complementarity is expected to increase food web productivity (Poisot *et al.* 2013). I highlighted the strong pieces of evidence of resource partitioning at all trophic levels in species-

rich forests. Let us consider the case of resource partitioning in the use of different substrates: first, tree species richness is increasing resource partitioning, for example, by increasing the complementarity of mycorrhizal associations and thus foraging mechanisms. Then, tree diversity increases the diversity of tree products offered to the consumer communities (i.e., herbivores and decomposers), which increases the resource niche size, and thus favors resource partitioning among consumers (Fig. 3). The same causal cascade would be expected for spatial and temporal resource partitioning: first, the plant community benefits from it (e.g., crown complementarity for light interception or phenological complementarity); then, the consumer community and the processes they carry out benefit from the tree products spatio-temporal complementarity (Fig. 3).

Lack of spatio-temporal aspects

A major characteristic of species-rich forests is their spatial heterogeneity due to the tree species spatial distribution. Increasing tree species richness is expected to increase forest spatial heterogeneity and stabilize ecosystem functioning (Wang *et al.* 2021). The consequences of

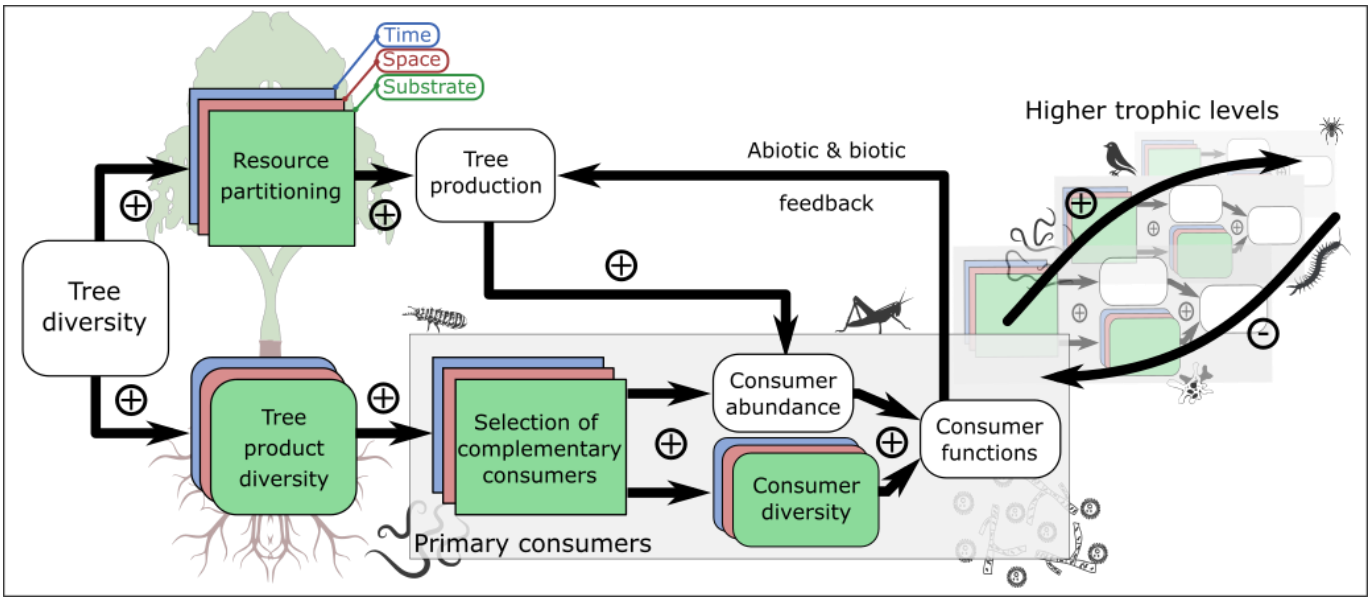


Fig. 3: Conceptual framework of tree diversity effects on ecosystem functioning. Black arrows represent the causal relationships between the ecosystem parameters. Colored boxed highlight the substrate (green), spatial (red) and temporal (blue) partitioning or complementarity of resources, tree products, consumer communities and functions.

spatio-temporal heterogeneity; such as crown structural complementarity (Williams *et al.* 2017), or tree phenology (Sapijanskas *et al.* 2014); have been thoroughly explored in a tree productivity perspective. However, the effects of tree diversity on the spatial and temporal distribution of tree products, and thus, the consequences for higher trophic levels and carbon cycling remain rarely explored. For example, how increasing tree spatial heterogeneity would affect litter distribution on the ground and how such changes will affect decomposition processes remain unknown. Moreover, as the soil microbiome is related to tree composition (Pei *et al.* 2016), it is crucial to understand how increasing tree spatial and temporal heterogeneity will affect soil microbial dynamics and processes. Taken together, the diversity-driven carbon cycle is more and more recognized, but the effects of tree diversity on forest spatial and temporal heterogeneity and the relevance for carbon cycling in forests remain unclear.

Objectives

The aim of this thesis is to understand the mechanisms behind tree diversity effects on forest carbon cycling and how these mechanisms are mediated by microbial communities and tree diversity-induced spatial heterogeneity (Fig. 4). In the first chapter (Chapter I), my colleagues and I investigated how tree diversity effects on litter decomposition are mediated by litterfall patterns and microbial processes. In the second chapter (Chapter II), we explored how tree diversity affects soil microbial communities and their functions. Then, in the third chapter (Chapter III), we synthesized these findings to understand how tree diversity effects on soil microbial biomass and carbon concentrations are mediated by tree diversity effects on environmental conditions. Finally, we explored the implication of our results for climate change mitigation and their consequences for reforestation projects (Chapter IV). Together, my studies aim to give a holistic view of tree diversity effects on forest carbon cycling and its mediation by the microbial communities and the diversity-driven spatial heterogeneity.

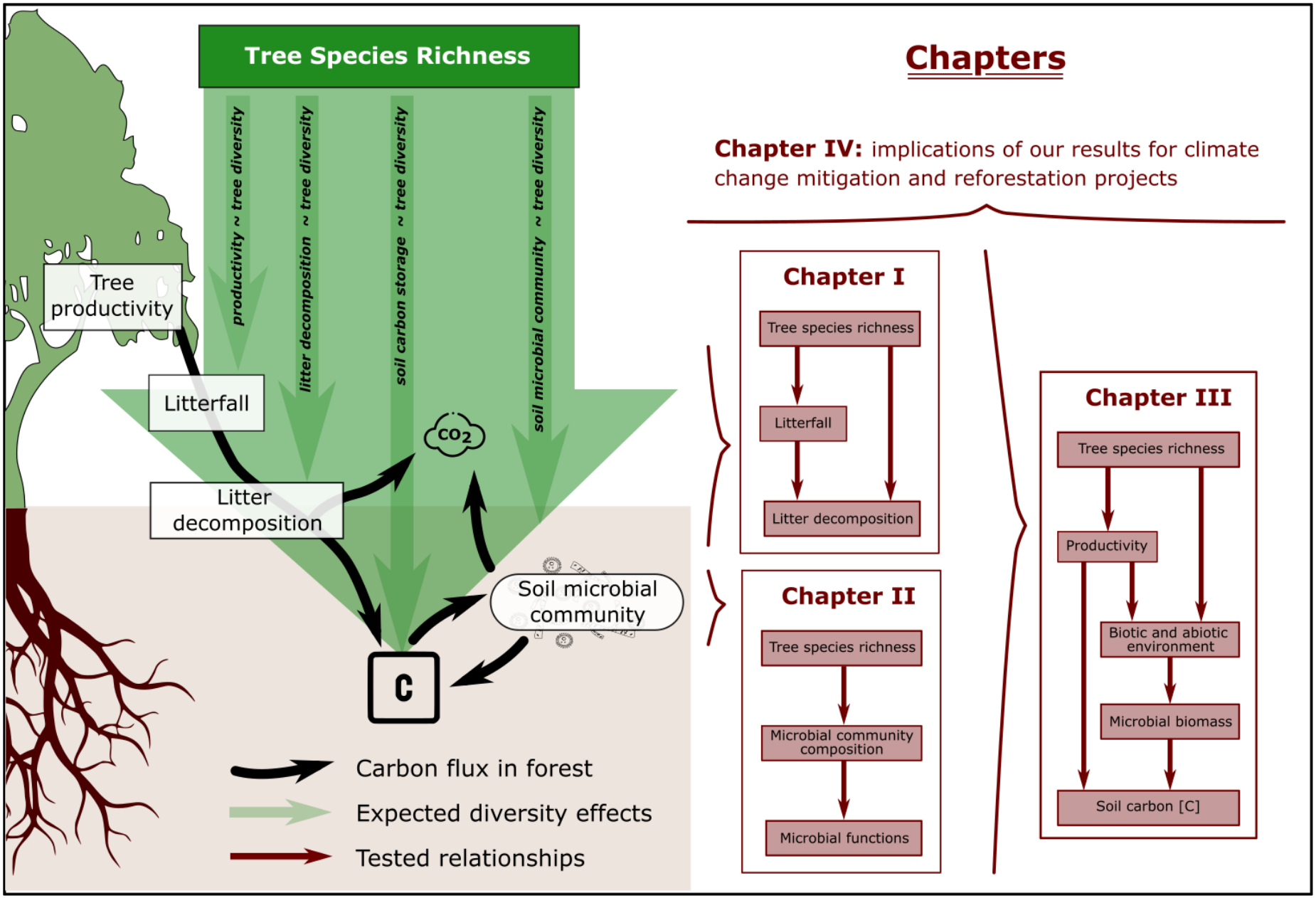


Fig. 4: Conceptual figure linking tree diversity effects on forest carbon cycle and the associated chapters.

Experimental design

Our studies have been performed within the Chinese subtropical biodiversity-ecosystem functioning tree experiment BEF-China (Fig. 5; Bruelheide *et al.* 2014) located in Southeast China. This biome has the highest average net ecosystem productivity among Asian forests (Yu *et al.* 2014) and is thus important for the study of carbon cycling and its determinants. Our sampling was based on the TreeDì sampling design focusing on tree-tree interactions (Trogisch *et al.* 2021). This design aims to study the effect of tree-tree interactions on ecosystem functions by following pairs of trees (i.e., tree species pairs: TSP, Fig. 6.A) from twelve tree species along a plot diversity gradient ranging from 1 to 16 species (Fig. 5, Bruelheide *et al.* 2014). The neighbors of a TSP are defined as the ten trees directly adjacent in the planting grid (Fig. 6.A). Each TSP was replicated three times in each richness level of the broken stick design (see "broken stick design", Bruelheide *et al.* 2014), resulting in 180 TSPs in total. Our sampling consisted of three sampling periods (Fig. 6.B): (i) September 2018 for the soil sampling (Chapter II-III) and the installation of litter traps (Chapter I), (ii) December 2018 from the collection of litter after litterfall and the installation of the decomposition experiments (Chapter I), and (iii) September 2019 to sample the decomposition experiments (Chapter I).

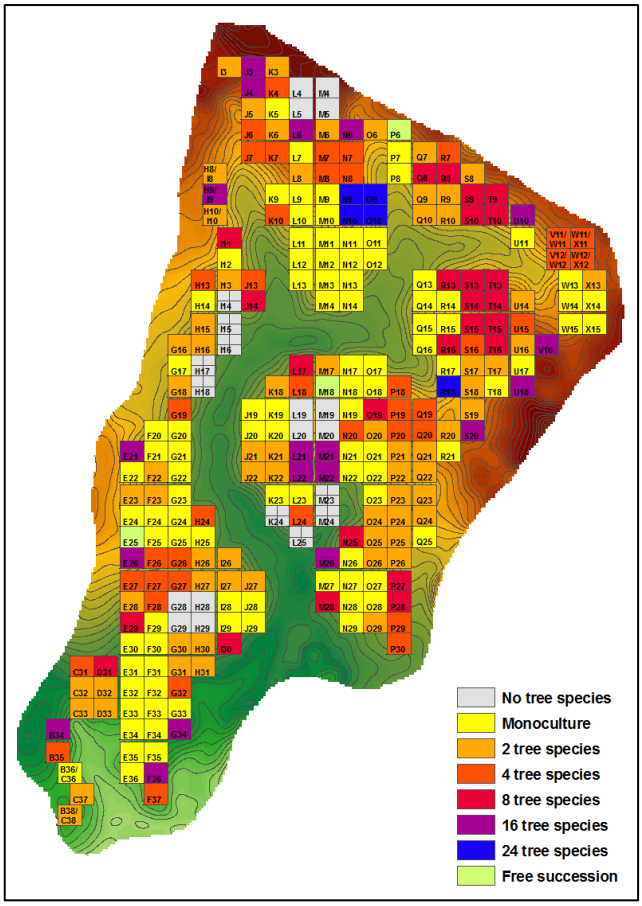


Fig. 5: BEF-China Site A: elevation plot and diversity treatments (Bruelheide *et al.* 2014). The plot elevation ranging from 105 to 280 m.

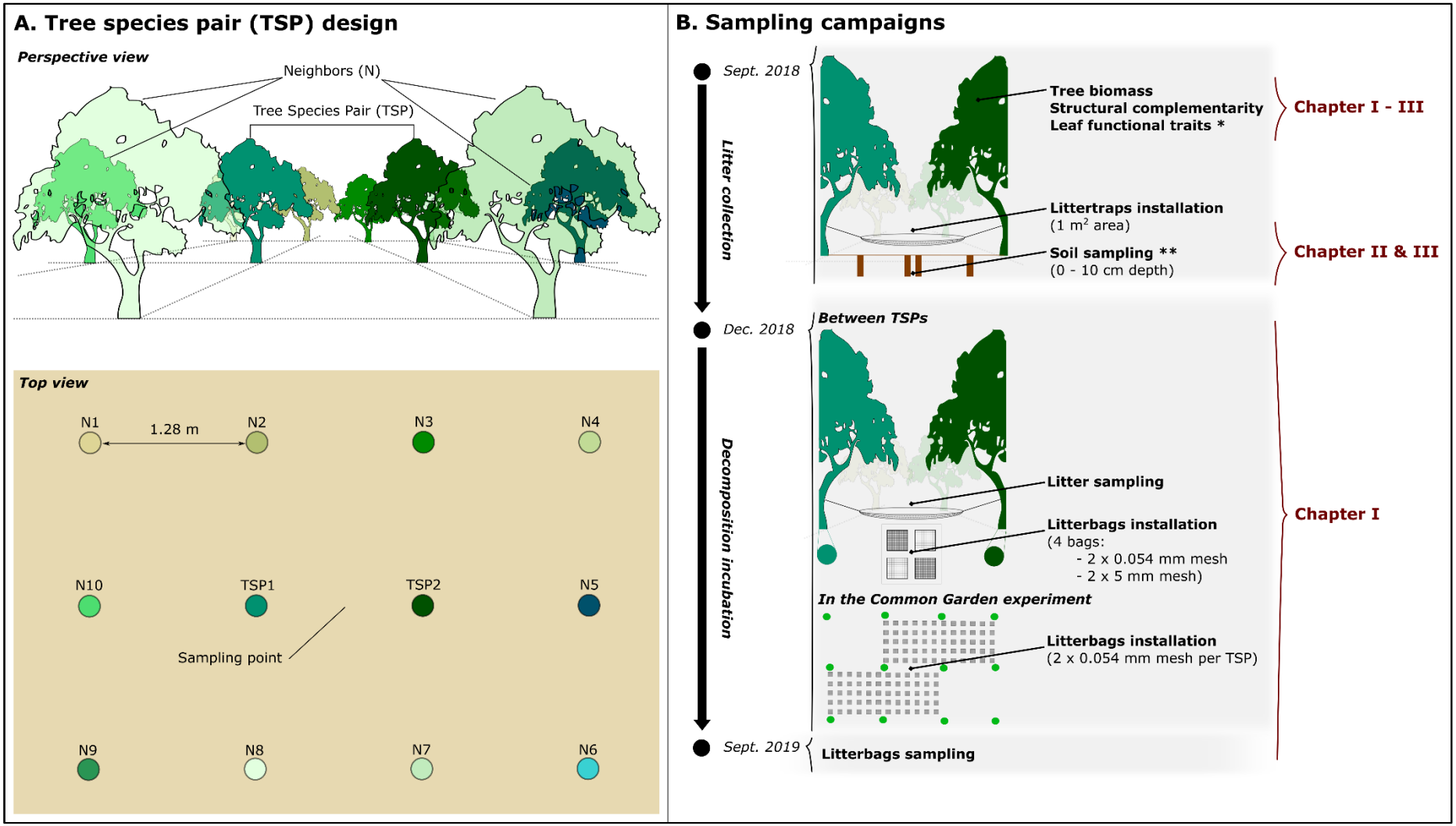


Fig. 6: A. Tree species pair experimental spatial design, and B. Description of the sampling campaigns. *: tree biomass was estimated from the measurements of the TreeDì project P5G (Mariem Saadani, Prof. Dr. Helge Bruelheide), crown structural complementarity was measured by the project P1G (Maria D. Perles Garcia, Dr. Matthias Kunz, Prof. Dr. Goddert von Oheimb), leaf functional traits were measured by the project P2G (Andréa Davrinche, Dr. Sylvia Haider). **: soil sampling and measurements were performed in collaboration with the project P7G (Bala Singavarapu, Dr. Tesfaye Wubet), and P8C (Dr. Jianqing Du, Dr. Kai Xu, Prof. Dr. Yanfan Wang)

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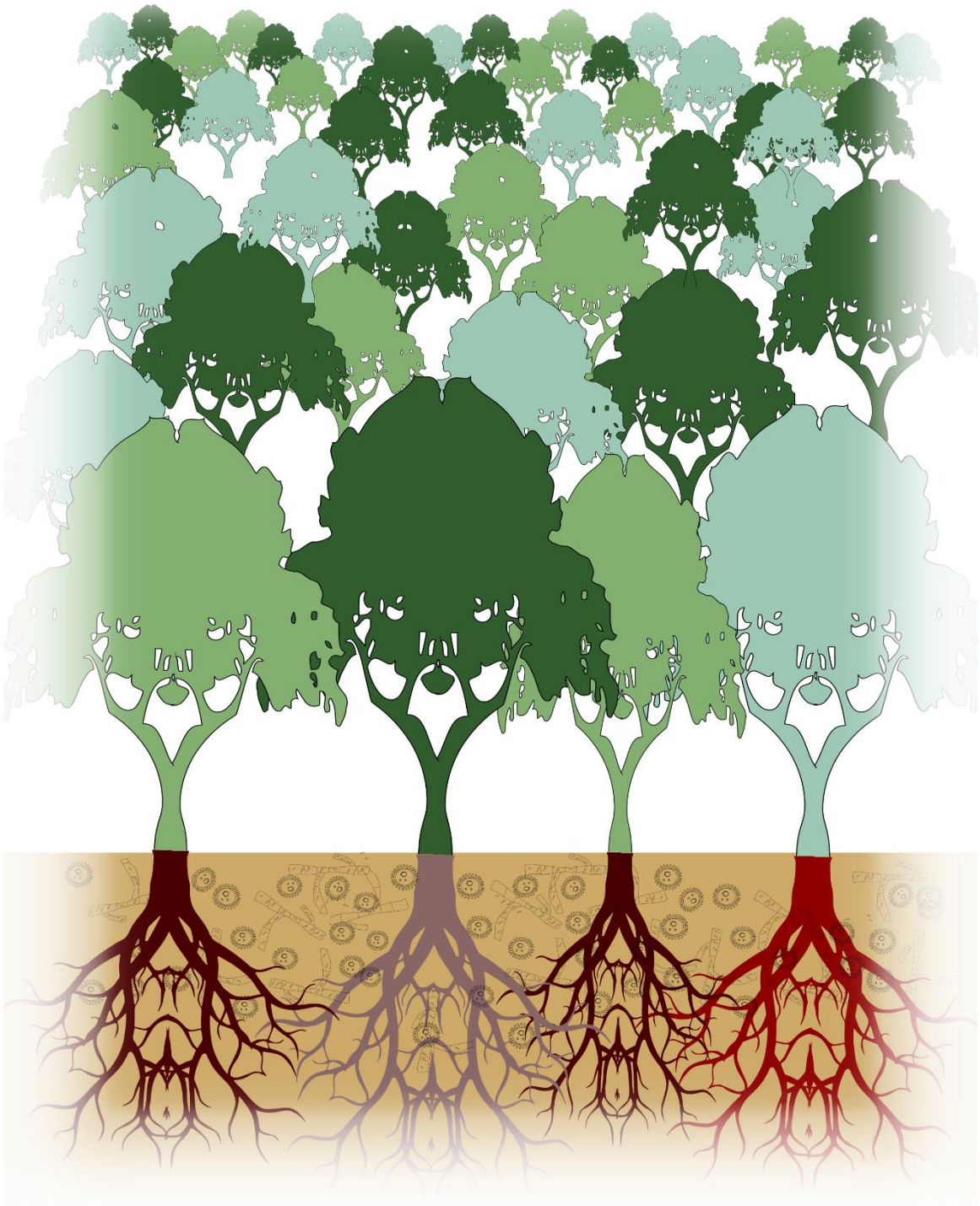

Chapter I

Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes

Chapter I - Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes

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Abstract

Forest ecosystems are critical for carbon fixation in both above- and belowground compartments. Increasing tree diversity enhances forest productivity and litter decomposition through soil organisms. Litter diversity increases litter decomposability (i.e., the susceptibility of litter to decomposition) by increasing the diversity of substrates offered to decomposers. However, the relative importance of the litter decomposability and the decomposer community in mediating tree diversity effects on decomposition remains unknown. Moreover, how tree diversity modulates the spatial distribution of litterfall, and consequently, litter decomposition has rarely been tested.

Here, we studied tree diversity effects on decomposition using litter bags with different mesh sizes and how such effects are mediated by the amount of litterfall, litter diversity, decomposability and soil microorganisms in a large-scale tree diversity experiment in subtropical China (BEF-China Experiment). In addition, we examined how leaf litter decomposability is affected by the litter functional identity and diversity. Finally, we tested how leaf functional traits, tree biomass, and forest spatial organization drive the spatial patterns of litterfall.

We found evidence that tree species richness increased litter decomposition by increasing litter species richness and the amount of litterfall. Moreover, we showed that the majority of litter decomposition (84-87%) is performed by soil microorganisms in this subtropical forest. Changes in the amount of litterfall and microbial decomposition explained 19-37% of total decomposition variance with similar effect sizes. In addition, up to 20% of microbial decomposition variance was explained by litter decomposability, while litter decomposability was determined by the litter nutrient content, functional diversity, and species richness. In addition, our results show that tree species richness increased the amount of litterfall (+200% from monoculture to 8-species neighborhood) and litter species richness (1:1 relationship between tree and litter species richness). We further demonstrated that species-specific amount of litterfall increased with increasing tree biomass and proximity to the trees, but not with specific leaf area. These drivers of litterfall increased the spatial heterogeneity of litter distribution in the plot, thus influencing litter decomposability, and thereby litter decomposition. Together, our findings highlight multiple mass- and diversity-mediated effects of tree diversity on ecosystem properties driving forest carbon and nitrogen cycling. Therefore, we conclude that considering spatial variability in biotic properties will improve our mechanistic understanding of biogeochemical cycles and ecosystem functioning.

Introduction

Forest ecosystems have been highlighted for their carbon fixation potential in both above- and belowground compartments (Bastin *et al.* 2019; Lewis *et al.* 2019), especially in species-rich forests (Liang *et al.* 2016; Liu *et al.* 2018; Xu *et al.* 2020). Recycling of tree dead organic matter (e.g., litter or dead wood decomposition) controls the release of carbon and other nutrients from the aboveground compartment into the soil (Seibold *et al.* 2021; Wardle *et al.* 2004), while preventing dead organic matter accumulation (Minderman 1968). Recycling processes become even more important in highly productive ecosystems, such as subtropical Chinese forests (Yu *et al.* 2014), where high amounts of dead organic matter are released (Liu *et al.* 2018), and where it is therefore critical to understand the drivers of decomposition processes.

Decomposition of leaf litter is the main recycling process in forests, including the fragmentation of litter, its incorporation into the soil, and its mineralization due to enzymatic activities (Coûteaux *et al.* 1995; Hättenschwiler 2005; Wardle *et al.* 2002). Tree species richness was shown to increase decomposition (Gartner and Cardon 2004; Gessner *et al.* 2010; Joly *et al.* 2017; Trogisch *et al.* 2016), thus enhancing the incorporation of organic matter into the soil compartment (Gartner and Cardon 2004; Lange *et al.* 2015). Litter decomposition is carried out by meso- and macro-decomposers (García-Palacios *et al.* 2013) interacting with microbial communities (Bradford *et al.* 2002; Joly *et al.* 2018). Tree species richness, and as a consequence litter species richness, is expected to increase decomposer biomass and diversity by providing a higher diversity of substrates and increasing niche partitioning of the decomposer community (Ebeling *et al.* 2014; Finke and Snyder 2008; Hooper *et al.* 2000; Scherber *et al.* 2010). In addition, litter species richness should increase litter decomposition by increasing litter decomposability (Lin and Zeng 2018; Zhou *et al.* 2020); i.e., the ability of litter to decompose when measured in a controlled environment (Freschet *et al.* 2012).

However, the relative contribution of litter decomposability and soil decomposer community in mediating tree diversity effects on litter decomposition remains untested.

Litter decomposability quantifies how decomposition responds to changing substrate; i.e., the effect of litter on decomposition when controlling for the effects on decomposer community or environmental conditions. Litter decomposability is strongly driven by leaf functional trait identity and diversity (Freschet *et al.* 2012; Rosenfield *et al.* 2020; Zhou *et al.* 2020). For example, high-quality litter, related leaf functional traits like nutrient stoichiometry (i.e., high quality litter with lower C:N and C:P ratios), enhances litter decomposition by increasing the availability of limiting nutrients (Fanin *et al.* 2012; Patoine *et al.* 2020; Zhang *et al.* 2018). Moreover, higher litter species richness promotes litter decomposability by increasing litter chemical dissimilarity and favoring nutrient transfer from nutrient-rich leaves to nutrient-poor leaves (Schimel and Hättenschwiler 2007). However, the relative contributions of litter composition and diversity on decomposability remain rarely tested, especially in a large pool of species and species mixtures (Lin *et al.* 2021).

Changes in tree diversity affect the amount of litterfall and litter species richness at the plot level (Huang *et al.* 2017). For example, tree species richness was shown to increase forest productivity (Huang *et al.* 2018), including litterfall biomass (Huang *et al.* 2017). In species-rich forests, the spatial arrangement of tree species in the plot (i.e., tree planting pattern) is also expected to influence the spatial distribution of litter and, thus, litter composition and decomposition. Moreover, we could expect litter distribution across space to be affected by species identity and leaf morphological traits. For example, as leaf size increases, leaves should be transported further away from the source tree (Chandler *et al.* 2008). However, little is known about the effects of leaf morphological traits and tree productivity on spatial patterns of litterfall distribution and the consequences for decomposition processes.

In this study, we aim to mechanistically understand tree species richness effects on leaf litter decomposition by considering the amount of litterfall and litter composition, the factors (e.g., tree biomass, leaf traits and tree spatial organization) that affect litter composition, its decomposability, as well as the mediation by microbial processes. We hypothesized that (Fig. I.1) tree species richness would increase litter decomposition (H1), and that litter decomposition would be carried out mainly by the soil microbial community (H2). Further, increasing litter decomposability should increase microbial decomposition (H3), and we expect litter diversity and nutrient availability (e.g., litter N, P content) to increase litter decomposability (H4). Finally, we hypothesized the spatial distribution of litterfall to be driven by tree biomass, leaf morphological traits, and the spatial distribution of the trees in the plot (H5).

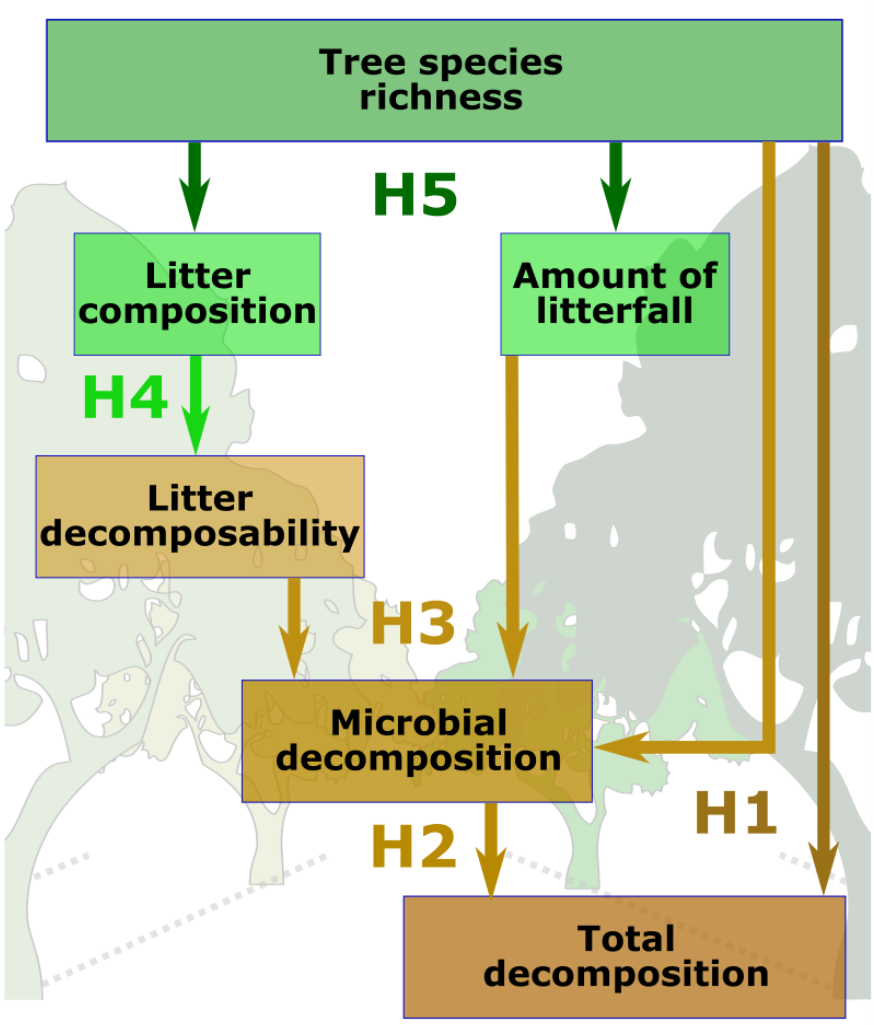

Fig. I.1: Conceptual framework of the study. Relationships between the different hypotheses tested in this study: **H1** - tree species richness increases litter decomposition; **H2** - litter decomposition is carried out mainly by the soil microbial community; **H3** - microbial decomposition increases with litter decomposability (i.e., litter decomposition measured in a controlled environment); **H4** - litter diversity and nutrient availability (e.g., litter C, N, P content) increases litter decomposability; **H5** - the litter composition is driven by tree biomass, leaf morphological traits, and the spatial distribution of the trees in the plot.

Materials and methods

Study site

The study site is located in south-east China near the town of Xingangshan (Jiangxi province, 29.08-29.11° N, 117.90-117.93° E). Our experimental site is part of the BEF-China experiment (site A; Bruelheide *et al.* 2014), which was planted in 2009 after a clear-cut of the previous commercial plantations. The region is characterized by a subtropical climate with warm, rainy summers and cool, dry winters with a mean annual temperature of 16.7 °C and a mean annual rainfall of 1.821 mm (Yang et al. 2013). Soils in the region are Cambisols and Cambisol derivatives, with Regosol on ridges and crests (Geißler *et al.* 2012; Scholten *et al.* 2017). The natural vegetation consists of species-rich broad-leaved forests dominated by *Cyclobalanopsis glauca*, *Castanopsis eyrei*, *Daphniphyllum oldhamii*, and *Lithocarpus glaber* (Bruelheide *et al.* 2011; Bruelheide *et al.* 2014).

Study design

To identify the effect of tree spatial organization on litterfall distribution and decomposition, we measured litterfall and decomposition between tree species pairs (i.e., TSP) across various neighborhoods. Each TSP consisted of two trees next to each other (1.28 m), and we defined its neighborhood as the ten trees directly adjacent in the planting grid (Trogisch et al. 2021). Each TSP was replicated three times in five tree species richness levels (1, 2, 4, 8, and ≥ 16 species), when available according to the experimental design (see "broken stick design"; Bruelheide *et al.* 2014). In total, we surveyed 24 combinations of tree species resulting in a total of 180 TSPs in 52 plots (Suppl. I-S1).

Litterfall sampling

In September 2018, a litter trap of 1 m² was set up at a height of 1 m above the soil surface between each TSP (Suppl. I-S1). Litter was collected in December 2018 to cover the main litterfall season in the region (Huang *et al.* 2017). To measure litterfall composition, each leaf

of the litter trap was sorted and identified to species level. Each species' litter was dried at 40ºC for two days and weighed (± 0.1 g). Litter species richness was assessed as the number of species identified in the trap, and the total amount of litterfall was calculated as the sum of the dried biomass of all species.

Litter decomposition experiments

We performed two complementary decomposition experiments: one in the TSPs to measure microbial and total decomposition, and one in a Common Garden experimental field site to assess decomposability (i.e., the susceptibility of litter to decompose measured in controlled conditions Suppl. I-S1).

For both experiments, litterbags (10 cm x 10 cm), with different mesh sizes (see details below) were filled with 2 g (± 0.01 g) of dried litter according to litter trap species composition (i.e., species-specific biomasses) of the different TSPs. Therefore, the litter composition of the litterbags exactly matched the litter composition (i.e., species-specific biomasses) collected in the corresponding TSP. The litterbags for both experiments were installed in December 2018 and collected in September 2019, i.e., after nine months of decomposition. The litterbags were water-cleaned and dried at 40 ºC for two days. The residual litter was weighed (± 0.01 g) and milled.

Decomposition experiment in between the TSPs

To assess total litter decomposition (total C and N loss, including fauna-mediated decomposition) and microbial decomposition (microbial C and N loss, excluding fauna-mediated decomposition), two large-mesh (5 mm mesh, total litter decomposition) and two small-mesh (0.054 mm mesh, microbial decomposition) litterbags were set up between the TSPs, respectively, with plot-specific litter. Small-mesh litter bags excluded meso- and macro-detritivores by using a fine mesh size (0.054 mm-mesh) to assess microbial decomposition,

while large-mesh litter bags were built using a 5 mm-mesh in the upper half of the bag to provide access to macro-decomposers, and a 0.054 mm-mesh only at the bottom to prevent loss of fine leaf litter particles to access to total litter decomposition. All litterbags were covered by a 1 m x 1 m grid to prevent heavy rainfalls from dislocating the litterbags (1 cm mesh size, see Suppl. I-S1).

Decomposition experiment in the Common Garden

The Common Garden setting consisted of a monoculture stand of *Schima superba*, a species that was not included in the TSP experiment; thereby, we were able to exclude any home-field advantages (Fanin *et al.* 2021). *Schima superba* was not part of the litter mixtures of the decomposition experiment and was chosen to maximize the phylogenetic distance with our target species and minimize environmental heterogeneity within the plot (i.e., productive species with closed canopy). *Schima superba*'s litter was removed from the ground before deploying the litterbags at a distance of 10 cm from each other in two blocks (one TSP replicate per block, Suppl. I-S1). To measure litter decomposability, two small-mesh litterbags (0.054 mm mesh) representing the litter composition of each TSP were incubated in the Common Garden experiment.

Leaf and litter trait measurements

Leaf functional traits were assessed at the species- and plot-level in September 2018, following Davrinche and Haider (2021). For each TSP species in each plot, several leaf samples were collected, and the reflectance spectra were measured using ASD FieldSpec® 4 High-Resolution Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom). Leaf functional traits were predicted from the reflectance spectra of a calibration dataset of the same species, where both reflectance spectra and leaf functional traits were measured. For leaf morphological traits – specific leaf area (SLA, leaf area divided by dry weight) and leaf dry matter content (LDMC, ratio of leaf dry mass to fresh mass – fresh and dry weights were

measured before and after drying for 72 h at 80°C. To obtain SLA, leaf areas were measured from scans with a resolution of 300 dpi of the fresh leaves using the WinFOLIA software (Regent Instruments, Quebec, Canada. Leaf chemical contents; carbon (C), nitrogen (N), phosphorus (P) contents; were measured from dried leaves ground into a fine powder (Mixer Mill 400, Retsch, Haan, Germany). About 5 mg of leaf powder was used to determine C and N content with an elemental analyzer (Vario EL Cube, Elementar, Langenselbold, Germany); a 200 mg subsample was used to measure P content via nitric acid digestion and spectrophotometry using the acid molybdate technique. The filtrate resulting from nitric acid digestion was analyzed with atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany) for magnesium (Mg), calcium (Ca) and potassium (K) content. The relation between the leaf spectra of the calibration samples and the leaf traits was analyzed in the software Unscrambler X (version 10.1, CAMO Analytics, Oslo, Norway) to predict species- and plot-specific leaf functional traits. For each litterbag, we calculated the total amount of nutrients (i.e., C, N, P, Mg, Ca, K) as the sum of all species contribution, and leaf morphological traits (i.e., SLA and LDMC) community weighted means (Garnier *et al.* 2004). In addition, we calculated the variance of each functional trait (i.e., C, N, P, Mg, Ca, K, SLA, LDMC) within the litterbags.

Litter C and N content after decomposition were measured from the residual litter with an elemental analyzer (Vario EL Cube, Elementar, Langenselbold, Germany). To estimate soil contamination, the ash content of the sample was measured using the loss on ignition method as:

$$soil\ content\ \left[g_{soil}/g_{sample}\right] = \frac{ash_{sample}\left[\frac{g_{ash}}{g_{sample}}\right]}{ash_{soil}\left[\frac{g_{ash}}{g_{soil}}\right]} = \frac{ash\left[\frac{g_{ash}}{g_{sample}}\right]}{1-SOM\left[\frac{g_{SOM}}{g_{soil}}\right]}, \text{ where } ash_{soil} = (1 - SOM)$$

The carbon and nitrogen content in the litter sample were corrected for soil contamination after:

$$[C]_{litter} = [C]_{sample} - [C]_{soil} \times soil\ content$$

$$[N]_{litter} = [N]_{sample} - [N]_{soil} \times soil\ content$$

See Suppl. I-S2 for details

Decomposition measures

C and N loss (%) in the litterbags between December 2018 and September 2019 were used as a measure of the total decomposition (i.e., measured via the large mesh-size in the TSP experiment), microbial decomposition (i.e., using small mesh-size in the TSP experiment), and itter decomposability (i.e., using small mesh-size in the Common Garden experiment).

Statistical methods

A description of all the variables used in this study can be found in Suppl I-S1. All data handling and statistical calculations were performed using the R statistical software version 4.1.0 (R Core Team 2021). All R scripts used for this project can be found in our GitHub repository (https://github.com/remybeugnon/Beugnon-et-al-2021_Tree-diversity-effects-on-litter-decomposition). All following linear multiple-predictors models were tested in R using the 'lm' function (R Core Team, 2021), and statistical hypotheses (i.e., residuals normality, homoscedasticity, homogeneity of variance) of the following linear models were tested in Suppl. I-S3 using the 'model_check' function from the 'performance' package (Lüdecke *et al.* 2020).

Tree diversity effect on carbon and nitrogen loss (H1)

We used linear models and normal distribution assumptions to test the effects of neighborhood tree species richness on total decomposition ("C loss" and "N loss" measured between the TSPs) and microbial decomposition ("C loss" and "N loss" measured between the TSPs when soil meso- and macro-fauna were excluded). In addition, we used linear models and normal

distribution assumptions to test the effects of litter species richness on litter decomposability ("C loss" and "N loss" measured in the Common Garden Experiment).

Tree diversity effect on the amount of litterfall and litter species richness

We used linear models and normal distribution assumptions to test the effect of neighborhood tree species richness on the amount of litterfall, and litter species richness.

Mediation of tree species richness effects on litter decomposition

To test the effects of litter species richness on litter decomposability ("C loss" and "N loss" in the Common Garden experiment), we used linear models and normal distribution assumptions. To test the effects of litter species richness, amount of litterfall, and decomposability ("C loss" and "N loss" in the Common Garden experiment) on litter microbial decomposition ("C loss" and "N loss" between the TSPs when soil meso- and macro-fauna were excluded), we used linear multiple predictor models and normal distribution assumptions where all predictors values were rescales using the R function 'scale' (R Core Team 2021). To test the effects of litter species richness, amount of litterfall, and litter microbial decomposition ("C loss" and "N loss" between the TSP when soil meso- and macro-fauna were excluded) on litter decomposition ("C loss" and "N loss" between the TSP when soil meso- and macro-fauna were included), we used linear multiple predictor models and normal distribution assumptions where all predictors values were rescales using the R function 'scale' (R Core Team 2021 - H2). All previously cited model output can be found in Suppl. I-S3.

To test the mediation of tree species richness effects on litter decomposition by litterfall abundance and species richness effects on decomposability, we implemented the previous relationships in a Structural Equation Model (SEM) framework (see Suppl. I-S3 for model structure). Our SEM was fitted using the R 'sem' function from the 'lavaan' package (Rosseel 2012). The quality of our model fit on the data was estimated using three complementary

indices: (i) the root-mean-squared error of approximation (RMSEA), (ii) the comparative fit index (CFI), and (iii) the standardized root mean squared residuals (SRMR), a model fit was considered acceptable when RMSEA < 0.10, CFI > 0.9 and SRMR < 0.08.

Litterfall composition effect on litter decomposability (H4)

To test the effects on litter functional identity and diversity on litter decomposability: first, we summarized changes in litter functional identity (i.e., total amount of C, N, P, Mg, Na, K, and the CWM of the litter SLA and LDMC in the litterbag) using a principal component analysis (PCA); second, we summarized changes in litter functional diversity (i.e., variance of C, N, P, Mg, Na, K, SLA and LDMC in the litterbag) using a PCA, and third, we tested the effects of litter species richness and litter functional identity and diversity on litter decomposability.

The first two axes of the litter functional identity PCA covered 76% of the litter functional identity variance between the litterbags (Suppl. I-S3). The first axis (i.e., "Litter nutrient content" axis) was correlated with the chemical content (total amount of C, N, P, Mg, Na, K) of material in the litterbag, while the second axis (i.e., "Litter morphology" axis) was correlated with the litter morphological traits (i.e., CWM of SLA and LDMC within the litterbag). We extracted the first two axes of the PCA ("Litter nutrient content" and "Litter morphology") for the following analyses. The first two axes of the litter functional diversity PCA explained 91% of the variance in litter functional diversity between the litterbags (Suppl. I-S3). We extracted the first two axes of the PCA ("Litter fun. diversity 1" and "Litter fun. diversity 2") for the following analysis. To test the effects of litter species richness, litter nutrient content, morphology and functional diversity on litter decomposability (i.e., "C loss" and "N loss" in the Common Garden experiment), we used linear multiple predictor models and normal distribution assumptions where all explanatory variables were rescaled using the R function 'scale' (R Core Team 2021). Explanatory variables were selected using forward and backward step selection based on AIC, R 'step' function from 'stats' package (R Core Team 2021).

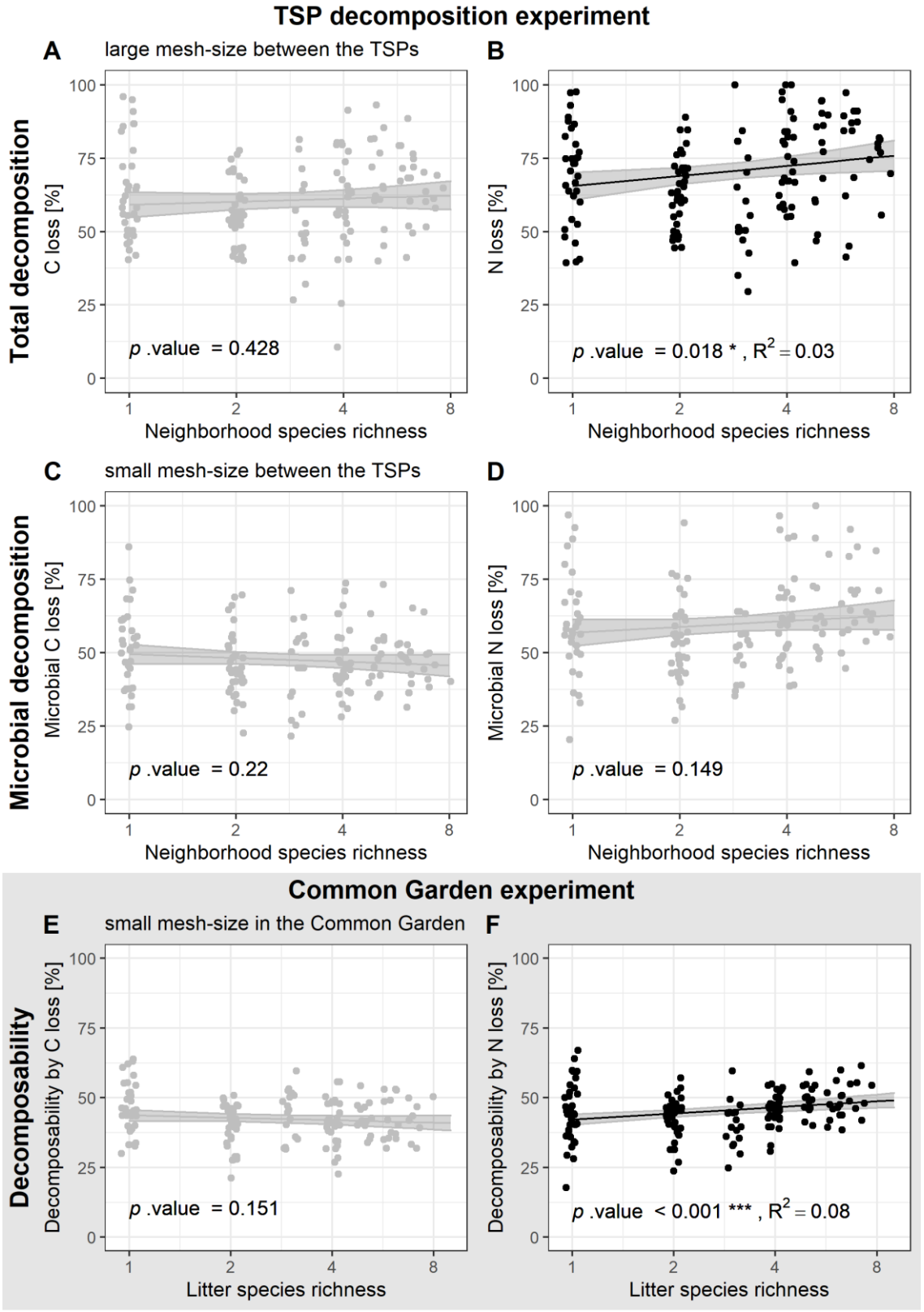

Fig. I.2: Neighborhood tree species richness effect on total litter decomposition using large mesh-size litterbags (5 mm mesh, A & B), microbial decomposition using small mesh-size litterbags (0.054 mm mesh, C & D), and litter species richness effect on litter decomposability measured under controlled conditions in the Common Garden experiment using small-mesh size litterbags (0.054 mm mesh, E & F). The values represent carbon and nitrogen loss (in %) after nine months of decomposition in a subtropical Chinese forest. For better readability, the values were jittered and non-significant relationships (i.e., p-value > 0.05) were grayed. Significance levels: ".": *p*-value < 0.1, "*": *p*-value < 0.05, "**": *p*-value < 0.01, and "***: *p*-value < 0.001).

Tree biomass, functional traits and planting pattern effects on litterfall composition (H5)

To test the effects of tree biomass ("log(biomass)"), leaf morphology ("SLA", LDMC was removed from the model due to the high correlation with SLA, Suppl. I-S3), the tree proximity to the traps ("1/dist") on amount of species-specific litterfall in our traps, we fitted linear mixed effect multiple predictor models with normal distribution assumptions using the R 'lmer' function from 'lmerTest' package (Kuznetsova *et al.* 2017). Species identity was used as random factor and the total amount of litter from other species in the litter trap was used as a covariate to control for TSP productivity. Explanatory variables were rescaled using the R function 'scale' (R Core Team 2021) and selected using forward and backward step selection based on AIC (R 'step' function from 'lmerTest' package, Kuznetsova *et al.* 2017).

Results

Tree species richness increases decomposition

Our analyses showed that after nine months of decomposition, neighborhood tree species richness did not affect carbon loss (p-value = 0.428, Fig. I.2.A), but significantly increased litter nitrogen loss significantly (estimate ± SE = 5.00 ± 2.08, p-value = 0.018, Fig. I.2.B). However, tree species richness did not affect carbon nor nitrogen loss during microbial decomposition (p-value = 0.220, Fig. I.2.C, and p-value = 0.149, Fig. I.2.D). In addition, litter species richness increased litter decomposability measured in the controlled environment. In detail, litter species richness did not affect carbon loss (p-value = 0.151, Fig. I.2.D) but increased nitrogen loss (3.15 ± 0.85, p-value < 0.001, Fig. I.2.F).

Tree species richness affects litterfall with consequences for litter decomposition

Our model revealed a positive effect of neighborhood tree species richness on the amount litterfall and litter species richness (estimate ± SE = 52.3 ± 8.24, p-value < 0.001; 1.00 ± 0.05, p-value < 0.001, respectively; Fig. I.3.A). In the Common Garden experiment, where litter decomposability was investigated, litter species richness of the litterbags increased litter N loss

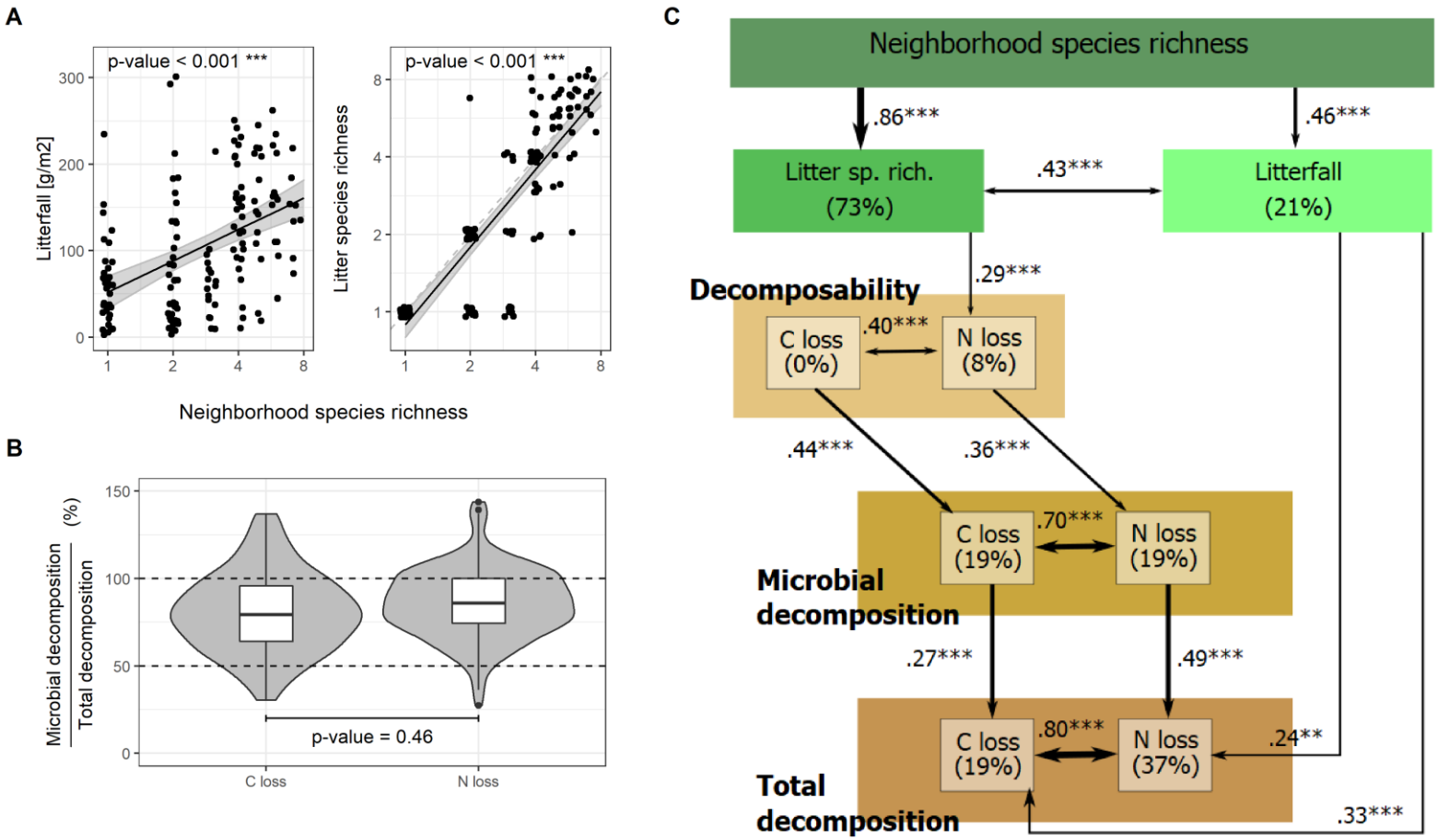

Fig. I.3 Tree species effect on the amount of litterfall and litter species richness, as well as consequences for litter decomposition. A. Neighborhood species richness effect on the amount of litterfall and litter species richness (values were jittered for better readability). B. Percentage of total decomposition carried out by the microbial community. C. Structural equation model linking neighborhood species richness, litterfall (i.e., litter species richness: "Litter sp. rich.", and amount of litterfall: "Litterfall") and decomposition processes (i.e., Decomposability in terms of litter "C loss" and "N loss" in a Common Garden experiment, microbial decomposition in terms of litter "C loss" and "N loss", and total decomposition in terms of "C loss" and "N loss"). Only significant paths (*p-value* < 0.05) are reported with an arrow in the figure (see the whole model structure in Suppl. I-S3). Arrow widths were scaled by the standardized effect size of significant relations. Correlations between nodes were drawn with double-headed arrows, while causal relations were drawn with one-way arrows. The variance explained by the model (R^2, in %) is shown after each node name. Significance levels: ".": *p*-value < 0.1, "*": *p*-value < 0.05, "**": *p*-value < 0.01, and "***: *p*-value < 0.001).

(0.29 ± 0.07, *p*-value < 0.001, Fig. I.3.C), and explained up to 8% of its variance but did not affect litter C loss. The total and microbial litter decompositions were investigated in the TSP where the litter was collected. Microbial C loss increased with C loss measured in controlled conditions (i.e., decomposability, 0.43 ± 0.05, *p*-value < 0.001), explaining 19% of the variance in microbial C loss (Fig. I.3.C). Similarly, microbial N loss increased with increasing litter decomposability (0.36 ± 0.06, *p*-value < 0.001), explaining up to 19% of the variance in microbial N loss. Microbial decomposition represented the major part of litter decomposition: 84% (± 40%) of C loss and 87% (± 22%) of N loss were carried out by the microbial community (Fig. I.3.B). Litter microbial C loss and the amount of litterfall explained up to 19% of litter C loss, both increasing litter C loss (0.31 ± 0.09, *p*-value < 0.001, and 0.26 ± 0.05, *p*-value < 0.001, respectively, Fig. I.3.C). Similarly, microbially-mediated N loss and the amount of litterfall increased total litter N loss (0.50 ± 0.05, *p*-value < 0.001, and 0.23 ± 0.08, *p*-value = 0.003), explaining 37% of the variance in litter N loss.

Litter decomposability is leaf trait based

Our analyses showed that, in controlled environmental conditions, litter species richness and functional trait identity and diversity (Fig. I.3.A) explained up to 2% and 17% of litter carbon and nitrogen loss variance, respectively (Fig. I.3.B., Suppl. I-S3). Our models showed that only N loss increased with litter species richness (estimate ± SE = 2.55 ± 0.73, *p*-value < 0.001) and with increasing litter functional diversity (0.45 ± 0.19, *p*-value = 0.017). Moreover, both C and N loss increased with increasing litter nutrient content (1.02 ± 0.39, *p*-value = 0.009; 2.10 ± 0.51, *p*-value < 0.001, respectively).

Amount and composition of litterfall is affected by tree biomass, and tree spatial organization

Our analyses of litterfall composition highlighted the effect of tree biomass and the spatial arrangements of the trees at the locations of litter collection (Fig. I.4.C),

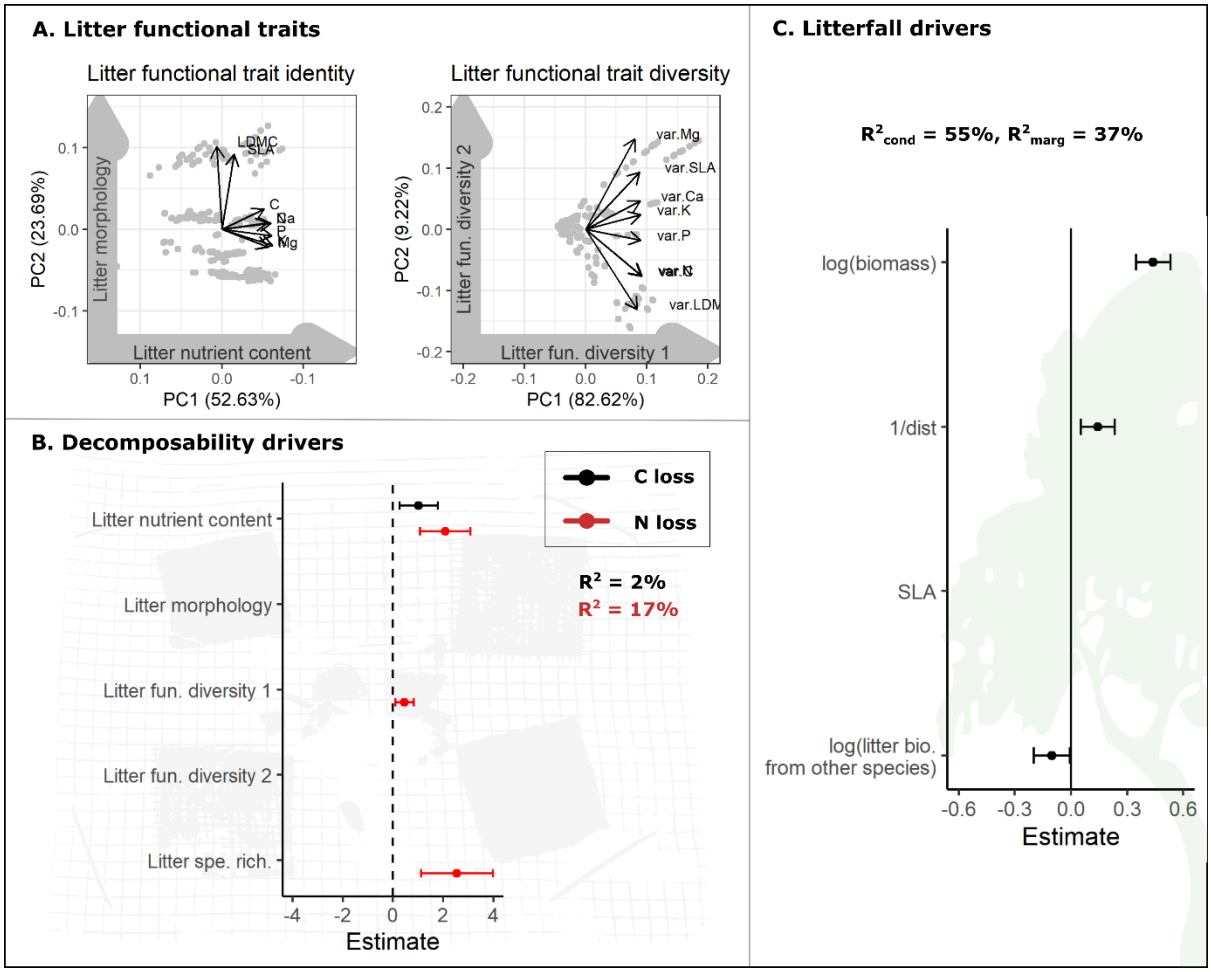

Fig. I.4: Litter functional trait identity and diversity (A), decomposability drivers (B), and drivers of the amount of species-specific litterfall (C). A. Primary Component Analysis (PCA) of litter functional trait identity and diversity. Litter functional trait identity consisted of litter chemical composition (litterbag C, N, P, Mg, Na, K content) and litter leaf morphological traits (litterbag community weighted mean SLA and LDMC), and litter functional trait diversity consisted of litter leaf functional trait variance within the litterbags (C, N, P, Mg, Na, K, SLA and LDMC variances). B. Effect of litter nutrient content (PCA litter functional identity first axis), morphology (PCA litter functional identity second axis), functional diversity (PCA litter functional diversity first two axes), and litter species richness ("Litter spe. rich.") on litter decomposability (in term of carbon and nitrogen loss in black and red, respectively). The plot shows the results of the multi-predictor model fit after a step AIC selection procedure. For selected variables, confidence intervals (95%) were drawn around the standardized effect estimate with a full line for significant effects (p-value < 0.05) and a dashed line for non-significant effects. C. Effect of tree biomass ("log(biomass)"), tree closeness to the litter-trap ("1/dist"), leaf morphology (i.e., SLA) and other species litter biomass in the trap ("log(litter bio. from other species)") on species-specific litterfall amount collected in the trap. The plot shows the results of the multi-predictor linear mixed effect model, using litter species as a random factor, after a step AIC selection procedure. For selected variables, confidence intervals (95%) were drawn around the standardized effect estimate with a full line for significant effects (p-value < 0.05) and a dashed line for non-significant effects.

as these three aspects together explained up to 45% of the variance in species-specific litter biomass. Species-specific litter biomass increased with tree biomass (estimate ± SE = 0.43 ± 0.05, *p*-value < 0.001) and the proximity to the trees (0.14 ± 0.05, *p*-value = 0.002), but was not affected by leaf morphology (i.e., SLA was excluded during model selection). In addition, the amount of litter from other species in the litter trap reduced species-specific litter biomass (-0.10 ± 0.05, *p*-value = 0.038).

Discussion

We studied the effects of tree species richness on leaf litter decomposition considering the amount of litterfall and its composition, litter decomposability, and the role of the microbial community in the decomposition process. Our results confirmed our hypotheses by showing that tree species richness promoted litter decomposition (H1) and was mainly carried out by microbial decomposers (H2). Microbial decomposition increased with litter decomposability (H3), with the latter being driven by litter species richness and leaf functional trait identity and diversity (H4). In addition, we showed a positive effect of tree species richness on the amount of litterfall and litter species richness (H5), while litter species-specific biomass increased with increasing proximity to the trees as well as with tree biomass (H5). Notably, these findings highlight the complex interplay among tree litter diversity, leaf traits related to litter decomposability, and the spatial arrangement of trees in determining microbial decomposition processes in subtropical forest ecosystems.

Relationship between litter decomposition and soil microorganisms

We found that litter decomposition is mostly performed by soil microbial communities in this studied Chinese subtropical forest (H2). This observation is in contrast with previous measurements of woody litter decomposition, made in the same experiment, showing the significant role of soil meso- and macrofauna (Pietsch *et al.* 2019). However, it could be explained by the low abundance of soil meso- and macrofauna we observed during the

experiment (Suppl. I-S4) and in the respective region (Wang *et al.* 2007; Xu *et al.* 2006). Therefore, changes in litter decomposition were primarily explained by changes in microbial decomposition. Notably, soil fauna removal even increased the decomposition rate in some samples (Fig. 3.B), suggesting top-down control of microbial decomposers by meso- and macrofauna communities (Patoine *et al.* 2020). For instance, the presence of bacterial and fungal feeders could reduce microbial biomass (Crowther *et al.* 2013; Tobias-Hünefeldt *et al.* 2021), and/or the disturbance of fungal hyphae in the early stage of decomposition could reduce fungal activity (Ristok *et al.* 2019).

Tree diversity mass and diversity effects on decomposition

Our results showed a positive effect of the amount of litter on total decomposition but not microbial decomposition. Increasing the litter cover on the ground may favor other groups of decomposers such as meso- and macro-fauna decomposer by providing suitable environmental conditions (Gottschall *et al.* 2019; Joly *et al.* 2017; Korboulewsky *et al.* 2016). Therefore, more investigation is be needed to better understand the interplay between soil microbial community, meso-/macro-fauna community, and litter decomposition. In particular, we need to understand how soil microbial community and soil fauna detritivores interact (Joly *et al.* 2020; Ristok *et al.* 2019) as well as their environmental drivers (Cesarz *et al.* 2020; Phillips *et al.* 2021) to better understand their combined effects on soil carbon dynamics. Interestingly, we showed that both diversity effect pathways – (i) diversity effects on litter decomposition by increasing litterfall (i.e., mass effect), and (ii) diversity effects on litter decomposition through litter species richness and microbial decomposition – had similar effect size, highlighting the concurrence of tree diversity mass (i) and diversity (ii) effects on litter decomposition through litterfall (Sonkoly *et al.* 2019). Together, tree diversity effects on ecosystem functions are multicausal due to combined mass and diversity effects, both being equivalent driving forces of ecosystem function.

Nutrient content and litter diversity drive litter decomposability

Litter decomposability measurements allowed us to isolate the litter effect on decomposition from decomposer and environmental effects (García-Palacios *et al.* 2013; Lin *et al.* 2021; Zhang *et al.* 2018). Consistent with our expectations, we observed a positive effect of litter decomposability on microbial decomposition. Moreover, we estimated that up to 20% of litter decomposition is driven by variations in litter decomposability. These results support previous observations showing that litter is a driving force in litter decomposition (e.g., Fanin *et al.* 2012; Joly *et al.* 2017; Rosenfield *et al.* 2020; Zhang *et al.* 2018).

Together, litter nutrient content and litter diversity are driving litter effects on decomposition which was also observed in earlier studies (Fanin *et al.* 2012; Joly *et al.* 2017; Liu *et al.* 2020; Zhou *et al.* 2020). Two main mechanisms can explain these observations: increasing leaf nutrient contents provided to the decomposer community reduce stoichiometric limitations (Fanin *et al.* 2012; Rosenfield *et al.* 2020), and increasing substrate diversity leads to a higher niche partitioning of the decomposer community (Ebeling *et al.* 2014; Hooper *et al.* 2000). In addition, litter species richness could favor nutrient transfer between species-specific litter (Liu *et al.* 2020), for example, by transferring nutrients such as nitrogen from nitrogen-rich species to nitrogen-poor species through the fungal hyphae (Schimel and Hättenschwiler 2007). However, only a small fraction of the litter decomposability was explained by our models (i.e., 2% of C loss and 17% of N loss); thus other key aspects are still missing in our models to better predict decomposability drivers. These missing litter properties may include chemical components like polyphenols and tannins contents (Ristok *et al.* 2019) or structural components such as celluloses, hemicelluloses or lignin (Austin and Ballaré 2010; Fioretto *et al.* 2005; Hättenschwiler *et al.* 2005).

Tree diversity and functional drivers of litterfall spatial distribution

Litterfall is the significant carbon flux from the canopy to the forest floor; therefore, an increase in litterfall increases litter decomposition and soil carbon storage (Xu *et al.* 2018). We demonstrated that tree species richness increased the amount of litterfall, confirming previous findings (Huang *et al.* 2017). Moreover, species-specific litterfall increased with increasing tree biomass and proximity to the trees. These results provide some of the first empirical evidence of tree diversity effects on the spatial heterogeneity of litterfall composition at small spatial scales (i.e., a fraction of meters around the sampling point) and suggest a trait- and distance-based mediation of litterfall effects on decomposition in forests. Thus, our results emphasize the importance of considering small-scale processes and plot spatial heterogeneity to understand ecosystem functioning. Moreover, these small-scale processes and their drivers are potentially vital in understanding above- and belowground drivers of biodiversity, on top of plot-, field- and landscape-level drivers (Le Provost *et al.* 2021).

Spatially heterogeneous distribution of litter composition and leaf trait effects on decomposition may cause spatial heterogeneity in litter decomposition and thus nutrient cycling. The distance-based mediation of litterfall will promote litter decomposition at two levels: on the one hand, a small part of litter originating from more distant trees could enhance decomposition by increasing litter diversity (Gessner *et al.* 2010; Joly *et al.* 2017; Trogisch *et al.* 2016; Zhang *et al.* 2018). On the other hand, the most litter will accumulate close to the source tree, increasing litter decomposition due to increased litterfall and homefield advantages (Fanin *et al.* 2021; Vogel *et al.* 2013). The accumulation of species-specific litter close to each tree may favor species-specific decomposer communities (such as found in grassland soils; Bezemer *et al.* 2010). Therefore, spatial heterogeneity of litter at the plot level will sustain a high decomposer meta-community diversity (Hooper *et al.* 2000). A diverse meta-community is expected to promote ecosystem functioning (Grman *et al.* 2018; Häussler *et al.* 2020; Mori

et al. 2018) and stability (Mougi and Kondoh 2016; Wang *et al.* 2021). However, these novel insights need further theoretical and empirical investigation to map and predict litter composition, decomposition, and decomposer meta-community dynamics at the plot level. Therefore, spatial experiments and modeling at small-scales are essential to understand litter dispersal and the consequences for decomposition and mineralization processes that determine nutrient availability for plants.

Conclusion

The present study provides new mechanistic insights into the impact of tree diversity on litter decomposition in subtropical forests and its consequences for carbon and nitrogen cycling. We showed that tree diversity enhances litter decomposition by increasing the amount of litterfall and litter species richness, highlighting the multiple effects of tree diversity on litter decomposition. Moreover, we suggest that litter mass and diversity effects of tree diversity are two significant pathways to understand tree diversity effects on ecosystem functioning, and thus, both aspects of tree diversity should be better explored in the future. Moreover, we showed the key role of the spatial distribution of litterfall and thus the consequences for litter decomposition. Further research should consider the spatial distribution of trees to understand the spatial heterogeneity of tree products such as litterfall and root exudates, and thus the consequences for ecosystem functions like carbon and nitrogen cycling in forests.

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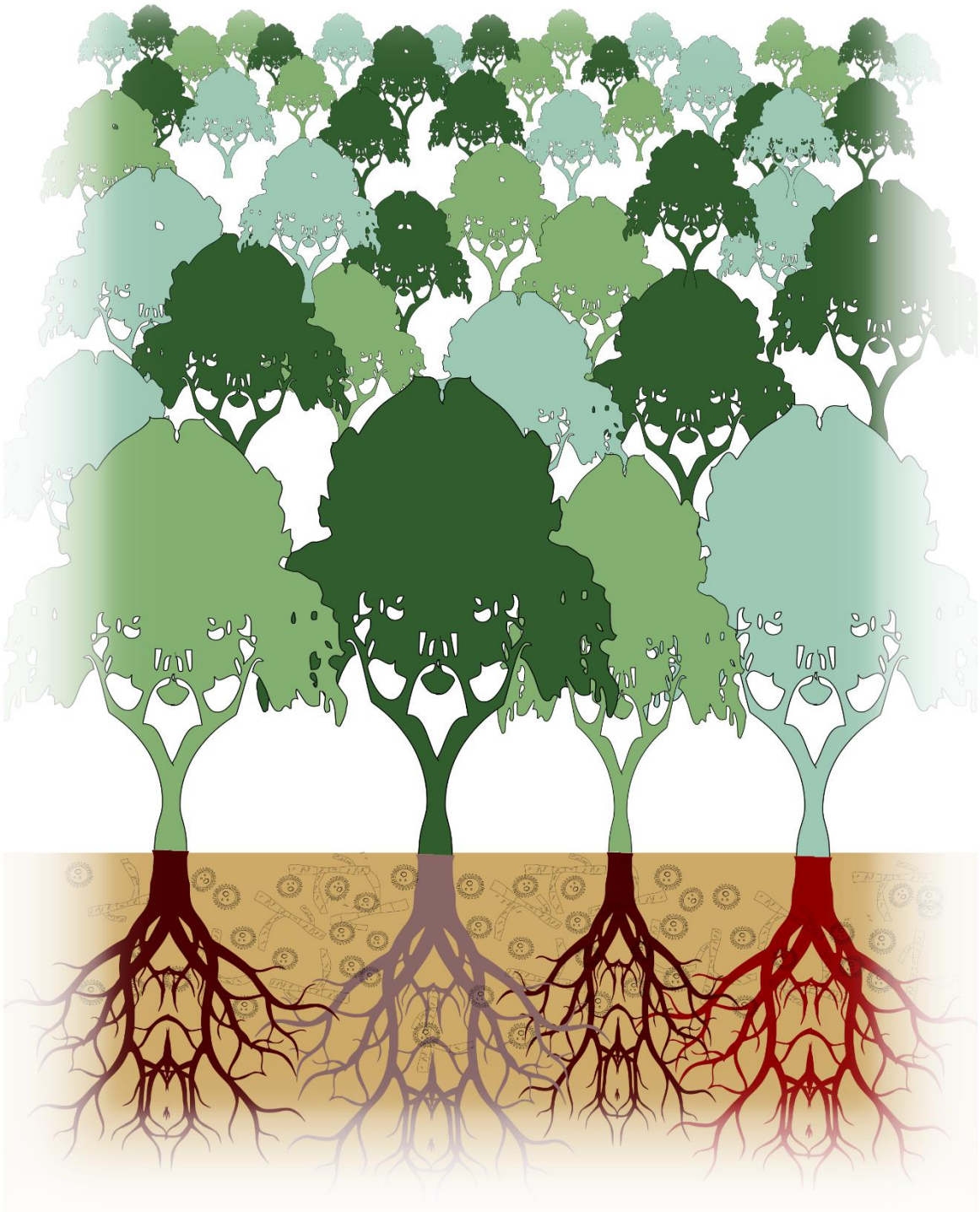
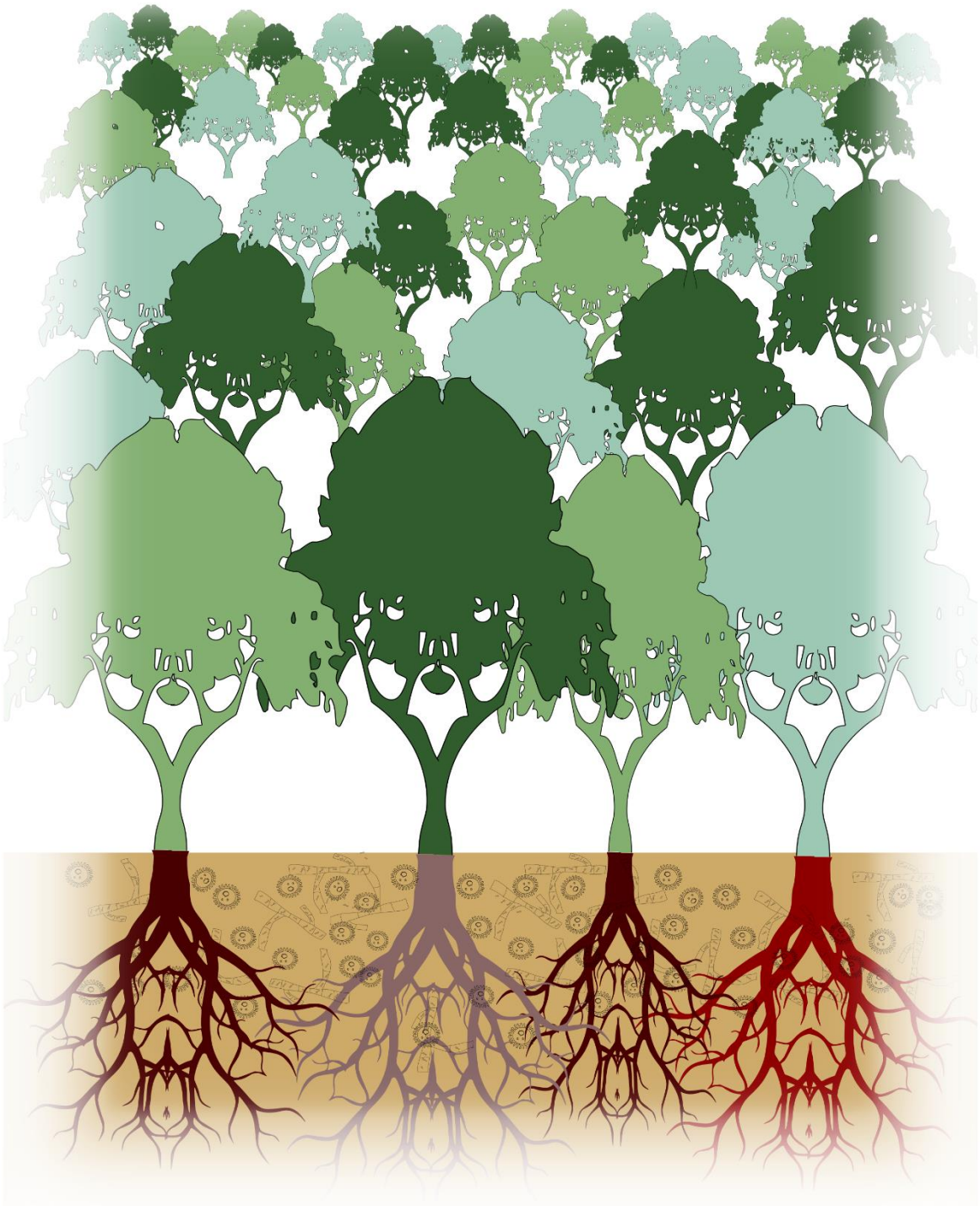
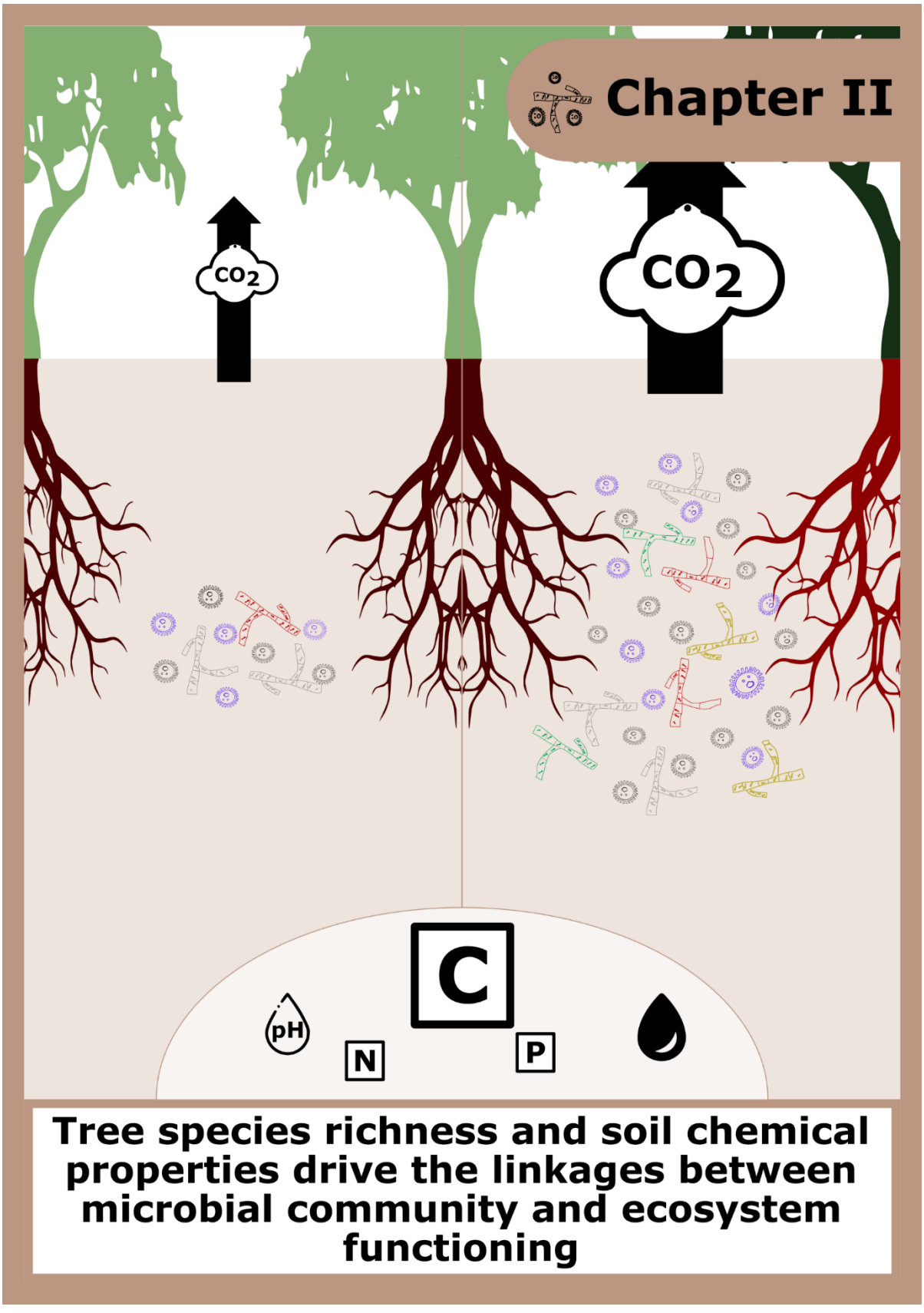


Transition I - II

In the first chapter, my colleagues and I highlighted the positive effects of tree species richness on leaf litter decomposition. We showed that tree diversity enhanced litter decomposition by promoting the litter susceptibility to decompose (i.e., litter decomposability). Tree litter decomposability was explained by the litter composition itself driven at plot level by tree biomass and tree plantation patterns. We demonstrateed the key role of soil microbial community to carry out litter decomposition; therefore, in my second chapter, I explored the consequences of tree species richness on the linkages between soil microbial community facets (i.e., biomass, taxonomic and functional profiles) and functions (i.e., soil heterotrophic respiration).





Tree species richness and soil chemical properties drive the linkages between microbial community and ecosystem functioning

Chapter II - Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning

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Abstract

Microbial respiration is critical for soil carbon balance and ecosystem functioning. Previous studies suggest that plant diversity influences soil microbial communities and their respiration. Yet, the linkages between tree diversity, microbial biomass, microbial diversity, and microbial functioning have rarely been explored. In this study, we measured two microbial functions (microbial physiological potential, and microbial respiration), together with microbial biomass, microbial taxonomic and functional profiles, and soil chemical properties in a tree diversity experiment in South China, to disentangle how tree diversity affects microbial respiration through the modifications of the microbial community. Our analyses show a significant positive effect of tree diversity on microbial biomass (+25% from monocultures to 24-species plots), bacterial diversity (+12%), and physiological potential (+12%). In addition, microbial biomass and physiological potential, but not microbial diversity, were identified as the key drivers of microbial respiration. Although soil chemical properties strongly modulated soil microbial community, tree diversity increased soil microbial respiration by increasing microbial biomass rather than changing microbial taxonomic or functional diversity. Overall, our findings suggest a prevalence of microbial biomass over diversity in controlling soil carbon dynamics.

Introduction

A thorough understanding of the soil carbon balance is essential to mitigate recent increases in atmospheric carbon concentrations and the resulting climate change (Davidson and Janssens 2006; IPCC 2013; Lal 2004; Trumbore 1997). Soil heterotrophic respiration is a critical process for the soil carbon balance and ecosystem functions such as climate regulation, nutrient cycling, and plant productivity (Schlesinger and Andrews 2000; Singh *et al.* 2010). Microorganisms are the main contributors to soil heterotrophic respiration, and microbial respiration is tightly linked to microbial community properties (Delgado-Baquerizo *et al.* 2016a; Liu *et al.* 2018; McGuire and Treseder 2010; Monson *et al.* 2006; Wieder *et al.* 2013). In turn, soil microbes and their functioning are determined by the biotic and abiotic environmental conditions (Delgado-Baquerizo *et al.* 2016b; Maaroufi and Long 2020; Gottschall *et al.* 2019).

Microbial properties are strongly affected by the vegetation type (Durán and Delgado-Baquerizo 2020) and its diversity (Pei et al. 2016). Consequently, plant community composition and diversity mediate microbial control over the soil carbon balance (Beugnon *et al.;* Pei *et al.* 2016; Xu *et al.* 2020; Lange *et al.* 2015; Schmidt *et al.* 2011). Plant diversity can increase litter and rhizosphere carbon inputs into the soil, thereby enhancing the quality and quantity of resources for the soil microbial community (Eisenhauer *et al.* 2017; Huang *et al.* 2017). This increase of rhizosphere carbon was shown to enhance soil carbon storage (Fornara and Tilman 2008; Lange *et al.* 2015) by increasing soil microbial biomass and activity (Lange *et al.* 2015; Chen *et al.* 2019). However, how plant diversity modulates the microbial community and how this affects soil carbon dynamics is not well understood. In addition, abiotic conditions, such as climate and soil chemical properties (soil carbon, nitrogen and phosphorus concentrations, pH, and humidity) also drive the assembly and functioning of soil microbial communities (Delgado-Baquerizo *et al.* 2016b; Maaroufi and Long 2020; Thoms *et al.* 2010; Rousk *et al.* 2010). For example, soil organic carbon content is generally correlated

with microbial biomass and activity (Lange *et al.* 2015; Miltner *et al.* 2012), while nitrogen and phosphorus-limited soils exhibit reduced microbial biomass and microbial community diversity (Delgado-Baquerizo *et al.* 2017; Fanin *et al.* 2012). Importantly, the effect of abiotic conditions on soil microbes greatly depends on which facet of the microbiota is assessed (Louca *et al.* 2016; Cao *et al.* 2020; Bao *et al.* 2020).

Soil microbial abundance, taxonomic and functional diversity can be assessed in terms of microbial biomass (i.e., through phospholipid fatty acid biomarkers or substrate-induced respiration measurements), taxonomic community composition and diversity (i.e., taxonomic profile through 16S rRNA gene and ITS amplicon sequencing or phospholipid fatty acid [PLFA] biomarker measurements), or potential functioning (i.e., functional profile through shotgun metagenomics or qPCR of functional genes), respectively (Fig. II.1). Realized functions can be assessed by community level physiological profiling (i.e., physiological potential through MicroResp ® measurements) or microbial respiration measurements (Fig. II.1). For example, the taxonomic diversity of soil microbes generally correlates with functional diversity (Galand *et al.* 2018), but these relationships may decouple as results of microbial functional redundancy and the different sensitivities of microbial facets to environmental changes (Louca *et al.* 2016; Kuang *et al.* 2016; Jurburg and Salles 2015). Alternatively, combining several measurements of the soil microbial community may provide a deeper understanding of soil microbial functioning; however, the different facets of soil microbial communities are rarely assessed together.

Taken together, soil microbial biomass, taxonomic and functional profiles are three key facets of the microbial community shown to be critical for microbial respiration (Chen *et al.* 2020; Liu *et al.* 2018; Trivedi *et al.* 2016), but they have not been studied together. Consequently, little is known about the potential correlations between these microbial facets, and their relationship to microbial functions (Chen *et al.* 2020; Liu *et al.* 2018; Trivedi *et al.* 2016; Hale

et al. 2019). For example, microbial respiration is tightly linked to the total microbial biomass and the microbial taxonomic profile (Delgado-Baquerizo *et al.* 2016a; Liu *et al.* 2018; McGuire and Treseder 2010; Monson *et al.* 2006; Wieder *et al.* 2013), but the microbial functional profile has been shown to be more relevant than the taxonomic profile to predict microbial realized functions (Chen *et al.* 2020; Hale *et al.* 2019; Chen and Sinsabaugh 2021). Moreover, microbial respiration is strongly limited by the microbial physiological ability to process the available substrates (Allison *et al.* 2010; Eisenhauer *et al.* 2010). Therefore, the microbial physiological potential to process substrate is expected to be a powerful predictor of microbial respiration and functions (Allison *et al.* 2010; Bonner *et al.* 2018). The physiological potential is believed to be dependent on the microbial biomass, as well as the taxonomic and functional profiles (Bárány *et al.* 2014; Bonner *et al.* 2018; Chodak *et al.* 2016; Lagomarsino *et al.* 2007). By predicting enzymatic activity (Trivedi *et al.* 2016; Chen and Sinsabaugh 2021), the microbial functional profile is hypothesized to be more closely related to the physiological potential of the soil microbial community than microbial biomass or taxonomic profile. However, no study has tested the individual or combined ability of these different microbial facets to predict the microbial physiological potential. A better understanding of the relationship between microbial facets and realized microbial function may facilitate the integration of soil microbial processes into soil carbon flux models (Crowther *et al.* 2019; Hall *et al.* 2018; Malik *et al.* 2020; Sainte-Marie *et al.* 2021).

To mechanistically understand tree diversity and soil chemical properties effects on microbial functions, we sampled a subtropical forest experiment in China (Bruelheide *et al.* 2014), and explored the contribution of different facets of the microbial community to microbial functions by bringing these microbial facets and functions together in a common framework. This biome has the highest average net ecosystem productivity among Asian forests (Yu *et al.* 2014) and is thus ideal for the study of carbon cycling and its determinants. In 2018, we collected 150

samples in 52 plots from a tree diversity experiment established in 2009. Across a tree species richness gradient, we measured soil microbial respiration, biomass, taxonomic and functional profiles, and physiological potential, along with soil chemical properties (carbon, nitrogen, and phosphorus concentrations, soil humidity, and pH).

We hypothesized that (H1) tree diversity would drive microbial community facets (microbial biomass, taxonomic and functional profile) and increase soil microbial functioning (microbial physiological potential and respiration); (H2) soil microbial biomass, taxonomic and functional profiles would be tightly correlated with each other and together drive microbial functions; (H3) microbial physiological potential would link microbial biomass, taxonomic and functional profiles to microbial respiration; and (H4) that environmental conditions (tree diversity and soil chemical properties) would co-determine soil respiration by modulating the microbial community facets.

Materials and methods

Only key procedures are provided here, further details about the materials and methods are available in Suppl. II - S1.

Study site, study design, and sampling

Our study site was located in south-east China in the Jiangxi province (29.08-29.11° N, 117.90-117.93° E). Sampling took place in BEF-China, a tree diversity experiment, including tree species mixture plots (1, 2, 4, 8, and 16 tree species per plot, Fig. II.1) (Bruelheide *et al.* 2014). To account for the role of tree diversity and soil quality, we collected 150 soil samples across different levels of tree diversity randomly distributed in the landscape (Fig. II.1, Suppl. II - S2). We sampled from mid-August to late-September 2018, before the litterfall season. To avoid spatio-temporal autocorrelation, the daily sample location was chosen randomly; and to control for the distance to the trees, each sample was extracted between a pair of trees. For each pair of trees, we extracted four soil cores (5 cm diameter; 10 cm depth), 5 cm and 20 cm away from

the center point between the tree pair (Fig. II.1). A composite sample was built from these four cores by homogenizing with a 2 mm sieve.

Soil quality analyses

Soil moisture was measured from 25 g of soil by drying at 40°C for two days. A subsample was used to measure soil pH in a 1:2.5 soil-water solution. In addition, to measure soil total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP), 200 g of soil were homogenized, ground with a ball mill, and sieved at 0.25 mm. Soil total organic carbon was measured by a TOC Analyzer (Liqui TOC II; Elementar Analysensysteme GmbH, Hanau, Germany). Soil total nitrogen was measured on an auto-analyzer (SEAL Analytical GmbH, Norderstedt, Germany) using the Kjeldahl method (Bradstreet 1954). Soil total phosphorus concentration was measured after wet digestion with H_2SO_4 and $HClO_4$ by a UV-VIS spectrophotometer (UV2700, SHIMADZU, Japan). Carbon to nitrogen and carbon to phosphorus ratios were calculated as TOC:TN and TOC:TP, respectively.

Soil microbial biomass

Microbial biomass was measured using phospholipid fatty acid (PLFA) analysis. PLFAs were extracted from 5 g of frozen soil following Frostegård *et al.* (Frostegård *et al.* 1991). Biomarkers were assigned to microbial functional groups according to Ruess *et al.* (Ruess and Chamberlain 2010, see Suppl. II-S3). Total microbial biomass was calculated as the sum of biomasses of all microbial groups. The ratio of bacteria to fungi (B:F) was calculated as the ratio of the sum of all bacterial biomass markers to the sum of all fungal biomass markers. Active microbial biomass was measured from 6 g of soil using the substrate-induced respiration method following Scheu *et al.* (Scheu 1992).

Soil microbial taxonomic profile

Microbial DNA was extracted from freeze-dried soil samples using PowerSoil DNA Isolation Kit (MO BIO Laboratories Inc., Carlsbad, CA, United States). DNA concentrations were

checked with a NanoDrop spectrophotometer (Thermo Fisher Scientific, Dreieich, Germany), and the extracts were adjusted to 10–15 ng/µl. The bacterial and fungal amplicon libraries were prepared following Schöps *et al.* (Schöps *et al.* 2018) and Nawaz *et al.* (Nawaz *et al.* 2019).

Bioinformatic analysis was performed using the Quantitative Insights into Microbial Ecology – QIIME 2 2020.2 (Bolyen *et al.* 2019). The forward and reverse reads were demultiplexed, primer sequences were trimmed, denoised, and grouped into Amplicon Sequence Variants (ASVs) using cut-adapt for chimera removal (Martin 2011, via q2-cutadapt) and DADA2 for non-target taxa removal (Callahan *et al.* 2016, via q2-dada2). ASV tables were imported into R with the phyloseq package (McMurdie and Holmes 2013). The fungal and bacterial ASVs were rarefied to 16,542 and 28,897 reads per sample, respectively. OTU richness, Shannon diversity, Pielou evenness, and Gini dominance indices were calculated using the microbiome package (Lahti *et al.* 2017). We inspected the correlations between these indices and focused our analyses on Shannon diversity index (Suppl. II - S4.A).

Soil microbial functional profile

DNA was extracted with the FastDNA Spin Kit for Soil (MP Biomedicals, USA) following the manufacturer's instructions. DNA concentrations were checked with a NanoDrop spectrophotometer (Thermo Fisher Scientific, Dreieich, USA), and DNA concentrations were quantified with the QuantiFluor dsDNA kit (Promega, USA) and a microplate reader (SpectraMax M5, Molecular Devices). DNA was diluted to 50 ng/µl with sterile water and stored at -20 °C. Microbial functional genes coding for enzymes involved in carbon catabolism processes, which are central to soil carbon cycling (Liang *et al.* 2017, see Suppl. II-S5), were quantified following Zheng *et al.* (Zheng *et al.* 2018) using a high-throughput quantitative-PCR-based chip (HT-qPCR; SmartChip Real-time PCR system, WaferGen Biosystems, Fremont, USA).

To compare abundance patterns across functional genes, we scaled each functional gene abundance between 0 and 1 across all samples using the z-transformation, and we summed the scaled abundance of functional genes related to carbon catabolism (i.e., "Cata", Suppl. II - S5). To quantify the evenness of the functional gene abundances, the functional gene Pielou evenness was calculated using the R 'diversity' from the 'vegan' package ("FG evenness").

Soil microbial physiological potential

Microbial physiological potential indices were calculated from substrate-induced respiration assays using the MicroResp.® method (Campbell *et al.* 2003). This method is used to assess the potential response of the living microbial community (i.e., active and dormant) to substrate addition. Fourteen substrates from three chemical classes (i.e., saccharides, amino-acid, and carboxylic acids) were selected to cover complementary biochemical pathways and to create a gradient of molecular weights (ranging from 89 to 221 $g.mol^{-1}$), and a gradient of carbon oxidation states (ranging from -2 to 3 e^-, Suppl. II - S6). CO_2 measurements were used to calculate substrate-induced respiration efficiency (i.e., "SIR efficiency") and substrate-induced respiration response range (i.e., "SIR range"). SIR efficiency was calculated as the Pielou evenness (from R 'diversity' function package vegan) of the CO_2 production of all substrates. SIR range was defined as the difference in CO_2 production between oxalic acid and alanine, the two substrates on the upper and lower extremes of carbon oxidation. We performed sensitivity analyses to explore the effects of substrate selection on these indices, which showed that substrate selection did not alter our results and conclusions (Suppl. II - S6).

Soil microbial respiration

Soil microbial respiration was measured on 6 g of fresh soil following Scheu *et al.* (Scheu 1992) without adding any substrate or water, thereby reflecting the actual respiration at the site.

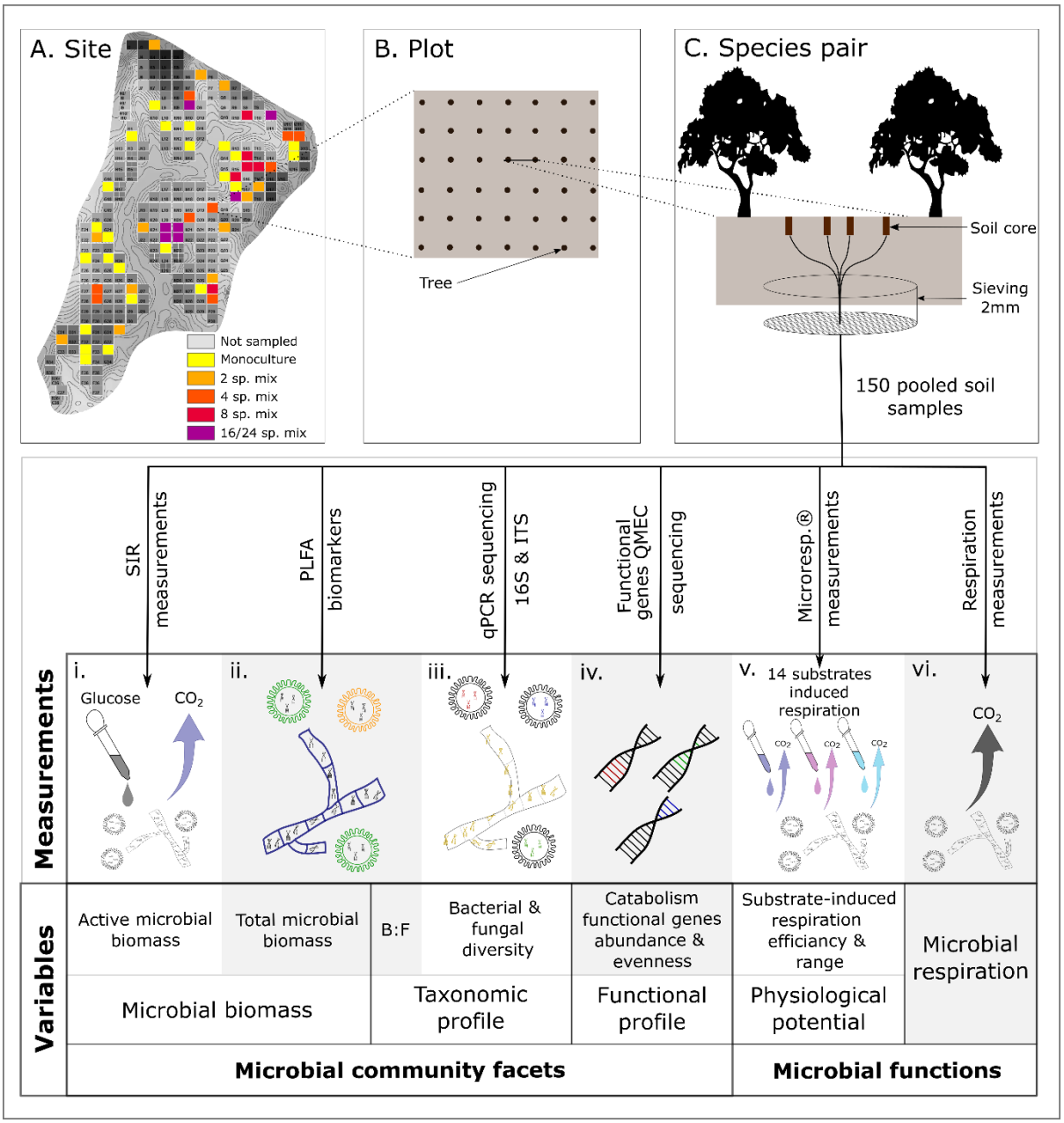


Fig. II.1: Sampling and measurement design. Sampling design: **A.** plot layout of the BEF China experimental platform (site A), **B.** plot tree planting grid pattern, **C.** soil core sampling design in tree species pairs, and treatment of samples. **Measurements:** (i.) quantification of active microbial biomass by substrate-induced respiration method (i.e., SIR, Scheu *et al.* 1992), (ii.) quantification of total microbial biomass and bacterial to fungal biomass ratio (B:F ratio) by measurement of soil microbial phospholipid fatty acids (PLFAs), (iii.) qualification of microbial profile by qPCR sequencing of soil 16S and ITS sequences, (iv.) quantification of functional genes related to carbon catabolism by quantitative microbial element cycling (QMEC, Zheng *et al.* 2018), (v.) quantification of carbon dioxide released during six hours after induction by a range of substrates using MicroResp.® method (Campbell *et al.* 2003), (vi.) quantification of soil microbial respiration by the O_2-microcompensation method.

Active microbial biomass (with substrate addition) and microbial respiration (without substrate addition) were measured on the same sample and machine. To test the robustness of our results, all following analyses were run with and without active microbial biomass.

Statistical analyses

All data handling and statistical analyses were performed using the R statistical software version 4.0.3, and all R scripts used for this study can be found in our GitHub repository (https://github.com/remybeugnon/Beugnon-Du_et_al_2021_Microbial_community_and_functions).

All metrics inferred from soil measurements are summarized in the Suppl. II - S4. In order to avoid any model-fit deviation due to scale differences between variables, all explanatory variables were centered and divided by two standard deviations for our analyses using the R rescale function from the arm package. For each analysis, we compared the drivers' effect sizes defined as the standardized estimate of a given variable in the model, where the response variable was centered and divided by two standard deviations.

Tree diversity effects on soil microbial community facets and functions

We used linear models and normal distribution assumptions to test the effects of tree species richness on soil microbial biomass (total and active microbial biomass), taxonomic profile (B:F ratio and Shannon diversity of bacterial and fungal communities), functional profile (catabolic functional gene abundance and evenness), physiological potential (SIR efficiency and range), and microbial respiration. Possible non-linear relations (i.e., quadratic, polynomial, and logarithmic relationships) were tested and are shown in Suppl. II - S7.A. The linear relationships were chosen when the difference in AIC with the best model (i.e., model with the lowest AIC) was lower than four. All previous linear models were tested in R using the lm function, and statistical hypotheses of the following linear models were tested in Suppl. II - S7.B using the model_check function from the performance package in R.

Relationships between soil microbial facets and microbial functions

We tested the correlations between the microbial community facets (soil microbial biomass, taxonomic and functional profiles) using Pearson correlation tests. We used linear multivariate models and normal distribution assumptions to test the effects of microbial biomass (total and active microbial biomass), taxonomic profile (B:F ratio and Shannon diversity of bacterial and fungal communities), and functional profile (catabolic functional gene abundance, and evenness) on soil microbial physiological potential (SIR efficiency and range), and soil microbial respiration. Explanatory variables (microbial biomasses, taxonomic and functional profile indices) were selected using forward and backward step selection based on AIC (i.e., R step function from stats package). A variance partitioning analysis was performed on the final set of variables to disentangle the effects of microbial biomass, taxonomic and functional profiles using the R varpart function from the vegan package. All previous linear multivariate models were tested in R using the lm function and statistical hypotheses of the following linear models were tested in Suppl. II - S8 using the model_check function from the performance package in R.

Cascading effects of the different soil microbial community facets on microbial physiological potential and microbial respiration

We tested the relationships between soil microbial biomass, taxonomic and functional profiles, physiological potential, and soil microbial respiration using a Structural Equation Modeling (SEM) framework. Microbial biomass, taxonomic and functional profiles were linked to each other by correlations, and their effects on physiological potential indices and soil microbial respiration were modeled with causal relations (directed paths). Our SEM was fitted using the R sem function from the lavaan package (Rosseel 2012). The model fit to our data and model quality were estimated using three complementary indices: (i) the root mean square error of approximation (RMSEA), (ii) the comparative fit index (CFI), and (iii) the standardized root

mean squared residuals (SRMR). Model fits were considered acceptable when RMSEA < 0.10, CFI > 0.9 and SRMR < 0.08. All statistical hypotheses and complete outputs can be found in Suppl. II - S9 and II - S10.

Effects of tree species richness and soil quality on relationships between the soil microbial community and their functions

To test the effects of tree species richness and soil chemical properties on the relationship between the soil microbial community facets and microbial respiration, we added the causal effects of soil chemical properties and tree species richness on the variables of our previous SEM model. To assess which group of response variables (i.e., soil microbial biomass, taxonomic profile, functional profile, physiological potential, and microbial respiration) was the most affected by soil chemical properties and tree species richness, the effects of soil chemical properties and tree species richness on each response group were summarized by summing all the absolute standardized effects of soil quality or tree species richness on the given response group. Additionally, to assess the importance of each soil chemical property and tree species richness, we summed the absolute standardized effects of each soil chemical property and tree species richness. All statistical hypotheses and complete outputs can be found in Suppl. II - S9 and II - S11.

Results

Tree diversity enhances the soil microbial biomass, diversity and functions

Our analyses showed that tree species richness enhanced soil microbial community properties and functions. Total microbial biomass and bacterial diversity increased significantly with tree species richness (total microbial biomass: estimate ± SE = 0.020 ± 0.007, *p*-value = 0.003; bacteria diversity: 0.017 ± 0.007, *p*-value = 0.011; Fig. II.2). Tree species richness significantly increased soil microbial community substrate-induced respiration efficiency (SIR efficiency: 0.022 ± 0.007, *p*-value = 0.001) and tended to increase microbial respiration (0.013 ±0.007, *p*-

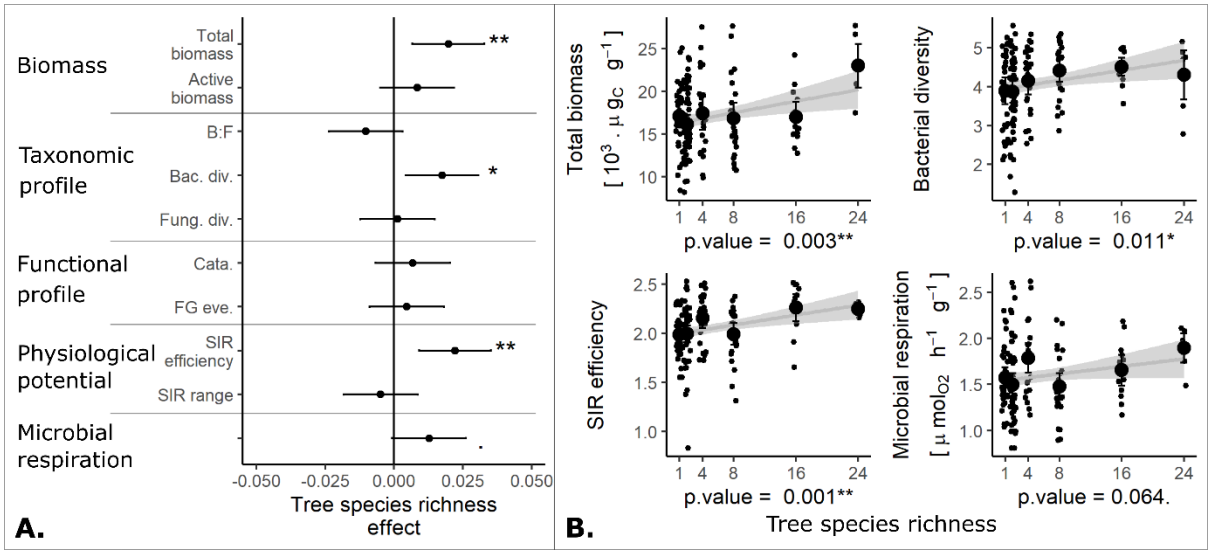


Fig. II.2: Tree species richness effects on soil microbial community facets and functions. A. Effect of tree species richness on microbial biomass (i.e., "Total biomass" and "Active biomass"), taxonomic profile (i.e., bacteria to fungi ratio: "B:F", bacteria Shannon diversity: "Bac. div.", and fungi Shannon diversity: "Fung. div."), functional profile (i.e., the abundance of catabolism functional genes: "Cata" and functional genes evenness: "FG eve."), physiological potential (i.e., substrate-induced respiration efficiency: "SIR efficiency", and substrate-induced respiration response range: "SIR range"), and microbial respiration. **B.** Relations between tree species richness and total microbial biomass, bacteria Shannon diversity (i.e., "Bacteria diversity"), SIR efficiency, and microbial respiration. The significance levels were standardized across the panels (".": *p*-value < 0.1, "*": *p*-value < 0.05, "**": *p*-value <0.01 and "***": *p*-value < 0.001: ***).

value = 0.064, Fig. II.2). Notably, the tree diversity effect on total biomass and basal respiration were mostly driven by high values in 24-species tree communities for microbial biomass and lower variability for respiration (Fig. II.2, Suppl. II - S7.A).

Soil microbial community facets are strongly correlated

We observed a positive correlation between total soil microbial biomass and active microbial biomass (Pearson correlation: cor = 0.45, *p*-value < 0.001), as well as a positive correlation between the functional profile variables (cor = 0.57, *p*-value < 0.001). In addition, the bacteria to fungi ratio (B:F) was negatively correlated to microbial biomass and the Shannon diversity of fungi (see Fig. II.3A, and Suppl. II - S8), while the Shannon diversity of fungi was positively correlated to active microbial biomass (cor = 0.20, *p*-value = 0.014; Fig. II.3A, Suppl. II - S8).

Soil microbial community facets drive soil microbial functions

We tested the effects of soil microbial biomass and taxonomic and functional profile on microbial community physiological potential and respiration using linear models and AIC-based model selection. Soil microbial community facets explained up to 50% of the variance in microbial respiration, but only 19% and 4% of the variance in SIR efficiency and range, respectively (Fig. II.3B). For all microbial functions, microbial biomass was the main driver by explaining up to 43% of microbial respiration, 14% of SIR efficiency, and 2% of substrate-induced respiration response range (Fig. II.3B, Suppl. II - S8). Together, microbial taxonomic and functional profile only explained a small part of the variance in microbial respiration (taxonomic profile: 6% and functional profile: <1%, Suppl. II - S8), substrate-induced respiration efficiency (taxonomic profile: 1% and functional profile: 2%, Suppl. II - S8), and substrate-induced respiration response range (functional profile: 1%, Suppl. II - S8). Active microbial biomass effects on microbial functions were consistent by increasing all functions (Fig. II.3B, Suppl. II - S8).

Soil microbial facets interact in mediating microbial respiration

We tested the combined effects of soil microbial biomass, taxonomic and functional profiles on microbial physiological potential and respiration using an SEM framework. The addition of microbial physiological potentials ("R^2 with") improved the variance explained of microbial respiration compared to the model considering microbial biomass and taxonomic and functional profile only (R^2_{with} = 57% in Fig. II.4 *vs.* $R^2_{without}$ = 50% in Fig. II.3B). There were combined positive effects of microbial biomass, fungal diversity, and physiological potential on microbial respiration (active microbial biomass effect: estimate ± SE = 0.590 ± 0.060, *p*-value < 0.001; fungi diversity: 0.128 ± 0.058, *p*-value = 0.027; SIR efficiency: 0.176 ± 0.062, *p*-value = 0.005; SIR range: 0.213 ± 0.057, *p*-value < 0.001, Fig. II.4, Suppl. II - S10). Soil microbial physiological potential, especially SIR efficiency, was strongly affected by soil

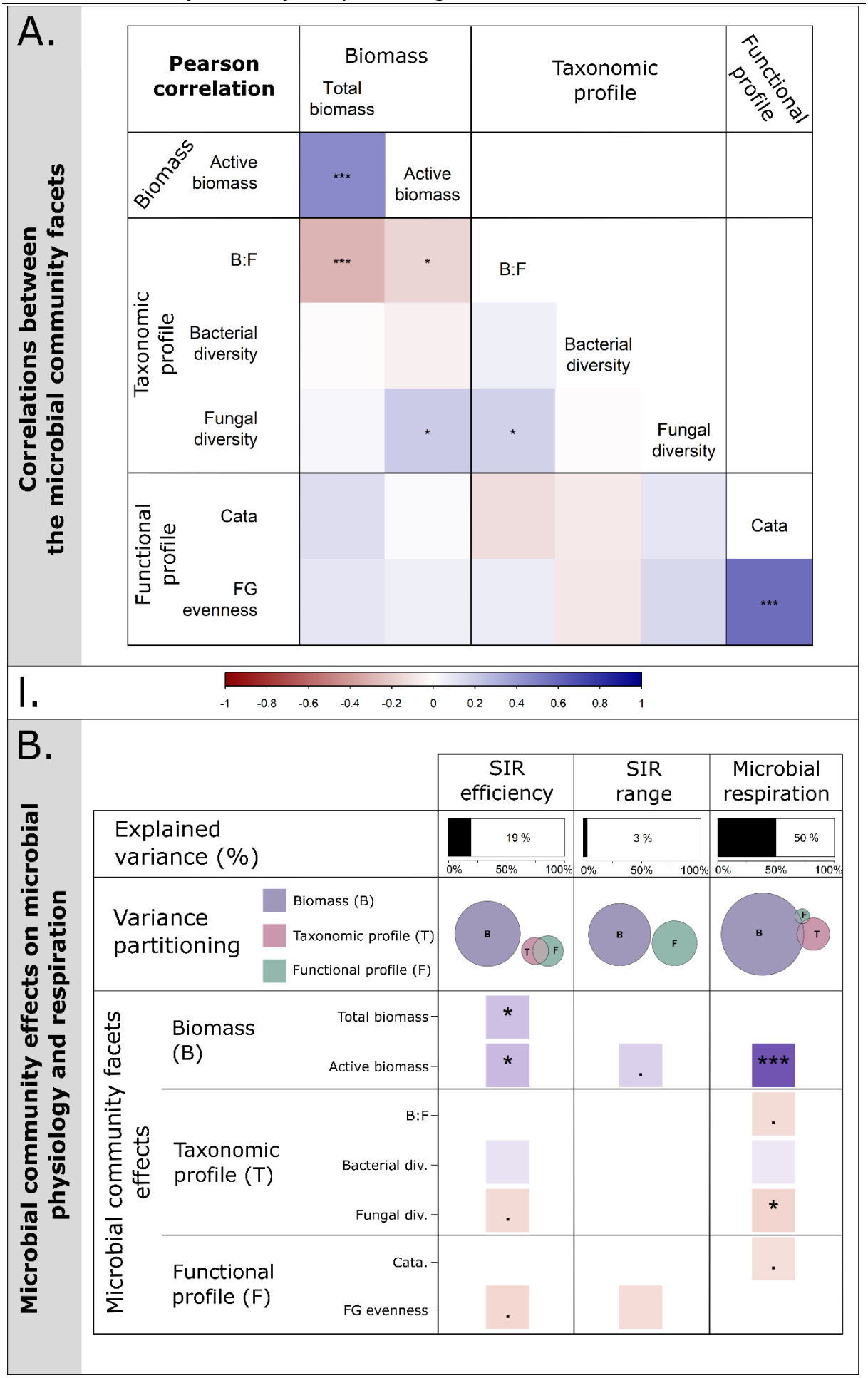

A.
Correlations between the microbial community facets
Pearson correlation
Biomass
Total biomass
Taxonomic profile
Functional profile
Biomass
Active biomass
***
Active biomass
Taxonomic profile
B:F
***
*
B:F
Bacterial diversity
Bacterial diversity
Fungal diversity
*
*
Fungal diversity
Functional profile
Cata
Cata
FG evenness
***
I.
-1 -0.8 -0.6 -0.4 -0.2 0 0.2 0.4 0.6 0.8 1
B.
Microbial community effects on microbial physiology and respiration
SIR efficiency
SIR range
Microbial respiration
Explained variance (%)
19 %
3 %
50 %
0% 50% 100%
Variance partitioning
Biomass (B)
Taxonomic profile (T)
Functional profile (F)
B
T
F
Microbial community facets effects
Biomass (B)
Total biomass
Active biomass
*
*
.
***
Taxonomic profile (T)
B:F
Bacterial div.
Fungal div.
.
.
*
Functional profile (F)
Cata.
FG evenness
.
.

Fig. II.3: Correlations between soil microbial community facets (A.), and effect of soil microbial community facets on microbial functions (B.). A. Correlation matrix of soil microbial community facets: microbial biomass (i.e., "total biomass" and "active biomass"), taxonomic profile (i.e., bacteria to fungi ratio: "B:F", bacteria Shannon diversity, and fungi Shannon diversity), functional profile (i.e., the abundance of catabolism functional genes: "Cata" and functional genes evenness: "FG evenness"). **B. Effects of microbial community facets on substrate-induced respiration efficiency and response range (i.e., "SIR efficiency" and "SIR range", respectively), and microbial respiration.** The explained variance (in %) of the model after model selection is displayed in the first row. The model variance partitioning between the different microbial facets (i.e., biomass, taxonomic and functional profile) is displayed in the second row. For each response variable (i.e., column), the circles are proportional to the part of explained variance and the intersects to the shared variance between two groups of variables. The last rows display the standardized effect sizes of the selected variables. The significance levels were standardized across the panels (".": *p*-value < 0.1, "*": *p*-value < 0.05, "**": *p*-value <0.01 and "***": *p*-value < 0.001: ***). **l. Color scale**. The colored bar represents both the correlation strength in A. and the effect size of the microbial community facets in B. both between -1 and 1.

microbial biomass and functional profile (total microbial biomass effect: 0.209 ± 0.083, *p*-value = 0.012; active microbial biomass: 0.258 ± 0.082, *p*-value = 0.002; and functional genes evenness: -0.179 ± 0.089, *p*-value = 0.045, Fig. II.4, Suppl. II - S10). The total effect size (i.e., sum of effects) of soil microbial biomass on microbial respiration was 0.672 (direct effect = 0.590, indirect effect = 0.082), while the total effect size of microbial taxonomic profile was 0.128 (only direct effect = 0.128), that of functional profile 0.031 (only indirect = 0.031), and that of physiological potential was 0.389 (only direct effects). Overall, we observed a strong effect of microbial biomass (i.e., a quantity-related measure, total effect: 0.672), but minor to neutral effects of microbial diversity (i.e., diversity measures, total effect of taxonomic and functional diversity: 0.159)

Soil quality shapes the relationship between the soil microbial community and microbial functions

The addition of tree diversity and soil chemical properties to our model increased the explained variance of microbial respiration (R^2_{with} = 68% in Fig. II.5C *vs*. $R^2_{without}$ = 57% in Fig. II.4) and explained part of soil microbial biomass variance ($R^2_{microbial\ biomass}$ = 46% Fig. II.5C, Suppl. II - S11). Soil chemical properties (i.e., soil carbon, nitrogen, and phosphorus contents, soil pH,

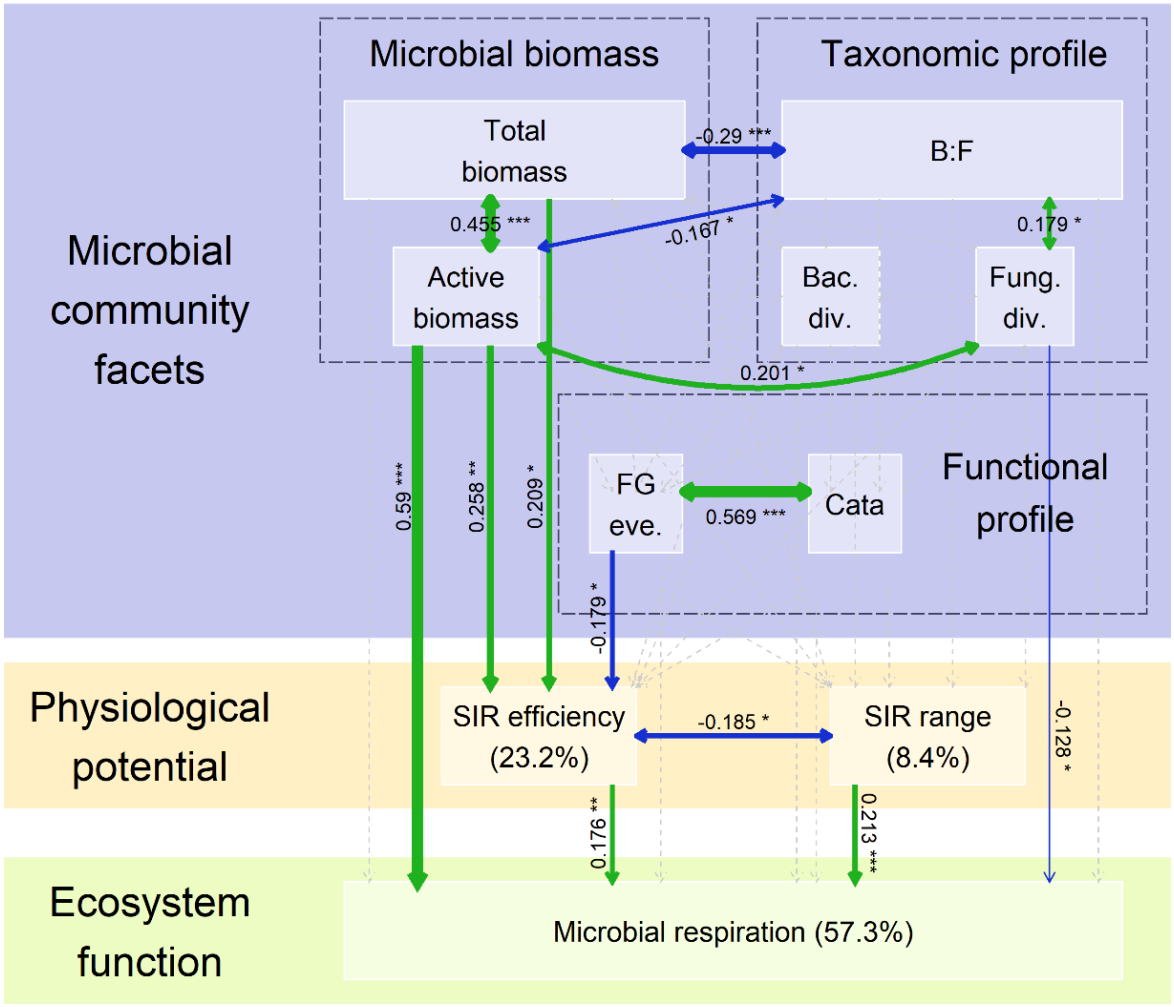


Fig. II.4. Structural equation model based on the effects of microbial community facets (i.e., microbial biomass: "Total biomass" and active microbial biomass, "Active biomass"; and, taxonomic profile: bacteria to fungi ratio, "B:F"; bacterial and fungal Shannon diversity, "Bac. div." and "Fung. div." respectively), genetic profile (i.e., carbon catabolism functional genes abundance: "Cata", and evenness: "FG eve."), and physiological potential (i.e., substrate-induced respiration efficiency and response range: "SIR efficiency" and "SIR range") on ecosystem function (i.e., "Microbial respiration"). Correlations between nodes are drawn with double-headed arrows, while causal relations were drawn with one-way arrows and are based on hypotheses explained in the main text; arrow widths are sized by the absolute effect size. Green and blue arrows stand for positive and negative relations between nodes, respectively, and significant relations between nodes are drawn with full lines, while non-significant relations are displayed with dashed lines, and the significance levels were standardized ("."): p-value < 0.1., "*": p-value < 0.05, "**": p-value <0.01, and "***": p-value < 0.001). For each endogenous variable (i.e., response variable), the part of variance explained (R^2, in %) was added after the variable name.

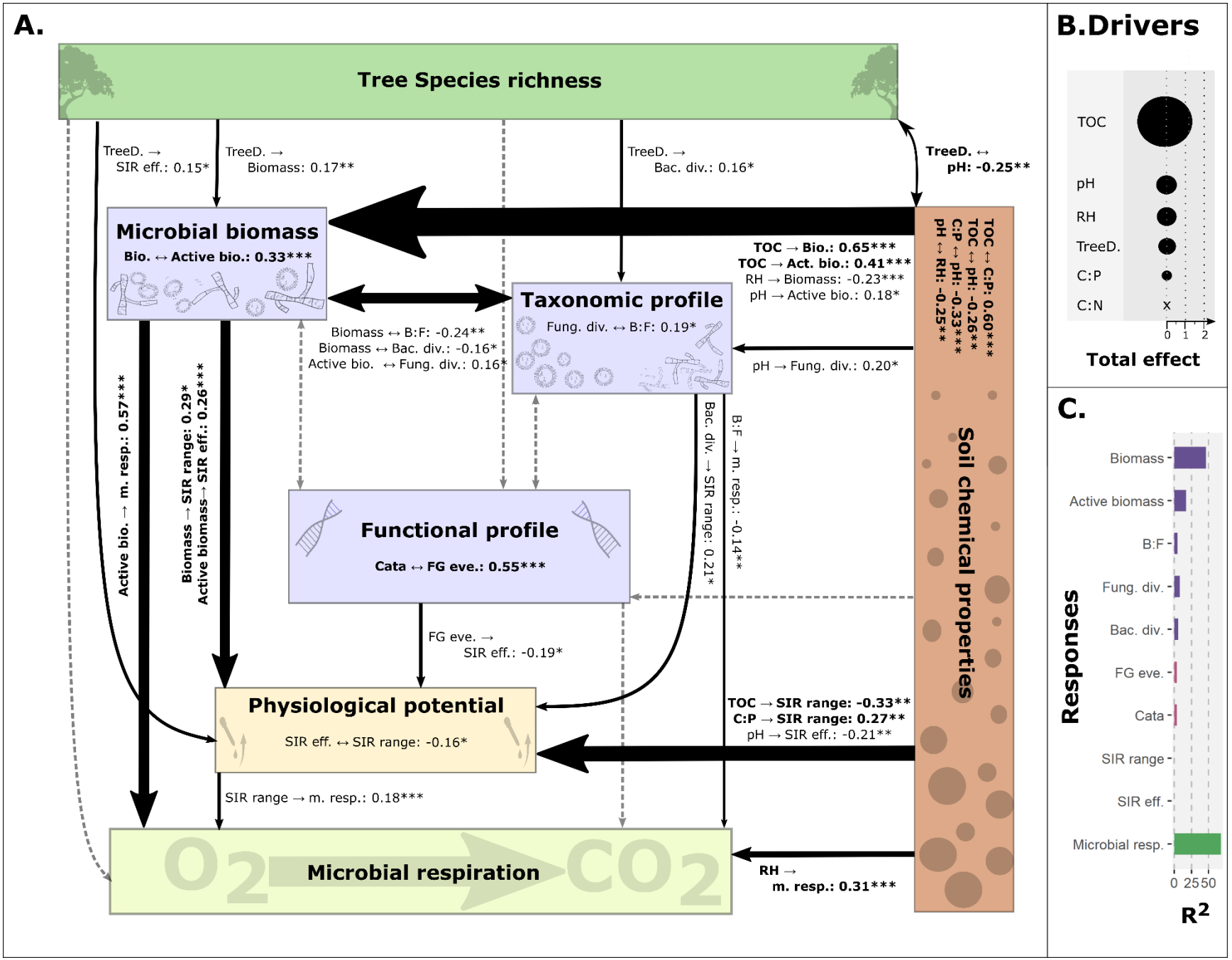
and humidity) affected all soil microbial properties and their interrelationships (microbial biomass, taxonomic and functional profiles, physiological potential, and microbial respiration) with the strongest effect on soil microbial biomass (total effect on microbial biomass: 1.474, total effect on taxonomic profile: 0.199, no effect on functional profile, total effect on physiological potential: 0.799, total effect on microbial respiration: 0.312; Fig. II.5C, Suppl. II - S11). TOC was the most important aspect of soil quality with a total effect of 1.383, while the total effect of all other soil properties together reached 1.400 (Fig. II.5B). Moreover, TOC and pH affected most of the microbial facets, while the other soil chemical properties affected only one or a few of the microbial facets (Fig. II.5A). For example, soil humidity increased microbial respiration but decreased total microbial biomass (0.312 ± 0.054, *p*-value< 0.001 and -0.234, *p*-value < 0.001, respectively); while, carbon to phosphorus ratio only increased SIR range (0.269 ± 0.098, *p*-value = 0.006, Fig. II.5, Suppl. II - S11).

Tree diversity effects on soil microbial respiration are mediated by the microbial community facets

In addition, tree species richness affected soil microbial biomass and taxonomic profile, and the community physiological potential with a positive effect on total microbial biomass (0.173 ± 0.063, *p*-value = 0.006), bacterial diversity (0.164 ± 0.082, *p*-value = 0.045), and SIR efficiency (0.152 ± 0.073, *p*-value = 0.038, Fig. II.5A, Suppl. II - S11). By increasing microbial biomass and physiological potential, tree species richness indirectly increased microbial respiration (indirect effect: 0.014).

Discussion

Our results show a positive effect of tree diversity on the measured soil microbial community facets and functions (H1). By integrating soil microbial biomass, taxonomic and functional profiles into a single framework, our analyses show how these different facets of the soil microbial community are linked to each other (H2) and mediate the effect of tree diversity and


A.
Tree Species richness
TreeD. → SIR eff.: 0.15*
TreeD. → Biomass: 0.17**
TreeD. → Bac. div.: 0.16*
TreeD. ↔ pH: -0.25**
Microbial biomass
Bio. ↔ Active bio.: 0.33***
Taxonomic profile
Fung. div. ↔ B:F: 0.19*
TOC → Bio.: 0.65***
TOC → Act. bio.: 0.41***
RH → Biomass: -0.23***
pH → Active bio.: 0.18*
Biomass ↔ B:F: -0.24**
Biomass ↔ Bac. div.: -0.16*
Active bio. ↔ Fung. div.: 0.16*
pH → Fung. div.: 0.20*
TOC ↔ C:P: 0.60***
TOC ↔ pH: -0.26**
C:P ↔ pH: -0.33***
pH ↔ RH: -0.25**
Soil chemical properties
Active bio. → m. resp.: 0.57***
Biomass → SIR range: 0.29*
Active biomass → SIR eff.: 0.26***
Bac. div. → SIR range: 0.21*
B:F → m. resp.: -0.14**
Functional profile
Cata ↔ FG eve.: 0.55***
FG eve. → SIR eff.: -0.19*
Physiological potential
SIR eff. ↔ SIR range: -0.16*
TOC → SIR range: -0.33**
C:P → SIR range: 0.27**
pH → SIR eff.: -0.21**
SIR range → m. resp.: 0.18***
O2
Microbial respiration
CO2
RH → m. resp.: 0.31***
B.Drivers
TOC
pH
RH
TreeD.
C:P
C:N
x
0 1 2
Total effect
C.
Biomass
Active biomass
B:F
Fung. div.
Bac. div.
FG eve.
Cata
SIR range
SIR eff.
Microbial resp.
Responses
0 25 50
R2

.

Fig. II.5. Structural equation model based on the effects of soil chemical properties and tree species richness on microbial community –ecosystem functioning linkages. A Structural equation model summary. Each node represents a group of variables, and each arrow summarizes all the significant effects between all the variables of two nodes. Correlations between nodes are drawn with double-headed arrows, while causal relations are drawn with simple arrows; arrow widths are sized by the sum of the absolute standardized effect size of significant relations between all variables of the two nodes. When no significant relations were found between any variables of two nodes, the arrows are drawn with dashed lines. Significant relationships between variables were specified in the figure (".": p-value < 0.1., "*": p-value < 0.05, "**": p-value <0.01, and "***": p-value < 0.001). **B** Total effects of soil chemical properties and tree diversity ("Drivers") on soil microbial facets and functions. The total effect size of the exogenous variables (i.e., tree species richness: "TreeD", total organic carbon: "TOC", soil pH: "pH", soil relative humidity: "RH", soil carbon to phosphorus ratio: "C:P", and soil carbon to nitrogen ratio: "C:N") on the microbial community facets (i.e., total microbial biomass: "Bio", active microbial biomass: "Active bio.", bacterial and fungal Shannon diversity: "Bac. div" and "Fung. div.", bacteria to fungi ratio: "B:F", catabolism functional genes abundance and evenness: "Cata" and "FG eve.") et functions (substrate-induced respiration efficiency and response range: "SIR eff." and "SIR range", and microbial respiration: "m. resp.") are shown by circles sized according to the sum of absolute standardized effect sizes. **C** Model explanatory power. R^2 values of response variables (y-axis) for the model are displayed on the x-axis. See Supplementary II - S11 for more details.

soil chemical properties on microbial respiration (H3 - H4). Our results highlight that soil microbial biomass and physiological potential are the main drivers of microbial respiration (H3). In turn, the microbial physiological potential is strongly affected by microbial biomass and functional gene evenness. Our results suggest that the relationship between soil microbial facets and realized functions are dependent on soil biochemistry. Taken together, our study presents a comprehensive framework of tree diversity effects on microbial community facets and functioning, providing novel insights into the most crucial variables for modeling changes in microbe-driven ecosystem functioning. For example, focusing our future investigations on tree species richness, soil carbon content, pH, and moisture will allow us to better predict soil microbial biomass as well as functioning.

Soil microbial community facets drives soil microbial functions

Our analyses showed strong positive effects of active microbial biomass and the functional gene evenness on microbial physiological potential and microbial respiration, as expected based on previous studies (Lange *et al.* 2015; Trivedi *et al.* 2016; Wieder *et al.* 2013).

Increasing microbial biomass *per se* increases the number of cells processing substrates and breathing, which results in enhanced total microbial respiration. We found that fungal diversity reduced microbial respiration, which contrasts with previous findings which suggest a strong positive effect of fungal diversity on microbial respiration (Liu *et al.* 2018). Potentially, high fungal diversity coincided with or was related to low availability of easily degradable substrates and dominance of more recalcitrant carbon sources (Paterson *et al.* 2008), but see (Kramer *et al.* 2016).

In addition, we found that microbial physiology had a positive effect on microbial respiration by mediating functional gene evenness and part of microbial biomass effects on microbial respiration. Substrate-induced respiration methods like MicroResp.® introduce to the microbial community a range of substrates which target different oxidation pathways (Liang *et al*. 2017, Parterson *et al*. 2008) in order to quantify the community's physiological profile (Campbell *et al.* 2003). This method provides an overview of the microbial community potential under resource-rich conditions, and may also not adequately reflect microbial respiration *in situ*, where different oxidation pathways may not be evenly activated. However, in longer physiological processes, such as litter decomposition, where litter chemical composition is changing with time (Berg 2000; Moretto *et al.* 2001), several oxidation pathways are successively activated. Therefore, information on the community's potential to evenly cover a large range of physiological pathways (i.e., provided by MicroResp® measurements) may become critical.

By bringing together the different facets of the microbial community, we showed the complementary effects of these microbial community facets on microbial realized functions, the significance of microbial biomass to explain microbial respiration, and the mediation of microbial community facets effects on microbial respiration by the microbial physiological potential. This new insight on the links between microbial community facets and realized

functions would now need to be considered in future efforts to model microbial processes in soils (Sainte-Marie *et al.* 2021; Crowther *et al.* 2019; Kyker-Snowman *et al.* 2020).

Soil chemical properties drive the soil microbial community - microbial functions relationships

We found that soil chemical properties were the strongest drivers of linkages between the soil microbial community and soil functioning by affecting all facets of the microbial community and microbial respiration. Soil organic carbon content had strong positive effects on both microbial biomass and microbial physiological potential, while soil pH affected microbial biomass, taxonomic profile and physiological potential; however, the soil chemical properties (i.e., soil carbon to phosphorus ratio, and soil humidity) had less pronounced effects on fewer facets. For example, soil humidity decreased microbial biomass but increased microbial respiration, while soil C:P ratio only increased substrate-induced respiration response range. These inconsistent effects of soil chemistry on the different facets of the microbial community were expected from previous studies showing different soil variables and selection mechanisms for microbial taxonomic and functional profiles (Chen *et al.* 2020; e.g., Liu *et al.* 2018; Trivedi *et al.* 2016). However, our analyses highlighted soil carbon content as the main driver of the microbial community, affecting microbial biomass, taxonomic profiles, and physiological potential. Together, these effects enhanced microbial respiration. The major significance of soil carbon in structuring soil microbial communities is well known and supported by many previous local- (e.g., Eisenhauer *et al.* 2010; Chodak *et al.* 2016) to global-scale studies (Crowther *et al.* 2019; e.g., Delgado-Baquerizo *et al.* 2016b).

Consequently, one might expect a negative feedback effect of soil microbial respiration on organic carbon content, due to the increase of soil carbon mineralization by the microbial community. However, high microbial respiration and microbial biomass are two strong indicators of microbial transformation of plant residues and soil organic carbon to microbial

necromass (Buckeridge *et al.* 2020; Lange *et al.* 2015; Miltner *et al.* 2012; Schmidt *et al.* 2011; Trumbore 1997). This transformation of easily decomposable plant material to microbial necromass may increase soil carbon residency time, and therefore soil carbon storage (Sainte-Marie *et al.* 2021). Our results provide novel insights on a positive tree diversity-induced feedback of soil carbon content on soil carbon storage by increasing soil microbial biomass and functioning. However, further empirical and theoretical studies are needed to mechanically test the effects of soil carbon chemical pools on soil bioprocesses as well as soil carbon sequestration. This requires a better description and measurement of the soil carbon chemical pools (Sainte-Marie *et al.* 2021; Buckeridge *et al.* 2020). Furthermore, mechanistic and dynamic models need to be built and calibrated on temporal data to predict soil carbon dynamics (Sainte-Marie *et al.* 2021; Kyker-Snowman *et al.* 2020), and to consider the context-dependency of the microbial processes to biotic and abiotic environmental conditions (Cesarz *et al.* 2020; Tedersoo *et al.* 2016; Chodak *et al.* 2016; Kyker-Snowman *et al.* 2020).

Tree diversity effects on soil respiration mediated via changes in the soil microbial community

We observed a positive effect of tree species richness on the different facets of the microbial community and its functions. Our results demonstrate that tree species richness drives soil microbial functions, such as microbial respiration, by modifying the soil microbial community: microbial biomass and diversity. Such positive effects of tree diversity on microbial biomass were shown in the past across biomes. They were explained by an increase of tree productivity and thus of tree carbon release into the soil (e.g., root exudation, Eisenhauer *et al.* 2017; litter production, Huang *et al.* 2017; Huang *et al.* 2018). Additionally, tree diversity is expected to increase substrate diversity available to soil microorganisms (Chapman *et al.* 2013; Eisenhauer *et al.* 2013; Eisenhauer *et al.* 2017; Thoms *et al.* 2010). Such an increase in substrate diversity could explain the enhancement of substrate-induced respiration efficiency observed by

selecting microbial communities adapted to diverse substrate inputs (Brandt *et al.* 2004). These results suggest a double effect of tree diversity on the microbial community. On the one hand, tree diversity maintains higher microbial biomass by increasing tree productivity and carbon inputs into the soil. On the other hand, tree diversity increases the heterogeneity of the organic inputs (Hooper *et al.* 2000), and maintains a higher level of functioning by increasing microbial physiological potential. In this study, the positive effect of tree diversity on microbial respiration was mostly driven by enhanced microbial biomass.

Conclusion

In conclusion, we showed that tree diversity and soil carbon content drive microbial respiration through their effects on the different soil microbial community facets. We identified microbial biomass as the main predictor of microbial respiration, by incorporating the different soil microbial community facets and their drivers in a common framework. These results suggest a positive tree diversity-induced feedback of soil carbon content on soil carbon storage by increasing soil microbial biomass and respiration. These novel insights should be considered in efforts to model soil carbon dynamics and feedbacks to atmospheric carbon concentrations (Crowther *et al.* 2019) as well as the ecosystem consequences of reforestation approaches (Domke *et al.* 2020; Tong *et al.* 2020; Veldkamp *et al.* 2020; Lewis *et al.* 2019).

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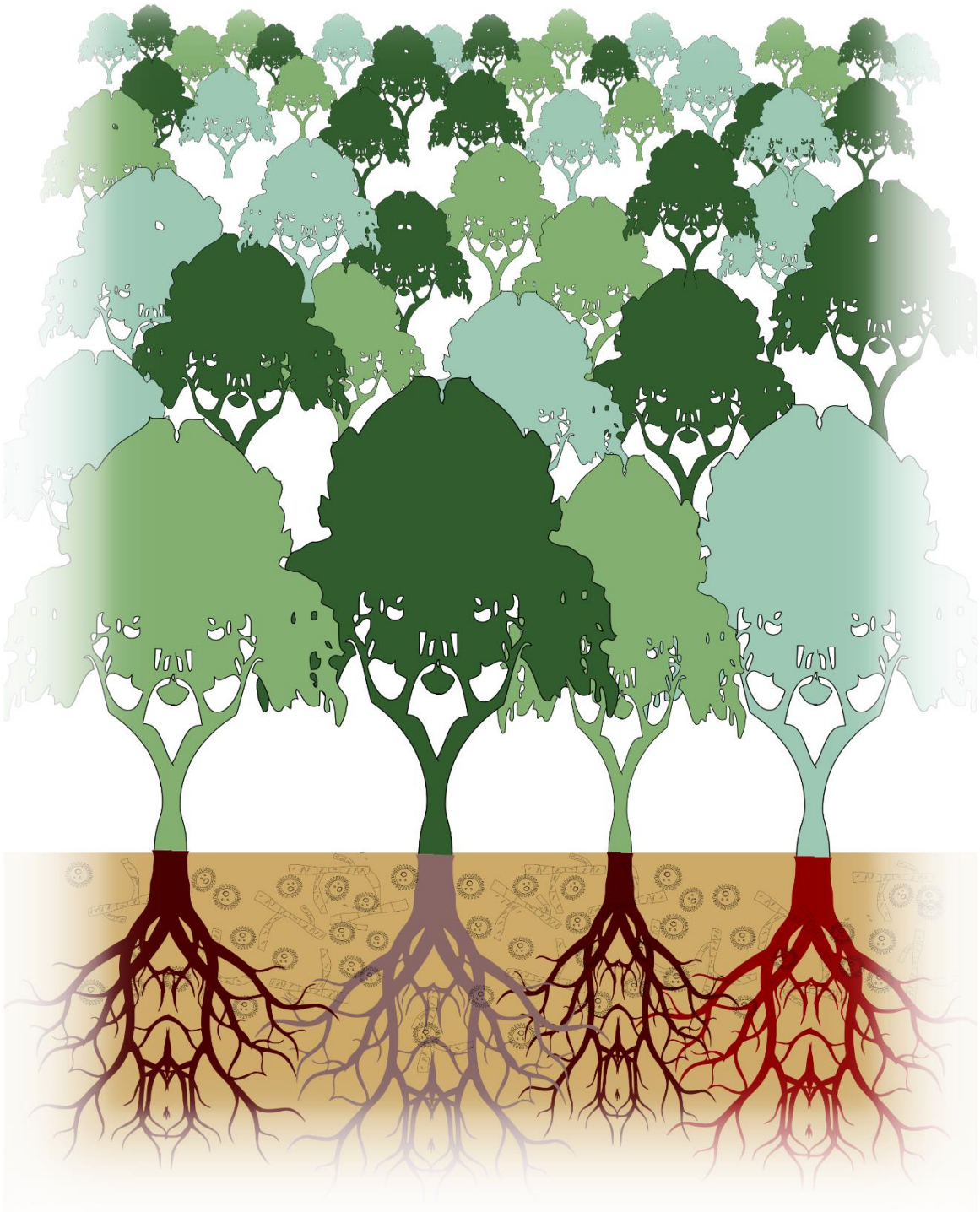
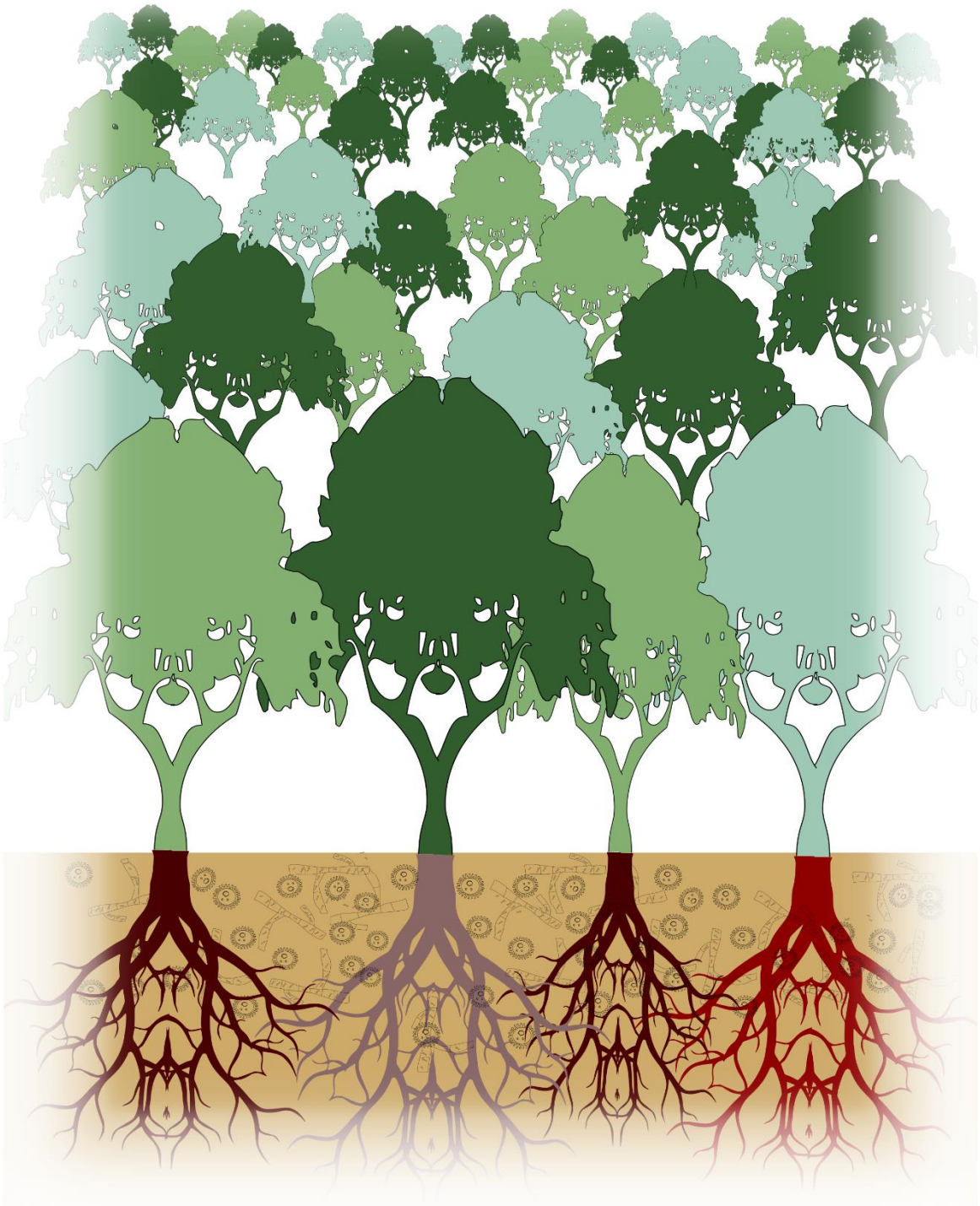
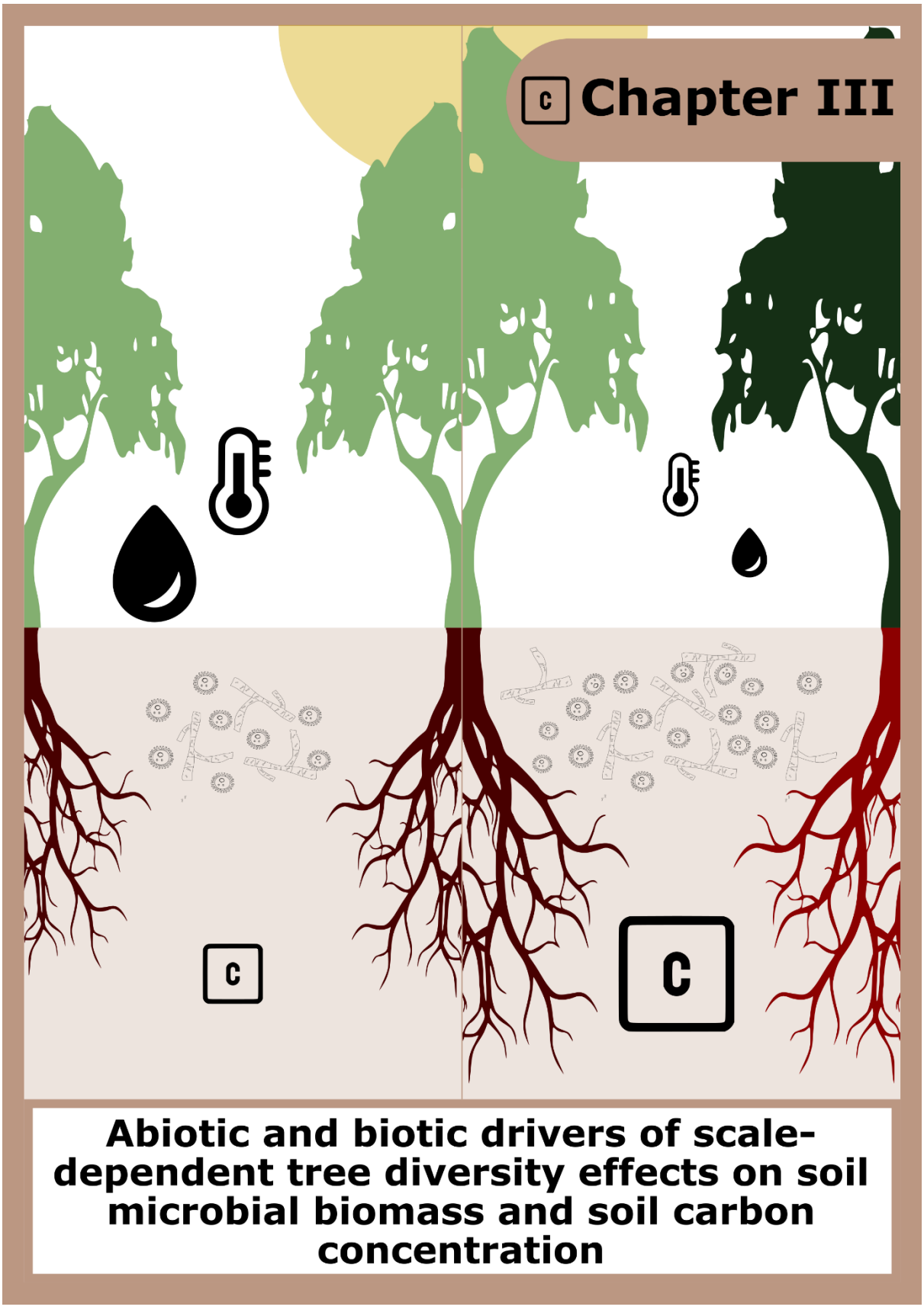


Transition II - III

In the second chapter, my colleagues and I showed that tree diversity increase soil microbial respiration by increasing microbial biomass rather than changing microbial taxonomic or functional diversity. Overall, these findings suggest a prevalence of microbial biomass over diversity in controlling soil carbon dynamics. Therefore, in my third chapter, I explored the abiotic and biotic environmental mediation of tree diversity effects on soil microbial biomass and soil carbon concentrations. In the third chapter, we adopted a whole-ecosystem approach of tree diversity effects on forests carbon cycling by considering several forest carbon pools such as tree biomass, litterfall, and soil carbon.





Abiotic and biotic drivers of scale-dependent tree diversity effects on soil microbial biomass and soil carbon concentration

Chapter III - Abiotic and biotic drivers of scale-dependent tree trait effects on soil microbial biomass and soil carbon concentration

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Abstract

Forest ecosystems have been highlighted for their carbon fixation potential in both above- and belowground compartments, especially in species-rich forests. Soil microbial communities are strongly linked to soil carbon sequestration, and it is suggested that this link is mediated by the tree community, likely due to modifications of micro-environmental conditions (i.e. micro-climate, soil quality, and biotic conditions). We further expect that these relationships will depend on the scale considered, with local (i.e., at the level of a tree species pair, TSP) and neighborhood (i.e., the surrounding trees of a TSP) scale processes influencing soil conditions.

We studied soil carbon concentration and the microbial community composition of 180 TSPs along a gradient of tree species richness ranging from 1 to 16 per plot in the Chinese subtropical forest experiment (BEF-China). Tree productivity and different tree functional traits were measured at both the TSP level and neighborhood level. We tested the effects of tree productivity, functional trait identity and dissimilarity on soil carbon concentrations, and if these links were mediated by the soil microbial biomass and micro-environmental conditions.

Tree productivity, together with tree functional traits, modulated micro-environmental conditions with substantial consequences for soil microbial biomass. Especially, soil microbial biomass was modified by root morphological traits at both TSP and neighborhood levels. However, the effects of the root morphological traits on microbial biomass were highly scale-dependent, with a positive effect of root morphological traits at the TSP level but a negative effect at the neighborhood level. Moreover, our analyses showed a strong positive correlation between soil microbial biomass and soil carbon concentration. We found that soil carbon concentrations increased with historical carbon concentrations, themselves strongly affected by the plot topography. However, soil carbon concentrations decreased over time. Besides, soil carbon concentration increased with tree productivity and root morphological traits at the neighborhood level.

Altogether, these results imply that mechanistic studies on the drivers of microbial biomass and soil carbon sequestration need to consider the different spatial scales at which the underlying mechanisms act. Moreover, quantification of the different soil carbon pools is critical to the understanding of microbial community–soil carbon stock relationships.

Introduction

The rapid increase in atmospheric carbon is one of the main causes of climate change and becomes a major threat to life on Earth (IPCC 2013). Atmospheric carbon concentrations can be reduced by both reducing carbon emissions and increasing carbon fixation. Forest ecosystems have been identified to be capable of mitigating increases in atmospheric carbon dioxide by capturing and fixing it aboveground and storing it both above and below the ground (Bastin *et al.* 2019; Lewis *et al.* 2019). Belowground carbon storage provides a high potential for atmospheric carbon control due to the long residence time of carbon in soil (Trumbore 1993). In forests, soil carbon stocks are driven by the balance between soil carbon influx (e.g., due to photosynthesis) and efflux (e.g., due to soil respiration and erosion), but our understanding of their balance and the driving factors is still limited.

Forest diversity enhances forest productivity: tree biomass and litterfall quantity as well as root biomass and exudation (Eisenhauer *et al.* 2017; Huang *et al.* 2017; Huang *et al.* 2018; Xu *et al.* 2020; Zheng *et al.* 2019). Therefore, tree diversity is expected to increase carbon influxes in soil and consequently soil carbon concentration (Liu *et al.* 2018). Moreover, the kinetic energy of throughfall as a determinant of soil erosion under forest is influenced by neighborhood tree species richness (Goebes *et al.* 2015). The same holds true for interrill erosion. Thus, different tree morphologies have to be considered, when assessing soil erosion under forest, which can affect soil carbon concentrations and nutrient fluxes on small scales (Seitz *et al.* 2015). In addition, recent studies have started linking soil carbon concentration to tree roots (Adamczyk *et al.* 2019). Specifically, morphological traits were shown to control the release of both root carbon (i.e., either by desiccation or exudation) to the soil (Sun *et al.* 2020) and to drive soil organic matter decomposition (Adamczyk *et al.* 2019). For example, with a higher specific root length (SRL), root carbon exudation and desiccation increase due to a higher density of fine roots (Bergmann *et al.* 2020; Sun *et al.* 2020; Wen *et al.* 2019).

Additionally, soil carbon concentrations have been linked to the mycorrhizal association of tree roots (Frey 2019), with trees associating with arbuscular mycorrhizal (AM) fungi having lower topsoil carbon concentrations, while tree stands with ectomycorrhizal (EM) fungi having higher soil carbon concentrations at large spatial scales (Averill *et al.* 2014; Averill and Hawkes 2016; Craig *et al.* 2018). These differential effects of the mycorrhizal association on soil carbon concentrations are expected to be driven by the difference in fungal metabolic pathways (Crowther *et al.* 2019). On top of that, fungal colonization increases with the increase of cortical tissues, themselves being positively correlated with root diameter (RD; Bergmann *et al*. 2020). Thus, root diameter should determine fungal association effects on soil carbon concentrations by modulating fungal colonization.

Tree-derived carbon substrates, such as litter and root exudates, are processed by soil biota. As microorganisms are the main consumers of soil organic matter, they should reduce soil carbon concentrations. However, recent studies highlighted that increased microbial activity can increase soil carbon concentrations by transferring higher amounts of microbial necromass to stable carbon pools (Buckeridge *et al.* 2020; Lange *et al.* 2015; Miltner *et al.* 2012; Schmidt *et al.* 2011; Trumbore 1993). Further, soil microbial community composition and its functioning are strongly influenced by the above-mentioned root traits (i.e. root functional trait identity) and thereby by the tree community composition due to species-specific traits and relations among these traits (Lareen *et al.* 2016; Pei *et al.* 2016). For example, root traits related to root biomass (e.g., RD, SRL) and to litter mass production may increase substrate availability for soil microorganisms with increasing species richness (Bardgett *et al.* 2014; Hooper *et al.* 2000). Besides, species-rich plant communities have also been shown to increase microbial biomass and diversity (Chapman *et al.* 2013; Eisenhauer *et al.* 2010; Lange *et al.* 2015) and, as a consequence, soil carbon concentrations (Li *et al.* 2019). For example, high litter diversity has been linked to an increase in microbial biomass (Thoms *et al.* 2010; Ushio *et al.* 2008). Further,

plant species richness has been shown to increase soil microbial biomass (Xu *et al.* 2020) and the relative proportion of fungi over bacteria by enhancing root biomass as well as the amount and diversity of root exudates (Eisenhauer *et al.* 2017). Moreover, the dissimilarity between root traits is expected to increase resource partitioning of soil microbial species, which should increase soil food web complexity (Kramer *et al.* 2016), and the overall microbial biomass, as shown in consumer communities (Eisenhauer *et al.* 2013; Scherber *et al.* 2010). However, the underlying mechanisms linking primary producers and the microbial community to soil carbon concentrations have rarely been investigated.

Next to root traits, environmental conditions such as climate, soil chemistry, and biotic interactions strongly influence microbial community abundance and composition (Gottschall *et al.* 2019). Recent global studies have shown that climate and soil chemistry are the two main drivers of microbial biomass and composition in drylands (Delgado-Baquerizo *et al.* 2016), but also along large climate gradients from arid to humid (Bernhard *et al.* 2018). In particular, temperature and soil water content increase microbial biomass by increasing microbial activity and growth (Delgado-Baquerizo *et al.* 2016). Moreover, soil chemistry has been highlighted as a major driver of microbial community composition and functioning (Maaroufi and Long 2020). For instance, reduced water availability increases the osmotic pressure which, due to salt concentration and pH, constrains microbial biomass and alters community composition (Aciego Pietri and Brookes 2009; Delgado-Baquerizo *et al.* 2017; Wichern *et al.* 2006). Moreover, substrate limitation (e.g., high carbon to nitrogen ratio and/or carbon to phosphorus ratio) can reduce microbial biomass (Delgado-Baquerizo *et al.* 2017). Besides, a change from alkaline to neutral or acid soil pH coincides with qualitative differences in microbial habitats (Bernhard *et al.* 2018). Next to these abiotic parameters, a positive link between understory plant diversity and soil microbial biomass and activity was found in temperate forests (Eisenhauer *et al.* 2011), while empirical evidences remain inconsistent (Xu *et al.* 2020).

Microbial community composition and processes are closely related to micro-environmental conditions, which are co-determined by tree community composition. Tree community effects on micro-climatic conditions can be manifold. For example, soil moisture can be affected by tree specific root length, as this trait affects the hydraulic lift (Burgess *et al.* 1998). Moreover, tree diversity can stabilize the micro-climate, as forests with a higher hydraulic diversity were shown to increase ecosystem resilience to drought (Anderegg *et al.* 2018). Additionally, species-rich forests were shown to have higher spatial complementarity in tree crowns and canopy closure (Kunz *et al.* 2019; Williams *et al.* 2017), and thereby a lower local temperature under the canopy (Frenne *et al.* 2021) with subsequent effects on soil microbial processes (Gottschall *et al.* 2019). Tree community composition can also modify soil chemistry, such as soil pH and nutrient availability (Reich *et al.* 2005), with significant consequences for the relative proportion of fungi over bacteria (Thoms *et al.* 2010; Rousk *et al.* 2010). Further, forest understory plant communities are connected to the tree community composition and diversity (Germany *et al.* 2017). Tree diversity, for example, has been identified to increase the cover of forbs, while the proportion of forest-specific understory species increased with canopy cover (Vockenhuber *et al.* 2011). However, herb layer productivity is not necessarily affected by neither tree layer diversity (Germany *et al.* 2017), nor herb layer diversity (Both *et al.* 2011).

Forest ecosystems are horizontally structured, this is particularly important when it comes to species-rich forests. At a given location in the forest, the tree species composition can differ from the total species richness of the forest. As a consequence, sampling and observations are highly dependent on the scale considered (i.e., scale-dependency effect). Further, soil erosion can explain small scale changes like concurrently increasing carbon concentrations downslope, in hollows and valleys and that soil fertility is strongly influenced by topography (Scholten *et al.* 2017), as well as the transition from alkaline to acid soil pH (Slessarev *et al.* 2016). In order to take this scale-dependency into account, we considered two levels in this study: the local

level (i.e., between two neighboring trees) and the neighborhood level (i.e., the ten trees directly surrounding the two focal trees). We assume that the mechanisms driving soil functions and community composition are mediated by the tree community at both levels. For example, litter falling on the ground during litterfall may influence the neighborhood level, while root exudation into soils is expected to have local-level effects related to the closest trees (Walker *et al.* 2003).

In this study, we aim to mechanistically understand tree diversity, productivity, functional identity and dissimilarity effects on soil carbon concentration and its mediation by the soil microbial biomass and local environmental conditions (i.e. micro-climatic conditions, soil chemical quality, and biotic environment) across different spatial scales (Fig. III.1). We based our study on the BEF-China experiment and investigated two adjacent trees that will be called in the following a tree species pair (TSP). TSPs of a specific species combination were followed through plots with a species richness gradient ranging from 1 to 16. For each TSP, we measured soil chemical properties, soil microbial biomass, and environmental conditions to mechanistically describe and understand tree productivity and functional trait effects on soil carbon concentrations.

We assume tree diversity and productivity as well as functional trait identity and dissimilarity to drive soil carbon concentration (H1). In addition to that, tree diversity, productivity and functional identity and dissimilarity effects on soil carbon concentrations are expected to be mediated by soil microbial biomass (H2). Besides, we expected tree community effects on soil microbial biomass to be mediated by micro-environmental conditions (micro- climate, soil quality, and biotic environment; H3). Finally, we expected tree productivity and functional trait identity and dissimilarity effects on soil microbial biomass and soil carbon concentration to be scale-dependent (H4). All hypotheses described above must be seen with respect to the spatial scales. We expected that mechanisms related to root

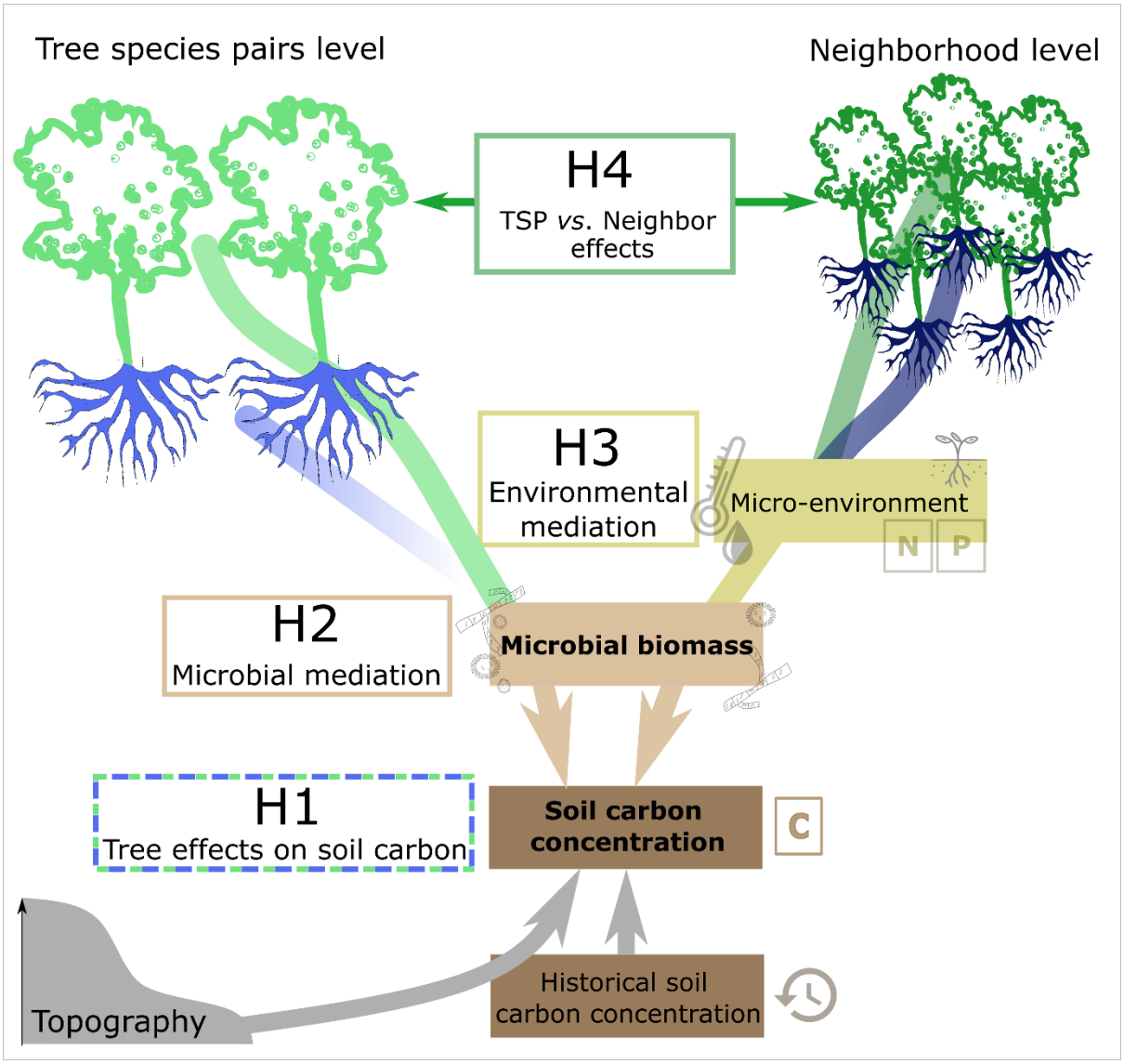

Fig. III.1: Conceptual framework of the study. Relation between the different hypotheses tested in the study: **H1** - tree productivity and functional trait identity and dissimilarity drive soil carbon concentration; **H2** - tree productivity and functional identity and dissimilarity effects on soil carbon concentrations are expected to be mediated by soil microbial biomass; **H3** - tree community effects on soil microbial biomass are mediated by micro-environmental conditions (micro-climate, soil quality, and biotic environment); and **H4** - tree productivity and functional trait identity and dissimilarity effects on soil microbial biomass are scale-dependent.

traits, such as root biomass inputs, are important at the TSP level. However, mechanisms related to the plot level, such as temperature or humidity, are likely to act at the neighborhood level. In order to control for soil history and topography effects on erosion and, therefore soil carbon concentration, we considered historical soil carbon concentration (measured before the

onset of tree interactions) and plot topography (i.e., plot altitude, slope, and curvature) as covariates in our analyses (Fig. III.1).

Material and methods

Study site

The study site is located in south-east China nearby the town of Xingangshan (Jiangxi province, 29.08-29.11° N, 117.90-117.93° E). Our experimental site is part of the BEF-China experiment (site A, Bruelheide *et al.* 2014), and it was planted in 2009 after a clear-cut of the previous commercial plantation. The region is characterized by a subtropical climate with warm, rainy summers and cool, dry winters with a mean temperature of 16.7 °C and a mean rainfall of 1,821 mm (Yang *et al.* 2013). Soils in the region are Cambisols and Cambisol derivatives, with Regosol on ridges and crests (Geißler *et al.* 2012; Scholten *et al.* 2017). The natural vegetation consists of species-rich broad-leaved forests dominated by *Cyclobalanopsis glauca*, *Castanopsis eyrei*, *Daphniphyllum oldhamii*, and *Lithocarpus glaber* (Bruelheide *et al.* 2011; Bruelheide *et al.* 2014).

Study design

We selected 24 combinations of tree species pairs (TSPs) and followed these TSPs across five plot species richness levels (1, 2, 4, 8, and 16 species). A TSP consists of two tree species next to each other. The neighbors of a TSP are defined as the ten trees directly adjacent in the planting grid (Suppl. III-S1.A-B). Each TSP was replicated three times in each richness level when available (see "broken stick design", Bruelheide *et al.* 2014), resulting in 180 TSPs in total (Suppl. III-S1.C-D).

Plot topography

A digital elevation model (DEM) was interpolated in 2015 from elevation measurements with a differential global positioning system (DGPS) using the ordinary kriging algorithm and a cell

size of 5 m x 5 m. The plot mean slope, altitude, plan curvature (Curv. PL), and profile curvature (Curv. PR) were calculated from the DEM (Scholten *et al*. 2017).

Micro-climate modeling

The daily air temperature was recorded using 35 data loggers (HOBO® Pro v2, U23-001) installed at 1 m height in the center of 35 plots across the experiment, while a meteorological station was set up in the central part of the experimental site (see Suppl. III-S2.A for more details, Bruelheide *et al.* 2014). To cover our full experimental area, the air temperature was modeled for all of our experimental plots using the available logger data. We modeled the temperature measurements of the 35 data loggers (i.e., daily minimum, mean, and maximum temperature) as a function of the meteorological station measurements (i.e., daily temperature, rainfall, and solar radiation), plot topography (i.e., latitude, longitude, altitude, orientation, slope, plot curvature, and mean annual solar radiation), forest vertical stratification (i.e. effective number of layers index, "ENL", see below) and plot species richness (see Suppl. III-S2 for more details). Spatio-temporal trends for the whole experiment were estimated using Gaussian radial basis functions (functions auto_basis, eval_basis from the FRK package, see Suppl. III-S2.C andWikle *et al.* 2019). Our model fits explained more than 90% of the loggers' temperature measurement variability. The fitted models were used to predict daily minimum, mean, and maximum temperature for all experimental plots with a standard error from 0 °C to 2 °C during our sampling period (Suppl. III-S2).

Field sampling

Our field measurements were performed from mid-August to the end of September 2018, before the litterfall season. To avoid spatio-temporal autocorrelation, each day another sampling area was randomly chosen. Between the two trees of each TSP, understory plant cover was estimated on a five-level factorial scale from 'no understory plant' to 'mainly understory plants'.

Starting from the center of the TSP, we extracted two soil cores with 5 cm diameter and 10 cm depth, 5 cm away from the center (Suppl. III-S1.B). Two additional cores of the same dimensions were taken 20 cm away from the center in the direction of each tree. A composite soil sample was built from these four soil cores and sieved with a 2 mm mesh size. Root fragments contained in the sieving residues were air-dried at 40°C for two days and weighed (± 0.01 g), while the composite soil samples were stored at -20°C.

The litter cover between the two trees of each TSP was estimated on a five-level factorial scale from 'no-litter' to 'litter layer thicker than five centimeters'. Leaf litter was collected excluding green understory plant residuals, air-dried at 40°C for two days, and milled to powder. Carbon and nitrogen concentrations were measured by micro-combustion from a subsample of 4 mg (Elementar Vario El III analyzer, Elementar, Hanau, Germany).

Soil analyses

Soil moisture was measured from a subset of 25 g soil by drying the soil at 40 °C for two days. A subsample was used to quantify soil pH in a 1:2.5 soil-water solution. Soil total nitrogen (TN) was determined on an auto-analyzer (SEAL Analytical GmbH, Norderstedt, Germany) using the Kjeldahl method (Bradstreet 1954). Soil total phosphorus (TP) was measured after wet digestion with H_2SO_4 and $HClO_4$ using a UV-VIS spectrophotometer (UV2700, SHIMADZU, Japan). Soil total organic carbon (TOC) was measured by a TOC Analyzer (Liqui TOC II; Elementar Analysensysteme GmbH, Hanau, Germany). TOC in 2010 was quantified in a previous study (Scholten *et al.* 2017) at the plot level using the micro-combustion method (Elementar Vario El III analyzer, Elementar, Hanau, Germany).

Soil microbial biomass

Soil microbial biomass was measured using phospholipid fatty acid (PLFA) analysis. PLFAs were extracted from 5 g of frozen soil following Frostegård *et al.* (1991). Biomarkers were

assigned to microbial functional groups according to Ruess and Chamberlain (2010) using markers to assign bacteria (gram-positive bacteria: i15:0, a15:0, i16:0, i17:0; gram-negative bacteria: cy17:0, cy19:0; general bacteria markers: 16:1ω5; 16:1ω7), arbuscular mycorrhizal fungi (20:1ω9), and saprophytic and ectomycorrhizal fungi (18:1ω9 and 18:2ω6,9, see Suppl. III-S3).

Tree functional traits

Tree biomass

Tree biomass was predicted for all TSPs and neighbors using tree basal area (BA) and species-specific allometric relationships estimated on the TSP trees. (1) Circumference at breast height (CBH) was measured in September 2018 for all TSPs and direct neighbors in order to calculate the basal area of these trees as $BA = \frac{(CBH)^2}{4\pi}$. (2) Tree height was measured for the TSP trees, and tree biomass was calculated following Huang *et al.* (2017). BA and TSP tree biomass were used to estimate species-specific allometric BA-biomass relationships (see Suppl. III-S4). (3) These species-specific allometric relationships were used to calculate the TSP biomass (i.e., sum of the two-tree biomass) and neighborhood biomass (i.e., sum of neighbors' biomass).

Leaf traits

For each tree species of the experiment, 10 samples consisting of 10 to 25 pooled fresh leaves were collected across all diversity levels from mid-August to October 2018 (Davrinche and Haider 2021). Each sample was dried at 80 °C for two days and milled 5 min at 26 shakes per second. Carbon and nitrogen concentrations were measured by micro-combustion from a subsample of 5 mg (Elementar Vario El III analyzer, Elementar, Hanau, Germany).

Root traits

Root functional traits were measured from BEF-China Site A from September to October 2013 using two to three tree individuals per species per diversity level. First-order roots were

collected, cleaned, scanned, and analyzed by WinRHIZO (Regent Software, Canada). After measurements, roots were air-dried at 60°C for two days and weighed. Average RD (in mm) and SRL (in $m.g^{-1}$) were calculated from the measurements of each species at all species richness levels (Bu *et al.* 2017). The mycorrhizal status of the tree species was determined from the literature (Haug *et al.* 1994; Hawley and Dames 2004; Wang and Qiu 2006).

Root functional trait variables

We considered three functional root traits that are related to soil processes (Bardgett *et al.* 2014): root diameter (RD), specific root length (SRL), and mycorrhizal tree association (i.e. AM or EM). For each TSP, two trait variables were calculated at both the TSP level and the neighborhood level. At the TSP level, we calculated trait community-weighted mean (CWM, Garnier *et al.* 2004) and trait functional richness (FRic) – defined as the range between the TSP trait values (Villéger *et al.* 2008) – of the above-mentioned root functional traits. At the neighborhood level, we calculated community-weighted means and functional dispersion (FDis) – defined as the weighted variance of the trait values within the neighborhood (Laliberté and Legendre 2010). All measures were weighted using tree BA. Calculations were made using the 'dbFD' function from the 'FD' package in R (Laliberté *et al.* 2014).

Forest vertical stratification

A terrestrial laser scanning campaign took place in February-March of 2019 using a FARO Focus S120 and a FARO Focus X130 laser scanner (FARO Europe, Korntal-Münchingen, Germany; seePerles-Garcia *et al.* 2021). The scanner was set up on a tripod at 1.3 m height in the center of each plot and a fully three-dimensional point cloud (360° x 305° field of view) with a spatial resolution of 6 mm at a distance of 10 m was acquired.

For each plot the Effective Number of Layers (ENL, Ehbrecht *et al.* 2016) was computed. First the scans were filtered using a statistical outlier removal filter (SOR, N=10, SD=3) in

CloudCompare 2.9.1 software. Taking into account the dimensions of each plot (~667 m²), each point cloud was clipped in a 20m square around the scan center (~400 m²). The point clouds were voxelized into a voxel grid of 5 cm voxels using R package VoxR (Lecigne *et al.* 2018). Then, they were grouped in vertical slices of 50 cm and, for each slice, we quantified the proportion of filled voxels. The ENL was the result of calculating the inverse Simpson-Index: $ENL = 1 / \sum_{i=1}^{n} p_i^2$, were n refers to the number of slices, calculated as ($height_{max}$ – $height_{min}$) / 50cm; and p_i is the proportion of filled voxels of the i_{th} slice.

A high ENL value indicates more evenly distributed layers, which can be an indication of higher crown complementarity and, thus, increased of canopy packing (Ehbrecht *et al.* 2016).

Litterfall measurement

From September to December 2018, the freshly fallen leaf litter between the two trees of each TSP was collected in a 1 m^2 litter trap (1 cm mesh). The collected litter was identified to species level, air-dried at 40 °C for two days, and weighed (± 0.01 g). Annual amounts of litter carbon (i.e. "$C_{litterfall}$") and nitrogen (i.e. "$N_{litterfall}$") deposited on the ground were calculated using species-specific leaf carbon and nitrogen contents and species-specific litter mass collected in the traps. We calculated the litterfall carbon to nitrogen ratio ($CN_{litterfall}$) from these measurements.

Statistical analyses

A description of all the variables used in this study can be found in Suppl. III-S5.A. All data handling and statistical calculations were performed using the R statistical software version 3.6.1. All R scripts used for this project can be found in our GitHub repository (i.e., https://github.com/remybeugnon/Beugnon-et-al-2021_Soil-carbon-and-microbial-biomass-drivers).

In order to avoid any deviation due to scale differences between variables, all explanatory variables were centered and divided by two standard deviations for our analyses using the R

'rescale' function from the 'arm' package. Collinearity of root trait indices was inspected by Pearson's correlation (Suppl. III-S6); highly correlated variables were excluded by our model selection algorithm. We first tested the effects of tree species richness on our productivity and structural variables (i.e., TSP biomass, neighborhood biomass, ENL, $C_{litterfall}$, and $CN_{litterfall}$) using linear models and normal distribution assumptions. Similarly, we used linear models to control for the effects of topography (plot slope, plan curvature, profile curvature and altitude) on soil historical carbon concentration.

Drivers of soil carbon concentration (H1). We used linear models and normal distribution assumptions to test the effects of initial soil carbon concentration (i.e., $[C]_{2010}$), topography, tree productivity variables, litterfall carbon deposition, and C:N ratio, and root functional traits on soil carbon concentration (i.e., $[C]_{2018}$). Explanatory variables were selected by a both-way step selection based on AIC (R 'step' function from the 'stats' package with back- and forward selection). We estimated the drivers of soil carbon concentrations from the final model. All significant variables of the model output (p-value < 0.05) were implemented with the effects of topography on soil historical C concentration and, when applicable, with tree diversity effects on productivity in a Structural Equation Model (SEM). Our SEM was fitted using the R 'sem' function from the 'lavaan' package (Rosseel 2012). The quality of our model fit on the data was estimated using three complementary indices: (i) the root-mean-squared error of approximation (RMSEA), (ii) the comparative fit index (CFI), and (iii) the standardized root mean squared residuals (SRMR), a model fit was considered acceptable when RMSEA < 0.10, CFI>0.9 and SRMR<0.08.

Drivers of soil carbon concentration mediated by soil microbial biomass (H2). We used the same procedure to select drivers of microbial biomass. All selected drivers of microbial biomass were implemented in the above described SEM structure. The relation between

microbial biomass and soil carbon concentration (i.e., causal relation direction or correlation) was tested by comparing the models AIC.

Drivers of microbial biomass mediated by micro-environmental conditions (H3). Micro-environmental conditions were described by (i) micro-climatic conditions, (ii) soil chemical quality conditions, and (iii) biotic conditions. Correlations between micro-environment variables were explored in Suppl. III-S7.A.

(i) Micro-climatic conditions were estimated using both soil humidity (RH) and air temperature. The air temperature was used at the plot level on the day of sampling (minimum, average, and maximal temperature, 'T.min', 'T.mean', 'T.max', respectively) and during the week before sampling (minimum, average, and maximal temperature, 'T.min.week', 'T.mean.week', 'T.max.week', respectively, see Suppl. III-S7.B.1). The first axis of the PCA projection was negatively correlated with temperature variables (Suppl. III-S7.B.2.2). Given that the first PCA axis was negatively correlated with temperature indices and to simplify the presentation to the readers, we used the positive value of the vector for the first PCA axis as a proxy for air temperature variables in further analyses. (ii) To describe soil quality conditions, we used soil carbon to nitrogen ratio ('C:N'), and carbon to phosphorus ratio ('C:P'). (iii) Biotic conditions were described by using field measurements of understory plant cover, soil root biomass, litter cover, and leaf chemical traits (i.e., litter carbon and nitrogen contents).

For each micro-environmental variable, we used linear models and normal distribution assumptions to test the effects of tree productivity, litterfall carbon deposition and C:N ratio, and root functional traits. Explanatory variables were selected by a both-way step selection based on AIC. We used linear models and normal distribution assumptions to test the effects of micro-environmental variables on soil microbial biomass. Explanatory variables were selected by a both-way step selection based on AIC. We estimated the drivers of microbial

biomass from the final model. All variables selected and their relations to tree variables were implemented in our previous SEM.

All the statistical assumptions of our linear models were tested using the "*check_model*" function from the R package '*performance'* (Suppl. III-S8).

Results

Local history and topography effects on soil carbon concentrations

On average, forest soil carbon concentrations slightly decreased over time (mean = -0.33 g yr-1, sd = 0.86 g yr-1), but we also observed high variability in the data (from -3.00 g yr-1 to +1.85 g yr-1, Fig. III.2.A). Soil carbon concentration measured in 2018 increased with historical soil carbon concentrations measured in 2010 before the experiment (estimate ± sd = 0.263 ± 0.077, Fig. III.2.D-F, Suppl. III-S9). As historical soil carbon concentrations were affected by local topography (slope: 0.175 ± 0.038, plan curvature: 0.357 ± 0.038, R^2 = 10%, Fig. III.2.B), topography indirectly affected soil carbon concentrations measured in 2018 by the modification of historical soil carbon concentrations (Fig. III.2.E-F).

Tree species richness effects on tree productivity

At the neighborhood level, plot tree species richness increased the different aspects of tree productivity: tree biomass (0.427 ± 0.073, R^2 = 18%), litterfall production (i.e. “C.litterfall”, 0.416 ±0.078, R^2 = 17%), and forest vertical stratification (i.e. ENL, 0.248 ± 0.070, R^2 = 32% when accounting for topography effects, Fig. III.2.C). However, we could not detect any effects of neither plot species richness nor TSP species richness on TSP biomass (Fig. III.2.C). These different aspects of forest productivity were correlated to each other (Pearson correlation: neighborhood biomass – ENL = 0.38, neighborhood biomass – "C litterfall" = 0.4, TSP biomass – "C litterfall" = 0.25, ENL – "C litterfall" = 0.61).

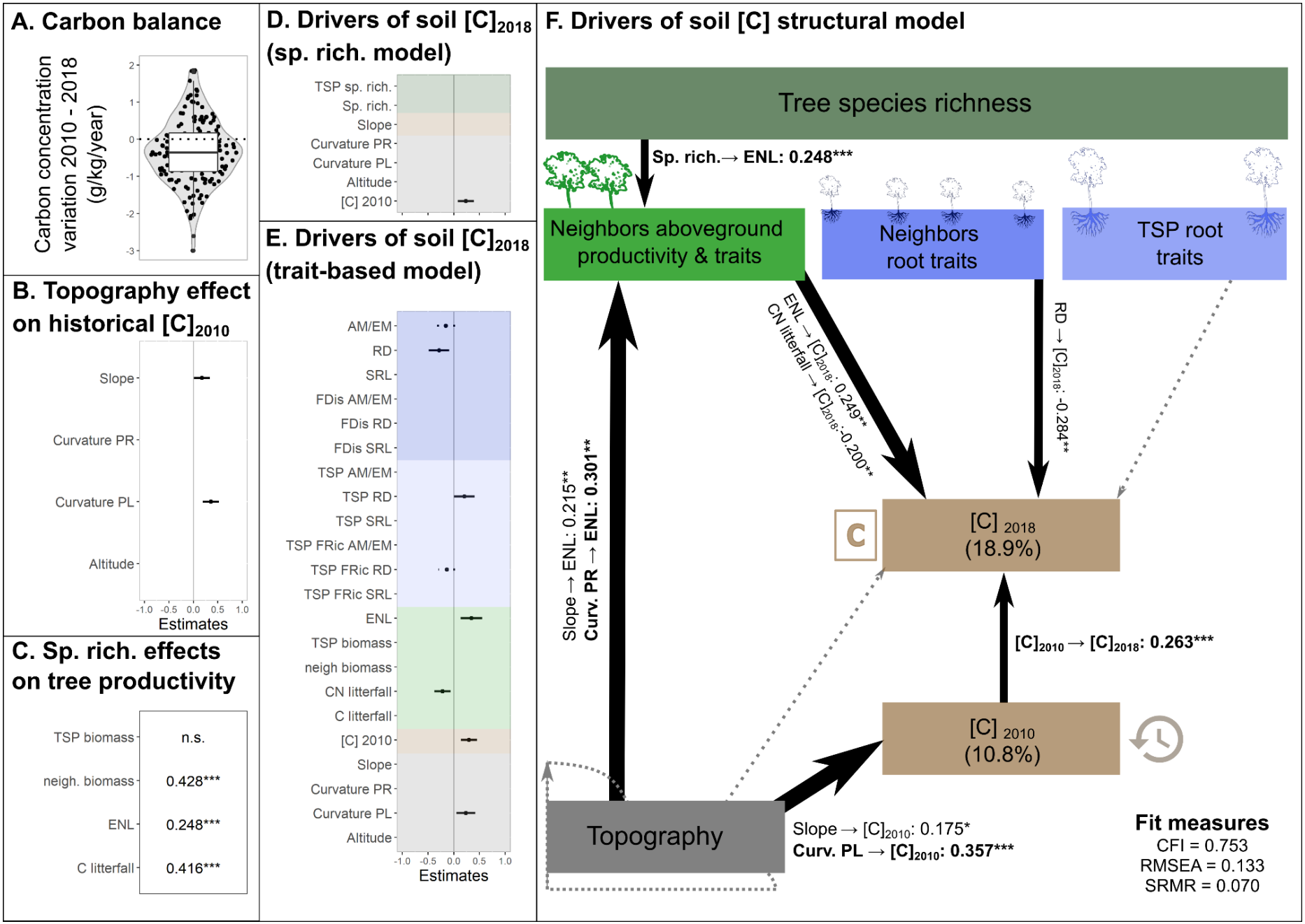
A. Carbon balance
Carbon concentration variation 2010 - 2018 (g/kg/year)
B. Topography effect on historical [C]2010
Slope
Curvature PR
Curvature PL
Altitude
Estimates
C. Sp. rich. effects on tree productivity
TSP biomass n.s.
neigh. biomass 0.428***
ENL 0.248***
C litterfall 0.416***
D. Drivers of soil [C]2018 (sp. rich. model)
TSP sp. rich.
Sp. rich.
Slope
Curvature PR
Curvature PL
Altitude
[C] 2010
E. Drivers of soil [C]2018 (trait-based model)
AM/EM
RD
SRL
FDis AM/EM
FDis RD
FDis SRL
TSP AM/EM
TSP RD
TSP SRL
TSP FRic AM/EM
TSP FRic RD
TSP FRic SRL
ENL
TSP biomass
neigh biomass
CN litterfall
C litterfall
[C] 2010
Slope
Curvature PR
Curvature PL
Altitude
Estimates
F. Drivers of soil [C] structural model
Tree species richness
Sp. rich.→ ENL: 0.248***
Neighbors aboveground productivity & traits
Neighbors root traits
TSP root traits
ENL → [C]2018: 0.249**
CN litterfall → [C]2018: -0.200**
RD → [C]2018: -0.284**
Slope → ENL: 0.215**
Curv. PR → ENL: 0.301**
C
[C] 2018 (18.9%)
[C]2010 → [C]2018: 0.263***
[C] 2010 (10.8%)
Topography
Slope → [C]2010: 0.175*
Curv. PL → [C]2010: 0.357***
Fit measures
CFI = 0.753
RMSEA = 0.133
SRMR = 0.070

Fig. III.2: Tree diversity effects on tree productivity and consequences for soil carbon concentration, while controlling for soil history and topography effects. A. Soil carbon balance between 2010 and 2018. B. Topography effect on historical soil carbon concentrations. For each driver of soil historical carbon concentration on the y-axis (i.e., slope, plan curvature: "Curvature PL", profile curvature: "Curvature PR", altitude), the dot represents the estimated effect of the driver on historical soil carbon concentration, the line represents the 95% confidence interval for a given estimated value. The drivers excluded during model selection have neither estimates nor confidence intervals. **C. Tree species richness effect on tree productivity.** For each response variable on the y-axis – TSP biomass, neighborhood biomass (i.e. "neigh. biomass"), forest vertical stratification (i.e., "ENL"), and litterfall carbon deposition (i.e. "C litterfall") – the standardized estimate of plot tree species richness (i.e. "Sp. Rich.") was shown with the significance of the relationship. *N.B.* ENL model controlled for topography effects. **Tree species richness (D.) and tree productivity and functional traits effects (E.) on soil carbon concentration ("Soil C 2018") controlling for soil history ("Soil C 2010") and topography effects (i.e. "Slope", profile curvature: "Curvature PR", plan curvature: "Curvature PL" and "Altitude").** For each driver on the y-axis, the dot represents the estimated effect of the driver on soil carbon concentrations; the line represents the 95% confidence interval for a given estimate value. Estimates and confidence intervals were drawn in dashed lines when the effect of the driver on soil carbon concentration was non-significant (i.e. p-values > 0.05). The drivers excluded during model selection have neither estimates nor confidence intervals. Six groups of explanatory variables were built: species richness variables (i.e. TSP species richness: "TSP sp. rich.", plot species richness: "Sp. rich."), soil history variables (i.e. "Soil C 2010"), plot topography (i.e. "Slope", "Curvature PR", "Curvature PR", "Altitude"), neighborhood root trait indices (i.e. neighbors' AM versus EM tree association: "AM/EM", community weighted mean of root diameter and specific root length: "RD" and "SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "FDis AM/EM", "FDis RD", and "FDis SRL", respectively), TSP root trait indices (i.e. TSP' AM versus EM tree association: "TSP AM/EM", community weighted mean of root diameter and specific root length: "TSP RD" and "TSP SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "TSP FRic AM/EM", "TSP FRic RD", and "TSP FRic SRL", respectively), aboveground productivity and traits (i.e. "TSP biomass", neighbor biomass: "neigh biomass", litterfall C:N ratio: "CN litterfall", litterfall carbon deposition: "C litterfall"). **F. Structural equation model showing the relationships between topography (i.e. "Slope", "Curv. PR" and "Curv. PL"), soil history (i.e. "$[C]_{2010}$"), tree species richness, tree aboveground productivity and functional traits (i.e. "ENL" and "CN.litterfall") and root functional traits (i.e. "RD"), and soil carbon concentration (i.e. "$[C]_{2018}$").** Each node represents a group of variables (selected from panels B.-E.), and each arrow summarizes all the significant effects between all the variables of two nodes. Arrow widths were sized by the sum of the standardized effect size of significant relations between all variables of the two nodes. When non-significant relations were found between any variables of two nodes, the arrows were drawn with dashed lines. The variance in soil carbon concentration explained by the model (R^2, in %) was added after the node name, see Suppl. III-S9 for detailed output. The significance levels were standardized across the panel (p-value > 0.05: "n.s.", p-value < 0.05: *, p-value <0.01: ** and p-value < 0.001: ***).

Tree effects on soil carbon concentrations

Plot tree species richness did not affect soil carbon concentrations (Fig. III.2.C), but tree productivity, especially, forest vertical stratification (i.e., ENL), affected by tree species richness, increased soil carbon concentrations (0.249 ± 0.083, Fig. III.2.D-F). In contrast, litterfall C:N ratio decreased soil carbon concentration (-0.200 ± 0.077, Fig. III.2.D-F, Suppl. III-S9). Belowground, one root morphological trait, root diameter (RD), strongly influenced soil carbon concentration. At the neighborhood level, RD decreased soil carbon concentration (-0.286 ± 0.101), while at the TSP level, RD increased soil carbon concentration (0.206 ± 0.126). The latter became non-significant (i.e. p-value = 0.126) once taken together with the other variables in the SEM framework (Fig. III.2.F, Suppl. III-S9).

Tree effects on soil microbial biomass

Our analyses showed a positive effect of tree species richness on soil microbial biomass (0.202 ± 0.079, R^2 = 3%, Fig. III.3.A). By considering tree functional traits and productivity, we got a better understanding of the variability in soil microbial biomass (R^2 = 14%, $AIC_{\text{sp. rich. based model}}$ = 222 *vs.* $AIC_{\text{trait based model}}$ = 210). We found that soil microbial biomass increased with tree productivity (i.e., ENL, 0.172 ± 0.037) and was strongly affected by root morphological traits. At the neighborhood level, soil microbial biomass decreased with increasing RD (-0.359 ± 0.100) and specific root length (SRL) functional dissimilarity (-0.216 ± 0.102), while at the TSP level, soil microbial biomass increased with RD (0.308 ± 0.116) and SRL (0.223 ± 0.103, Fig. III.3.B). We did not observe any significant effect of tree mycorrhizal association on soil microbial biomass.

Relationship between soil microbial biomass and soil carbon concentration

We found a strong positive correlation between soil carbon concentration and soil microbial biomass (Pearson-correlation = 62.7%, p-value < 0.001, Fig. III.3.C). Taken together with the other drivers of soil carbon and microbial biomass, we tested the directionality of the

relationship between soil carbon concentration and soil microbial biomass (Fig. III.3.D). The AIC comparison between the models was in favor of the model with a causal effect from soil carbon concentration to soil microbial biomass and the model taking into account both causal links (i.e., soil carbon concentration effect on microbial biomass and *vice versa*). The latter, being the most conservative model, is given in Fig. III.3.E. This SEM showed a strong positive effect of soil carbon concentration on microbial biomass (0.506 ± 0.145, Fig.3.E), but a non-significant effect of soil microbial biomass on soil carbon concentration (p-value = 0.57, Suppl. III-S10). Additionally, root functional trait effects on soil microbial biomass remained strong (neighborhood root traits total effect = 0.285, TSP root traits total effect = 0.438, Fig. III.3.E, Suppl. III-S10), but the tree productivity effect on soil microbial biomass was mediated by soil carbon concentration (p-value = 0.103, Fig. III.3.E, Suppl. III-S10).

Tree effects on micro-environmental conditions

Tree species richness effects on micro-environmental conditions were limited to a negative effect on air temperature (-0.208 ± 0.082, R^2 = 3%) and a positive effect on the amount of litter collected on the ground (0.168 ± 0.080, R^2 = 2%, Fig. III.4.A). However, the trait-based model showed the major role of trees in controlling environmental conditions. Aboveground, forest vertical stratification (i.e., ENL) reduced air temperature (-0.406 ± 0.078), plant cover, and amount of litter (-0.472 ± 0.008 and -0.294 ± 0.083, respectively), but also root biomass (-0.389 ± 0.091), and litter C:N ratio (-0.306 ± 0.089), while litterfall C:N ratio increased C:N ratio of the residual litter on the ground (0.233 ± 0.077), but also decreased soil humidity (-0.247 ± 0.077), soil nitrogen and phosphorus contents (-0.189 ± 0.082 and -0.186 ±0.080), and plant cover (-0.305 ± 0.085, Fig. III.4.B). Belowground, environmental conditions were mostly affected by the root morphological traits (RD and SRL). These effects were inconsistent with the scale considered (i.e. TSP *vs.* neighborhood levels, Fig. III.4.B). While SRL decreased soil

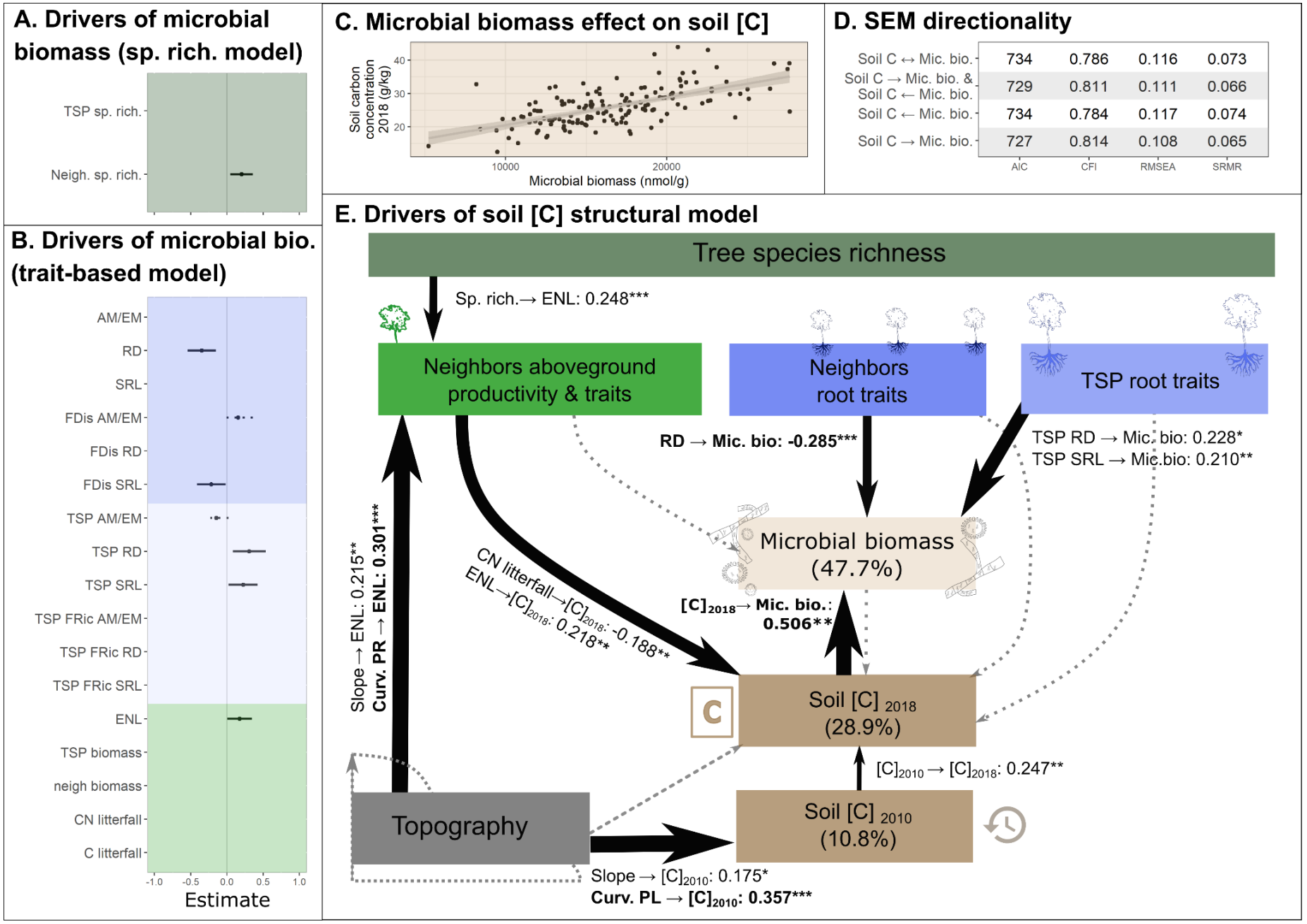
A. Drivers of microbial biomass (sp. rich. model)
TSP sp. rich.
Neigh. sp. rich.
B. Drivers of microbial bio. (trait-based model)
AM/EM
RD
SRL
FDis AM/EM
FDis RD
FDis SRL
TSP AM/EM
TSP RD
TSP SRL
TSP FRic AM/EM
TSP FRic RD
TSP FRic SRL
ENL
TSP biomass
neigh biomass
CN litterfall
C litterfall
-1.0 -0.5 0.0 0.5 1.0
Estimate
C. Microbial biomass effect on soil [C]
Soil carbon concentration 2018 (g/kg)
40
30
20
10000
20000
Microbial biomass (nmol/g)
D. SEM directionality
Soil C ↔ Mic. bio. 734 0.786 0.116 0.073
Soil C → Mic. bio. & Soil C ← Mic. bio. 729 0.811 0.111 0.066
Soil C ← Mic. bio. 734 0.784 0.117 0.074
Soil C → Mic. bio. 727 0.814 0.108 0.065
AIC CFI RMSEA SRMR
E. Drivers of soil [C] structural model
Tree species richness
Sp. rich.→ ENL: 0.248***
Neighbors aboveground productivity & traits
Neighbors root traits
TSP root traits
RD → Mic. bio: -0.285***
TSP RD → Mic. bio: 0.228*
TSP SRL → Mic.bio: 0.210**
Microbial biomass (47.7%)
[C]2018→ Mic. bio.: 0.506**
CN litterfall→[C]2018: -0.188**
ENL→[C]2018: 0.218**
Slope → ENL: 0.215**
Curv. PR → ENL: 0.301***
C
Soil [C] 2018 (28.9%)
[C]2010 → [C]2018: 0.247**
Topography
Soil [C] 2010 (10.8%)
Slope → [C]2010: 0.175*
Curv. PL → [C]2010: 0.357***

Fig. III.3: Biotic drivers of soil microbial biomass (A.-B.) and relationship with soil carbon concentrations (C.-E.). Tree species richness (A.), and tree productivity and functional trait effects (B.) on soil microbial biomass. For each driver on the y-axis, the dot represents the estimated effect of the driver on soil microbial biomass; the line represents the 95% confidence interval for a given estimate value. Estimates and confidence intervals were drawn in dashed lines when the effect of the driver on soil microbial biomass was non-significant (i.e. p-values > 0.05). The drivers excluded during model selection have neither estimates nor confidence intervals. Four groups of explanatory variables were built: species richness variables (i.e. TSP species richness: "TSP sp. rich.", plot species richness: "Sp. rich."), neighborhood root trait indices (i.e. neighbors' AM versus EM tree association: "AM/EM", community weighted mean of root diameter and specific root length: "RD" and "SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "FDis AM/EM", "FDis RD", and "FDis SRL", respectively), TSP root trait indices (i.e. TSP' AM versus EM tree association: "TSP AM/EM", community weighted mean of root diameter and specific root length: "TSP RD" and "TSP SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "TSP FRic AM/EM", "TSP FRic RD", and "TSP FRic SRL", respectively), aboveground productivity and traits (i.e. "TSP biomass", neighbor biomass: "neigh biomass", litterfall C:N ratio: "CN litterfall", litterfall carbon deposition: "C litterfall"). **C. Linear regression between soil carbon concentration and soil microbial biomass. D. Directionality of the relationship between soil carbon concentration and soil microbial biomass tested in the SEM including the drivers of soil microbial biomass (A.-B.) and soil carbon concentration (Fig. III.2.F.). F. Structural equation model showing the relationships between topography (i.e. "Slope", profile curvature: "Curv. PR" and plan curvature: "Curv. PL"), soil history (i.e. "$[C]_{2010}$"), tree species richness, tree aboveground productivity and functional traits (i.e. "ENL" and "CN.litterfall"), root functional traits (i.e. "RD"), soil carbon concentration (i.e. "$[C]_{2018}$"), and soil microbial biomass.** Each node represents a group of variables (selected from A.B. and Fig. III.2.F.) and each arrow summarizes all the significant effects between all the variables of two nodes. Arrow widths were sized by the sum of the standardized effect size of significant relations between all variables of the two nodes. When no significant relations were found between any variables of two nodes, the arrows were drawn with dashed lines. The variance in soil carbon concentration and microbial biomass explained by the model (R^2, in %) were added after the node name, see Suppl. III-S10 for detailed output. The significance levels were standardized across the panel (p-value > 0.05: "n.s.", p-value < 0.05: *, p-value <0.01: ** and p-value < 0.001: ***).

humidity (-0.290 ± 0.087), plant cover and amount of litter (-0.262 ± 0.105 and -0.365 ± 0.116, respectively) at TSP level, it increased soil nitrogen content (0.214 ± 0.093) at the neighborhood level. Similarly, RD decreased plant cover and the amount of litter (-0.212 ± 0.103 and -0.254 ± 0.115, respectively) but increased soil phosphorus content (0.408 ± 0.097). Moreover, root functional trait dissimilarity and richness also played a major role in controlling soil quality and biotic conditions at both TSP and neighborhood level (Fig. III.4.B). In addition,

plant cover was positively correlated to root biomass and amount of litter (Pearson correlation: plant cover ~ root biomass = 0.30, plant cover ~ amount of litter = 0.37, Suppl. III-S7).

Micro-environmental mediation of tree effects on microbial biomass

Microbial biomass was affected by micro-climate, soil quality, and biotic conditions (Fig. III.5.A). Both air temperature and soil humidity decreased soil microbial biomass (-0.379 ± 0.072 and -0.221 ± 0.066, respectively). In addition, soil microbial biomass increased with increasing soil nitrogen content (0.385 ± 0.066) and increasing litter C:N ratio (0.240 ± 0.068, Fig. III.5.A). By adding these drivers to the previous structural model, we explained up to 54% of the variability in soil microbial biomass (Fig. III.5.B). Microbial biomass was mostly affected by variations in soil carbon concentration (total effect: 0.562) and micro-environmental conditions (total effect: 0.610), which were themselves strongly mediated by tree productivity and functional traits (total effect: on soil carbon concentration = 0.733, on micro-environmental conditions = 2.308, Fig. III.5.B, Suppl. III-S11). In addition, our analyses revealed that soil carbon concentration was driven by tree productivity and functional traits at the neighborhood scale, while soil microbial biomass was driven by root functional traits at both investigated scales. The strongest effect on soil microbial biomass was exerted by variations in micro-environmental conditions, which were themselves strongly influenced by tree productivity and functional traits at both TSP and neighborhood scales (Fig. III.5.B).

Discussion

The present study revealed strong effects of forest diversity, productivity, and functional traits on soil carbon concentrations as well as the underlying biotic and abiotic drivers at different local spatial scales of tree species pairs (TSPs) in a tree diversity experiment. In addition to the effects of topography, our analyses showed a strong positive effect of tree species richness on tree productivity (i.e., tree biomass, amount of litterfall, and forest vertical stratification). Tree productivity and tree functional traits modulated micro-environmental conditions, such as

micro-climate, soil quality, and biotic conditions. These changes in micro-environmental conditions had consequences for soil microbial biomass (e.g., an increase of temperature decreased soil microbial biomass). In addition, root functional traits modulated soil microbial biomass at both TSP and neighborhood levels. Soil microbial biomass was strongly correlated to soil carbon concentration, and our analyses found more support for a positive effect of soil carbon concentration on soil microbial biomass than vice versa. Moreover, soil carbon concentration increased with tree productivity and root morphological traits at the neighborhood level. Taken together, these findings for the first time show how tree diversity and productivity, and functional traits shape forest abiotic and biotic conditions and soil functioning, and how these effects are highly scale-dependent; these findings reconciling previous inconsistent findings and calling for a more thorough consideration of scale in soil ecological studies.

Tree diversity enhances productivity with consequences for environmental conditions

Our analyses confirmed previous results showing increased productivity with tree species richness (Huang *et al.* 2017; Huang *et al.* 2018; Kunz *et al.* 2019; Perles-Garcia *et al.* 2021). Interestingly, our results highlighted that tree species richness simultaneously enhances tree biomass, litter production, and forest vertical stratification. This positive effect of tree species richness is also expected belowground (Liu *et al.* 2018; Liu *et al.* 2020a; Xu *et al.* 2020). However, efforts are still needed to a finer quantification of belowground productivity, particularly so over time (Liu *et al.* 2020a). A major challenge is developing non-invasive quantification methods of belowground biomass (Clark *et al.* 2011; Metzner *et al.* 2014; Mooney *et al.* 2012).

Tree productivity combined with root functional traits allowed us to explore how tree effects are mediated by micro-environmental conditions: micro-climate, soil quality, and biotic conditions. Our results, by showing a negative effect of forest vertical stratification on

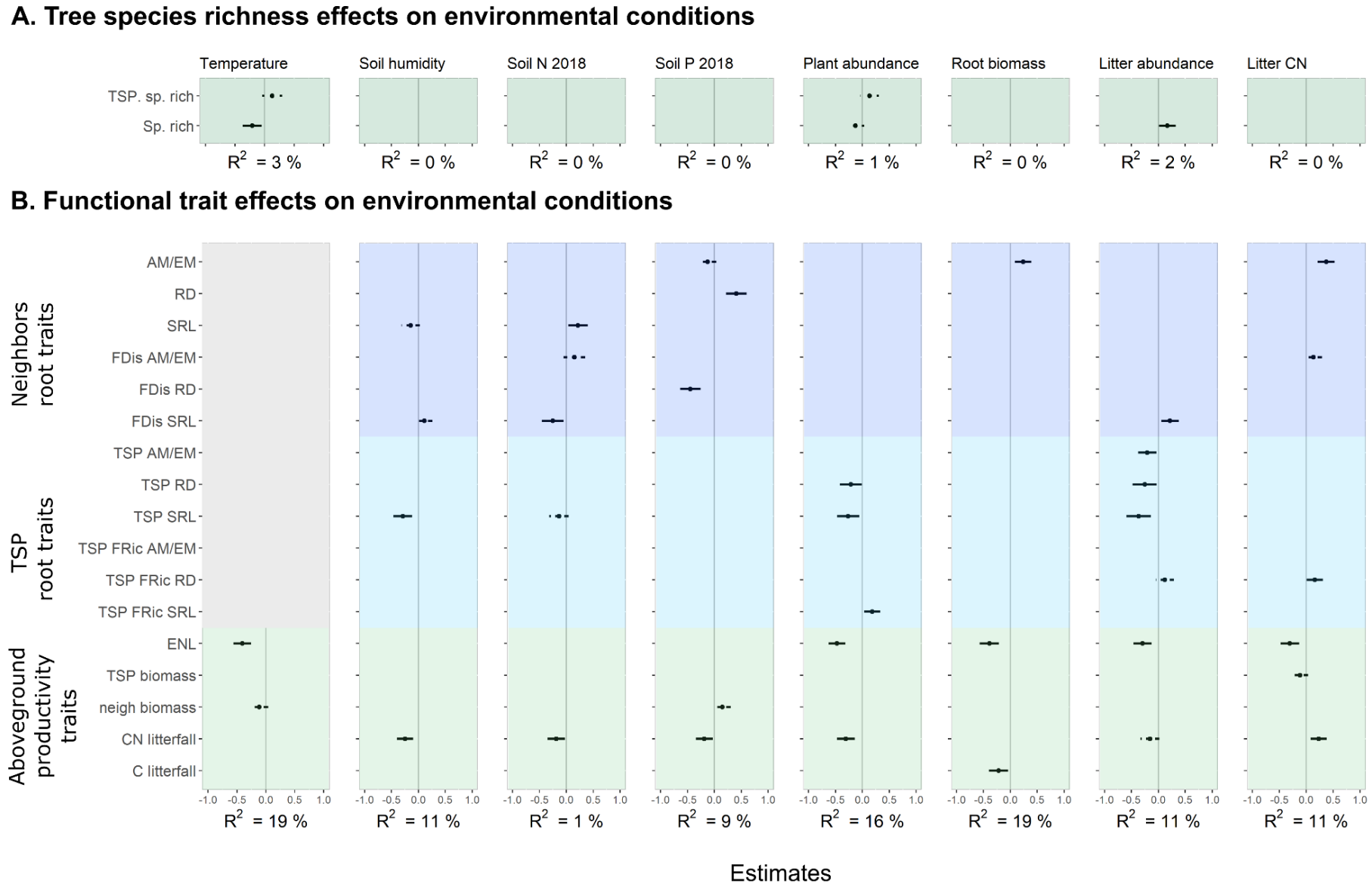
A. Tree species richness effects on environmental conditions
Temperature
Soil humidity
Soil N 2018
Soil P 2018
Plant abundance
Root biomass
Litter abundance
Litter CN
TSP. sp. rich
Sp. rich
R2 = 3 %
R2 = 0 %
R2 = 0 %
R2 = 0 %
R2 = 1 %
R2 = 0 %
R2 = 2 %
R2 = 0 %
B. Functional trait effects on environmental conditions
Neighbors root traits
TSP root traits
Aboveground productivity traits
AM/EM
RD
SRL
FDis AM/EM
FDis RD
FDis SRL
TSP AM/EM
TSP RD
TSP SRL
TSP FRic AM/EM
TSP FRic RD
TSP FRic SRL
ENL
TSP biomass
neigh biomass
CN litterfall
C litterfall
-1.0 -0.5 0.0 0.5 1.0
R2 = 19 %
R2 = 11 %
R2 = 1 %
R2 = 9 %
R2 = 16 %
R2 = 19 %
R2 = 11 %
R2 = 11 %
Estimates

Fig. III.4: Tree species richness (A.), and tree productivity and functional traits effects (B.) on micro-environmental variables. For each driver on the y-axis, the dot represents the estimated effect of the driver on the micro-environmental variable, the line represents the 95% confidence interval for a given estimate value. Estimates and confidence intervals were drawn in dashed lines when the effect of the driver was non-significant (i.e. p-values > 0.05). The drivers excluded during model selection have neither estimates nor confidence intervals. Four groups of explanatory variables were built: species richness variables (i.e. TSP species richness: "TSP sp. rich.", plot species richness: "Sp. rich."), neighborhood root trait indices (i.e. neighbors' AM versus EM tree association: "AM/EM", community weighted mean of root diameter and specific root length: "RD" and "SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "FDis AM/EM", "FDis RD", and "FDis SRL", respectively), TSP root trait indices (i.e. TSP' AM versus EM tree association: "TSP AM/EM", community weighted mean of root diameter and specific root length: "TSP RD" and "TSP SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "TSP FRic AM/EM", "TSP FRic RD", and "TSP FRic SRL", respectively), aboveground productivity and traits (i.e. forest vertical stratification: “ENL”, "TSP biomass", neighbors biomass: "neigh biomass", litterfall C:N ratio: "CN litterfall", litterfall carbon deposition: "C litterfall"). In the case of air temperature (i.e. "Temperature"), only tree aboveground productivity and functional traits were considered in the trait-basal model.

temperature, confirmed previous findings emphasizing the role of forests as a heat buffer (Frenne *et al.* 2019). In the same line, we found negative effects of tree-specific root length on soil water availability, which can be explained by increased water uptake with a denser root system (Zhang *et al.* 2020). This increase in water consumption, consequently decreasing soil water availability, would increase the competition for water between trees and understory plants and would explain the negative effects of specific root length on understory productivity (i.e., plant cover and root biomass). In addition to the belowground competition, our results suggested an aboveground competition for light with negative effects of forest vertical stratification on understory productivity (Hakkenberg *et al.* 2020; Mueller *et al.* 2016). Besides, we confirmed the role of trees in controlling soil nitrogen and phosphorus contents by modifying litter C:N ratio and root morphological traits related to desiccation and exudation (i.e., N and P-rich compounds, Bardgett *et al.* 2014; Sun *et al.* 2017).

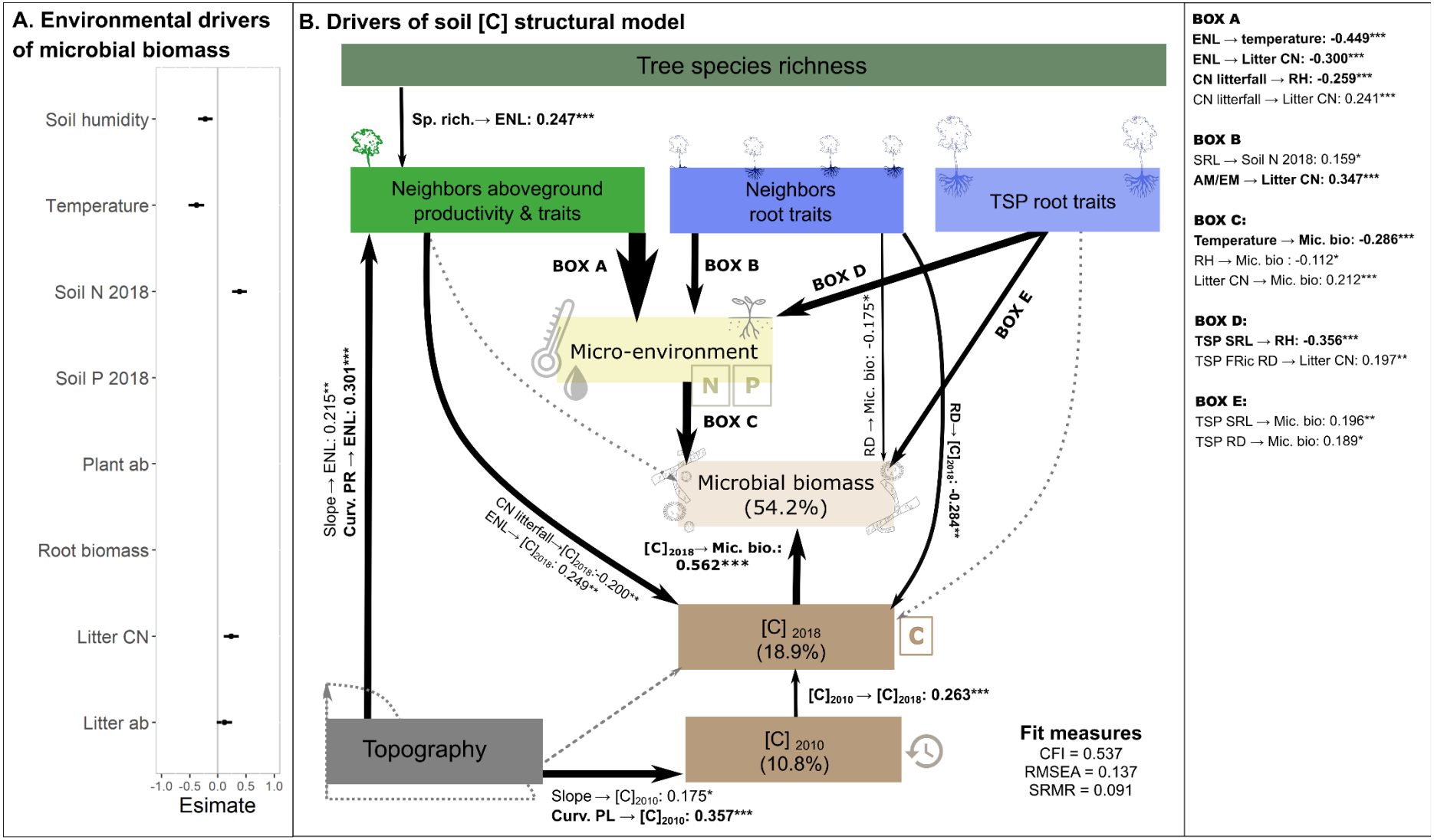
A. Environmental drivers of microbial biomass
Soil humidity
Temperature
Soil N 2018
Soil P 2018
Plant ab
Root biomass
Litter CN
Litter ab
-1.0 -0.5 0.0 0.5 1.0
Esimate
B. Drivers of soil [C] structural model
Tree species richness
Sp. rich.→ ENL: 0.247***
Neighbors aboveground productivity & traits
Neighbors root traits
TSP root traits
BOX A
BOX B
BOX C
BOX D
BOX E
Micro-environment
N
P
Microbial biomass (54.2%)
[C] 2018 (18.9%)
C
[C] 2010 (10.8%)
Topography
Slope → ENL: 0.215**
Curv. PR → ENL: 0.301***
CN litterfall→[C]2018:-0.200**
ENL→ [C]2018: 0.249**
RD → Mic. bio: -0.175*
RD→ [C]2018: -0.284**
[C]2018→ Mic. bio.: 0.562***
[C]2010 → [C]2018: 0.263***
Slope → [C]2010: 0.175*
Curv. PL → [C]2010: 0.357***
Fit measures
CFI = 0.537
RMSEA = 0.137
SRMR = 0.091
BOX A
ENL → temperature: -0.449***
ENL → Litter CN: -0.300***
CN litterfall → RH: -0.259***
CN litterfall → Litter CN: 0.241***
BOX B
SRL → Soil N 2018: 0.159*
AM/EM → Litter CN: 0.347***
BOX C:
Temperature → Mic. bio: -0.286***
RH → Mic. bio : -0.112*
Litter CN → Mic. bio: 0.212***
BOX D:
TSP SRL → RH: -0.356***
TSP FRic RD → Litter CN: 0.197**
BOX E:
TSP SRL → Mic. bio: 0.196**
TSP RD → Mic. bio: 0.189*

Fig. III.5: Mediation of tree effects on soil microbial biomass by micro-environmental conditions. A. Effects of micro-environmental conditions on microbial biomass. For each driver of microbial biomass on the y-axis, the dot represents the estimated effect of the driver on microbial biomass, the line represents the 95% confidence interval for a given estimated value. The drivers excluded during model selection have neither estimates nor confidence intervals. **B. Structural equation model showing the relationships between topography (i.e. "Slope", profile curvature: "Curv. PR" and plan curvature: "Curv. PL"), soil history (i.e. "$[C]_{2010}$"), tree species richness, tree aboveground productivity and functional traits (i.e. "ENL" and "CN.litterfall") and root functional traits (i.e. "RD"), soil carbon concentration (i.e. "$[C]_{2018}$"), soil microbial biomass, and microclimatic conditions (i.e. "temperature", soil relative humidity : "RH", Soil nitrogen concentration: "Soil N 2018", litter collected on the ground C:N ratio: "Litter CN").** Each node represents a group of variables (selected from A., Fig. III.3.E., and Fig. III.4.B.) and each arrow summarizes all the significant effects between all the variables of two nodes. Arrow widths were sized by the sum of the standardized effect size of significant relations between all variables of the two nodes. When no significant relations were found between any variables of two nodes, the arrows are drawn with dashed lines. The variance in soil carbon concentration and microbial biomass explained by the model (R^2, in %) were added after the node name, see Suppl. III-S11 for detailed output. The significance levels were standardized across the panels (p-value > 0.05: "n.s.", p-value < 0.05: *, p-value <0.01: ** and p-value < 0.001: ***).

Micro-environmental conditions and root morphological traits drive microbial biomass

We showed that three micro-environmental parameters drove soil microbial biomass: temperature, soil humidity, and litter C:N ratio. In contrast to our expectations, soil microbial biomass decreased with increasing air temperature. Notably, we sampled during summer with an average daily temperature of 27°C ±3°C and an average maximum daily temperature of 35°C ±8°C. These high temperatures may exceed the thermal niche of some microbial taxa and thus repress microbial growth (Barcenas-Moreno *et al.* 2009). Surprisingly, high soil humidity also reduced total soil microbial biomass as well as both fungal and bacterial biomass. This is in contrast with previous findings showing no effect or a positive effect of soil humidity on soil microbial biomass (Serna-Chavez *et al.* 2013; see Pei *et al.* 2017 for subtropical forests). However, the local precipitation regime in September (i.e., heavy rains interspersed by some dry spells) and the topography of the study site with valleys where water accumulates, may have favored anoxic conditions and repressed soil microbial biomass.

Soil microbial biomass and soil carbon concentration are strongly related

Our analyses highlighted a robust positive correlation between soil microbial biomass and soil carbon concentrations. We expected feedback mechanisms between soil microbial biomass and soil organic carbon (Clemmensen *et al.* 2013; Lange *et al.* 2015). On the one hand, soil microbial growth is maintained and limited by soil organic carbon availability (see chapter 7, Bollag and Stotzky 1993). On the other hand, soil organic carbon is consumed and processed by soil microbes and is altered by their activity (Clemmensen *et al.* 2013; Schmidt *et al.* 2011). Soil microbial biomass and soil organic carbon are strongly related to each other (Serna-Chavez *et al.* 2013; Xu *et al.* 2013) due to the equilibrium between microbial growth and soil carbon consumption. However, in the present study, we could only verify the strong positive effect of soil carbon concentration on soil microbial biomass, while the potential feedback effect of soil microbes on soil carbon accumulation (Lange *et al.* 2015) was not significant. Measurements of the different soil carbon pools and more detailed assessments of soil microbial community structure and the activities of main groups therein would be needed to understand the fluxes of carbon between these carbon pools and the role of soil microbes as main consumers and producers of soil carbon (Goto *et al.* 1994; Liski *et al.* 2005).

Soil carbon concentration dynamics in BEF-China

Our analyses showed a loss of soil carbon during the first ten years of the experiment. Site A of the BEF-China experiment was planted in 2009 after a clear-cut of the previous conifer plantation (Yang *et al.* 2013). Clear-cut harvestings are known to enhance soil carbon loss during the following decade (Li *et al.* 2019; Seedre *et al.* 2014). This is mainly caused by a massive input of deadwood to the soil acting as a primer of soil organic matter decomposition as well as by the removal of litterfall and exudation causing a shift in microbial physiology (Taylor *et al.* 2008). However, this average decrease of soil carbon concentrations was accompanied by a large range variability of plot-level values (ranging from -3.33 g yr-1 to 1.85

g yr-1), suggesting strong local drivers of soil carbon dynamics. First, we found a positive effect of soil historical carbon concentrations on current soil carbon concentrations. Second, we found that the topography effects on soil carbon concentration were mostly mediated by the topography effects on historical soil carbon concentrations (Liu *et al.* 2020b; Scholten *et al.* 2017). This result highlights the importance of soil history for *in situ* experiments and the need to consider historical variables in the analyses. Moreover, integrating time in our studies of BEF relationships and considering soil history already proved useful to understand the slope of BEF relationships as well as its change over time (Guerrero-Ramírez *et al.* 2017; Vogel *et al.* 2019).

Neighborhood tree traits and productivity are driving soil carbon concentrations

Once controlling for topography and soil history effects, neighborhood trees influenced soil carbon concentrations, both through above- and belowground mechanisms. Aboveground, soil carbon concentration was increased by forest vertical stratification, which decreased litterfall C:N ratio, i.e. increasing litter quality. The positive effects of forest vertical stratification can be related to two independent mechanisms: on the one hand, the increase of tree biomass production and thereby enhanced inputs to the soil (Liu *et al.* 2018); on the other hand, the reduction of erosion due to the reduction of the kinetic energy of throughfall with higher crown complementarity (i.e., higher ENL, Goebes *et al.* 2015; Seitz *et al.* 2015). Moreover, the negative effect of litterfall C:N ratio suggests reduced nitrogen limitation may contribute to soil carbon stabilization, which emphasizes the central role of the biotic processes transforming the fresh litter to stable carbon forms (Buckeridge *et al.* 2020).

Belowground, root diameter increased soil carbon concentrations. Root morphological traits, such as RD, have been related to belowground biomass allocation and productivity (Bardgett *et al.* 2014) and to increase soil carbon concentrations (Adamczyk *et al.* 2019). However, our measurements of root traits were based on species-specific values and did not consider trait

plasticity (Sun *et al.* 2017). Tree diversity and forest productivity have been shown to influence fine root traits, such as RD (Sun *et al.* 2017). Our study again stresses the need for non-invasive methods and measurements of belowground productivity and root traits (Bu *et al.* 2017; Sun *et al.* 2017). Such measures will allow us to consider trait plasticity and disentangle productivity and physiological effects.

Scale-dependent effects of root functional traits

Our results highlighted the importance of the scale considered to explain root functional traits' effects on the micro-environment, soil microbial biomass, and soil carbon concentrations. While micro-climate and soil quality (including soil carbon concentration) were mostly driven at the neighborhood level, biotic conditions like understory plant cover were mainly affected by the TSP root functional traits. Besides, soil microbial biomass was affected by micro-environmental conditions but also by root functional traits acting at both scales. At the TSP level, root morphological traits (SRL and RD) increased microbial biomass, while at the neighborhood level, RD decreased microbial biomass. This spatial dependency of root traits such as RD could be explained by complementary mechanisms. At TSP level, microbial biomass may benefit from root productivity and exudation (Bardgett *et al.* 2014; Eisenhauer *et al.* 2017), while at the neighborhood level, RD may be related to tree resource use (e.g., water) and therefore to the competition for resources between trees and the microbial community (Bernhard *et al.* 2018; Burgess *et al.* 1998). Such spatial dependency of the processes could explain the inconsistent results found in previous soil microbiology studies (Cesarz *et al.* 2020; Pei *et al.* 2016) and emphasize the need to consider space in our measurements and analyses of soil ecosystem functioning (Eisenhauer *et al.* 2020; Ettema and Wardle 2002).

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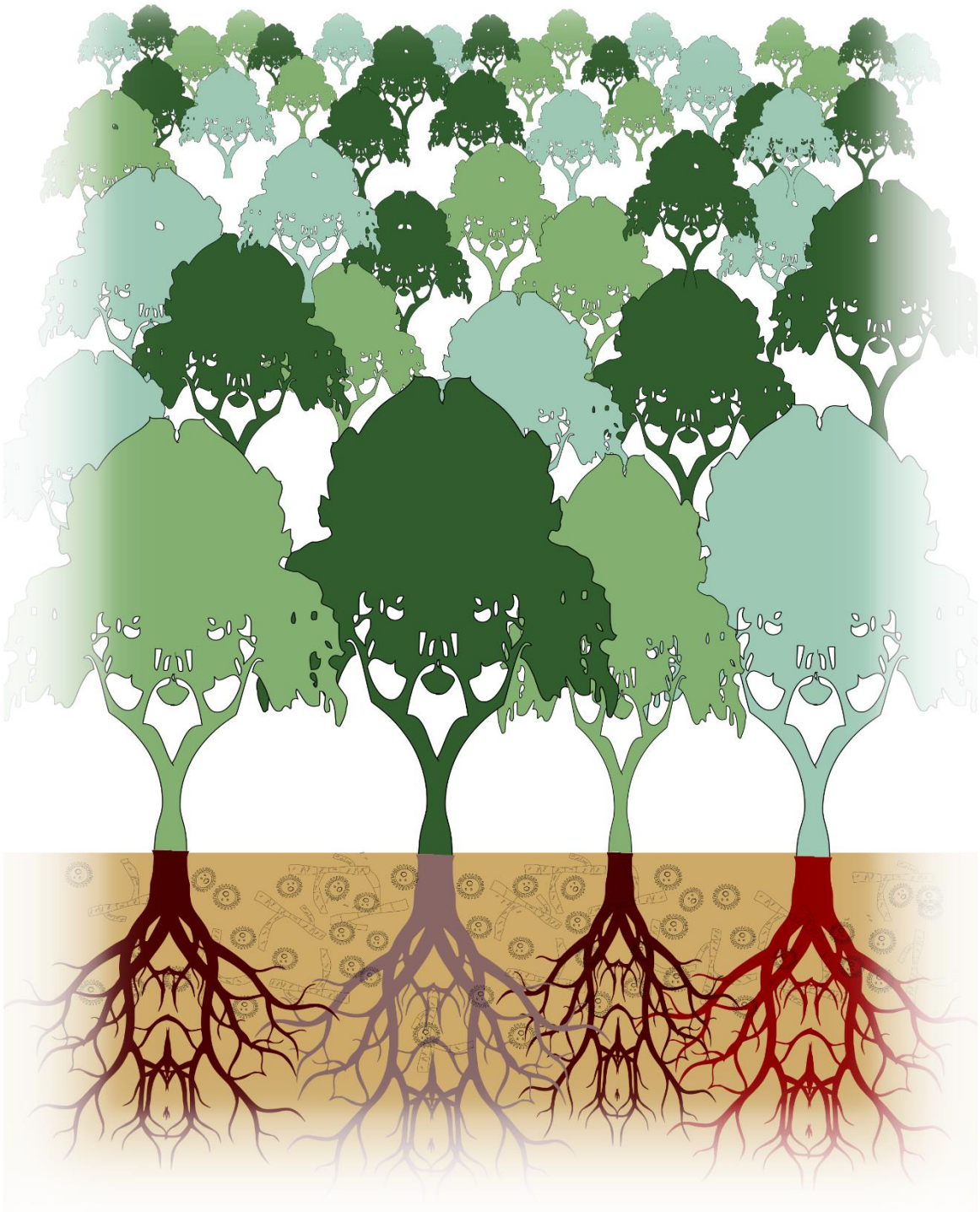
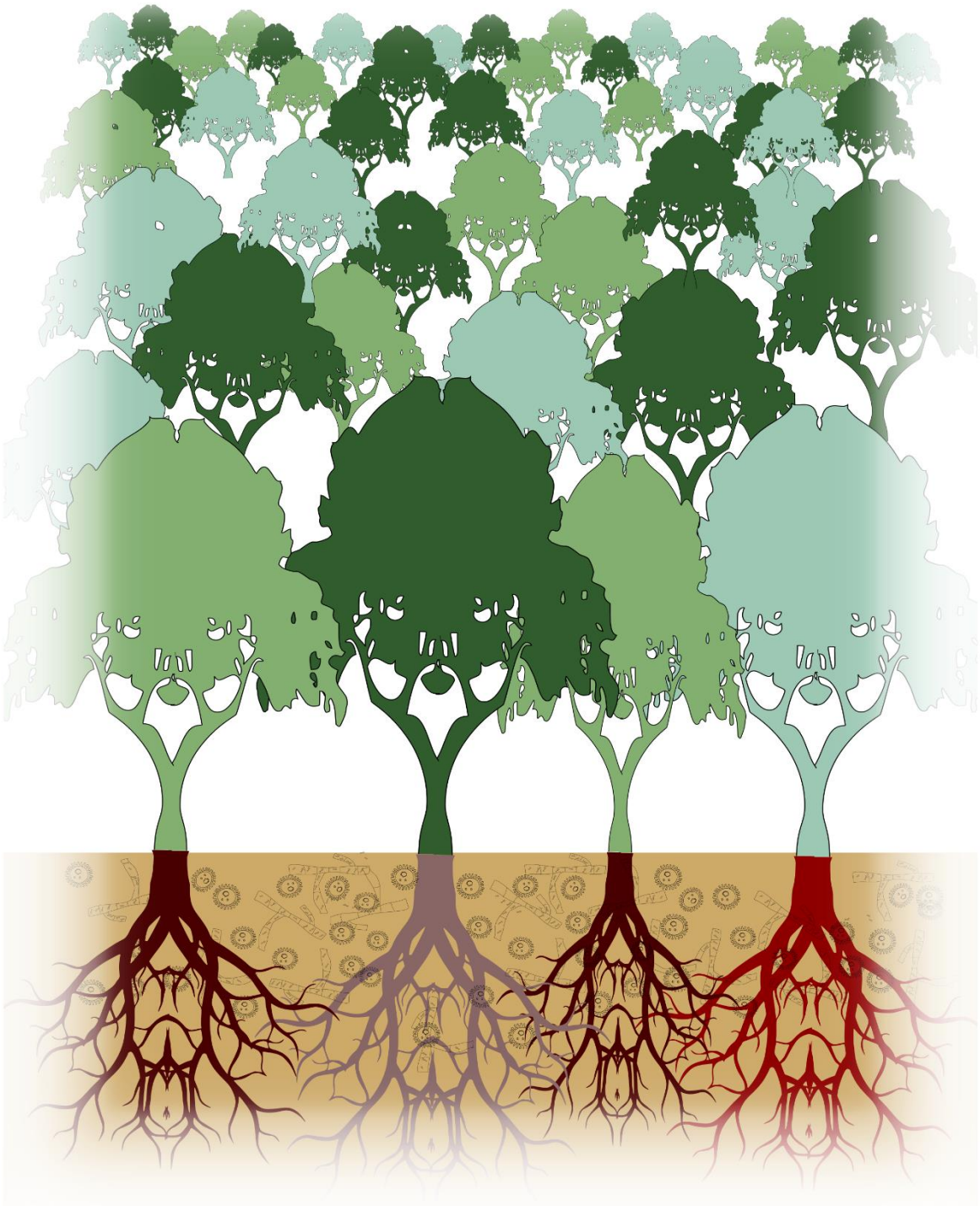
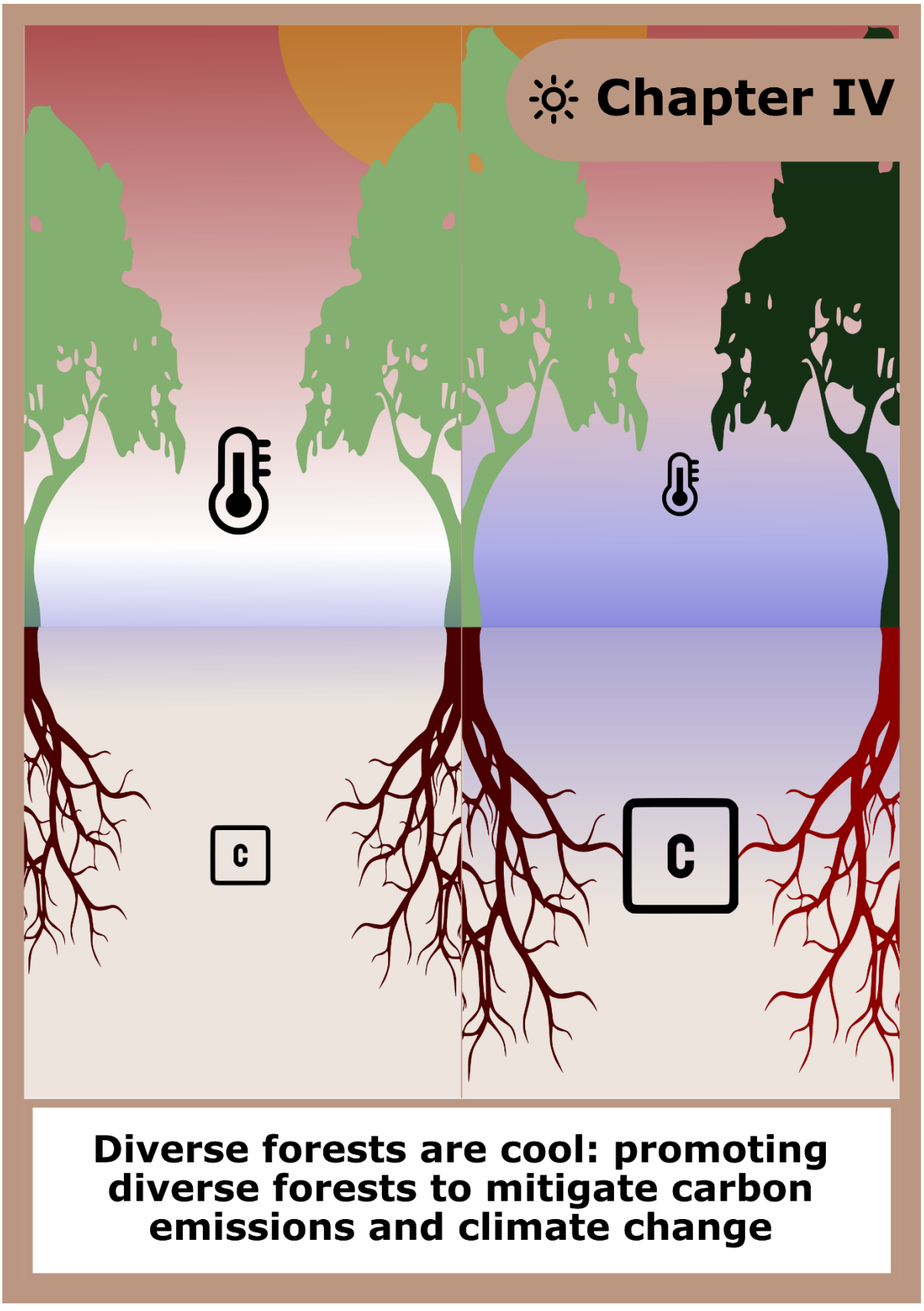


Transition III - IV

In the third chapter, my colleagues and I highlighted the positive effect of tree diversity on carbon storage in forests, by increasing tree aboveground productibity and soil carbon concentrations. Moreover, we highlighted the mechanisms behing tree diversity effects on soil carbon storage and the scale-dependency of these mechanisms. In this last chapter, we explored the implications of these results to mitigate increasing atmospheric carbon and how tree diversity could mitigate the effects of climate change for ecosystem functioning and human well-being.





Diverse forests are cool: promoting diverse forests to mitigate carbon emissions and climate change

Chapter IV – Diverse forests are cool: promoting diverse forests to mitigate carbon emissions and climate change

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Abstract

Climate change is one of the most pressing threats to humanity, inducing a global increase in temperatures and more frequent extreme climatic events. Considering this, global reforestation initiatives are proposed to capture carbon and mitigate climate change. Global restoration and reforestation programs and their targets have inspired both unparalleled enthusiasm worldwide and intense scientific criticism and debate regarding their feasibility and implementation. We agree that global reforestation forecasting and efforts require a nuanced discussion and approach. In that vein, we would like to emphasize the potential of increasing existing forest diversity to enhance climate change mitigation by increasing aboveground and belowground carbon storage. Moreover, we argue that focusing on planting diverse forests in reforestation efforts can help to reduce climate change effects on ecosystems: first, by increasing resistance and resilience to extreme climatic events, and second, by buffering microclimatic conditions in natural and urban areas. Diversifying forests plantations and reforestation projects may not always be feasible and cannot solve the climate crisis by itself. However, we highlight that a focus on diverse forests could maximize the benefits of reforestation programs by promoting sustainable land management.

Climate change and nature-based mitigation

Climate change threatens humanity and other life on Earth (IPCC 2013, 2021). The IPCC reports (2013, 2021) highlighted the crucial role of anthropogenic carbon dioxide (CO_2) emissions in climate change, estimating that CO_2 emissions contributed to about 0.75°C of the 1°C global warming over the last century (IPCC 2013, 2021). In addition to global warming, climate change induces more frequent and intense extreme climatic events, such as heatwaves and droughts. Enhancing photosynthetic carbon capture by increasing tree cover and restoring degraded forests has been suggested as one of the most effective approaches to mitigate climate change (Bastin *et al.* 2019; Lewis *et al.* 2019b). The IPCC (2013) projected that 1 billion ha of forest would be needed to keep global warming increases below 1.5°C by 2050 (IPCC 2013). This estimate was downscaled by Bastin *et al.* (2019), who predicted that planting 0.9 billion ha could store 205 Gt of carbon while investigating available areas for reforestation worldwide (Bastin *et al.* 2019). However, these numbers have been heavily criticized since their

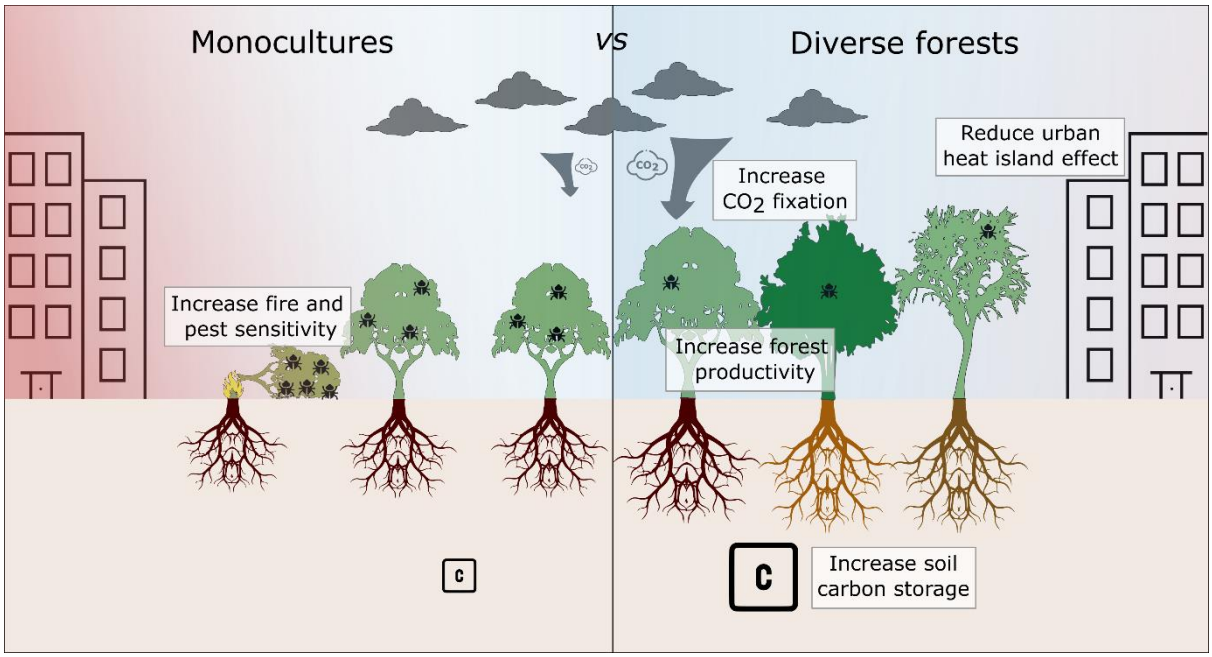

Figure IV.1: Conceptual figure of the effects of tree diversity on ecosystem properties related to climate change mitigation. Briefly, diverse forests have been shown to fix more carbon from the atmosphere, store more carbon above- and belowground, decrease the likelihood and severity of fires and pest outbreaks, and mitigate microclimatic conditions under climate change.

publication (Skidmore *et al.* 2019; Lewis *et al.* 2019a). The main concern is that the study overestimated the carbon storage potential of forests, thus underestimating the land area needed to achieve current carbon storage goals. Therefore, one major source of debate is that a global reforestation initiative to store 205 Gt of carbon would compete with other land uses (e.g., cropland, urban areas).

Diversifying forests to mitigate carbon emissions

There is increasing evidence that tree diversity has a positive effect on multiple measures of ecosystem functioning in forests (i.e., multifunctionality; Schuldt *et al.* 2018; Messier *et al.* 2021; Gamfeldt *et al.* 2013). Especially diverse forests were shown to increase aboveground (Huang *et al.* 2018; Duffy *et al.* 2017) and belowground (Xu *et al.* 2020; Liu *et al.* 2018) carbon storage (Fig. IV.1), e.g. by increasing tree complementarity while reducing soil carbon loss by erosion (Schuldt *et al.* 2018; Huang *et al.* 2018; Williams *et al.* 2017). For instance, in subtropical climates, species-rich forests of 20 tree species per ha store three times more carbon than monocultures (Liu *et al.* 2018). We argue that diversifying existing forests and reforestation projects will increase and stabilize forest carbon storage, therefore reducing the land needed for global reforestation projects, and thus the competition for land between reforestation projects and other important land uses. However, even if these patterns seem to be consistent globally (Xu *et al.* 2020), better global coverage of research across biomes is needed to predict the carbon storage potential of locally diversified forests. Promising initiatives in this context include the increasing availability of forest inventory data (e.g., Craven *et al.* 2020), the global network of tree diversity experiments (TreeDivNet; Verheyen *et al.* 2016), and global restoration initiatives with a biodiversity focus (e.g., Restor[1]). Likewise, promoting species-rich plantations will enhance the carbon storage potential of managed

[1] https://restor.eco/

forests in addition to reforestation projects. Transdisciplinary projects are needed to understand both biodiversity and production constraints and objectives (Messier *et al.* 2021). Here, we suggest that biodiversity-ecosystem functioning (BEF) research should take a sharp turn toward transdisciplinary research to better meet the practical demands of land managers, practitioners, and restoration initiatives (Messier *et al.* 2021). For instance, Mao *et al.* (2021) proposed and applied a holistic modeling framework to link biodiversity conservation and socio-economic goals in French mountain resort areas (Mao *et al.* 2021).

Diverse forests to mitigate the consequences of climate change

Climate change is expected to increase the frequency and intensity of extreme climatic events as well as biological responses to those events, such as drought, fire, and insect outbreaks (Messier *et al.* 2021; Pureswaran *et al.* 2018), increasing tree mortality and reducing forest heath. Climate change could contribute to reduce forest cover in the tropics by more than 200 million ha by 2050 (Bastin *et al.* 2019). Concurrently, tree diversity experiments have shown the high potential of diverse forests to buffer extreme climatic events (see Grossiord 2020 for context-dependencies; Fichtner *et al.* 2020). For example, tree diversity mitigates drought effects on forest productivity (Fichtner *et al.* 2020) by increasing the asynchronous response of tree species to climatic variability (Schnabel *et al.* 2019), thereby stabilizing ecosystem services (Messier *et al.* 2021; Gamfeldt *et al.* 2013). Likewise, increasing tree diversity stabilizes long-term carbon storage by reducing forests' susceptibility to fire and thus the net release of carbon dioxide (Messier *et al.* 2021). Moreover, diverse forests are naturally resistant to extreme insect outbreaks and herbivory pressure by supporting multitrophic biodiversity (Schuldt *et al.* 2018; Jactel *et al.* 2021). Given the many advantages that diverse forests provide, promoting diverse forests in existing forests and in reforestation projects present multiple benefits to protect forests from climate change in a sustainable way (Fig. IV.1).

Diverse forests to increase human well-being in cities

In cities - where most humans live - temperature increase is amplified by sealed surfaces and a lack of vegetation (so-called urban heat island effect), intensifying summer heatwaves, and exacerbating intense climatic effects on human well-being (IPCC 2021). Increasing urban tree cover and planting urban forests have been shown to reduce the urban heat island effect and to improve human well-being by shading surfaces (Gamfeldt *et al.* 2013). Urban forests could account for up to 1% of the total global reforestation potential (Bastin *et al.* 2019), which is an efficient space to improve millions of lives. Simultaneously, tree diversity increases aboveground productivity in forests (Huang *et al.* 2018; Duffy *et al.* 2017) and tree crown structural complementarity (Williams *et al.* 2017). Therefore, we expect tree diversity to increase canopy buffering of macroclimatic fluctuations (Frenne *et al.* 2021) and thus reduce the microclimatic temperature below the canopy under warm conditions (Gottschall *et al.* 2019). Increasing tree diversity in and around the urban matrix has the potential to enhance forest cooling effects (Fig. IV.1), but more experimental work is needed to explore this phenomenon and its magnitude. Here, we argue that public policy should take advantage of urban areas to plant diverse forests locally and contribute to climate change mitigation while increasing population well-being.

Outlook

We argue that diversifying existing forests and planting diverse forests through reforestation programs will promote forest carbon storage and can thus contribute to climate change mitigation. Moreover, increasing tree diversity will promote forest multifunctionality and protect forest functioning against climate change-induced threats (e.g., extreme climatic events, insect outbreaks). Finally, we suggest that tree diversity should be promoted in urban areas to locally buffer warming while improving human well-being. There is strong momentum for re-

/afforestation initiatives like the UN Decade on Ecosystem Restoration (2021-2030)[2], the Bonn Challenge[3], and the European Green Deal[4], as well as sustainable management of forests (see UN Sustainable Development Goals[5]: 6, 11, 13, 15). We acknowledge that reforestation is not possible everywhere and may also impose serious pitfalls, like the reduction of water availability or increase of social iniquity (Holl and Brancalion 2020). Therefore, to increase the likelihood of success of these initiatives, transdisciplinary approaches are needed to connect scientists, land managers, and politicians to address sustainable land use and climate change mitigation. Further research is essential to better assess how diverse forests will maximize reforestation potential to mitigate climate change. In particular, we need to determine the conditions under which diversifying forests is feasible (Holl and Brancalion 2020) and which tree community will provide the greatest benefits, and the limits under which diverse forests can mitigate the effects of climate change and extreme climatic events.

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[2] https://wedocs.unep.org/bitstream/handle/20.500.11822/30919/UNDecade.pdf?sequence=7
[3] https://www.bonnchallenge.org/content/challenge
[4] https://ec.europa.eu/info/strategy/priorities-2019-2024/european-green-deal_en
[5] https://sdgs.un.org/

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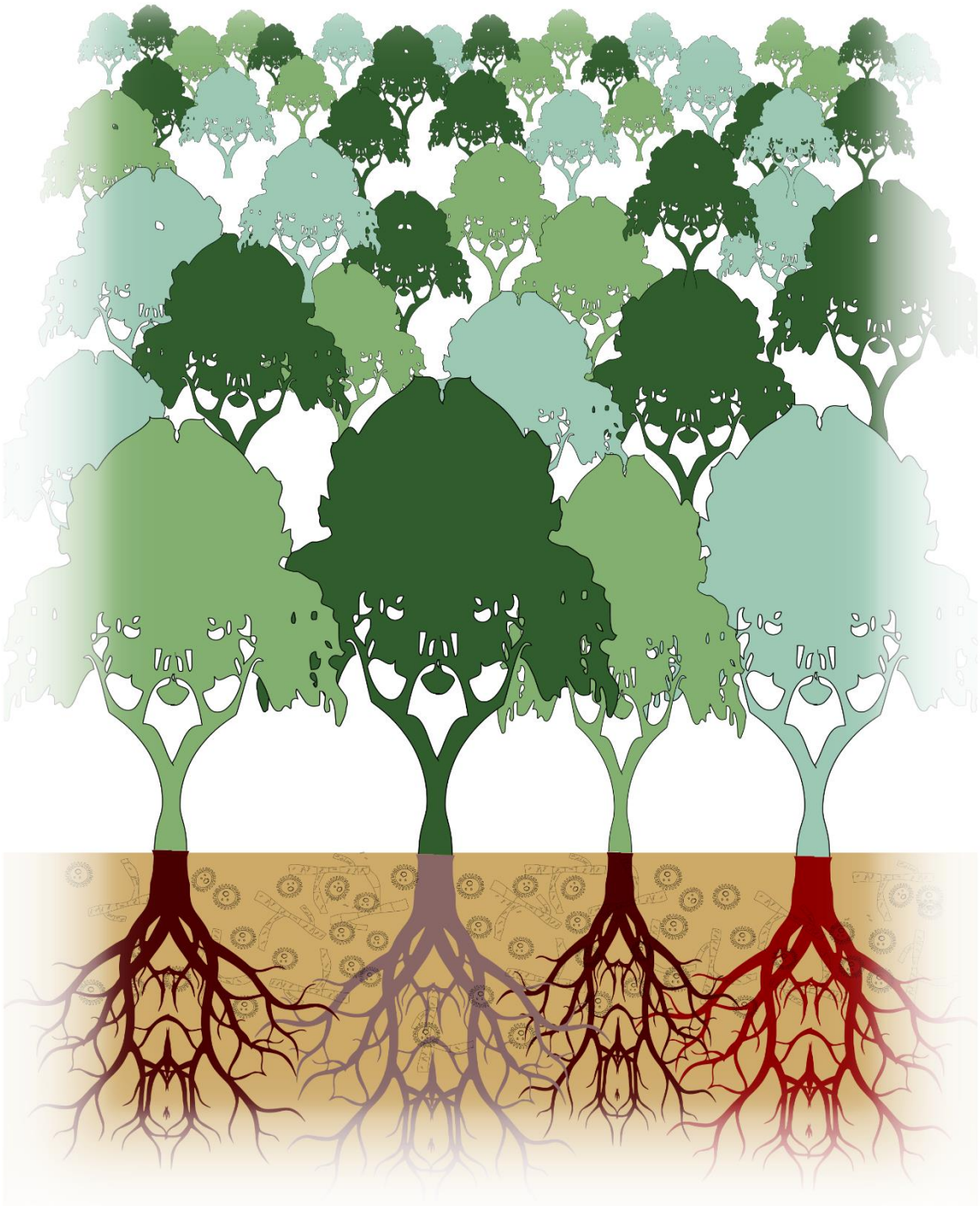

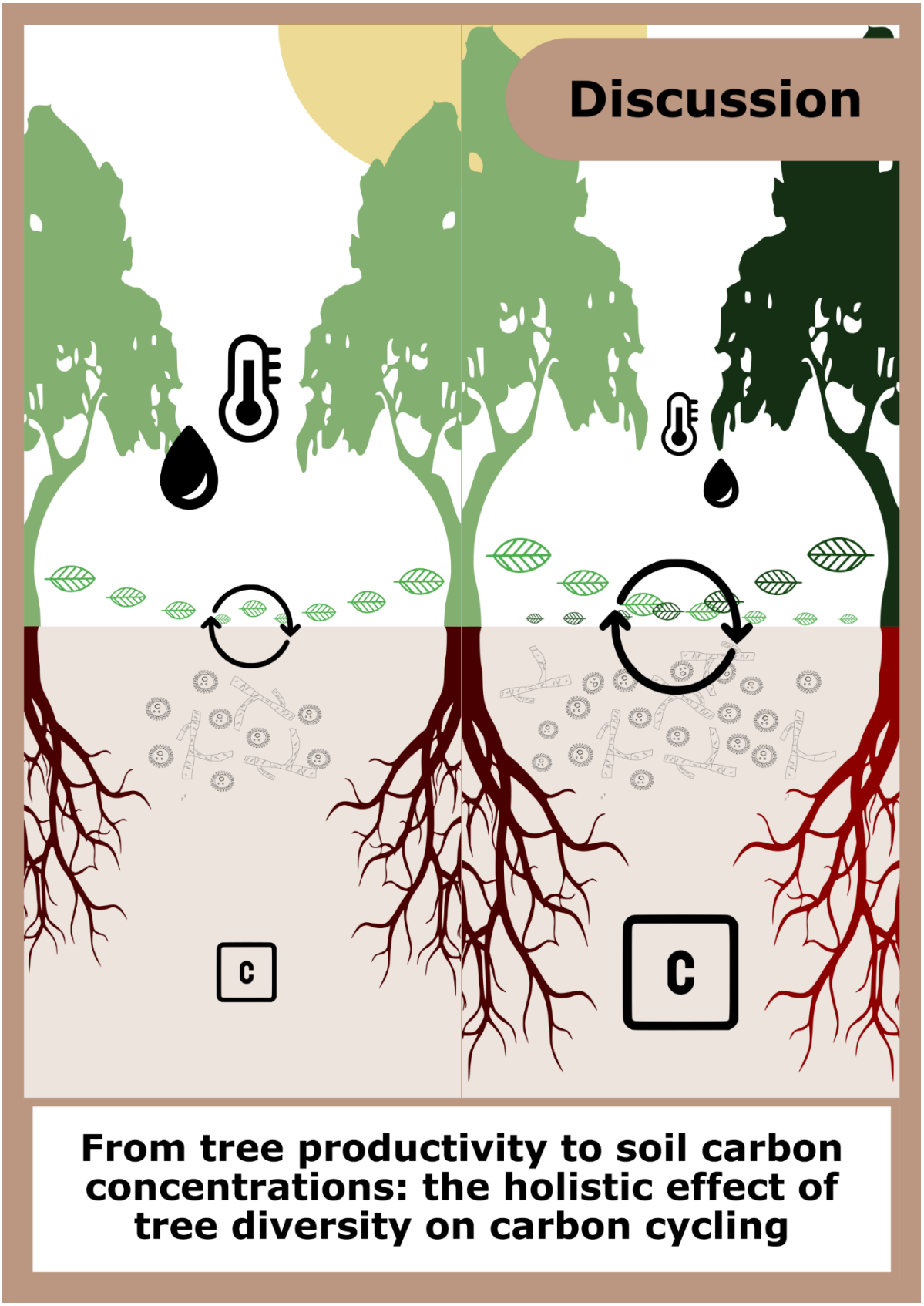

From tree productivity to soil carbon concentrations: the holistic effect of tree diversity on carbon cycling

General discussion

The first three chapters of this thesis aimed to explore the mechanisms behind tree diversity effects on carbon cycling in forests. Notably, we focused on microbial-based processes (Chapters I-III) and the consequences of tree diversity-induced spatial heterogeneity (Chapters I & III, Fig. 4). My colleagues and I considered several carbon cycling-related processes, such as tree biomass production, litterfall (Chapters I & III), litter decomposition (Chapter I), and *soil heterotrophic respiration*[1] (Chapter II). In addition, we explored the relationships between the microbial community composition and functions, and how tree diversity influenced these relationships (Chapter II). Following, we synthesized these results with a whole-ecosystem approach of tree diversity effects on carbon cycling by considering tree diversity effects on the main carbon compartments and their relationships in forests (Chapter III). Finally, in the last chapter, we explored the implications of diversifying plantations and re-/afforestation projects to enhance carbon sequestration, and the mitigating climate change effects on forests and human well-being (Chapter IV). In this final section, I first summarized the main findings of my thesis and highlighted the implications for future research and our societies.

Main findings

In this thesis, my colleagues and I highlighted how tree diversity affects carbon cycling in forests (Chapter I - III, Fig. 7). We showed that tree diversity effects on carbon cycling are manifold by affecting all compartments (e.g., above- and belowground) and processes (e.g., litterfall, decomposition, soil respiration) of the carbon cycle in forests (Chapters I – III, Fig. 7). Finally, we discussed the implication of diversifying forests in plantations and during reforestation initiatives. Moreover, we explored the benefits of diversifying forests to mitigate

[1] words in *italic* are defined in the Glossary page 2

extreme climatic events and microclimatic condition effects on forests and human well-being (Chapter IV).

(i) My colleagues and I demonstrated the positive effects of tree diversity on tree productivity, including litterfall (Chapters I & III). By increasing the amount and diversity of litterfall, tree diversity increased litter decomposition, and thus, the assimilation of tree products into the forest soil (Chapter I).

(ii) Our investigation showed the key role of microbial communities in controlling carbon dynamics by carrying out litter decomposition (Chapter I), *soil heterotrophic* respiration (Chapter II), and soil carbon stabilization (Chapter III). In addition, we showed how tree diversity increased soil microbial biomass (Chapter I-III) and functions (Chapter I-II). Moreover, we highlighted that tree diversity effects on soil microbial respiration are mediated primarily by soil microbial biomass rather than soil microbial community taxonomic or functional diversity.

(iii) The effects of tree diversity on microbial biomass were mediated by biotic and abiotic environmental conditions such as root functional traits, tree productivity, soil chemistry, and microclimate (Chapters II & III). For instance, tree diversity increased microbial biomass by reducing the local temperature, and thus, indirectly increased microbial processes.

(iv) We demonstrated the importance of considering neighborhood scale to understand tree diversity effects on ecosystem functioning (Chapters I & III). For example, in Chapter I, we showed that increasing tree diversity increased the spatial heterogeneity of litterfall with consequences for litter decomposition. In addition, we revealed in Chapter III the importance of investigating the different spatial scales at which tree functional traits affect soil microbial biomass and soil carbon concentrations.

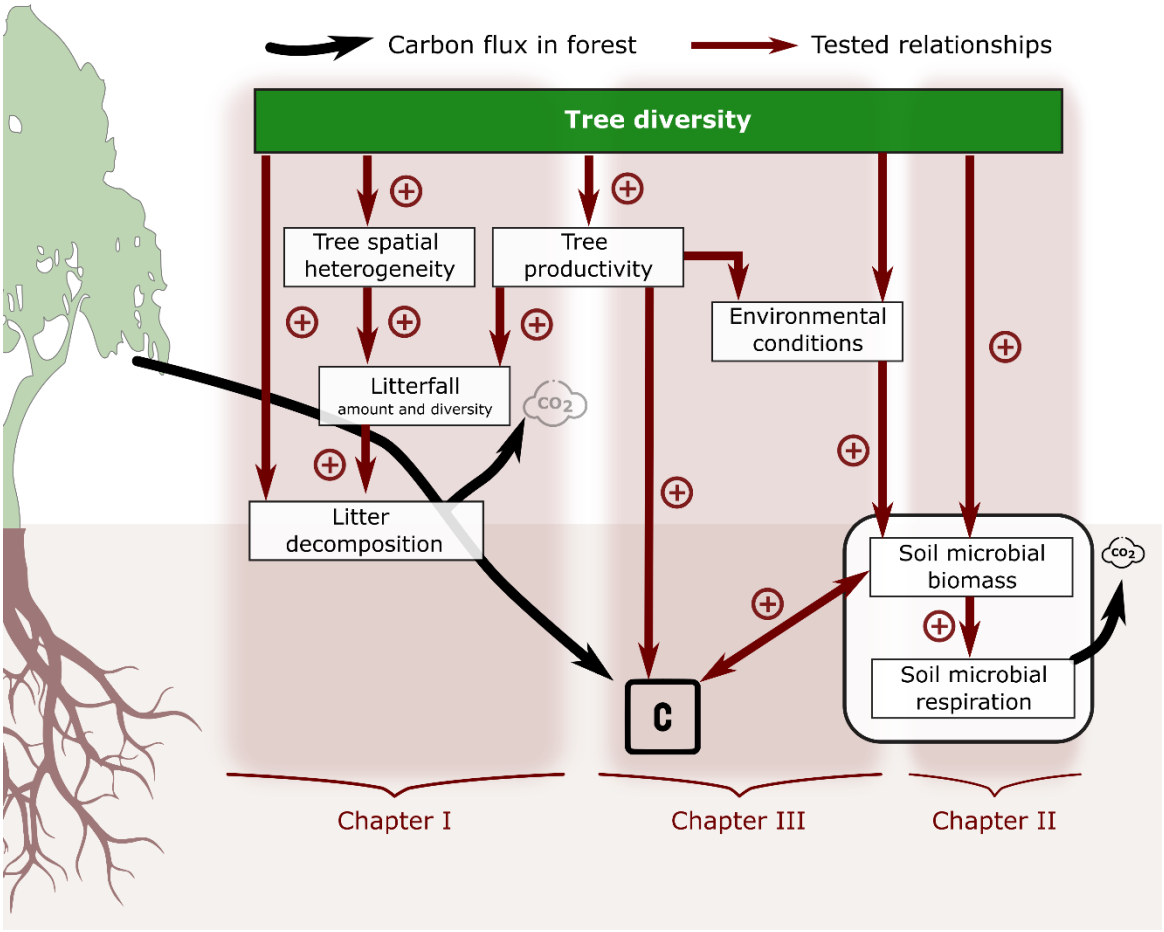

Fig. 7: microbial and spatial mediation of tree diversity effects on soil carbon cycling: visual summary of the main findings. Back arrows represent carbon fluxes between the different carbon compartments and processes (see Fig. 2). Red arrows indicate the results of tested relationships, a plus sign was added when the relationship was positive. Causal relations were drawn with single-headed arrows and correlations with double-headed arrows.

(v) We highlighted how planting diverse forests will promote climate change mitigation by increasing carbon fixation and storage, increasing forests resistance and resilience to climate change-induced threats (e.g., droughts, insect outbreaks), and mitigate microclimatic conditions in urban areas.

Together, our results suggest the crucial role of tree diversity in controlling forest functioning, the mechanisms behind tree diversity ~ carbon cycling relationships in forests, and the implication of diversifying forests for climate change mitigation.

Tree diversity effects on ecosystem functioning are manifold

Our results demonstrate the multiple effects of tree diversity on carbon cycling in forests by affecting every aspects (Fig. 7): from primary carbon inputs by photosynthesis (e.g., tree productivity, Chapters I & III) to the increase and stabilization of soil carbon by microbial transformation of freshly incorporated plant organic matter to stable microbial necromass (Chapter III, Buckeridge *et al.* 2020; Kästner and Miltner 2018). Moreover, we highlighted the interrelationships between all compartments and processes (Chapters I-III). For example, tree diversity increased on litter decomposition (Chapter I) by increasing the amount and diversity of litterfall and the microbial functioning (Chapter II). Due to these complex inter-relationships, this thesis reinforces the need for whole-ecosystem approaches to better understand the effects of biodiversity on ecosystems (Kay *et al.* 1999; Potvin *et al.* 2011; Shepherd 2004).

These new insights from a manipulative tree diversity experiment highlight the key role of tree diversity in maintaining upper trophic level diversity (Chapter II, Singavarapu *et al.* 2021) and functioning (Chapter I-III). In addition, diversity and functioning of upper trophic levels (e.g., soil microbial community) are expected to promote tree diversity (Albert *et al.* 2021; see Plant-Soil Feedback theory, Crawford *et al.* 2019; Miki *et al.* 2010; Mangan *et al.* 2010; Putten *et al.* 2016). Therefore, my thesis suggests that tree diversity, by promoting favorable environmental conditions, would enhance upper trophic level diversity and functioning, and thus tree diversity (Fig. 8). This positive feedback loop of tree diversity on tree diversity would suggest the self-maintenance of diversity in natural systems. Therefore, to understand the long-term consequences of planting diverse forests, future research should explore the successions of plant communities following a species-rich plantation to understand the long-term ecosystem effects of planting species-rich communities.

Being bigger makes you stronger, but diversity helps too

Tree diversity effects on ecosystem properties and functions are various; however, we can highlight two mechanisms: mass (i.e., the consequences of tree diversity ~ productivity relationships, Sonkoly *et al.* 2019) and diversity effects (i.e., the consequences of increasing tree products diversity, Fig. 8). We showed that higher tree biomass affected several aspects of carbon cycling in forests, such as litterfall, decomposition, and soil carbon concentrations (Chapters I & III). Moreover, we found similar mechanisms at the microbial community level, where increasing microbial biomass increased microbial respiration (Chapter II). In addition, we provided some evidence of diversity effects. For example, higher litter diversity increased litter decomposition (Chapter II), while crown structural complementarity reduced air temperature (Chapter III). Taken together, these results highlight the causal relationships behind tree diversity effects on forest functioning, as well as the complexity of the causal cascade resulting from these multiple causal relationships. For example, our results suggest a positive effect of tree diversity on soil microbial biomass due to changes in environmental conditions (Chapter III), while increasing soil microbial biomass promotes *heterotrophic respiration* (Chapter II) and soil carbon stabilization (Chapter III, Buckeridge *et al.* 2020; Kästner and Miltner 2018).

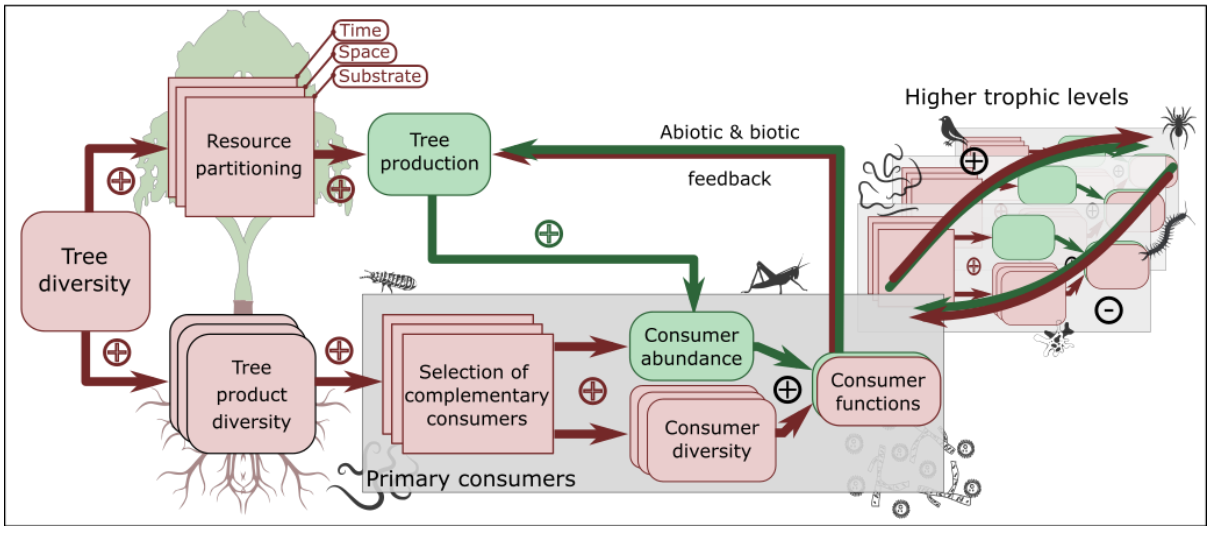

Fig. 8: Diversity (in red) and mass (in green) effects of tree diversity on ecosystem functioning (adapted from Fig. 3).

Tree diversity-induces spatial heterogeneity

A significant contribution of this thesis is the first demonstration that forest spatial heterogeneity is driven by tree diversity (Chapters I & III). Together with previous results showing higher crown (Perles-Garcia *et al.* 2021; Williams *et al.* 2017) or root (Guillemot *et al.* 2020) complementarity with increasing tree diversity, our results suggest that tree diversity effects on forest spatial heterogeneity are crucial to understand tree diversity effects on upper trophic level communities and functions. Moreover, the *sessile* nature of trees and the distance-based distribution of tree products (e.g., litter, Chapter I, Chandler *et al.* 2008) have structural consequences for the whole ecosystem, as shown in Chapters I & III; therefore, increasing tree diversity will *per se* will increase the forest heterogeneity. Our results suggest that the effect of tree-induced spatial heterogeneity appears at the local scale; however, how the spatial organization of tree species affects ecosystem functions remains unclear at the plot-level. For instance, parameters such as planting distances and spatial organization of tree species may become critical for forest functioning (Antony *et al.* 2012; Brazier and Mobbs 1993; Otsamo 2002; Uselis *et al.* 2020). Moreover, the distance-based effect of tree species may promote the non-linear distribution of products and lead to non-linear effects of tree diversity at the plot-level. Thus, estimates of processes such as decomposition or carbon storage at the plot level may differ greatly from traditionally measured averages. Therefore, this work emphasizes the need to consider the spatial distribution of forest processes and their relation to tree diversity in our sampling methods. Moreover, tree spatial distribution will determine possible tree-tree interactions. Tree-tree interactions may be crucial for ecosystem functioning (Fichtner *et al.* 2018). For instance, Fichtner *et al.* (2018) emphasized the importance of tree-tree interactions at the neighborhood scale to understand tree diversity effects on productivity. Therefore, tree-tree interactions are determined by tree diversity and the spatial distribution of tree species in the plot, highlighting the importance of local spatial scales for ecosystem functioning (Fichtner

et al. 2018; Williams *et al.* 2017) and suggesting a high spatial heterogeneity of interactions within forests.

Subtropical forest carbon cycle under microbial-control

Microbial communities are crucial for maintaining key ecological processes such as nitrogen fixation and nitrification. My results demonstrated role of microorganisms in controlling carbon cycling processes in subtropical forests (e.g., litter decomposition, Chapter I). Therefore, we showed that forest processes are driven by microbe, and we provided some first keys to understand tree diversity effects on soil microbial communities (Chapter II-III). However, our understanding of microbial community dynamics in forests remains scarce (Yokobe *et al.* 2018). For instance, litter is the primary interface between aboveground (Fanin *et al.* 2021) and belowground microbial communities. Before litterfall, leaves are exposed to the aboveground microbial community (Saadani *et al.* 2021); during litterfall, leaves get in contact with the belowground microbial community (Singavarapu *et al.* 2021). Therefore, litter decomposition is conducted by a mixed community resulting from the assemblage between aboveground and belowground microbial communities. However, little is known about the processes that lead to the formation of the decomposer community. We need to measure and follow the leaves' microbial community dynamics to better grasp microbial decomposition and the relative contribution of above- and belowground microbial communities. Here, both experimental and simulation-based approaches are needed to understand leaf microbial community dynamics and their drivers (Fanin *et al.* 2021).

Tree diversity control over environmental conditions

In Chapter III, we bring some first pieces of evidence for the control of tree diversity on microclimate promposed by Gottschall *et al.* (2019). In addition, in Chapter IV, we highlighted the potential of tree diversity to mitigate *extreme climatic events* (e.g., drought, flood) effects on tree productivity (Fichtner *et al.* 2020; but see Grossiord 2020 for context-dependencies),

and subsequently the implications for forest functioning (Schnabel *et al.* 2019). By stabilizing microclimatic conditions and reducing *extreme climatic events* effects on ecosystem function, tree diversity stabilizes ecosystem functions (Schnabel *et al.* 2019) and thus ecosystem services provided to human populations (FAO and UNEP 2020; Fichtner *et al.* 2020). However, the mechanisms linking tree diversity to microclimatic conditions remain unknown and require further investigation to understand the consequences of microclimatic buffering for ecosystem functioning.

Planting diverse forests to mitigate climate change

As suggested in Chapter IV, the positive effects of tree diversity on carbon storage in forests would help to maximize the potential of re-/afforestation initiatives to mitigate increasing atmospheric carbon and thus climate change (Bastin *et al.* 2019; Lewis *et al.* 2019). However, where and how diversifying forests is feasible remains to be identified (Holl and Brancalion 2020). For example, reforestation projects may lead to critical pitfalls such as reducing water availability and increasing soil salinity (Jackson *et al.* 2005) or exacerbating population inequalities (Holl and Brancalion 2020). Therefore, we need to clarify where re-/afforestation projects would be beneficial and how tree diversity could maximize these projects. In other words: we need to figure out "where" trees should be planted and "which" tree community should be planted. Therefore, the increasing availability of inventory data (Craven *et al.* 2020) together with the global network of tree diversity experiments (TreeDivNet, Verheyen *et al.* 2016) are promising initiatives to quantify tree diversity potential to mitigate climate change. In addition, few reforestation projects report progress and success rates, limiting our ability to learn from past experiences (Martin *et al.* 2021). Therefore, initiatives like Restor[2] will provide

[2] https://restor.eco/

unparalleled feedback for future projects and prevent us from repeating our mistakes (Holl and Brancalion 2020; Jackson *et al.* 2005).

Perspectives for future research

This thesis provides initial insights into tree diversity-induced spatial heterogeneity (Chapter I & III). Further research should focus on this second layer of diversity: the spatial heterogeneity of tree products, itsfunctional drivers, and the consequences for the overall food web and its functions (Fig. 3). According to my results, this new intermediate level representing the spatial heterogeneity within the ecosystem may become crucial to understand tree functions (e.g., productivity) and higher trophic levels drivers and functions (Chapter III). Le Provost *et al.* (2021) presented a spatially explicit framework by looking at aboveground and belowground diversity drivers across spatial scales: landscape-level (500-2000 m radius around the sampling point), field-level (75 m radius), and plot-level (50 – 50 m). Therefore, I would suggest extending this framework to a finer scale (i.e., within the ecosystem) to capture and understand plot spatial heterogeneity and the consequences for ecosystem functions. Following Le Provost *et al.* (2021), I would expect tree diversity-induced spatial heterogeneity to explain part of the plot-level heterogeneity, and thus the higher trophic level abundance, diversity, and functions.

Our understanding of tree diversity effects on ecosystem functioning may gain from exploring tree diversity-induced spatial heterogeneity; moreover, the effects of tree diversity on forest temporal asynchrony remain poorley understood (Fig. 3). This is especially true for the relationship between tree phenology and consumers phenology (van Schaik *et al.* 1993; Seifert *et al.* 2021). In their publication, Seifert *et al.* (2021) showed that herbivore community specialization increases between spring and fall, suggesting synchrony between leaf dynamics and herbivore community dynamics. Therefore, in species-rich forests that exhibit diverse tree phenology (Du *et al.* 2019; Huang *et al.* 2017), we might expect tree diversity-induced temporal asynchrony to drive consumer community and thus ecosystem functions. Further investigations

are needed to tackle this facet of tree diversity by following tree and consumer phenology across seasons and the consequences for ecosystem functions. Specifically, increasing tree litterfall asynchrony between the species will increase the number of freshly fallen litter inputs. Fresh litter inputs are expected to enhance litter and soil decomposition by a priming effect on the microbial community (Xu *et al.* 2018). Therefore, we would expect tree diversity to increase litter and soil decomposition by enhancing the fresh litter priming effect after each species fall.

Investigating spatio-temporal scales at the plot level requires high resolution and high temporal repetition of measurements (Gottschall *et al.* 2019). However, our current sampling methods are both limited in terms of resolution and unsustainable, often prioritizing efficiency over sustainability (Meyer *et al.* 2015). For instance, our first soil sampling in September 2018 required about 200 g of soil per sample to measure soil microbial community composition, biomass, physiology (MicroResp®), and respiration. Such a demand is not sustainable for repeated small-scale samplings. Moreover, mapping tree roots is often destructive as the entire root system must be excavated. Non-invasive methods for sustainable sampling are essential for investigating temporal and small spatial scales . One might look at the forest (above- and/or belowground) from three lenses: its physical structure (spatial arrangement and abundance of the different structural components such as branches, roots, rocks …), its chemical structure (i.e., the chemical composition such as soil carbon and nitrogen content, humidity), its biological structure (i.e., food web structure and biological processes such as decomposition), and external abiotic parameters such as temperature. Abovegroung, non-invasive methods to measure these different facets of the forests are numerous (Fig. 9); for instance, Terrestrial Laser Scanning used by Perles-Garcia *et al.* (2021) to measure aboveground physical structure, camera traps can be used to identify aboveground arthropod community (Droissart *et al.* 2021; Moore *et al.* 2021), caterpillar dummies to measure predation rate (Low *et al.* 2014; Howe *et*

al. 2009), and projects like AMMOD[3] allow for automated counting and identification of aboveground arthropod and plant species at larger scales. In addition, indirect methods such as measurements of the soundscape (Pijanowski *et al.* 2011) and smellscape (e.g., volatiles compound measurements; Tholl *et al.* 2021; Xiao 2020) are gaining importance and efficiency for determining species presense and dynamics. However, much progress is still needed belowground to widely open the "black box" (Fig. 9). For instance, new technologies based on X-ray (Mooney *et al.* 2012) and acoustic tomography (Bearce *et al.* 2014; Blum *et al.* 2004) are promising to improve mapping of soil structure (e.g., root, inorganic matrix, water, and air). However, these methods are still in the early stage of development and are not yet designed for *in situ* measurements. Likewise, a new method of mid-infrared spectrometry measurements would provide portable and non-invasive methods of soil chemistry (Ji *et al.* 2016), while requiring only a small amount of soil. Simultaneously, new sensors like EDAPHOLOG are promising avenues to identify and track soil microarthropods *in situ* (Dombos *et al.* 2017). However, measuring and identifying microbial communities and processes remains complex and soil consuming; some new methods are moving toward sustainability, for instance, *in situ* monitoring of microbial activity (Jin *et al.* 2020). In this vein, a method that consist in inserting and measuring chips will prevent repeated disturbances to the soil matrix and its communities. For example, methods like bait-lamina strips (Hamel *et al.* 2007) and TeaBags[4] (Keuskamp *et al.* 2013) to assess soil activity and decomposition, or microfluidic chips to sample soil microbial communities (Mafla-Endara *et al.* 2021; Pucetaite *et al.* 2021) are likely to gain importance in the coming years. Altogether, promising avenues consist in non-invasive measurements using tomography mapping of soil structures (e.g., seismic, acoustic, X-ray), spectrometry measurements of soil chemistry, image-based detection of soil organisms (e.g.,

[3] https://www.fona.de/en/measures/funding-measures/ammod_copy.php
[4] http://www.teatime4science.org/

EDAPHOLOG), and removable sampling chips (bait-lamina strips or microfluidic chips). All these previously mentioned methods should now be promoted in soil sciences to supportthe high spatial and temporal resolution of our samplings.

My thesis highlighted that tree diversity effects on ecosystem functioning are multifactorial and follow many pathways; therefore, having a holistic view of the ecosystem requires that numerous disciplines work together. Through this thesis, my colleagues and I promoted *interdisciplinary* approaches by bringing together experts of different fields such as plant ecologists, soil ecologists, cartographers, and microbiologists. The development of such *interdisciplinary* team is now a prerequisite for synthesizing broader research questions beyond disciplines like biodiversity-ecosystem functioning relationships (Kelly *et al.* 2019). Therefore,

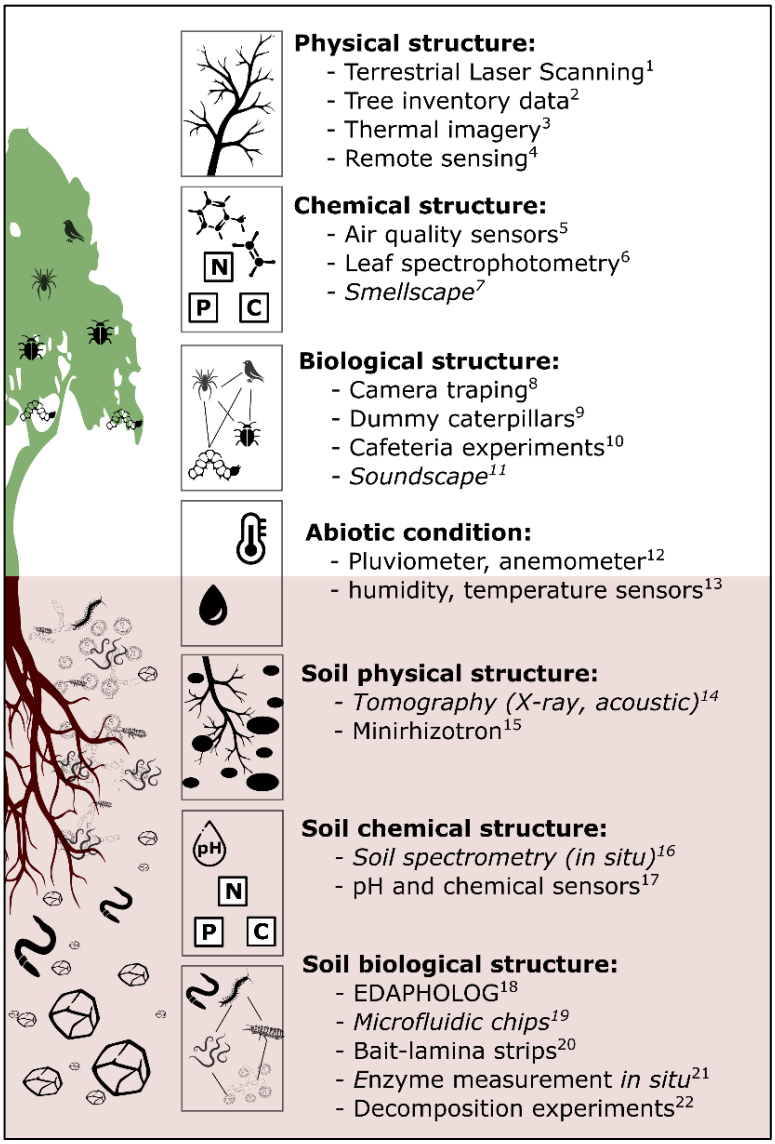

Fig. 9: Above- and belowground non-invasive measurement methods to access abiotic conditions and physical, chemical and biological structure of forests. Methods in italics are in development and not yet operational *in situ*.

References:

[1]: e.g. Kunz *et al.* (2019), Perles-Garcia *et al.* (2021)
[2]: Avery and Burkhart (2015)
[3]: Still *et al.* (2019); [4]: Wang and Gamon (2019)
[5]: Piedrahita *et al.* (2014)
[6]: Perez-Harguindeguy *et al.* (2013), e.g. Davrinche and Haider (2021)
[7]: e.g. volatile organic compounds Tholl *et al.* (2021) & Xiao (2020)
[8]: Dell *et al.* (2014)
[9]: Low *et al.* (2014), Howe *et al.* (2009)
[10]: Grime *et al.* (1996)
[11]: Pijanowski *et al.* (2011)
[12,13]: e.g. RX2100 Data Logger, HOBO Pendant® (ONSET, Bourne, USA)
[14]: Bearce *et al.* (2014), Blum *et al.* (2004), Mooney *et al.* (2012)
[15]: Svane *et al.* (2019)
[16]: Ji *et al.* (2016)
[17]: e.g. HOBOnet T21 (ONSET, Bourne, USA)
[18]: Dombos *et al.* (2017)
[19]: Mafla-Endara *et al.* (2021)
[20]: Kratz (1998), Eisenhauer *et al.* (2014)
[21]: Wallenstein and Weintraub (2008)
[22]: Keuskamp *et al.* (2013)

cohorts of doctoral researchers such as TreeDì in BEF-China (Trogisch *et al.* 2020) and in the Jena Experiment[5], provide nice examples of *interdisciplinary* teams built around a broader research question. However, one may question the feasibility of such *interdisciplinary* research in the context of a Ph.D. considering the duration of a doctoral project (e.g., three to four years in Germany) and of research fundings. This is especially true for time-related measurements which require years to build time series replicates. Therefore, to advance the understanding of temporal dynamics, long-term monitoring is needed to serve as a basis for these experiments.

Perspectives for our societies

This study is a step forward to the understanding of forest ecosystem functioning. Understanding the mechanisms shaping forests and driving their functions is critical to be able to predict biodiversity loss consequences on the potential ecosystem services such as wood production (FAO and UNEP 2020) or climate mitigation (Bastin *et al.* 2019; Lewis *et al.* 2019; IPCC 2013). Our results suggest that increasing tree diversity should enhance wood production as well as carbon storage (Chapter III, Xu *et al.* 2020). Moreover, tree diversity effects on these ecosystem services could be enhanced by selecting tree species base on their functional traits such as root and leaf characteristics. Together, these results are the first step to the prediction of ecosystem functioning and thus to our ability to provide accurate and efficient recommendations to practitioners. However, our results should be integrated into a larger framework to not only optimize few ecosystem functions, but also consider practitioners' needs and constraints (Messier *et al.* 2021). For instance, when tree productivity is a sufficient response variable for firewood production, millwork processes will require high-quality lumber (see ISO standards; Messier *et al.* 2021). In addition, our results suggest the relevance of tree-tree interactions and thus the importance of considering tree-tree interaction to guide planting

[5] http://the-jena-experiment.de/index.php/projects/

patterns in plantations and reforestation projects. Therefore, "planting diverse forests" may be an oversimplification of a problem that requires a higher integration of spatial, economic and social constraints (Messier *et al.* 2021). For example, if the goal of a planted forest is both storing carbon and producing wood for millwork, both aspects should be integrated into our research of suitable tree communities. Such questions can be solved by integrating goals (e.g., carbon storage and wood production) and their drivers (e.g., tree diversity, tree functional traits, including wood quality) in a simulation framework to predict ecosystem direction (Gaucherel *et al.* 2017; Gaucherel and Pommereau 2019). This approach would help us provide accurate and personalized recommendations to the practitioners (Mao *et al.* 2021; Messier *et al.* 2021). Exploring applicable and operational guidance for practitioners requires a greater *transdisciplinary* in BEF research to meet BEF goals and the practitioners' needs and constraints (see Chapter IV; Mao *et al.* 2021).

Finally, in times of international pandemic, global climate change, and loss of biodiversity, the relation between the scientists and the public becomes increasingly important to provide reliable information to the public. In particular, *science communication* makes it possible to demystify science for the general public by explaining both methods and results. Therefore, *science communication* is critical to provide reliable information to the public and fight conspiracy theories and fake news (Lewandowsky *et al.* 2017; McGee and Dawson 2020). In my opinion, engaging in *science communication* projects is not an option but a requirement for scientists, as is peer-reviewing (Tennant 2018). Consequently, more and more *science communication* projects are growing up, especially to inform and exchange with younger generations. The journal Frontiers for Young Minds allows researchers to write down their research for kids and young adults and provide a peer-reviewing by a scientific mentor and a young reviewer[6]. As part of this effort, Helen Philipps, Malte Jochum, and I edited a collection

[6] https://kids.frontiersin.org

about Soil Biodiversity[7] in Frontiers for Young Minds in the past few years to provide information about soil biodiversity, its drivers, and its functions.

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[7] https://kids.frontiersin.org/collections/11796/soil-biodiversity

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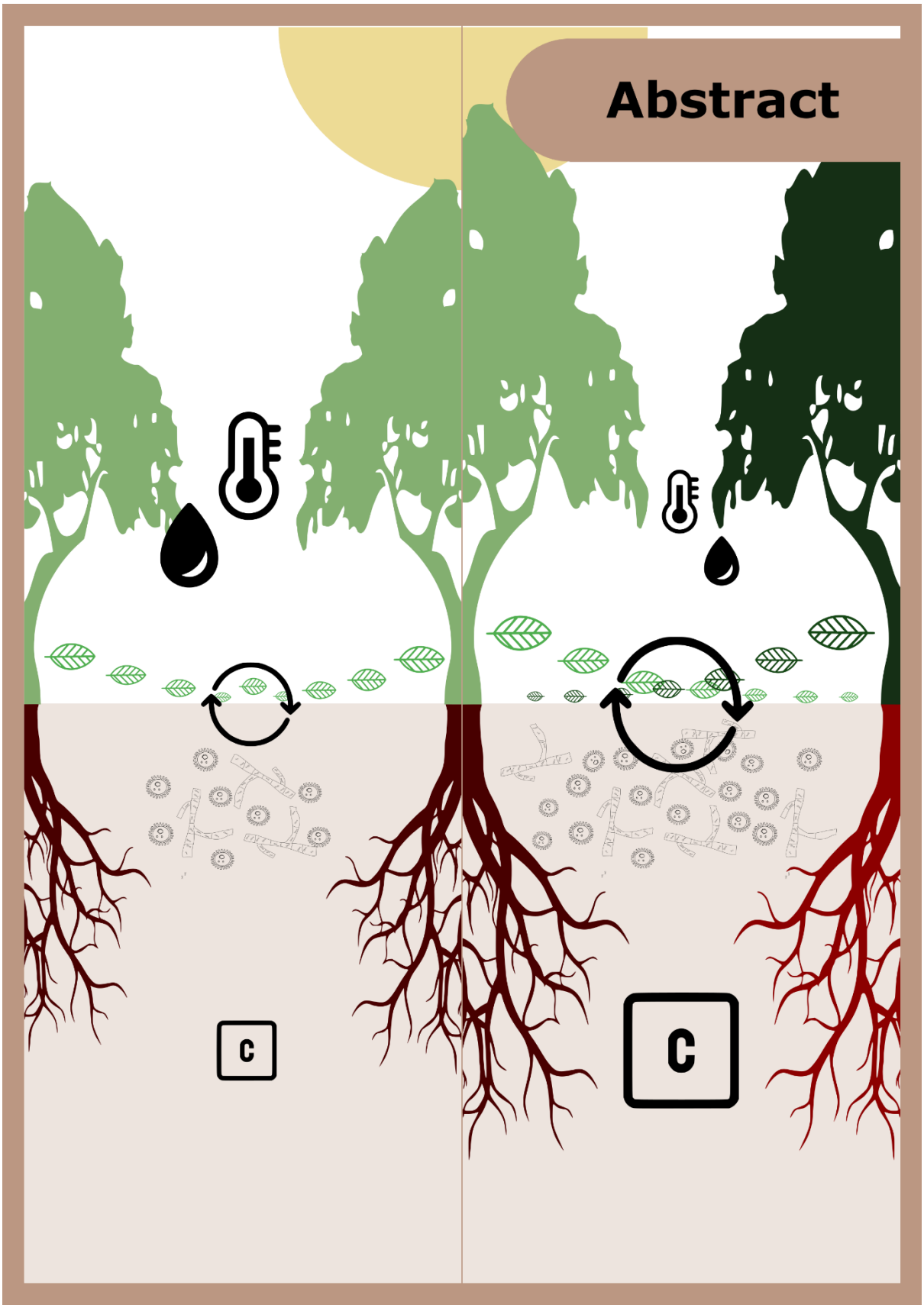
Abstract



Abstract

The loss of biodiversity is affecting all ecosystems on Earth, one of the greatest threats to biodiversity being climate change. Forests have been highlighted for their potential to mitigate climate change by storing carbon above- and belowground in soils. For decades, ecologists have built biodiversity-ecosystem functioning experiments (BEF experiments) aiming to understand the consequences of species loss for ecosystem functioning and services provided to humanity. The loss of tree diversity is expected to have cascading effects on the entire ecosystem and its functions, such as tree productivity and carbon storage.

In this thesis, I studied the effects of tree diversity loss on carbon cycling in subtropical Chinese forests. My goal was to explore the mechanisms behind tree diversity effects on carbon cycling by focusing on microbial-based processes and the consequences of tree diversity-induced spatial heterogeneity.

First, I reviewed the current state of knowledge of the mechanisms behind tree diversity of carbon cycling processes in forests. Second, my colleagues and I tested the effects of tree diversity on litterfall spatial patterns and the consequences for litter decomposition (Chapter I) and quantified the importance of microbial community in decomposition processes. Third, we explored the effects of tree diversity on relationships between soil microbial facets (i.e., biomass, taxonomic and functional composition) and soil microbial functions such as heterotrophic respiration (Chapter II). Fourth, we took a holistic approach to test the effects of tree diversity on soil microbial biomass carbon concentrations and their mediation by biotic and abiotic environmental conditions (Chapter III). Finally, we explored the consequences of diversifying forests for re-/afforestation initiatives and plantations to reduce atmospheric carbon levels, as well as the benefits of tree diversity for mitigating the effects of climate change on ecosystems and human well-being.

My literature review suggested that tree diversity effects on carbon cycling in forests are manifold and can be explained by the complementarity of species across trophic levels. This complementarity among species can include three aspects: the complementarity for substrate-use, the spatial and temporal complementarity between species. I have emphasized that spatial and temporal complementarity of tree species is gaining attention; however, the consequences of tree-induced spatio-temporal heterogeneity for higher trophic levels are still unknown. Across the different chapters of this thesis, I explored tree diversity effects on carbon cycling while considering tree diversity-induced spatial heterogeneity consequences. My colleagues and I highlighted the positive effects of tree diversity on tree productivity (i.e., tree biomass, litterfall, and crown complementarity, Chapters I & III). By increasing the amount and diversity of litterfall, tree diversity increased litter decomposition and subsequently the assimilation of tree products into the forest soils (Chapter I). Second, our investigation has shown the key role of microbial communities for forests carbon dynamics by carrying out litter decomposition (Chapter I), soil heterotrophic respiration (Chapter II), and soil carbon stabilization (Chapter III). In addition, we demonstrated how tree diversity increased soil microbial biomass (Chapters I-III) and functions (Chapters I-II). Most notably, tree diversity effects on soil microbial respiration were mainly mediated by soil microbial biomass rather than soil microbial community taxonomic or functional diversity. Third, the effects of tree diversity on microbial biomass were mediated by biotic and abiotic environmental conditions such as root functional traits, tree productivity, soil quality, and microclimate (Chapter II & III). For instance, tree diversity increased microbial biomass by lowering local temperature thereby indirectly increasing microbial processes. Taken together, we revealed the importance of considering space to understand biodiversity-ecosystem functioning relationships (Chapters I & III). For example, we showed that increasing tree diversity increases the spatial heterogeneity of litterfall, with consequences for litter decomposition (Chapter I). Finally, we argued that tree

diversity is a promising avenue to maximize the potential of re-/afforestation projects to mitigate increasing atmospheric carbon (Chapter IV). Moreover, we highlighted that diversifying forests in re-/afforestation initiatives can help to reduce climate change effects on ecosystems: first, by increasing resistance and resilience to extreme climatic events, and second, by buffering microclimatic conditions in natural and urban areas.

Tree diversity affects carbon cycling in forests by increasing tree productivity, the diversity of tree produces, and environmental conditions. My investigation highlighted that tree diversity effects on ecosystem functioning could be explained by both mass (i.e., increase of productivity with higher diversity) and diversity effects (i.e., increase of tree products diversity) on higher trophic levels and their functions. The linkages between tree diversity and the higher trophic levels are critical; for example, we showed the key role of microbial communities in driving carbon cycling in subtropical forests. Moreover, our results highlighted the high potential of diverse forests to mitigate climate change by enhancing carbon storage, and thus, reducing the competition between reforestation initiatives and other land use. In addition, at local scale, we found high potential for tree diversity to buffer microclimatic conditions and extreme climatic events. By looking at the potential mechanisms of tree diversity effects on ecosystem functioning, I emphasized the key role of tree diversity-induced spatial heterogeneity and the need to consider space and time in further research. This high resolution of the sampling will require the development of non-invasive *in situ* methods in order to conduct our research in a sustainable way. Ultimately, our results provide a holistic view of tree diversity effects on carbon cycling in forests. These results need to be combined with practitioner constraints and demands to enable feasible restoration projects.

Zusammenfassung

Der Verlust der biologischen Vielfalt wirkt sich weltweit aus und betrifft alle Ökosysteme der Erde. Eine der größten Bedrohungen für die biologische Vielfalt und den Menschen ist der Klimawandel. Wälder haben das Potenzial, den Klimawandel abzuschwächen, indem sie ober- und unterirdisch Kohlenstoff in den Böden speichern. Seit Jahrzehnten haben Ökologen Experimente zur Biodiversität und zum Funktionieren von Ökosystemen (BEF-Experimente) durchgeführt, um die Folgen des Artenverlusts für das Funktionieren von Ökosystemen sowie die für die Menschheit erbrachten Ökosystemdienstleistungen zu verstehen. Es wird davon ausgegangen, dass der Verlust der Baumvielfalt kaskadenartige Auswirkungen auf das gesamte Ökosystem und seine Funktionen hat, wie z. B. die Produktivität der Bäume und die Kohlenstoffspeicherung.

In dieser Arbeit habe ich die Auswirkungen des Verlusts der Baumvielfalt auf den Kohlenstoffkreislauf in subtropischen chinesischen Wäldern untersucht. Mein Ziel war es, die Mechanismen zu erforschen, die hinter den Auswirkungen der Baumvielfalt auf den Kohlenstoffkreislauf stehen, indem ich mich auf mikrobiell basierte Prozesse und die Folgen der durch die Baumvielfalt verursachten räumlichen Heterogenität konzentrierte.

Zunächst habe ich den aktuellen Wissensstand über die Mechanismen hinter der Baumvielfalt und den Kohlenstoffkreislaufprozessen in Wäldern untersucht. Zweitens haben meine Kollegen und ich die Auswirkungen der Baumvielfalt auf die räumlichen Muster des Streufalls und die Folgen für die Zersetzung der Streu getestet (Kapitel I) und die Bedeutung der mikrobiellen Gemeinschaft für die Zersetzungsprozesse quantifiziert. Drittens untersuchten wir die Auswirkungen der Baumvielfalt auf die Beziehungen zwischen den mikrobiellen Facetten des Bodens (d. h. Biomasse, taxonomische und funktionelle Zusammensetzung) und den mikrobiellen Funktionen des Bodens, z. B. der heterotrophen Atmung (Kapitel II). Viertens haben wir einen ganzheitlichen Ansatz gewählt, um die Auswirkungen der Baumvielfalt auf

die Kohlenstoffkonzentration der mikrobiellen Biomasse im Boden und deren Vermittlung durch biotische und abiotische Umweltbedingungen zu untersuchen (Kapitel III). Schließlich untersuchten wir die Folgen der Diversifizierung von Wäldern für Wiederaufforstungsinitiativen und das Potenzial von Plantagen, den atmosphärischen Kohlenstoffgehalt zu verringern, sowie die Vorteile der Baumvielfalt für die Abschwächung der Auswirkungen des Klimawandels auf Ökosysteme und das menschliche Wohlbefinden.

Meine Literaturrecherche ergab, dass die Auswirkungen der Baumvielfalt auf den Kohlenstoffkreislauf in Wäldern vielfältig sind und sich durch die Komplementarität der Arten auf verschiedenen trophischen Ebenen erklären lassen. Diese Komplementarität zwischen den Arten kann drei Aspekte umfassen: die Komplementarität bei der Substratnutzung sowie die räumliche und zeitliche Komplementarität zwischen den Arten. Ich habe hervorgehoben, dass die räumliche und zeitliche Komplementarität von Baumarten an Aufmerksamkeit gewinnt. Die Folgen der baumbedingten räumlich-zeitlichen Heterogenität für höhere trophische Ebenen sind jedoch noch nicht bekannt. In den verschiedenen Kapiteln dieser Arbeit habe ich die Auswirkungen der Baumvielfalt auf den Kohlenstoffkreislauf untersucht und dabei die Folgen der durch die Baumvielfalt bedingten räumlichen Heterogenität berücksichtigt. Meine Kollegen und ich haben die positiven Auswirkungen der Baumvielfalt auf die Baumproduktivität (d. h. Baumbiomasse, Streufall und Kronenkomplementarität, Kapitel I und III) hervorgehoben. Durch die Steigerung der Menge und Vielfalt des Streufalls erhöhte die Baumvielfalt die Zersetzung der Streu und in der Folge die Assimilation von Baumprodukten in den Waldboden (Kapitel I). Zweitens hat unsere Untersuchung gezeigt, dass mikrobielle Gemeinschaften eine Schlüsselrolle für die Kohlenstoffdynamik der Wälder spielen, indem sie den Streuabbau (Kapitel I), die heterotrophe Bodenatmung (Kapitel II) und die Stabilisierung des Kohlenstoffs im Boden (Kapitel III) übernehmen. Darüber hinaus haben wir gezeigt, wie die Baumvielfalt die mikrobielle Biomasse im Boden (Kapitel I-III) und die Funktionen

(Kapitel I-II) erhöht. Vor allem die Auswirkungen der Baumvielfalt auf die mikrobielle Bodenatmung wurden hauptsächlich durch die mikrobielle Bodenbiomasse und nicht durch die taxonomische oder funktionelle Vielfalt der mikrobiellen Bodengemeinschaft vermittelt. Drittens wurden die Auswirkungen der Baumvielfalt auf die mikrobielle Biomasse durch biotische und abiotische Umweltbedingungen wie funktionelle Eigenschaften der Wurzeln, Baumproduktivität, Bodenqualität und Mikroklima vermittelt (Kapitel II und III). Beispielsweise erhöhte die Baumvielfalt durch Senkung der lokalen Temperatur die mikrobielle Biomasse und steigerte damit indirekt die mikrobiellen Prozesse. Insgesamt haben wir gezeigt, wie wichtig die Berücksichtigung des Raums für das Verständnis der Beziehungen zwischen Biodiversität und Ökosystemfunktionen ist (Kapitel I und III). So haben wir beispielsweise gezeigt, dass mit zunehmender Baumvielfalt die räumliche Heterogenität des Streufalls zunimmt, was sich auf die Zersetzung der Streu auswirkt (Kapitel I). Schließlich haben wir argumentiert, dass die Baumvielfalt ein vielversprechender Weg ist, um das Potenzial von Aufforstungsprojekten zur Minderung des zunehmenden atmosphärischen Kohlenstoffs zu maximieren (Kapitel IV). Darüber hinaus haben wir gezeigt, dass die Diversifizierung der Wälder im Rahmen von Aufforstungsinitiativen dazu beitragen kann, die Auswirkungen des Klimawandels auf die Ökosysteme zu verringern: erstens durch die Erhöhung der Resistenz und Widerstandsfähigkeit gegenüber extremen Klimaereignissen und zweitens durch die Abpufferung mikroklimatischer Bedingungen in natürlichen und städtischen Gebieten.

Die Baumvielfalt beeinflusst den Kohlenstoffkreislauf in Wäldern, indem sie die Produktivität der Bäume, die Vielfalt der Baumarten und die Umweltbedingungen erhöht. Meine Untersuchung hat gezeigt, dass die Auswirkungen der Baumvielfalt auf das Funktionieren des Ökosystems sowohl durch die Masse (d. h. Produktivitätssteigerung bei höherer Vielfalt) als auch durch Diversitätseffekte (d. h. Steigerung der Vielfalt der Baumprodukte) auf höhere

trophische Ebenen und deren Funktionen erklärt werden können. Die Verbindungen zwischen der Baumvielfalt und den höheren trophischen Ebenen sind von entscheidender Bedeutung; so haben wir beispielsweise die Schlüsselrolle der mikrobiellen Gemeinschaften bei der Steuerung des Kohlenstoffkreislaufs in subtropischen Wäldern aufgezeigt. Darüber hinaus verdeutlichen unsere Ergebnisse das große Potenzial vielfältiger Wälder, den Klimawandel abzuschwächen, indem sie die Kohlenstoffspeicherung verbessern und damit die Konkurrenz zwischen Aufforstungsinitiativen und anderen Landnutzungen verringern. Darüber hinaus haben wir auf lokaler Ebene ein hohes Potenzial der Baumvielfalt zur Abfederung mikroklimatischer Bedingungen und extremer klimatischer Ereignisse festgestellt. Durch die Untersuchung der potenziellen Mechanismen der Auswirkungen der Baumvielfalt auf das Funktionieren von Ökosystemen habe ich die Schlüsselrolle der durch die Baumvielfalt bedingten räumlichen Heterogenität und die Notwendigkeit hervorgehoben, in der weiteren Forschung Raum und Zeit zu berücksichtigen. Die hohe Auflösung der Probenahmen erfordert die Entwicklung nicht-invasiver In-situ-Methoden, um unsere Forschung auf nachhaltige Weise durchführen zu können. Letztendlich liefern unsere Ergebnisse einen ganzheitlichen Blick auf die Auswirkungen der Baumvielfalt auf den Kohlenstoffkreislauf in Wäldern. Diese Ergebnisse müssen mit den Zwängen und Anforderungen der Praktiker kombiniert werden, um machbare Restaurationsprojekte zu ermöglichen.

Résumé

Dans le monde entier, la perte de biodiversité a des effets sur tous les écosystèmes, l'une des plus grandes menaces pesant sur la biodiversité étant le changement climatique. Les forêts ont montré leur haut potentiel pour lutter contre le changement climatique, de par leur capacité à accumuler du carbone dans leur parties aériennes mais aussi dans les sols. Depuis plusieurs décennies, les écologues ont construit des expériences sur la biodiversité et le fonctionnement des écosystèmes (*i.e.*, BEF experiments) pour comprendre les conséquences de la perte des espèces sur le fonctionnement des écosystèmes et les services que ces derniers procurent à l'humanité. Il est communément admis que la perte en diversité des arbres dans les forêts ait des conséquences sur l'ensemble de l'écosystème et ses fonctions, par exemple, la productivité de la forêt ou le stockage du carbone.

Pendant ma thèse, j'ai étudié l'effet de la perte de diversité des arbres sur le cycle du carbone en forêt subtropical chinoise. Mon but était de comprendre les mécanismes expliquant l'effet de la diversité en arbres sur le cycle du carbone tout en portant une attention particulière aux processus microbiens et aux conséquences de la diversité en arbres sur l'hétérogénéité spatiale des forêts.

Tout d'abord, j'ai effectué une synthèse de l'état actuel des connaissances sur les mécanismes sous-jacent à l'effet de diversité des arbres sur les processus lié au cycle du carbone dans les forêts. Ensuite, mes collègues et moi-même avons testé les effets de la diversité des arbres sur les schémas spatiaux de la chute des feuilles et les conséquences pour la décomposition de la litière (chapitre I) et nous avons quantifié l'importance de la communauté microbienne pour les processus de décomposition. Troisièmement, nous avons examiné les effets de la diversité des arbres sur les relations entre les facettes microbiennes du sol (c'est-à-dire la biomasse, la composition taxonomique et fonctionnelle) et les fonctions microbiennes du sol comme la

respiration hétérotrophe (chapitre II). Quatrièmement, nous avons adopté une approche plus holistique de l'écosystème pour étudier les effets de la diversité des arbres sur la biomasse microbienne et concentration en carbone des sols et leur médiation par l'environnement biotique et abiotique (chapitre III). Enfin, nous avons examiné les implications de la diversification des plantations et des forêts lors d'initiatives de reboisement pour réduire les niveaux de carbone atmosphérique, ainsi que les avantages de la diversité forestière pour atténuer les impacts du changement climatique sur les écosystèmes ainsi que le bien-être humain.

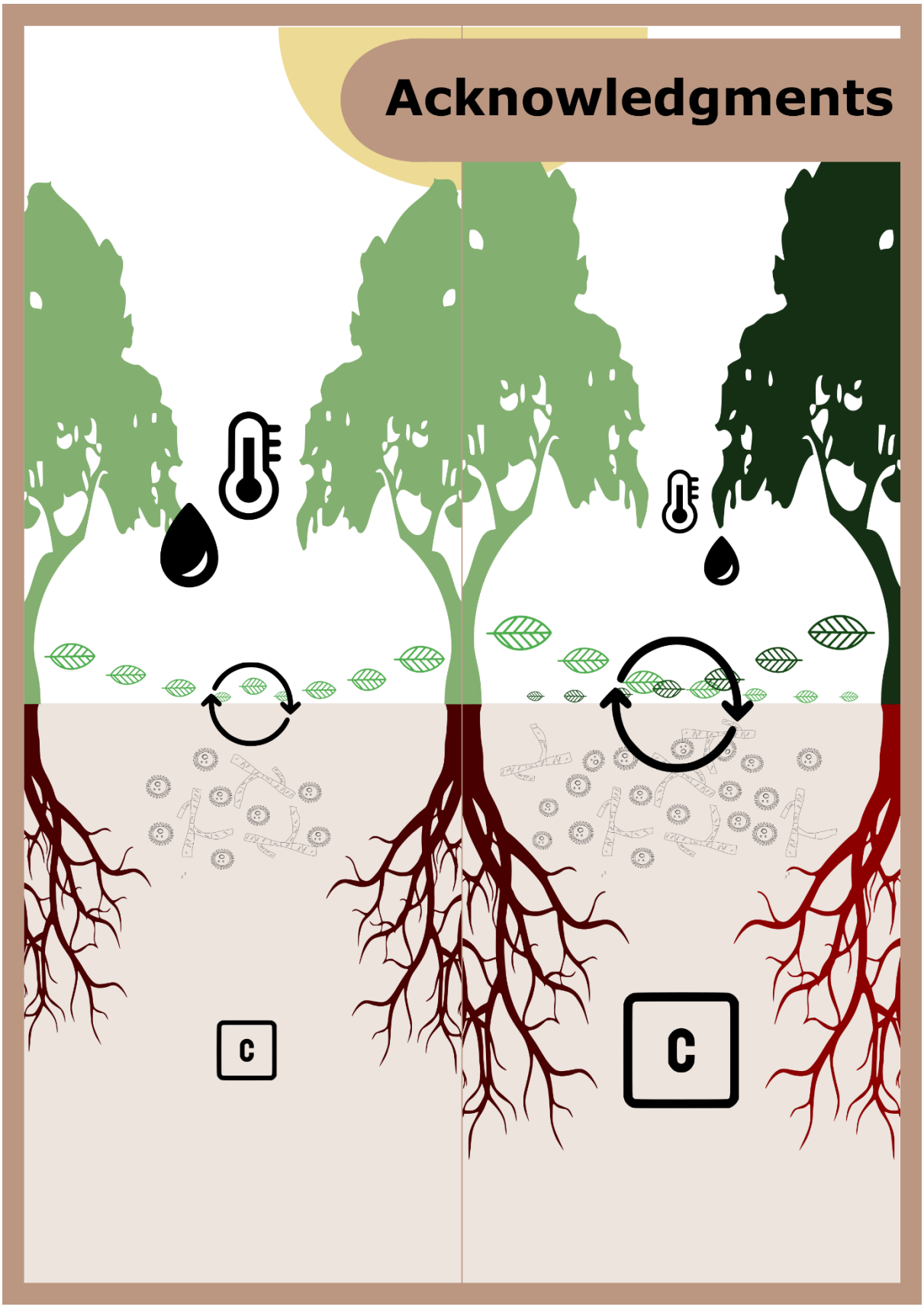
Ma revue de la littérature a révélé que les effets de la diversité des arbres sur le cycle du carbone dans les forêts sont divers et peuvent s'expliquer par la complémentarité des espèces à différents niveaux trophiques. Cette complémentarité interspécifique peut comprendre trois aspects : la complémentarité dans l'utilisation de substrats, et la complémentarité spatiale et temporelle entre les espèces. J'ai souligné que la complémentarité spatiale et temporelle des espèces d'arbres suscite de plus en plus d'intérêt, cependant, les conséquences de l'hétérogénéité spatio-temporelle induite par les arbres pour les niveaux trophiques supérieurs ne sont que peu connues. Dans les différents chapitres de cette thèse, j'ai examiné les effets de la diversité des arbres sur le cycle du carbone, en tenant compte des conséquences de l'hétérogénéité spatiale induite par la diversité des arbres. Mes collègues et moi-même avons souligné les effets positifs de la diversité des arbres sur la productivité des forêts (c'est-à-dire la biomasse des arbres, la litière et la complémentarité des canopées, chapitres I et III). En augmentant la quantité et la diversité de la litière, la diversité des arbres a augmenté la décomposition de la litière et, par la suite, l'assimilation de la biomasse produite par les arbres dans le sol forestier (chapitre I). Deuxièmement, notre étude a montré que les communautés microbiennes jouent un rôle clé dans la dynamique du carbone forestier via la décomposition de la litière (chapitre I), la respiration hétérotrophe du sol (chapitre II) et la stabilisation du carbone du sol (chapitre III).

En outre, nous avons montré comment la diversité des arbres augmente la biomasse microbienne du sol (chapitres I-III) et ses fonctions (chapitres I-II). Plus important encore, les effets de la diversité des arbres sur la respiration microbienne du sol étaient principalement affectés par la biomasse microbienne du sol plutôt que par la diversité taxonomique ou fonctionnelle de la communauté microbienne. Troisièmement, les effets de la diversité des arbres sur la biomasse microbienne étaient affecté par l'environnement biotique et abiotique telles que les propriétés fonctionnelles des racines, la productivité des arbres, la qualité du sol et le microclimat (chapitres II et III). Par exemple, la diversité des arbres a augmenté la biomasse microbienne en abaissant la température locale et a donc indirectement augmenté les processus microbiens. Dans l'ensemble, nous avons montré l'importance de la prise en compte de l'espace dans la compréhension des relations entre la biodiversité et les fonctions des écosystèmes (chapitres I et III). Par exemple, nous avons montré que lorsque la diversité des arbres augmente, l'hétérogénéité spatiale de la litière augmente, ce qui affecte la décomposition de la litière (chapitre I). Enfin, nous avons fait valoir que la diversité des arbres est un moyen prometteur de maximiser le potentiel des projets de reboisement pour atténuer l'augmentation du carbone atmosphérique (chapitre IV). En outre, nous avons montré que la diversification des forêts dans le cadre d'initiatives de reboisement peut contribuer à réduire les impacts du changement climatique sur les écosystèmes : premièrement, en augmentant la résistance et la résilience face aux événements climatiques extrêmes, et deuxièmement, en tamponnant les conditions microclimatiques dans les zones naturelles et urbaines.

La diversité des arbres influence le cycle du carbone dans les forêts en augmentant la productivité des arbres, la diversité des productions et les conditions environnementales. Mes recherches ont montré que les effets de la diversité des arbres sur le fonctionnement des écosystèmes peuvent s'expliquer à la fois par des effets de masse (c'est-à-dire une productivité accrue avec une plus grande diversité) et des effets de diversité (c'est-à-dire une diversité accrue

des produits des arbres) sur les niveaux trophiques supérieurs et leurs fonctions. Les liens entre la diversité des arbres et les niveaux trophiques supérieurs sont cruciaux. Par exemple, nous avons démontré le rôle clé des communautés microbiennes dans le contrôle du cycle du carbone dans les forêts subtropicales. En outre, nos résultats soulignent le grand potentiel des forêts diversifiées pour atténuer le changement climatique en améliorant le stockage du carbone et en réduisant ainsi la concurrence entre les initiatives de reboisement et les autres utilisations des terres. En outre, à l'échelle locale, nous avons constaté un fort potentiel de la diversité des arbres pour atténuer les conditions microclimatiques et les événements climatiques extrêmes. En explorant les mécanismes potentiels de l'impact de la diversité des arbres sur le fonctionnement des écosystèmes, j'ai mis en évidence le rôle clé de l'hétérogénéité spatiale causée par la diversité des arbres et la nécessité de prendre en compte l'espace et le temps dans les recherches futures. La haute résolution de l'échantillonnage nécessite le développement de méthodes in situ non invasives pour mener nos recherches de manière durable. En définitive, nos résultats fournissent une vision globale de l'impact de la diversité des arbres sur le cycle du carbone dans les forêts. Ces résultats doivent être combinés avec les contraintes et les exigences des acteurs locaux pour permettre des projets de restauration réalisables.

Acknowledgments



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This thesis was made possible by the BEF China platform and its many actors that maintain the facilities and keep the experiment running. I would like to especially thank Dr. Yang Bo, Dr. Li Shan, and Yuxi Xue for their support during the planning and achievement of my field campaigns. Without the responsiveness of Yang Bo to my phone call from the airport customs, Georg and I may still be stuck in Beijing Airport with our ethanol samples since December 2019. Moreover, I would like to thank my local helpers for their amaizing support: 在此，我由衷感谢所有帮助我完成我在中国野外采样和实验工作的人，你们的帮助是我顺利完成毕业论文的关键。我特别要感谢齐进泉同我一同完成野外采样工作，感谢齐益家、邬亚贞、程长容、施圆、徐慧敏、程秋琴等等对我实验室工作的帮助。还有一些帮过我但我不知道全名的人，同样予以衷心感谢。在中国的几个月里，你们给予我的许多热情的帮助，发展的珍贵的友情，我将铭记于心。

I would like to thank the TreeDì consortium and partners. You made this Ph.D. an incredible experience by providing me the best inspiration, support, and help I could imagine from the first day during the recruitment symposium to the redaction of this thesis. I wish to thank Stefan Trogisch for his technical and administrative support; I would not have made it to China without your help.

The TreeDì consortium allowed me to meet amazing people, and I am more than grateful to call them my friends. I would like to thank you so much for your help since 2018, particularly for the last weeks. A special thanks to Andréa Davrinche and Georg Albert, who supported me professionally and personally. I now owe you approximately two hundred diners; you will have to come far North one day. I would like to thank you so much for being present and providing essential inputs to this thesis. I hope we will find even more time to hang out once we are finally done with these theses. Andréa, I may not have survived our fieldwork if it wasn't for you; having another French fellow close by is quite a gift when you are far from anything you

know. Georg, even if I now need to climb three floors to see you, your presence and our talks were always comforting and inspiring to me. I hope we will now find some exciting projects to work on, and finally get a chance to go climbing together.

Furthermore, I would like to thank the members of my PAC for their guidance and crucial advice during our meetings. Sylvia Haider, having you in my PAC was probably one of the best choices I made. You helped me to put things into perspective and provided me guidance on the strategy to adopt for the Ph.D.

I would like to keep some words to thank my two supervisors, Simone Cesarz and Nico Eisenhauer; you are a tremendous supervising team by complementing one another in various ways. I cannot imagine better supervision than yours: you provided me incredible freedom as well as constant support and guidance. I will never thank you enough for your support, especially during the last few weeks when the deadlines became tight. Simone, your emotional support was critical during some difficult periods. Your knowledge of the lab's reality allowed me not to lose myself in too many side projects and random ideas. Nico, your supervision and constant support were the drivers of my success; you're a supervisor and a mentor to me. I hope that next year will be the good one to repeat our half-marathon; this time, let's start slower to survive it toward the end! During my interview, I promised you both that I would learn German, well I am a bit delayed on this project but I still made some kind of progress: Nico und Simone, ich möchte euch von Herzen für eure Unterstützung danken und auch für die Freiheit, die ihr mir gegeben habt. Ich hätte mir keine besseren Betreuer wünschen können.

I would like to thank all my collaborators and co-authors who provided insightful inputs throughout my different projects. I greatly appreciated the guidance and patience of Helge Bruelheide, Thomas Scholten, Steffen Seitz, Goddert von Oheim, Matthias Kunz, and Emma Ladouceur. The scope of this thesis couldn't have been covered without your insights. A special thanks go to my Chinese counterpart, Dr. Jianqing Du, it has been a really great joy for me to work with you during our different collaborations. I believe that our shared first-authored paper is an excellent example of our collaboration and the start of numerous projects together. In addition, I would like to thank Dr. Kai Xue and Prof. Yanfeng Wang for their guidance and time. Dr. Xue, our discussions have always been insightful to me; I thank you very much for sharing your expertise with me.

In addition, I would like to thank my informal collaborators and previous supervisors who brought me insight and guidance before and during this journey, namely, Sonia Kéfy, Vasilis Dakos, Paul Kardol, Clydecia Spitzer, Stephan Hättenschwiler, Nicolas Fanin, and François-

Xavier Joly. Stephan, Nicolas, and F-X, your guidance during my last field campaign brought me some hope when the sky was pretty cloudy. Further, I wish to acknowledge the help that the Theory in Biodiversity Science group members provided. Particularly, I would like to thank Benjamin Rosenbaum for his help during my statistical analyses and Benoît Gauzens for his scientific advice and friendship. Benoît, from next week onward, I might be able to finally find some time to join the Wednesday rugby trainings.

I want to express my deep appreciation to the Experimental Interaction Ecology (EIE) group members. I am particularly grateful for the administrative assistance given by Svenja Haenzel and the technical support provided by Alfred Lochner, Anja Zeuner, and Linnea Smith. You provided amazing help, which allowed me to work in an incredible environment. In addition, I would like to thank all my EIE colleagues for their scientific and personal support in the past few years. You always provided me the best of your craft, and you were always ready to help whatever was needed. I am particularly grateful for the advice given by Stephanie Jurburg, who became a mentor and a great friend, always available for a chat and to provide insightful guidance (as well as some scientific confrontations). Likewise, I am particularly grateful for the help of Lise Thouvenot. Working with you was of an incredible professional help, and the friendship we developed in the past few years was of great personal help. In the end, we probably lost hours/days chatting and gossiping in front of your door, but these moments were somehow needed too.

Moreover, I would like to thank my officemates that changed over the years but always bring a great office atmosphere. I wish to thank Helen Phillips, you were always around and present, especially when some situations became pretty overwhelming. Even though it was short, I was really glad to share the office with Guillaume Patoine and Ana Bonato Asato for some time. Our coffee machine investment is definitely one of the best of my all Ph.D. Furthermore, I am glad to have some time left with our two office newbies. You seem to be pretty strong not to be fed-up with Marie and me yet (or maybe you are, but you're too polite to tell us)! Last but not least, I would like to give special thanks to Marie Sünnemann for our great friendship and her support on a daily basis. You have endured my complaints for quite some time now and I wouldn't have survived these last weeks if it wasn't for you. More than an officemate, you're an incredible friend; I couldn't thank you enough for your constant professional and emotional support.

Without any doubt, I would like to acknowledge my students for their help with field and lab work. Thanks to your enrollment and work, I discovered the joys (and sometimes drawbacks)

of supervision. Georg Hähn, you were my first student, and you put the level pretty high for anyone coming after you. I enjoyed our work together; you always did way more than I would have expected and provided crucial help during our different field campaigns. I am sure that you will make a fantastic scientist. I will never forget our work and trips, especially, the climb of the yellow mountains! I am already looking forward to our next race together: pick a sport and I will follow. Henriette Christel, I am glad that I met you in China and had the chance to supervise your master thesis. I am glad to see you taking the path of the Ph.D., and I am looking forward to seeing your progress and successes.

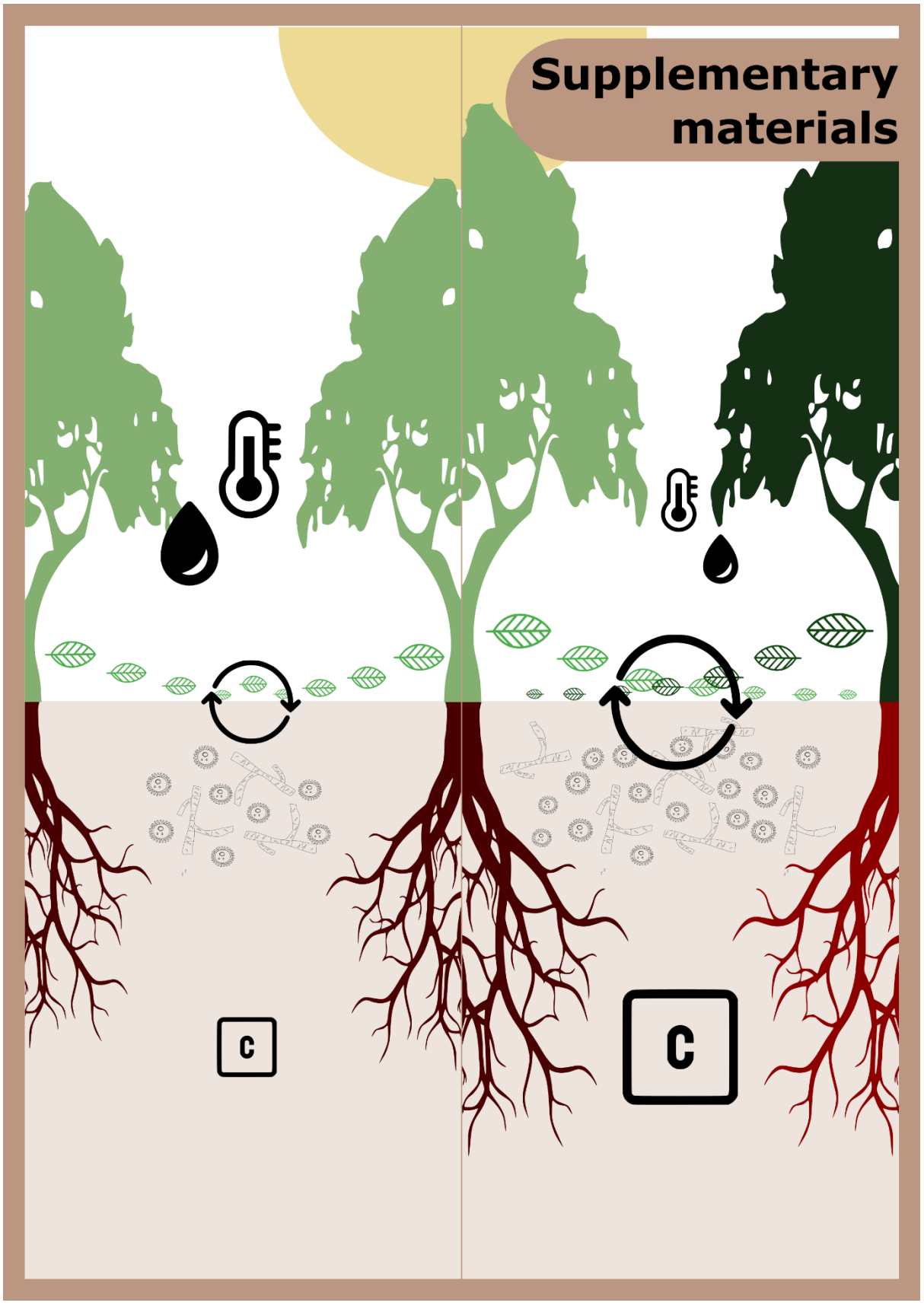
I would like to give a special thanks to COVID19; its constant presence and evolution prevented any routine in my life for almost two years. What better celebration could I have dreamed of for my birthdays than two quarantined Zoom parties?

I couldn't have completed this thesis without the constant support of my family and friends. Most were already cited above; I would like to add a special note to my Twitter friends (@barretocra and @GanaultPierre), we never or only quickly met in person, but you were a supportive presence all along this journey.

J'aimerais remercier mes amis de longue date. Paul Anfrey, je te remercie pour ta présence depuis de nombreuses années. Merci d'avoir continué à entretenir notre amitié même lorsque j'étais moins disponible. Adeline Dabé et Paul Ramette, merci de rester ces amis fidèles malgré la distance et nos rares contacts. Il fait toujours bon de vous revoir même après s'être perdus de vue pendant des années.

J'aimerais remercier mes parents pour leur constant soutien. Vous avez toujours su être là et me pousser sans jamais questionner mes décisions. Vous m'avez offert la chance de choisir ma voie et de poursuivre mes envies. Merci également d'avoir rempli mon cellier en me procurant moult pâté et conserve à chacun de mes passages.

Pour finir je voudrais remercier ma compagne Célia Lutrat. Nous allons bientôt en avoir fini avec nos thèses, ceci n'aura pas toujours été simple pour nous mais nous nous en sortons ! Merci d'avoir été présente pour moi et de m'avoir soutenu même lorsque j'ai décidé de partir m'installer à l'autre bout de l'Allemagne. Merci d'avoir su être patiente (ton point fort !) toutes ces années et d'avoir su me sortir la tête du guidon. Sans toi, je me serais sûrement perdu en chemin. Merci d'être à mes côtés et de me soutenir, j'espère pouvoir en faire autant pour toi maintenant. Le plus beau reste à venir pour nous, tous les deux d'une façon ou d'une autre (plus les deux chats et le petit chien).


Supplementary materials
C
C

Declaration of independent work

I, Rémy Beugnon, hereby affirm that I take note and accept the doctorate regulations of the Faculty of Biosciences, Pharmacy and Psychology of the University of Leipzig from the 30th of September 2019.

I further affirm that the presented thesis was prepared autonomously without inadmissible help. All aids used in this thesis as well as scientific ideas which are quoted from or based on other sources were cited at the respective point.

All people who helped me to prepared the conception, to select and analyze the materials of this thesis as well as to improve the manuscript are namely cited in the acknowledgments. With exception of the namely mentioned people no other persons were involved in the intellectual work. No Ph.D. consultant service was employed. Third parties did not get money's worth for benefits that were in conjunction with the content of this dissertation.

I declare that this dissertation has been neither presented nationally nor internationally in its entirely or in parts to any institution for the purpose of dissertation or other official or scientific examination and/or publishing.

Previously unsuccessful dissertations had not taken place.

The original document of the verification of the co-authors' parts are deposited in the office of the dean.

Leipzig, the 30th of September 2021

CV

Ph.D candidate in the German Center for Integrative Biodiversity Research (iDiv) Halle – Jena – Leipzig. I am working on tree diversity effects on soil microbial community and soil functioning including litter decomposition and soil carbon storage.
Research interest: BEF, ecosystem ecology, soil ecology, microbial ecology, food web ecology, synthesis

Rémy Beugnon

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04157 Leipzig (Germany)
Phone: +49 1520 33 43 829
E-Mail: remy.beugnon@idiv.de
Twitter: @BeugnonRemy
Web: https://remybeugnon.netlify.app/

Languages

French – native
English – fluent

Field skills

- Subtropical China field campaign
- Litterfall, insect and soil sampling
- Performing decomposition experiment

Lab skills

- Microbial biomass (e.g., PLFA)
- Microbial physiology (e.g., MicroResp®)
- Insect identification

Analysis skills

- Multivariate analysis (e.g. PCA, RDA)
- Frequentist statistic (e.g. linear, non-linear, mixed effects models)
- Spatio-temporal analysis
- Structural Equation Modelling
- Network analysis (basic knowledge)
- Bayesian statistics (basic knowledge)

Programming skills

R – advanced
Bash – basic knowledge
LaTeX – basic knowledge
Python/HTML/SQL/GIS – basic knowledge

Research experiences

07.2018 to now
Ph.D thesis - German Center for Integrative Biodiversity Research (iDiv) Halle – Jena – Leipzig , Leipzig (Germany)
Tree diversity effects on soil microbial communities and soil carbon dynamics
Supervision: Dr. Simone Cesarz, Prof. Dr. Nico Eisenhauer
Main topics: tree interactions effects on litterfall, decomposition, microbial community composition and functions and soil carbon storage

01.2018 to 06.2018
MSc. thesis - Institut des Sciences de l'Evolution de Montpellier ISME, Montpellier (France)
Modelling non-trophic interactions effects on community dynamics.
Supervision: Dr. Sonia Kéfi, Dr. Vasilis Dakos

04.2017 to 07.2017
Internship - Swedish University of Agricultural Sciences (SLU), Umeå (Sweden)
Root trait effects of alpine plant communities on plant-soil feedback effects performed in two greenhouse experiments.
Supervision: Dr. Paul Kardol

Education

09.2017-06.2018
Master's degree in biology, ecology and evolution – Université de Montpellier, France

09.2014-11.2018
Agricultural engineering diploma – Montpellier SupAgro, France

Publications

2019

Beugnon, Rémy; Steinauer, Katja; Barnes, Andrew D.; Ebeling, Anne; Roscher, Christiane; Eisenhauer, Nico (2019): *Plant functional trait identity and diversity effects on soil meso-and macrofauna in an experimental grassland*. In Advances in ecological research 61, p. 163-184. DOI: 10.1016/bs.aecr.2019.06.004

Cesarz, Simone; Schulz, Annika Eva; **Beugnon, Rémy**; Eisenhauer, Nico (2019): *Testing soil nematode extraction efficiency using different variations of the Baermann-funnel method*. In Soil Organisms 91 (2), p. 61. DOI: 10.25674%2Fso91201

2021

Beugnon, Rémy† & Du Jianqing†; Cesarz, Simone; Jurburg, Stephanie D.; Pang, Zhe; Singavarapu, Bala; Wubet, Tesfaye; Xue, Kai; Wangs, Yanfen[S] & Eisenhauers, Nico[S] (2021): *Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning*. In ISME Communications 1 (1), 1-11. DOI: 10.1038/s43705-021-00040-0

Beugnon, Rémy, Emma Ladouceur, Marie Sünnemann, Simone Cesarz[S] & Nico Eisenhauer[S] (2021): *Diverse forests are cool: promoting diverse forest to mitigate carbon emission and climate change*. In Journal of Sustainable Agriculture and Environment

Phillips, Helen R. P.; Bach, Elizabeth M.; Bartz, Marie L. C.; Bennett, Joanne M.; **Beugnon, Rémy**; Briones, Maria J. I. et al. (2021): *Global data on earthworm abundance, biomass, diversity and corresponding environmental properties.* In Scientific Data 8 (1), p. 136. DOI: 10.1038/s41597-021-00912-z.

Singavarapu, Bala; **Beugnon, Rémy**; Bruelheide, Helge; Cesarz, Simone; Du, Jianqing; Eisenhauer, Nico; Guo, Liang-Dong; Nawaz, Ali; Wang, Yanfen; Xue, Kai; Wubet, Tesfaye (2021): *Tree mycorrhizal type and tree diversity shape the forest soil microbiome.* In Environmental Microbiology

Thouvenot, Lise; Ferlian, Olga; **Beugnon, Rémy;** Künne, Tom; Lochner, Alfred; Thakur, Madhav P.; Türke, Manfred; Eisenhauer, Nico (2021): *Do invasive earthworms affect the functional traits of native plants?* In Frontiers in plant science 12, p. 424. DOI: 10.3389/fpls.2021.627573

In preparation

Beugnon, Rémy; Bu, Wensheng; Bruelheide, Helge; Davrinche, Andréa; Du, Jianqing; Haider, Sylvia; Kunz, Matthias; von Oheimb, Goddert; Perles-Garcia, Maria D.; Saadani, Mariem; Scholten, Thomas; Seitz, Steffen; Singavarapu, Bala; Trogisch, Stefan; Wang, Yanfen; Wubet, Tesfaye; Xue, Kai; Yang, Bo; Cesarz, SimoneS & Eisenhauer, NicoS (**under review**): *Abiotic and biotic drivers of scale-dependent tree trait effects on soil microbial biomass and soil carbon concentration*. In Ecological Monographs

Beugnon, Rémy; Eisenhauer, Nico; Bruelheide, Helge; Davrinche, Andréa; Du, Jianqing; Haider, Sylvia; Haehn, Georg; Saadani, Mariem; Singavarapu, Bala; Sünnemann, Marie; Thouvenot, Lise; Wang, Yanfen; Wubet, Tesfaye; Xue, Kai; Cesarz, Simone (**in prep.**): *Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes.*

Schnabel, Florian†; **Beugnon, Rémy**†; Bo, Yang†; Castro Izaguirre, Nadia Cristina; Cesarz, Simone; Eisenhauer, Nico; Garcia, Maria Dolores Perles; Haehn, Georg; Härdtle, Werner; Huang, Yuanyuan; Kunz, Matthias; Liu, Xiaojuan; Niklaus, Pascal A.; von Oheimb, Goddert; Pietsch, Katherina A.; Richter, Ronny; Schmid, Bernhard; Trogisch, Stefan; Wirth, Christian; Ma, Keping[S] & Bruelheide Helge[S] (**in prep.**): *The role of tree species richness for temperature buffering below forest canopies.*

Reviewer

Nature Communications, Scientific Reports, Pedobiologia, Soil Organisms

Teaching

2021 - Introduction to stats in R for bachelors and master students (12h)

Outreach

2019 to 2021 - Guest editor for Frontiers for Young Minds collection "Soil biodiversity"
2021 - Contribution to the Leipzig's Long Night of Sciences

Oral presentations and invited talks

2018 - *"Effect of non-trophic interactions on community dynamics",* Model in Ecology and Evolution conference – Monpellier, France

2019 - "Effects of tree functional diversity on soil community and function", iDiv conference – Leipzig, Germany

2020
"*To a mechanistical understanding of plant diversity effects on soil fauna community*", Laboratoire d'écologie alpine (LECA) – Grenoble, France

"*Abiotic and biotic mediations of scale dependent tree traits effects on soil carbon concentrations*", BES annual meeting 2020 – Virtual

2021
"*Tree diversity effects on litter decomposition and microbial processes* ", GfÖ annual meeting – Virtual

Professionalization courses

2021 - Third Party Funding Opportunities
2020
- Scientific writing
- Introduction to ggplot2
- Good scientific practices

2019
- Structural Equation Modeling
- Nematode identification course

Participation to institutional activities

09.2021 - Ph.D representative for iDiv Equal Opportunity comity
2021 - Interviews of senior researcher about "transdisciplinary research" for the GfÖ Twitter account
2018-2021
- Organization of afterwork activities for the Experimental Interaction Ecology (EIE) working group
- Organization of welcome packages for new members of the EIE working group

Article justifications

Nachweis über Anteile der Co-Autoren:

Title: Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes

Journal: Nature Communications (*under review*)

Autoren: Rémy Beugnon, Nico Eisenhauer, Helge Bruelheide, Andréa Davrinche, Jianqing Du, Sylvia Haider, Georg Haehn, Mariem Saadani, Bala Singavarapu, Marie Sünnemann, Lise Thouvenot, Yanfen Wang, Tesfaye Wubet, Kai Xue & Simone Cesarz

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Beiträge:

Rémy Beugnon: i. field sampling, ii. lab measurements, iii. project conceptual framework, iv. statistical analyses, v. manuscript writing

Nico Eisenhauer: i. funding; ii. project conceptual framework, iii. framing of the manuscript, iv. writing

Helge Bruelheide: i. project conceptual framework, ii. funding, ii. manuscript revision

Andréa Davrinche: i. field sampling, ii. lab measurements, iii. manuscript revision

Jianqing Du: i. project conceptual framework, ii. manuscript revision

Sylvia Haider: i. funding; ii. trait data; iii. manuscript revision

Georg Haehn: i. field sampling, ii. lab measurements, iii. manuscript revision

Mariem Saadani: i. field sampling, ii. manuscript revision

Bala Singavarapu: i. field sampling, ii. manuscript revision

Marie Sünnemann: i. project conceptual framework, ii. writing

Lise Thouvenot: i. project conceptual framework, ii. writing

Yanfen Wang: i. project conceptual framework, ii. manuscript revision

Tesfaye Wubet: i. project conceptual framework, ii. manuscript revision

Kai Xue: i. project conceptual framework, ii. manuscript revision

Simone Cesarz: i. funding; ii. project conceptual framework, iii. framing of the manuscript, iv. writing

Nachweis über Anteile der Co-Autoren, Rémy Beugnon
From tree to soil: microbial and spatial mediation of tree diversity effects on carbon cycling in Subtropical Chinese forests
Unterschriften:

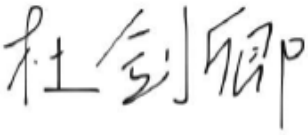
Rémy Beugnon

Prof. Dr. Nico Eisenhauer

Prof. Dr. Helge Bruelheide

Andréa Davrinche

Dr. Jianqing Du



Dr. Sylvia Haider

Georg Hähn

Mariem Saadani

Bala Singavarapu

Marie Sünnemann

Dr. Lise Thouvenot

Prof. Dr. Yanfen Wang

Dr. Tesfaye Wubet

Dr. Kai Xue

Dr. Simone Cesarz

Nachweis über Anteile der Co-Autoren:

Title: Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning

Journal: ISME Communications

Autoren: Rémy Beugnon & Jianqing Du, Simone Cesarz, Stephanie D. Jurburg, Zhe Pang, Bala Singavarapu, Tesfaye Wubet, Kai Xue, Yanfen Wang & Nico Eisenhauer

Beiträge:

Rémy Beugnon: i. field sampling, ii. lab measurements, iii. project conceptual framework, iv. statistical analyses, v. manuscript writing

Jianqing Du: i. lab measurements, ii. project conceptual framework, iii. contributed to statistical analyses, iv. manuscript writing

Dr. Simone Cesarz: i. contributed to project conceptual framework, ii. contributed to the framing of paper, iii. contributed to writing, iv. funding

Dr. Stephanie D. Jurburg: i. contributed to statistical analyses, ii.

contributed to writing Dr. Zhe Pang: i. lab measurements

Bala Singavarapu: i. field sampling, ii. lab measurements, iii. contributed to statistical analyses, iv. manuscript revisions

Dr. Tesfaye Wubet: i. provided lab support for microbial community profiling ii. bioinformatics, iii. contributed to manuscript revisions, iv. funding

Dr. Kai Xue: i. laboratory support, ii. contributed to project conceptual framework, iii. contributed to writing

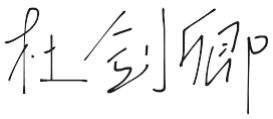
Prof. Dr. Yanfen Wang: i. lab support for measurements of soil properties and functional genes, ii. contributed to manuscript revisions, iii. funding

Prof. Dr. Nico Eisenhauer: i. contributed to project conceptual framework, ii. contributed to framing of paper, iii. contributed to writing, iv. funding

Nachweis über Anteile der Co-Autoren, Rémy Beugnon
From tree to soil: microbial and spatial mediation of tree diversity effects on carbon cycling in Subtropical Chinese forests
Unterschriften:

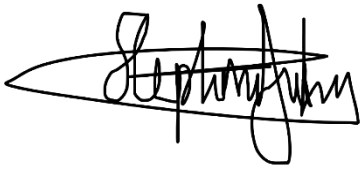
Rémy Beugnon

Jianqing Du



Dr. Simone Cesarz

Dr. Stephanie D. Jurburg



Dr. Zhe Pang

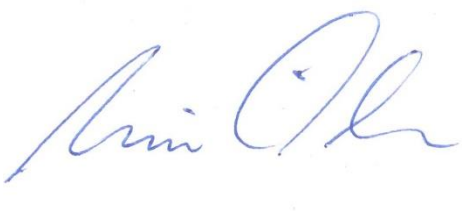
Bala Singavarapu

Dr. Tesfaye Wubet

Dr. Kai Xue

Prof. Dr. Yanfen Wang

Prof. Dr. Nico Eisenhauer



Nachweis über Anteile der Co-Autoren:

Title: Abiotic and biotic drivers of scale-dependent tree trait effects on soil microbial biomass and soil carbon concentration

Journal: Ecological Monographs (*under review*)

Autoren: Rémy Beugnon, Wensheng Bu, Helge Bruelheide, Andréa Davrinche, Jianqing Du, Sylvia Haider, Matthias Kunz, Goddert von Oheimb, Maria D. Perles-Garcia, Mariem Saadani, Thomas Scholten, Steffen Seitz, Bala Singavarapu, Stefan Trogisch, Yanfen Wang, Tesfaye Wubet, Kai Xue, Bo Yang, Simone Cesarz & Nico Eisenhauer.

Beiträge:
Rémy Beugnon: i. field sampling, ii. lab measurements, iii. project conceptual framework, iv. statistical analyses, v. manuscript writing

Dr. Wensheng Bu: i. field sampling, ii. lab measurements

Prof. Dr. Helge Bruelheide: i. securing funding, ii. experimental design, iii. trait and environmental measurements, vi. manuscript revisions.

Andréa Davrinche: i. field sampling (traits), ii. lab measurements (traits), iii. manuscript revisions

Jianqing Du: i. field sampling, ii. lab measurements, iii. manuscript revisions

Dr. Sylvia Haider: i. field sampling (traits), ii. lab measurements (traits), iii. manuscript revisions

Dr. Matthias Kunz: i. field sampling, iii. manuscript revisions

Prof. Dr. Goddert von Oheimb: i. securing funding, ii. manuscript revisions

Maria D. Perles-Garcia: i. field sampling, ii. data calculation, iii. manuscript revisions

Mariem Saadani: i. field sampling (Basal area), ii. manuscript revisions

Prof. Dr. Thomas Scholten: i. field sampling, ii. lab measurements, iii. manuscript revisions

Dr. Steffen Seitz: i. field sampling, ii. lab measurements, iii. manuscript revisions

Bala Singavarapu: i. field sampling, iii. manuscript revisions

Dr. Stefan Trogisch: i. field sampling, ii. manuscript revisions

Nachweis über Anteile der Co-Autoren, Rémy Beugnon
From tree to soil: microbial and spatial mediation of tree diversity effects on carbon cycling in Subtropical Chinese forests
Prof. Dr. Yanfen Wang: i. laboratory support, ii. manuscript revisions

Dr. Tesfaye Wubet: i. field sampling, ii. manuscript revisions

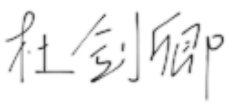
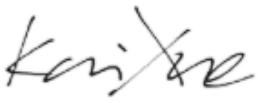
Dr. Kai Xue: i. laboratory support, ii. manuscript revisions

Dr. Bo Yang: i. site establishment, ii. microclimate measurements

Dr. Simone Cesarz: i. conceived the study, ii. secured relevant funds, iii. project conceptual framework, iv. laboratory support, v. manuscript revisions

Prof. Dr. Nico Eisenhauer: i. conceived the study, ii. secured relevant funds, iii. project conceptual framework, iv. manuscript revisions

Unterschriften:

Rémy Beugnon	**Dr. Wensheng Bu**	**Prof. Dr. Helge Bruelheide**
		
Andréa Davrinche	**Jianqing Du**	**Dr. Sylvia Haider**
		
Dr. Matthias Kunz	**Prof. Dr. Goddert von Oheimb**	**Maria D. Perles-Garcia**
		
Mariem Saadani	**Prof. Dr. Thomas Scholten**	**Dr. Steffen Seitz**
		
Bala Singavarapu	**Dr. Stefan Trogisch**	**Prof. Dr. Yanfen Wang**
		
Dr. Tesfaye Wubet	**Dr. Kai Xue**	**Dr. Bo Yang**
		
Dr. Simone Cesarz	**Prof. Dr. Nico Eisenhauer**	
		

Nachweis über Anteile der Co-Autoren:

Title: Diverse forests are cool: promoting diverse forests to mitigate carbon emissions and climate change

Journal: Journal of Sustainable Agriculture and Environment

Autoren: Rémy Beugnon, Emma Ladouceur, Marie Sünnemann, Simone Cesarz & Nico Eisenhauer.

Beiträge:

Rémy Beugnon: i. conceptual framework, ii. manuscript writing, iii. manuscript revisions

Dr. Emma Ladouceur: i. conceptual framework, ii. manuscript revisions

Marie Sünnemann: i. conceptual framework, ii. manuscript revisions

Dr. Simone Cesarz: i. conceptual framework, ii. manuscript revisions

Prof. Dr. Nico Eisenhauer: i. conceptual framework, ii. manuscript revisions

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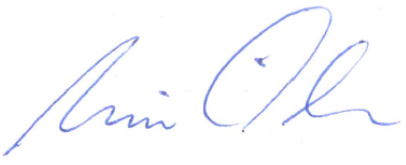

Beugnon, Rémy

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16-Sep-2021

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1

TO WHOME IT MAY CONCERN

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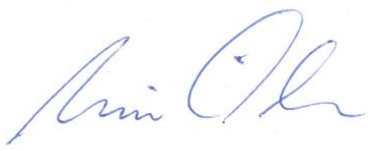


Prof. Dr. Nico Eisenhauer

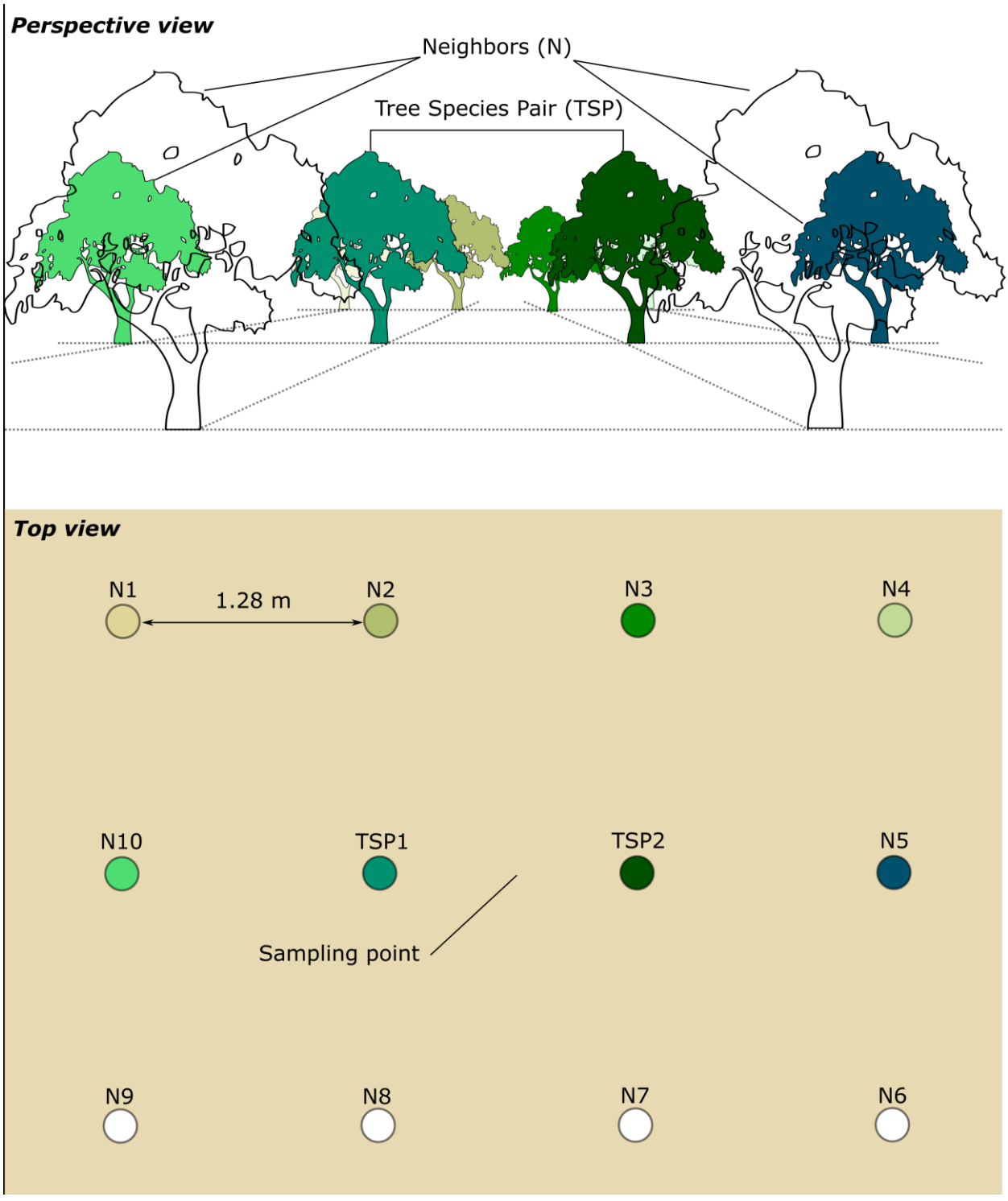
Scientific supplementary materials

Supplementary material: Chapter I - Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes

Supplementary material I – S1 Experimental design

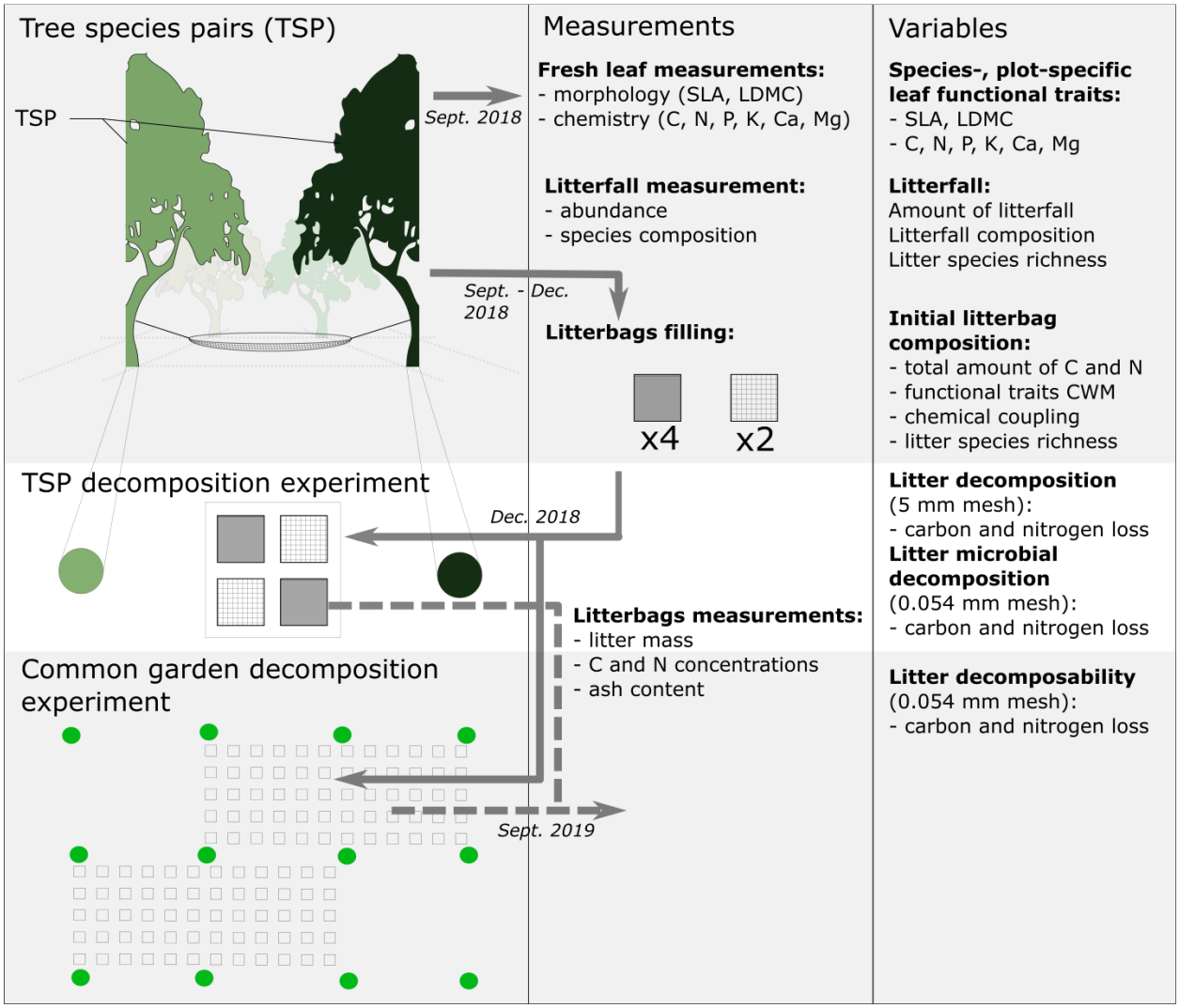
A. Plot design

Plantation design in BEF China plot with example of tree species pair (i.e., TSP) and its neighborhood.



B. Sampling design

Experimental design, realized measurements, and variables used in our study.



C. Tree species selection

List of tree species building the pairs of tree species in the different plots of Site A (BEF China experiment)

Species	Leaf persistence
Castanea henryi	deciduous
Castanopsis sclerophylla	evergreen
Choerospondias axillaris	deciduous
Cyclobalanopsis glauca	evergreen
Koelreuteria bipinnata	deciduous
Liquidambar formosana	deciduous
Lithocarpus glaber	evergreen
Nyssa sinensis	deciduous
Quercus fabri	deciduous
Quercus serrata	deciduous
Sapindus mukorossi	deciduous
Sapium sebiferum	deciduous

D. Tree Species Pairs (TSPs) selection

Sampling point description and attributes (paragraphs were added for readability)

Code	Site	Plot	Diversity level	Species 1	Species 2
26-E24	A	E24	1	*Liquidambar formosana*	*Liquidambar formosana*
33-E31	A	E31	1	*Quercus fabri*	*Quercus fabri*
34-E31	A	E31	1	*Quercus fabri*	*Quercus fabri*
27-E33	A	E33	1	*Lithocarpus glaber*	*Lithocarpus glaber*
28-E33	A	E33	1	*Lithocarpus glaber*	*Lithocarpus glaber*
1-E34	A	E34	1	*Castanea henryi*	*Castanea henryi*
2-E34	A	E34	1	*Castanea henryi*	*Castanea henryi*
37-F21	A	F21	1	*Quercus serrata*	*Quercus serrata*
38-F21	A	F21	1	*Quercus serrata*	*Quercus serrata*
10-G17	A	G17	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
29-G22	A	G22	1	*Lithocarpus glaber*	*Lithocarpus glaber*
22-G24	A	G24	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
23-G24	A	G24	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
36-G33	A	G33	1	*Quercus serrata*	*Quercus serrata*
30-H25	A	H25	1	*Nyssa sinensis*	*Nyssa sinensis*
3-I12	A	I12	1	*Castanea henryi*	*Castanea henryi*
24-I28	A	I28	1	*Liquidambar formosana*	*Liquidambar formosana*
25-I28	A	I28	1	*Liquidambar formosana*	*Liquidambar formosana*
14-K9	A	K9	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
8-L11	A	L11	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
9-L11	A	L11	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
13-L23	A	L23	1	*Choerospondias axillaris*	*Choerospondias axillaris*
43-N11	A	N11	1	*Sapindus mukorossi*	*Sapindus mukorossi*
46-N13	A	N13	1	*Sapium sebiferum*	*Sapium sebiferum*

Code	Site	Plot	Diversity level	Species 1	Species 2
47-N13	A	N13	1	*Sapium sebiferum*	*Sapium sebiferum*
11-O27	A	O27	1	*Choerospondias axillaris*	*Choerospondias axillaris*
21-Q13	A	Q13	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
r-21-Q13	A	Q13	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
35-Q16	A	Q16	1	*Quercus fabri*	*Quercus fabri*
15-R14	A	R14	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
16-R14	A	R14	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
44-R17	A	R17	1	*Sapindus mukorossi*	*Sapindus mukorossi*
45-W13	A	W13	1	*Sapium sebiferum*	*Sapium sebiferum*
32-W14	A	W14	1	*Nyssa sinensis*	*Nyssa sinensis*
51-C32	A	C32	2	*Castanea henryi*	*Castanea henryi*
52-C32	A	C32	2	*Castanea henryi*	*Nyssa sinensis*
96-C32	A	C32	2	*Castanea henryi*	*Nyssa sinensis*
95-C32	A	C32	2	*Nyssa sinensis*	*Nyssa sinensis*
97-C32	A	C32	2	*Nyssa sinensis*	*Nyssa sinensis*
53-F22	A	F22	2	*Castanea henryi*	*Castanea henryi*
54-F22	A	F22	2	*Castanea henryi*	*Castanea henryi*
55-F22	A	F22	2	*Castanea henryi*	*Nyssa sinensis*
98-F22	A	F22	2	*Nyssa sinensis*	*Nyssa sinensis*
87-H31	A	H31	2	*Liquidambar formosana*	*Liquidambar formosana*
86-H31	A	H31	2	*Liquidambar formosana*	*Sapindus mukorossi*
113-H31	A	H31	2	*Sapindus mukorossi*	*Liquidambar formosana*
112-H31	A	H31	2	*Sapindus mukorossi*	*Sapindus mukorossi*
118-I27	A	I27	2	*Sapium sebiferum*	*Sapium sebiferum*
81-J21	A	J21	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
82-J21	A	J21	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
83-J21	A	J21	2	*Koelreuteria bipinnata*	*Lithocarpus glaber*
92-J21	A	J21	2	*Lithocarpus glaber*	*Lithocarpus glaber*
72-K3	A	K3	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
73-K3	A	K3	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
75-K3	A	K3	2	*Cyclobalanopsis glauca*	*Quercus fabri*
64-O6	A	O6	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
65-O6	A	O6	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
66-O6	A	O6	2	*Castanopsis sclerophylla*	*Quercus serrata*
105-O6	A	O6	2	*Quercus serrata*	*Quercus serrata*
63-P26	A	P26	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
62-P26	A	P26	2	*Castanopsis sclerophylla*	*Quercus serrata*
102-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
103-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
104-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
74-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
76-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Quercus fabri*
77-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Quercus fabri*
100-Q21	A	Q21	2	*Quercus fabri*	*Quercus fabri*
101-Q21	A	Q21	2	*Quercus fabri*	*Quercus fabri*
84-Q7	A	Q7	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
85-Q7	A	Q7	2	*Koelreuteria bipinnata*	*Lithocarpus glaber*

Code	Site	Plot	Diversity level	Species 1	Species 2
93-Q7	A	Q7	2	*Lithocarpus glaber*	*Lithocarpus glaber*
94-Q7	A	Q7	2	*Lithocarpus glaber*	*Lithocarpus glaber*
69-S18	A	S18	2	*Choerospondias axillaris*	*Choerospondias axillaris*
70-S18	A	S18	2	*Choerospondias axillaris*	*Sapium sebiferum*
71-S18	A	S18	2	*Choerospondias axillaris*	*Sapium sebiferum*
119-S18	A	S18	2	*Sapium sebiferum*	*Sapium sebiferum*
r-120-S18	A	S18	2	*Sapium sebiferum*	*Sapium sebiferum*
88-T17	A	T17	2	*Liquidambar formosana*	*Liquidambar formosana*
89-T17	A	T17	2	*Liquidambar formosana*	*Liquidambar formosana*
90-T17	A	T17	2	*Liquidambar formosana*	*Sapindus mukorossi*
115-T17	A	T17	2	*Sapindus mukorossi*	*Sapindus mukorossi*
130-F27	A	F27	4	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
131-F27	A	F27	4	*Choerospondias axillaris*	*Castanopsis sclerophylla*
153-F27	A	F27	4	*Quercus serrata*	*Choerospondias axillaris*
161-F27	A	F27	4	*Sapium sebiferum*	*Choerospondias axillaris*
162-F27	A	F27	4	*Sapium sebiferum*	*Sapium sebiferum*
139-F28	A	F28	4	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
132-N20	A	N20	4	*Choerospondias axillaris*	*Choerospondias axillaris*
154-N20	A	N20	4	*Quercus serrata*	*Castanopsis sclerophylla*
155-N20	A	N20	4	*Quercus serrata*	*Quercus serrata*
156-N20	A	N20	4	*Quercus serrata*	*Sapium sebiferum*
163-N20	A	N20	4	*Sapium sebiferum*	*Castanopsis sclerophylla*
133-N8	A	N8	4	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
149-N8	A	N8	4	*Quercus fabri*	*Cyclobalanopsis glauca*
125-P19	A	P19	4	*Castanea henryi*	*Castanea henryi*
126-P19	A	P19	4	*Castanea henryi*	*Nyssa sinensis*
143-P19	A	P19	4	*Liquidambar formosana*	*Sapindus mukorossi*
148-P19	A	P19	4	*Nyssa sinensis*	*Sapindus mukorossi*
160-P19	A	P19	4	*Sapindus mukorossi*	*Sapindus mukorossi*
141-P29	A	P29	4	*Liquidambar formosana*	*Liquidambar formosana*
142-P29	A	P29	4	*Liquidambar formosana*	*Nyssa sinensis*
147-P29	A	P29	4	*Nyssa sinensis*	*Castanea henryi*
159-P29	A	P29	4	*Sapindus mukorossi*	*Castanea henryi*
146-W12/X12	A	W12/X12	4	*Lithocarpus glaber*	*Lithocarpus glaber*
176-P27	A	P27	8	*Cyclobalanopsis glauca*	*Quercus fabri*
181-P27	A	P27	8	*Koelreuteria bipinnata*	*Lithocarpus glaber*
166-R16	A	R16	8	*Castanea henryi*	*Liquidambar formosana*
171-R16	A	R16	8	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
175-R16	A	R16	8	*Choerospondias axillaris*	*Sapium sebiferum*
190-R16	A	R16	8	*Nyssa sinensis*	*Castanea henryi*
193-R16	A	R16	8	*Quercus serrata*	*Castanopsis sclerophylla*
194-R16	A	R16	8	*Quercus serrata*	*Quercus serrata*
198-R16	A	R16	8	*Sapindus mukorossi*	*Sapindus mukorossi*
199-R16	A	R16	8	*Sapindus mukorossi*	*Sapindus mukorossi*
200-R16	A	R16	8	*Sapium sebiferum*	*Quercus serrata*
201-R16	A	R16	8	*Sapium sebiferum*	*Sapium sebiferum*
165-S10	A	S10	8	*Castanea henryi*	*Castanea henryi*
170-S10	A	S10	8	*Castanopsis sclerophylla*	*Sapium sebiferum*

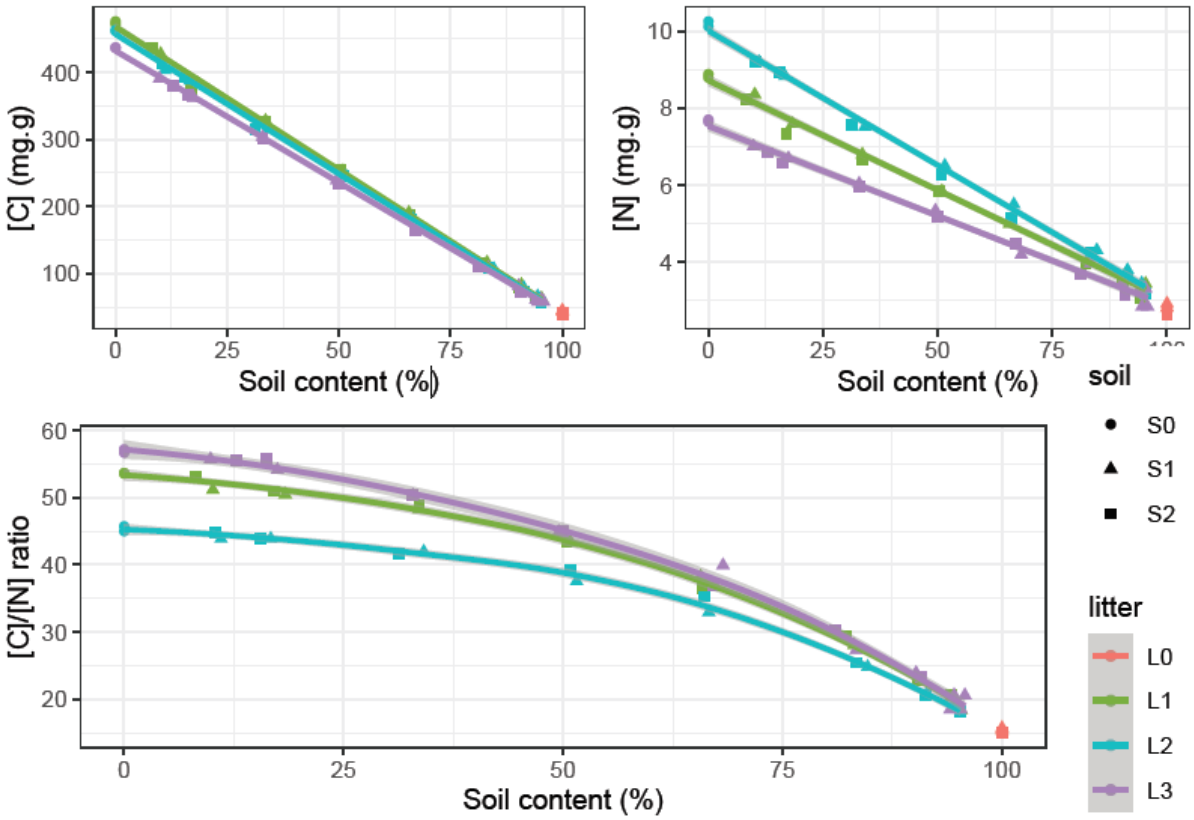
Code	Site	Plot	Diversity level	Species 1	Species 2
173-S10	A	S10	8	*Choerospondias axillaris*	*Castanopsis sclerophylla*
174-S10	A	S10	8	*Choerospondias axillaris*	*Choerospondias axillaris*
186-S10	A	S10	8	*Liquidambar formosana*	*Liquidambar formosana*
185-S10	A	S10	8	*Liquidambar formosana*	*Nyssa sinensis*
188-S10	A	S10	8	*Nyssa sinensis*	*Nyssa sinensis*
189-S10	A	S10	8	*Nyssa sinensis*	*Sapindus mukorossi*
197-S10	A	S10	8	*Sapindus mukorossi*	*Castanea henryi*
178-S14	A	S14	8	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
183-S15	A	S15	8	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
r-216-S15	A	S15	8	*Koelreuteria bipinnata*	*Lithocarpus glaber*
184-S15	A	S15	8	*Koelreuteria bipinnata*	*Quercus fabri*
191-T15	A	T15	8	*Quercus fabri*	*Quercus fabri*
220-L21	A	L21	16	*Liquidambar formosana*	*Choerospondias axillaris*
203-L22	A	L22	16	*Castanea henryi*	*Nyssa sinensis*
204-L22	A	L22	16	*Castanea henryi*	*Sapindus mukorossi*
217-L22	A	L22	16	*Liquidambar formosana*	*Castanea henryi*
219-L22	A	L22	16	*Liquidambar formosana*	*Liquidambar formosana*
218-L22	A	L22	16	*Liquidambar formosana*	*Nyssa sinensis*
221-L22	A	L22	16	*Lithocarpus glaber*	*Lithocarpus glaber*
222-L22	A	L22	16	*Quercus fabri*	*Quercus fabri*
230-L22	A	L22	16	*Sapium sebiferum*	*Castanopsis sclerophylla*
226-M21	A	M21	16	*Quercus serrata*	*Sapium sebiferum*
r-213-U10	A	U10	16	*Cyclobalanopsis glauca*	*Quercus fabri*
225-U10	A	U10	16	*Quercus serrata*	*Quercus serrata*
229-U10	A	U10	16	*Sapindus mukorossi*	*Sapindus mukorossi*
231-U10	A	U10	16	*Sapium sebiferum*	*Sapium sebiferum*
232-N9	A	N9	24	*Castanea henryi*	*Castanea henryi*
236-N9	A	N9	24	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
238-N9	A	N9	24	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
241-N9	A	N9	24	*Sapindus mukorossi*	*Nyssa sinensis*
234-R18	A	R18	24	*Castanopsis sclerophylla*	*Quercus serrata*
235-R18	A	R18	24	*Choerospondias axillaris*	*Quercus serrata*
239-R18	A	R18	24	*Nyssa sinensis*	*Nyssa sinensis*

Supplementary material I – S2 Soil contamination correction

Effect of soil contamination on litter carbon (C) and nitrogen (N) measurements

Estimation of soil contamination effect on C and N measurements

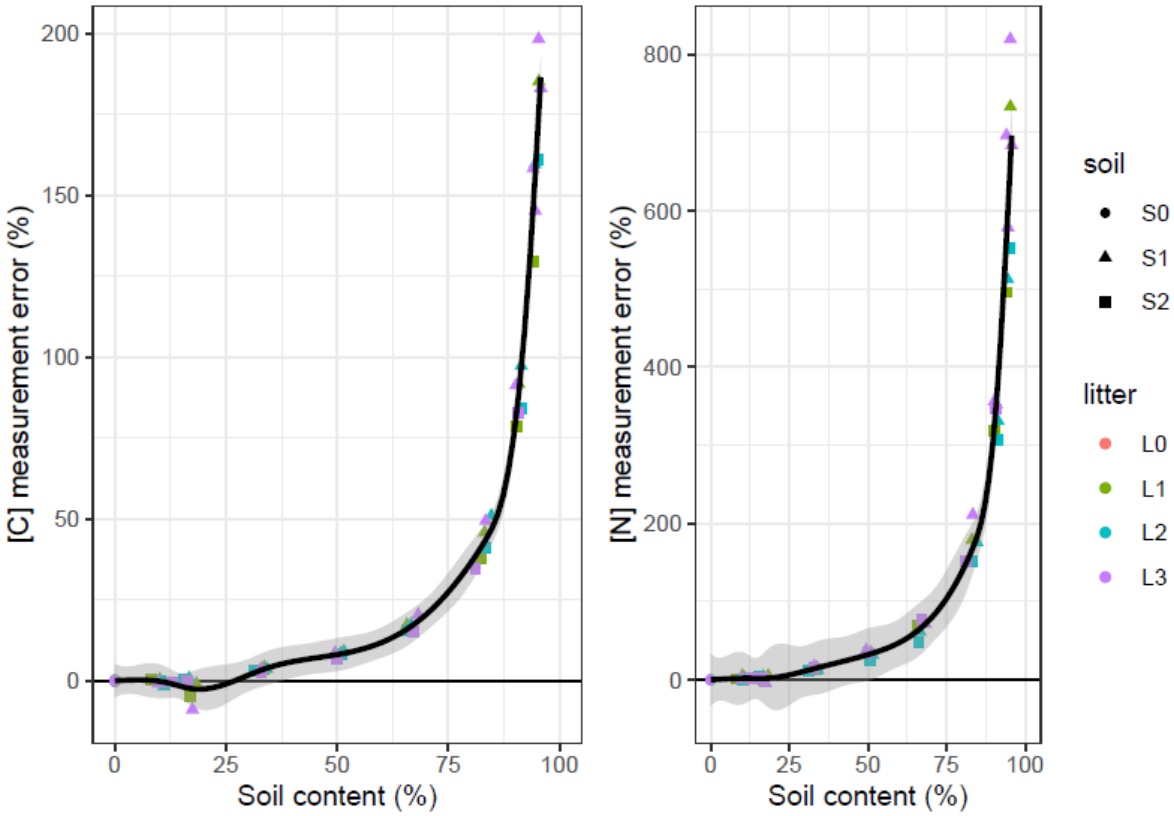
To test the effect of soil contamination on carbon and nitrogen measurements, we prepared calibration samples where soil contamination was manipulated from 0% to 100% of the total sample mass. The litter was collected in litter traps to avoid soil contamination from three monocultures (*Sapium sebiferum, Castanea Henryi, Liquidambar formosana*), soil was collected from two distant plots (K19 and T17) with contracting chemical composition (see Scholten *et al.* 2017). For each pair of soil and litter types, 1 g of soil:litter mix was prepared for the following ratio: 1:0, 5:1, 2:1, 1:1, 1:2, 1:5, 1:10, 0:1. The sample carbon and nitrogen content were measured with and elemental analyzer (Vario EL Cube, Elementar, Langenselbold, Germany)



Measurement error due to soil contamination

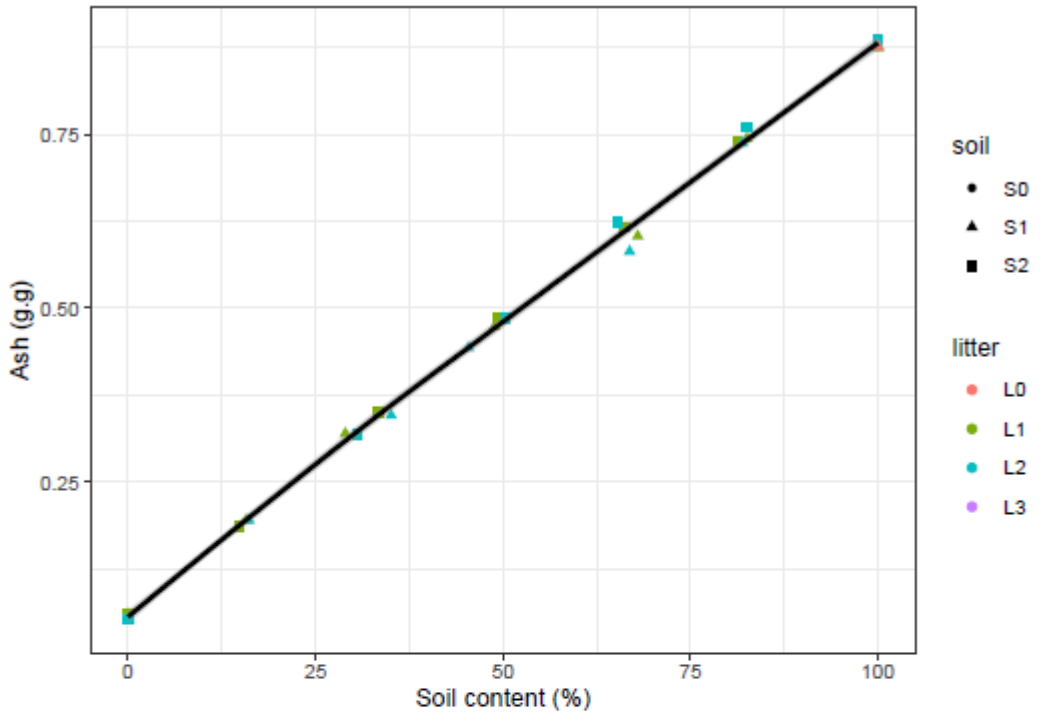
Measurement error calculation:

$$Measurement.error = 100 \times \frac{(measured - introduced)}{introduced}$$



Using ash measurements to estimate and correct soil contamination

To estimate soil contamination from our samples, we used measured ash content from our calibration samples and tested the linear relationship between soil contamination (%) and ash content (g.g). The ash content of the samples was measured using the loss on ignition method where the samples are incinerated in a muffle oven at 550 ◦ C (Nabertherm GmbH, Lilienthal, Germany)




```
##
## Call:
## lm(formula = ash.content ~ soil.conta, data = df.ash)
##
## Residuals:
##       Min        1Q    Median        3Q       Max
## -0.032487 -0.008449  0.000179  0.007138  0.022679
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept) 6.347e-02  3.756e-03    16.9  3.2e-16 ***
## soil.conta  8.231e-03  6.233e-05   132.1  < 2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.01208 on 28 degrees of freedom
##   (17 observations deleted due to missingness)
## Multiple R-squared:  0.9984, Adjusted R-squared:  0.9983
## F-statistic: 1.744e+04 on 1 and 28 DF,  p-value: < 2.2e-16
```

According to our measurements, soil contamination linearly increases ash content. In addition, litter ash content (estimate +/- SE = 0.063 +/- 0.004 g/g, i.e., model intercept) is neglectable in comparison to soil ash content (.886 +/- 0.004 g/g).

Therefore, we can estimate soil carbon and nitrogen addition into the sample using:

$$\Leftrightarrow soil.content = \frac{Ash_{sample}}{Ash_{soil}}$$

$$\Leftrightarrow soil.content = \frac{Ash_{sample}}{1 - SOM}, \text{ when } Ash_{soil} = 1 - SOM$$

$$\Rightarrow [C]_{litter} = [C]_{sample} - [C]_{soil} \times soil.content$$

$$\Leftrightarrow [C]_{litter} = [C]_{sample} - [C]_{soil} \times \frac{Ash_{sample}}{1 - SOM}$$

Equivalent for N content with:

$$[N]_{litter} = [N]_{sample} - [N]_{soil} \times \frac{Ash_{sample}}{1 - SOM}$$

Supplementary material I – S3 R Outputs

Contents

Fig. 2.A Decomposition C loss (%)

Model output

```
##
## Call:
## lm(formula = "C.loss_Ma1 ~ log(neigh.sp.rich)", data = df)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -50.755 -10.573  -1.088  10.112  38.701
##
## Coefficients:
##                   Estimate Std. Error t value Pr(>|t|)
## (Intercept)         59.175      2.236  26.461   <2e-16 ***
## log(neigh.sp.rich)   1.532      1.927   0.795    0.428
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 15.32 on 151 degrees of freedom
## Multiple R-squared:  0.00417,    Adjusted R-squared:  -0.002425
## F-statistic: 0.6322 on 1 and 151 DF,  p-value: 0.4278
```

Model quality

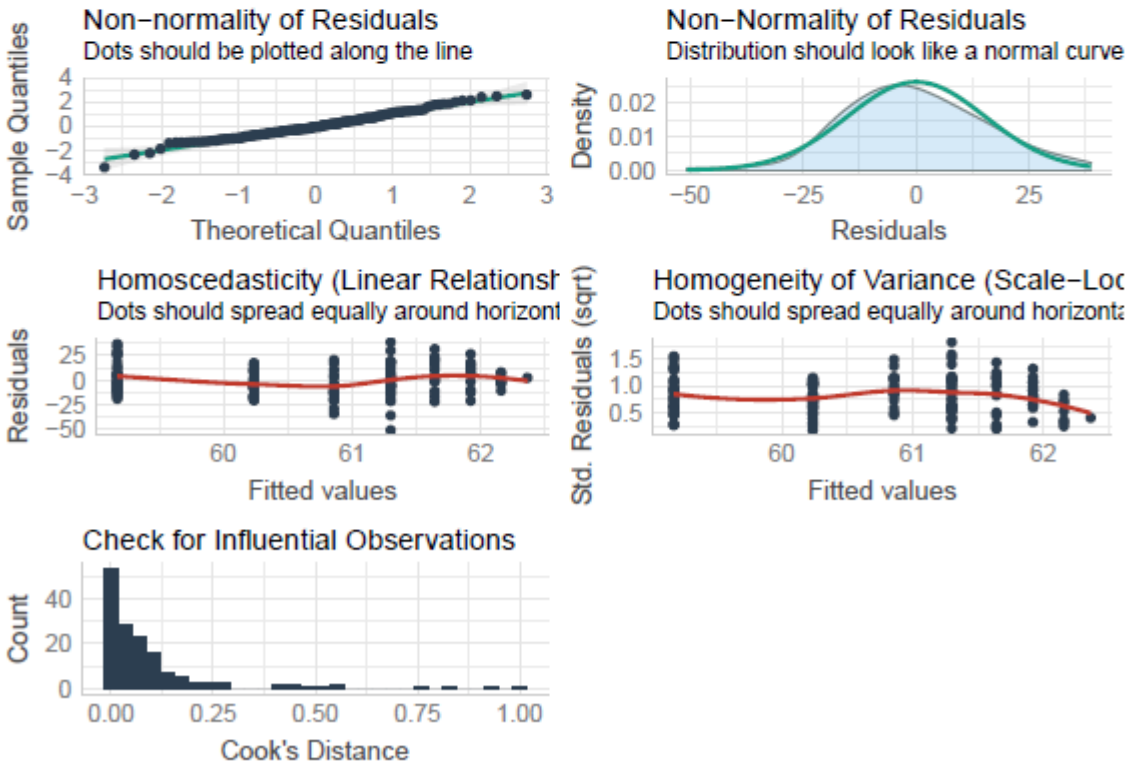


Fig. 2.B Decomposition N loss (%)

Model output

```
##
## Call:
## lm(formula = "N.loss_Ma1 ~ log(neigh.sp.rich)", data = df)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -41.429 -12.969   1.371  11.548  34.494
##
## Coefficients:
##                   Estimate Std. Error t value Pr(>|t|)
## (Intercept)         65.506      2.418  27.094   <2e-16 ***
## log(neigh.sp.rich)   4.989      2.083   2.395   0.0179 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 16.56 on 151 degrees of freedom
## Multiple R-squared:  0.03659,    Adjusted R-squared:  0.03021
## F-statistic: 5.735 on 1 and 151 DF,  p-value: 0.01785
```

Model quality

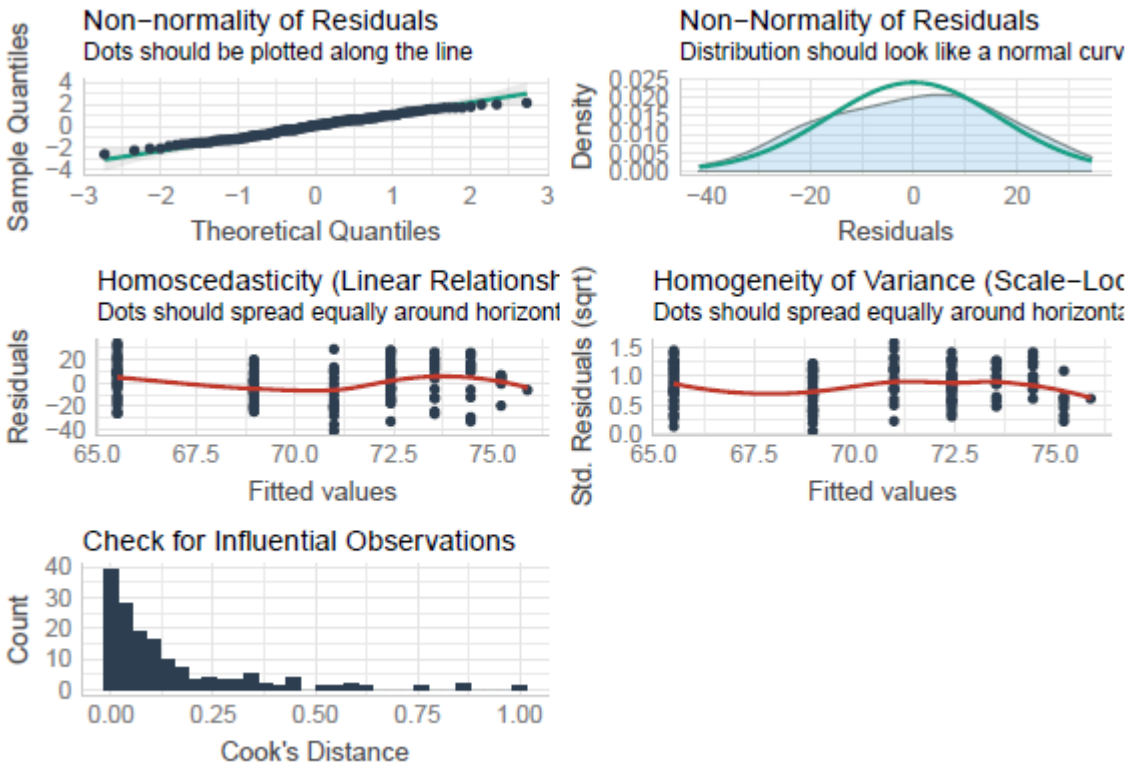


Fig. 2.C Microbial decomposition C loss (%)

Model output

```
##
## Call:
## lm(formula = "C.loss_M11 ~ log(neigh.sp.rich)", data = df)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -25.889  -7.769  -0.531   6.920  36.553
##
## Coefficients:
##                   Estimate Std. Error t value Pr(>|t|)
## (Intercept)         49.521      1.720  28.783   <2e-16 ***
## log(neigh.sp.rich)  -1.826      1.482  -1.231     0.22
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 11.79 on 151 degrees of freedom
## Multiple R-squared:  0.009943,   Adjusted R-squared:  0.003386
## F-statistic: 1.516 on 1 and 151 DF,  p-value: 0.2201
```

Model quality

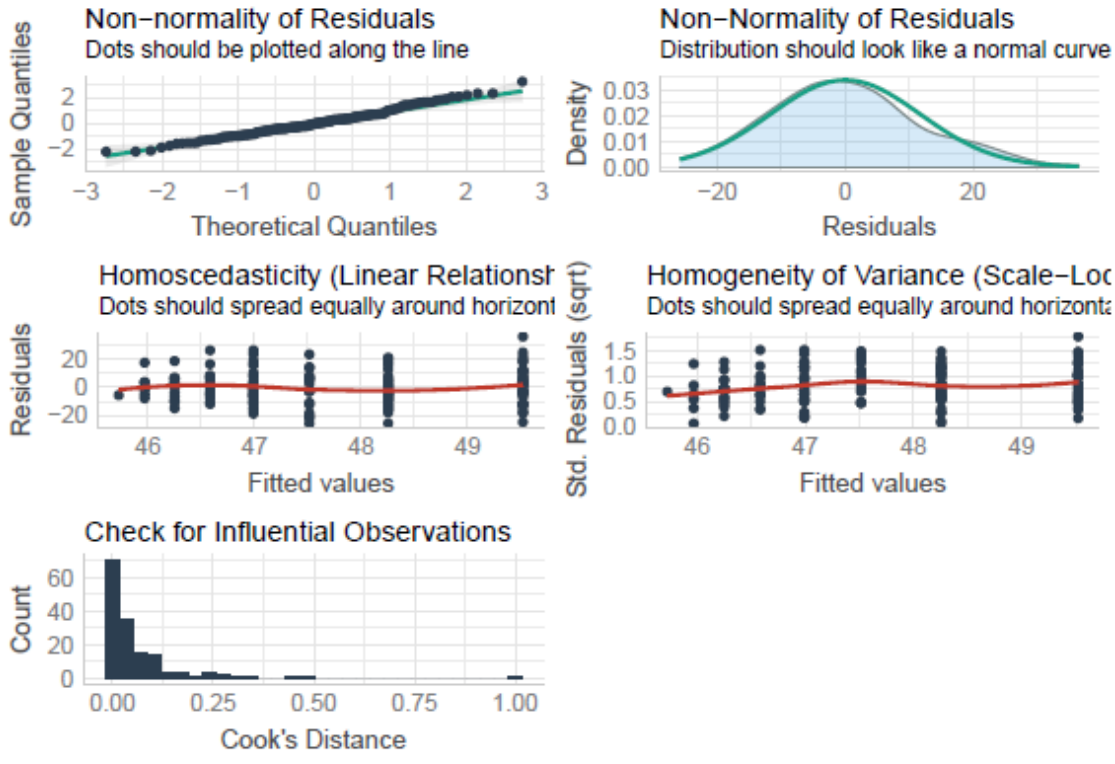


Fig. 2.D Microbial decomposition N loss (%)

Model output

```
##
## Call:
## lm(formula = "N.loss_M11 ~ log(neigh.sp.rich)", data = df)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -36.379 -10.818  -1.621   7.900  43.181
##
## Coefficients:
##                   Estimate Std. Error t value Pr(>|t|)
## (Intercept)         56.819      2.308  24.616   <2e-16 ***
## log(neigh.sp.rich)   2.885      1.989   1.451    0.149
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 15.81 on 151 degrees of freedom
## Multiple R-squared:  0.01374,    Adjusted R-squared:  0.007213
## F-statistic: 2.104 on 1 and 151 DF,  p-value: 0.149
```

Model quality

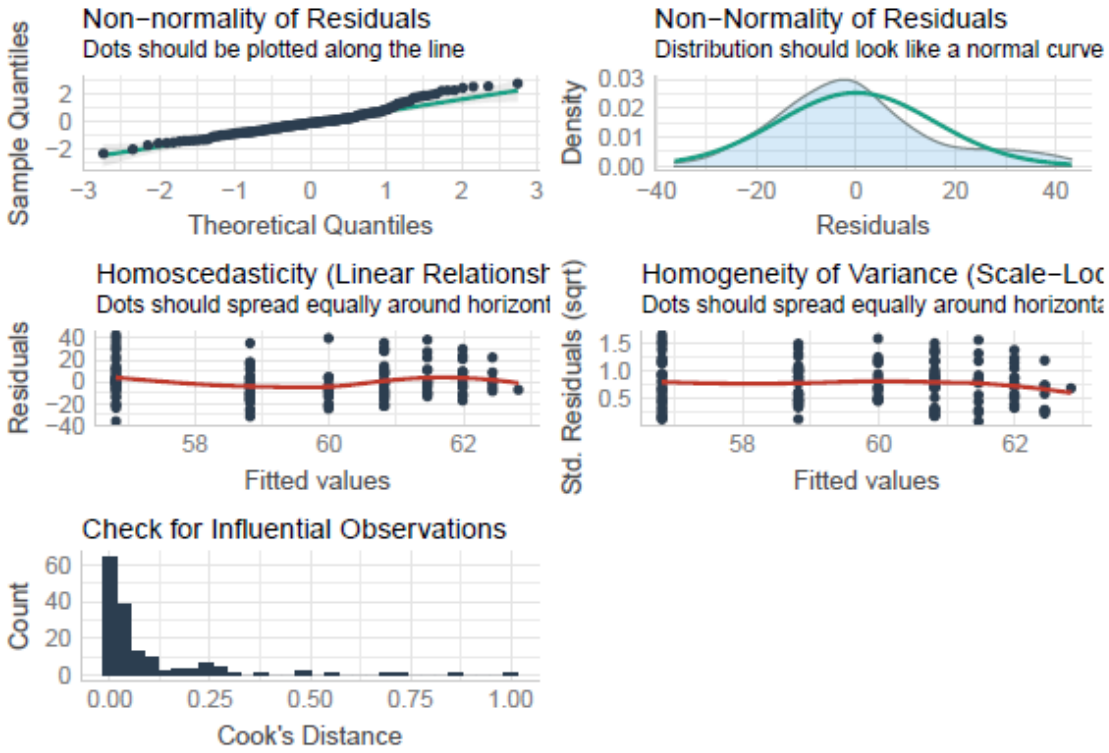


Fig. 2.E Decomposability C loss (%)

Model output

```
##
## Call:
## lm(formula = "C.loss_CC ~ log(lit.rich)", data = df)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -21.659  -5.099  -0.132   5.716  20.047
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)    43.7478     0.9935  44.032   <2e-16 ***
## log(lit.rich)  -1.2590     0.8716  -1.445    0.151
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 8.124 on 151 degrees of freedom
## Multiple R-squared:  0.01363,    Adjusted R-squared:  0.007099
## F-statistic: 2.087 on 1 and 151 DF,  p-value: 0.1507
```

Model quality

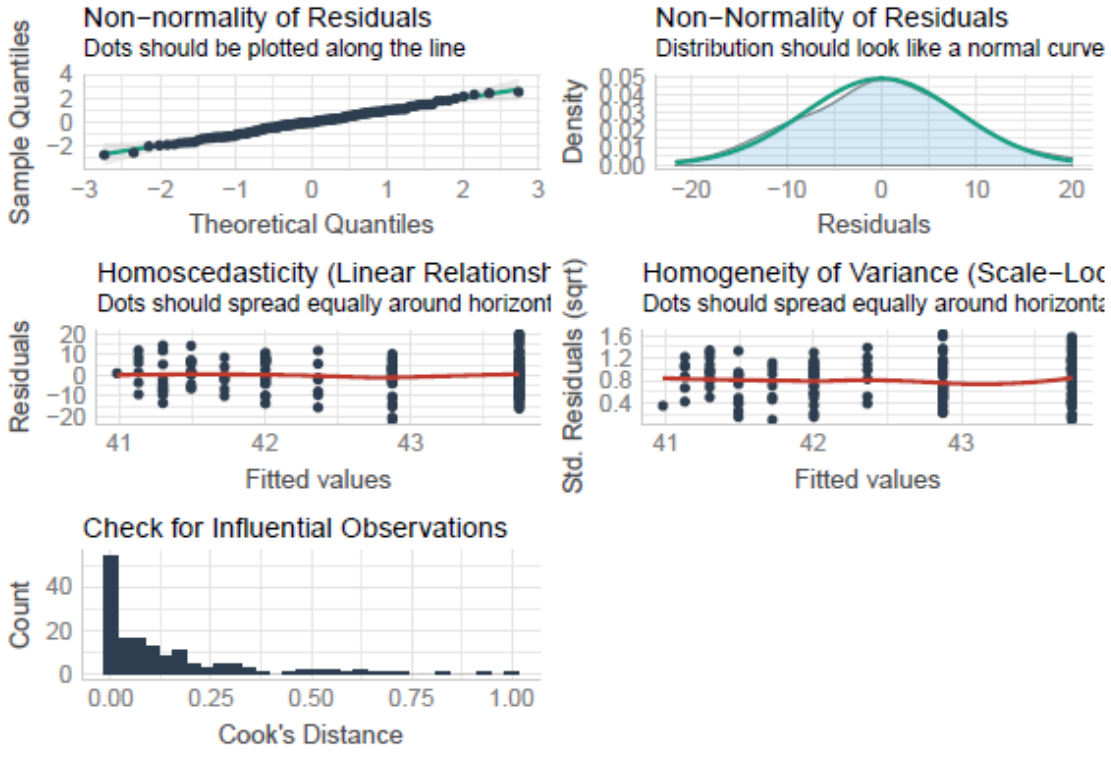
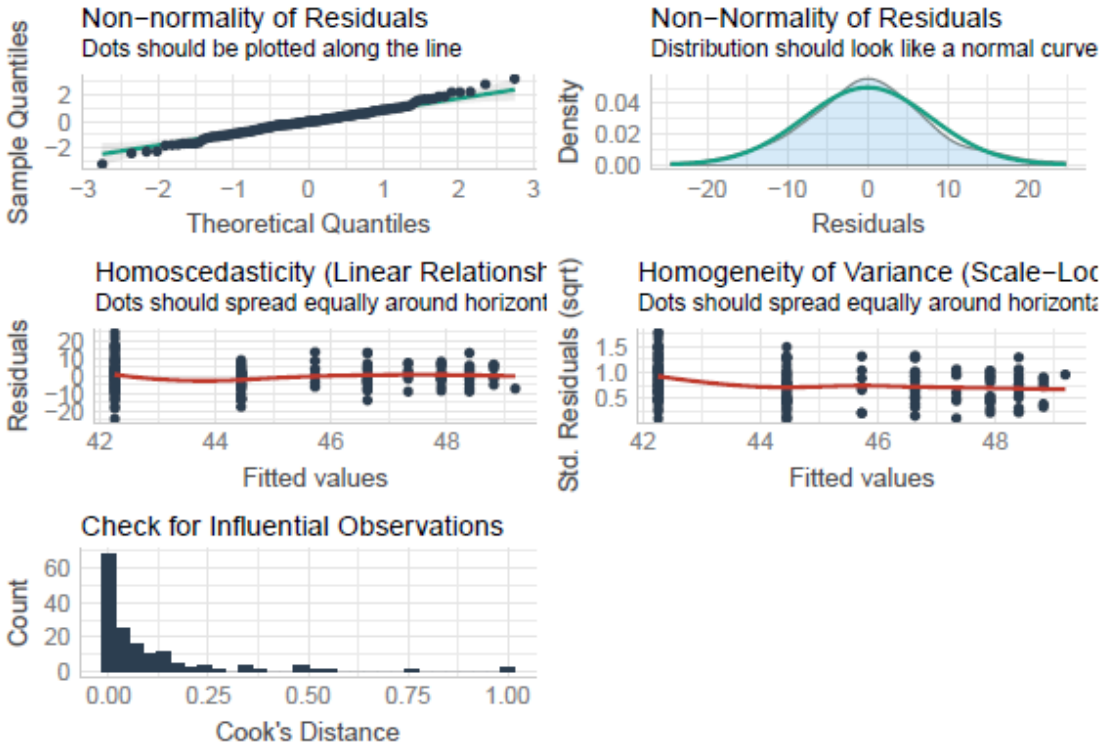


Fig. 2.F Decomposability N loss (%)

Model output

```
##
## Call:
## lm(formula = "N.loss_CG ~ log(lit.rich)", data = df)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -24.5090  -4.9002   0.0964   4.6015  24.6910
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)    42.2580     0.9720  43.476  < 2e-16 ***
## log(lit.rich)   3.1526     0.8527   3.697 0.000304 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 7.947 on 151 degrees of freedom
## Multiple R-squared:  0.08302,    Adjusted R-squared:  0.07694
## F-statistic: 13.67 on 1 and 151 DF,  p-value: 0.0003043
```

Model quality



Litter species richness

Model

```
##
## Call:
## lm(formula = "lit.rich ~ log(neigh.sp.rich)", data = df)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -3.4450 -1.2606 -0.2954  0.6351  4.6699
##
## Coefficients:
##                   Estimate Std. Error t value Pr(>|t|)
## (Intercept)         0.3649     0.1996   1.828   0.0695 .
## log(neigh.sp.rich)  2.8353     0.1720  16.488   <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 1.367 on 151 degrees of freedom
## Multiple R-squared:  0.6429, Adjusted R-squared:  0.6405
## F-statistic: 271.9 on 1 and 151 DF,  p-value: < 2.2e-16
```

Model quality .

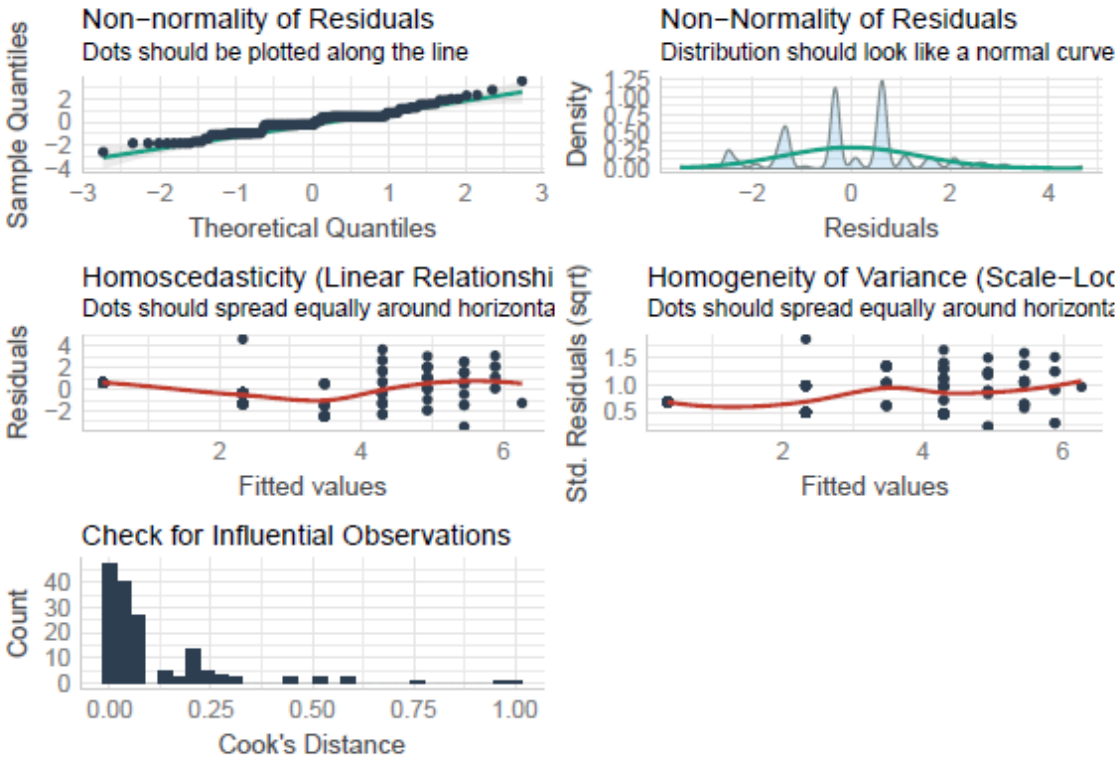


Fig. 3.B: Part of microbial decomposition in litter decomposition

Part of microbial decomposition in total C loss

$$\text{microbial contribution to } C_{loss} = \frac{C.loss_{microbial}}{C.loss_{total}}$$

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##   30.32   64.30   80.55   84.42   97.41  476.48
```

Part of microbial decomposition in total N loss

$$\text{microbial contribution to } N_{loss} = \frac{N.loss_{microbial}}{N.loss_{total}}$$

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##   27.31   74.62   86.59   87.16  100.62  190.34
```

Fig. 3.C: Structural equation model

SEM structure

Labels: "Ma" = total decomposition, "Mi" = microbial decomposition, "CG" = Common Garden (i.e., decomposability), "fall" = amount of litterfall, "lit.rich" = litter species richness, "neigh.sp.rch" = neighborhood tree species richness

```
form.sem =
  '
  C.loss_Ma1 ~ C.loss_Mi1 + fall + log.lit.rich + log.neigh.sp.rich
  N.loss_Ma1 ~ N.loss_Mi1 + fall + log.lit.rich + log.neigh.sp.rich
  C.loss_Ma1 ~~ N.loss_Ma1

  C.loss_Mi1 ~ C.loss_CG + fall + log.lit.rich + log.neigh.sp.rich
  N.loss_Mi1 ~ N.loss_CG + fall + log.lit.rich + log.neigh.sp.rich
  C.loss_Mi1 ~~ N.loss_Mi1

  C.loss_CG ~ log.lit.rich
  N.loss_CG ~ log.lit.rich
  C.loss_CG ~~ N.loss_CG

  fall ~ log.neigh.sp.rich
  log.lit.rich ~ log.neigh.sp.rich
  fall ~~ log.lit.rich
'
```

Hypotheses .

Causal relations

Response variable	Explanatory variable	Hypothesis
C.loss_Ma1	C.loss_Mi1	We expect total litter decomposition to be carried out by the microbial community
C.loss_Ma1	fall	We expect litter decomposition rate to increase with the amount of litterfall due to the addatation of the decomposer community to the higher amount of nutrients
C.loss_Ma1	log.lit.rich	We expect litter decomposition rate to increase with litter species richness due to the increase of litter complementarity
N.loss_Ma1	N.loss_Mi1	We expect total litter decomposition to be carried out by the microbial community
N.loss_Ma1	fall	We expect litter decomposition rate to increase with the amount of litterfall due to the addatation of the decomposer community to the higher amount of nutrients
N.loss_Ma1	log.lit.rich	We expect litter decomposition rate to increase with litter species richness due to the increase of litter complementarity
C.loss_Mi1	C.loss_CG	We expect microbial decomposition to increase with litter decomposability
C.loss_Mi1	fall	We expect litter decomposition rate to increase with the amount of litterfall due to the addatation of the decomposer community to the higher amount of nutrients

(continued)

Response variable	Explanatory variable	Hypothesis
C.loss_Mi1	log.lit.rich	We expect litter decomposition rate to increase with litter species richness due to the increase of litter complementarity
N.loss_Mi1	N.loss_CG	We expect microbial decomposition to increase with litter decomposability
N.loss_Mi1	fall	We expect litter decomposition rate to increase with the amount of litterfall due to the addatation of the decomposer community to the higher amount of nutrients
N.loss_Mi1	log.lit.rich	We expect litter decomposition rate to increase with litter species richness due to the increase of litter complementarity
C.loss_CG	log.lit.rich	We expect litter decomposition rate to increase with litter species richness due to the increase of litter complementarity
N.loss_CG	log.lit.rich	We expect litter decomposition rate to increase with litter species richness due to the increase of litter complementarity
fall	log.neigh.sp.r	We expect tree litterfall to increase with tree species richness
log.lit.rich	log.neigh.sp.ric	We expect litter species richness to increase with tree species richness

Correlations

Covariate 1	Covariate 2	Hypothesis
C.loss_Ma1	N.loss_Ma1	We expect carbon and nitrogen decomposition to be positively correlated
C.loss_Mi1	N.loss_Mi1	We expect carbon and nitrogen decomposition to be positively correlated
C.loss_CG	N.loss_CG	We expect carbon and nitrogen decomposition to be positively correlated
fall	log.lit.rich	We expect the amount of litterfall and litter species richness to be positively correlated as both positively affected by tree species richness

Model outputs

Summary .

Labels: "Ma" = total decomposition, "Mi" = microbial decomposition, "CG" = Common Garden (i.e., decomposability), "fall" = amount of litterfall, "lit.rich" = litter species richness, "ngh.sp.rch" = neighborhood tree species richness

```
## lavaan 0.6-7 ended normally after 42 iterations
##
##   Estimator                                         ML
##   Optimization method                           NLMINB
##   Number of free parameters                         32
##
##   Number of observations                           153
##
## Model Test User Model:
##
##   Test statistic                                10.994
##   Degrees of freedom                                12
##   P-value (Chi-square)                           0.529
##
## Parameter Estimates:
##
##   Standard errors                             Standard
##   Information                                 Expected
##   Information saturated (h1) model          Structured
##
## Regressions:
##                    Estimate  Std.Err  z-value  P(>|z|)   Std.lv  Std.all
##   C.loss_Ma1 ~
##     C.loss_Mi1        0.264    0.052    5.069    0.000    0.264    0.261
##     fall              0.319    0.092    3.468    0.001    0.319    0.314
##     log.lit.rich      0.185    0.158    1.168    0.243    0.185    0.181
##     log.ngh.sp.rch   -0.214    0.144   -1.486    0.137   -0.214   -0.210
##   N.loss_Ma1 ~
##     N.loss_Mi1        0.507    0.048   10.511    0.000    0.507    0.492
##     fall              0.235    0.081    2.904    0.004    0.235    0.232
##     log.lit.rich      0.090    0.139    0.649    0.516    0.090    0.089
##     log.ngh.sp.rch   -0.053    0.126   -0.423    0.672   -0.053   -0.053
##   C.loss_Mi1 ~
##     C.loss_CG         0.433    0.055    7.881    0.000    0.433    0.430
##     fall              0.046    0.091    0.502    0.616    0.046    0.045
##     log.lit.rich      0.196    0.156    1.255    0.210    0.196    0.195
##     log.ngh.sp.rch   -0.217    0.142   -1.532    0.125   -0.217   -0.216
##   N.loss_Mi1 ~
##     N.loss_CG         0.350    0.056    6.271    0.000    0.350    0.356
##     fall              0.110    0.089    1.229    0.219    0.110    0.111
##     log.lit.rich      0.235    0.154    1.530    0.126    0.235    0.239
##     log.ngh.sp.rch   -0.198    0.139   -1.429    0.153   -0.198   -0.202
##   C.loss_CG ~
##     log.lit.rich     -0.117    0.080   -1.454    0.146   -0.117   -0.117
##   N.loss_CG ~
##     log.lit.rich      0.288    0.077    3.722    0.000    0.288    0.288
```

```
##   fall ~
##     log.ngh.sp.rch    0.459    0.072    6.395    0.000    0.459    0.459
##   log.lit.rich ~
##     log.ngh.sp.rch    0.856    0.042   20.445    0.000    0.856    0.856
##
## Covariances:
##                    Estimate  Std.Err  z-value  P(>|z|)   Std.lv  Std.all
##  .C.loss_Ma1 ~~
##    .N.loss_Ma1        0.579    0.075    7.716    0.000    0.579    0.798
##  .C.loss_Mi1 ~~
##    .N.loss_Mi1        0.550    0.078    7.062    0.000    0.550    0.695
##  .C.loss_CG ~~
##    .N.loss_CG         0.379    0.082    4.604    0.000    0.379    0.401
##  .fall ~~
##    .log.lit.rich      0.197    0.040    4.901    0.000    0.197    0.432
##
## Variances:
##                    Estimate  Std.Err  z-value  P(>|z|)   Std.lv  Std.all
##    .C.loss_Ma1        0.827    0.095    8.746    0.000    0.827    0.803
##    .N.loss_Ma1        0.636    0.073    8.746    0.000    0.636    0.624
##    .C.loss_Mi1        0.807    0.092    8.746    0.000    0.807    0.803
##    .N.loss_Mi1        0.776    0.089    8.746    0.000    0.776    0.807
##    .C.loss_CG         0.980    0.112    8.746    0.000    0.980    0.986
##    .N.loss_CG         0.911    0.104    8.746    0.000    0.911    0.917
##    .fall              0.784    0.090    8.746    0.000    0.784    0.789
##    .log.lit.rich      0.266    0.030    8.746    0.000    0.266    0.268
```

R squared

```
##   C.loss_Ma1   N.loss_Ma1   C.loss_Mi1   N.loss_Mi1    C.loss_CG    N.loss_CG
##        0.197        0.376        0.197        0.193        0.014        0.083
##         fall log.lit.rich
##        0.211        0.732
```

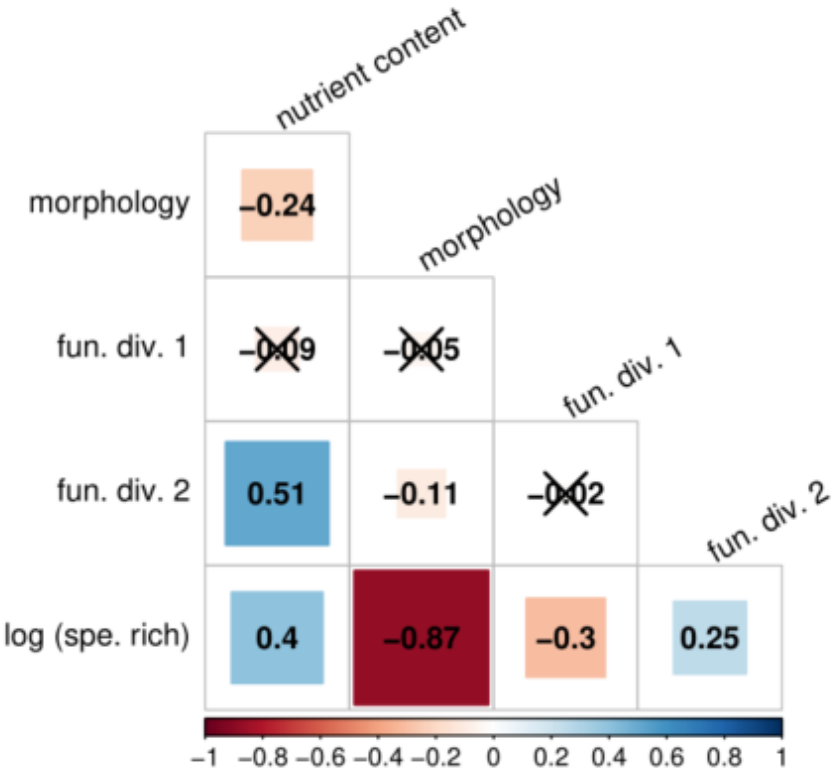
Model quality

```
##     DF    CFI  RMSEA   SRMR
## 12.000  1.000  0.000  0.031
```

Figure 4

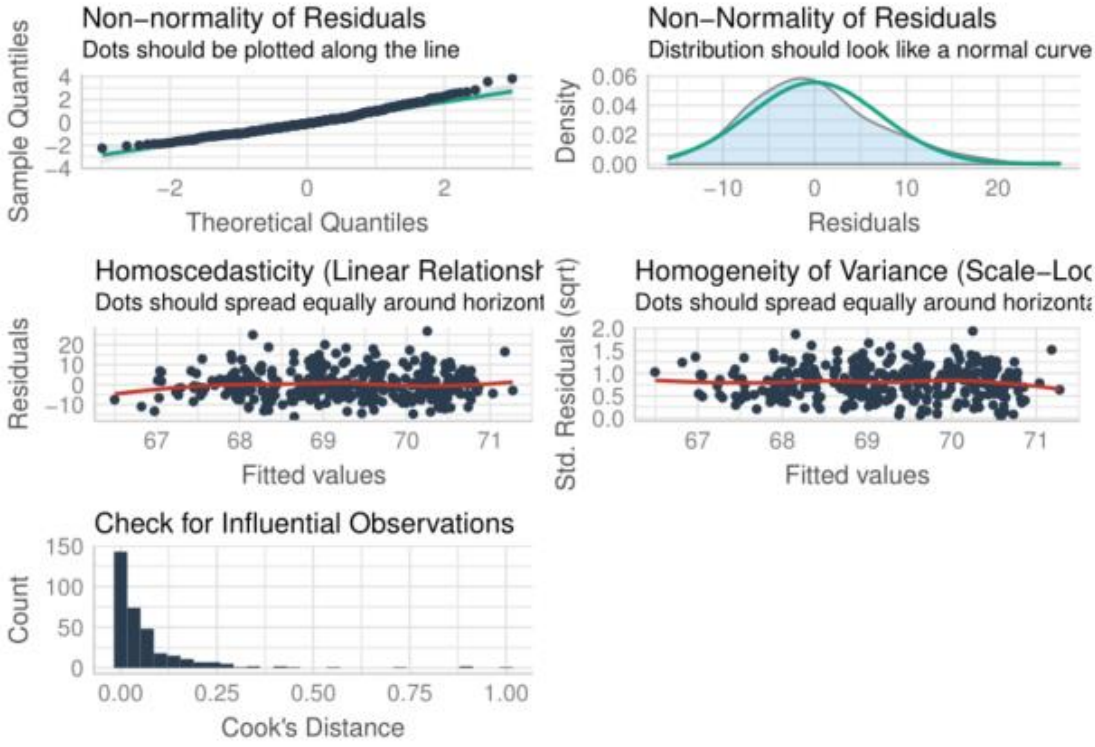
Fig. 4.A: Decomposability drivers

Correlation between explanatory variables



Decomposability C loss

```
##
## Call:
## lm(formula = C.loss ~ compo.pca.1, data = df)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -16.0580  -5.0609  -0.6945   3.9496  26.8027
##
## Coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  69.2268     0.3891 177.915  < 2e-16 ***
## compo.pca.1   1.0215     0.3897   2.621  0.00915 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 7.164 on 337 degrees of freedom
## Multiple R-squared:  0.01998,    Adjusted R-squared:  0.01707
## F-statistic: 6.872 on 1 and 337 DF,  p-value: 0.009155
```



Decomposability N loss

```
##
## Call:
## lm(formula = N.loss ~ div.pca.1 + compo.pca.1 + log(lit.rich),
##     data = df)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -25.5671  -4.8384  -0.5727   5.3752  29.4864
##
## Coefficients:
##               Estimate Std. Error t value Pr(>|t|)
## (Intercept)    69.7242     0.7842  88.909  < 2e-16 ***
## div.pca.1       0.4594     0.1909   2.406 0.016667 *
## compo.pca.1     2.0861     0.5152   4.049 6.38e-05 ***
## log(lit.rich)   2.5523     0.7333   3.481 0.000566 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 8.67 on 335 degrees of freedom
## Multiple R-squared:  0.1249, Adjusted R-squared:  0.1171
## F-statistic: 15.94 on 3 and 335 DF,  p-value: 1.041e-09
```

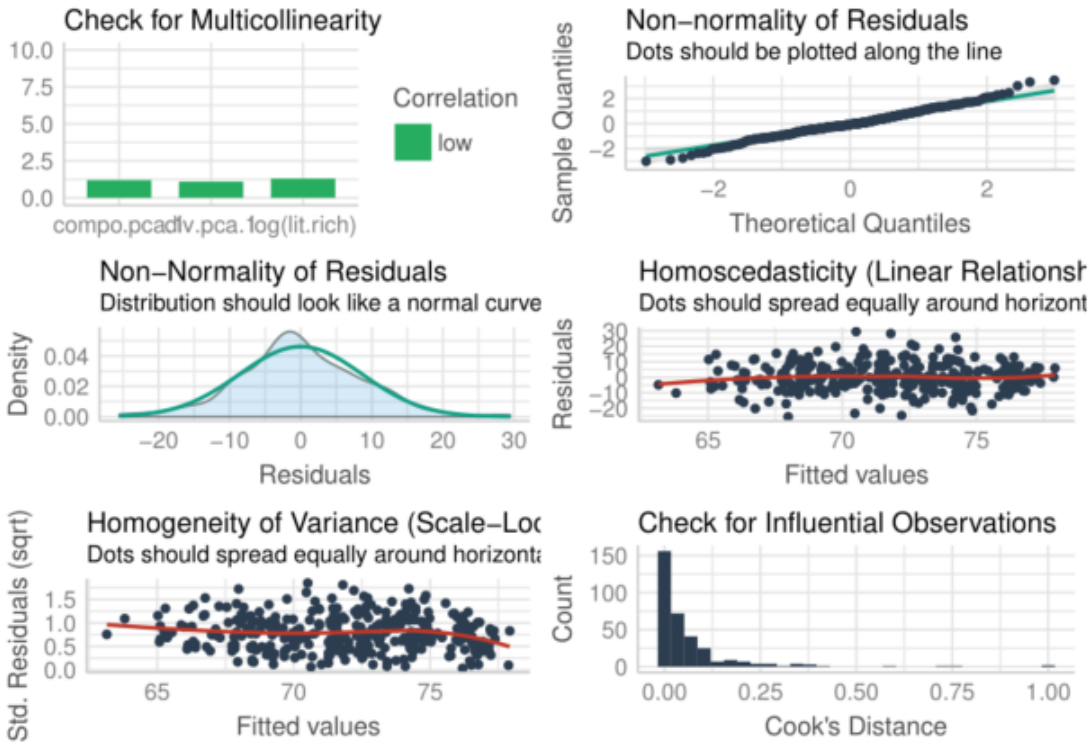
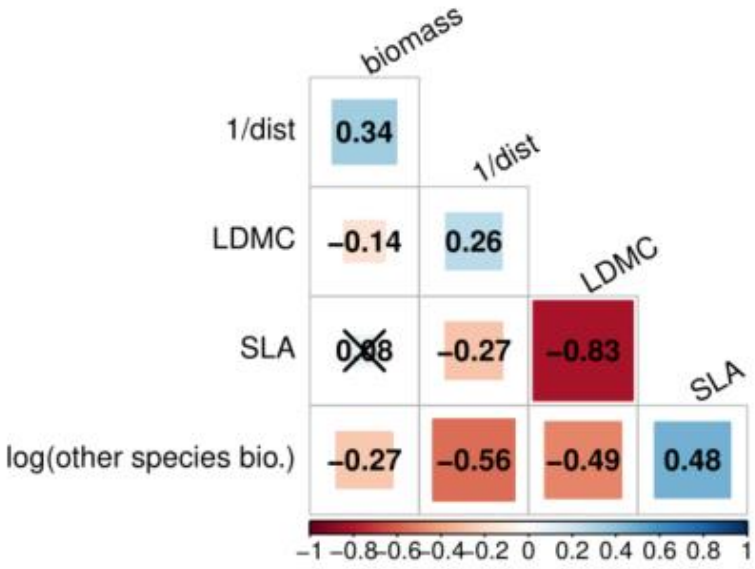
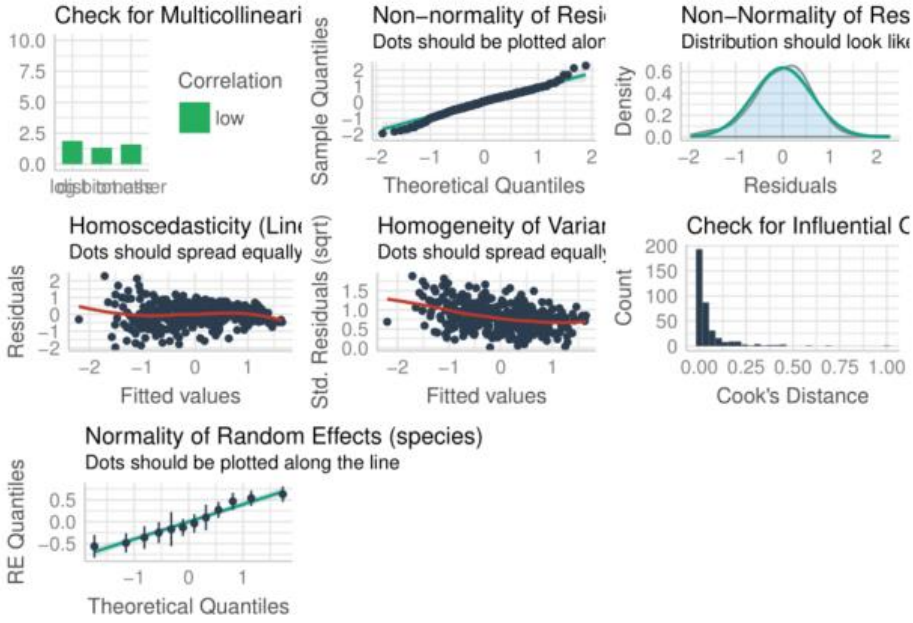


Fig. 4.B: Litterfall drivers

Correlation between explanatory variables



```
## Linear mixed model fit by REML. t-tests use Satterthwaite's method [
## lmerModLmerTest]
## Formula: log.litter.biomass.area ~ log.biomass + dist + tot.other + (1 |
##     species)
##    Data: df.stat
##
## REML criterion at convergence: 767.2
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -3.0497 -0.5819  0.0695  0.6145  3.5516
##
## Random effects:
##  Groups   Name        Variance Std.Dev.
##  species  (Intercept) 0.1785   0.4225
##  Residual             0.4107   0.6408
## Number of obs: 372, groups:  species, 12
##
## Fixed effects:
##              Estimate Std. Error        df t value Pr(>|t|)
## (Intercept)  -0.10092    0.12795  10.89923  -0.789  0.44707
## log.biomass   0.43985    0.04755 354.96121   9.251  < 2e-16 ***
## dist          0.14263    0.04644 367.58871   3.072  0.00229 **
## tot.other    -0.10310    0.04953 363.68207  -2.082  0.03809 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##             (Intr) lg.bms dist
## log.biomass  0.066
## dist        -0.014 -0.390
## tot.other    0.050  0.047  0.542
```



Supplementary material I – S4 Soil fauna sampling

Fauna collection protocol

In September 2019, we performed several fauna collection during our sampling campaign.

Soil mesofauna collection

Soil mesofauna was collected by heat extraction from two soil cores (5 cm diameter and 10 cm deep) sampled near the Common Garden experiment

Soil macrofauna collection

Soil macrofauna was collected by heat extraction from two soil cores (10 x 10 x 10 cm) sampled near the Common Garden experiment.

Ground macrofauna collection

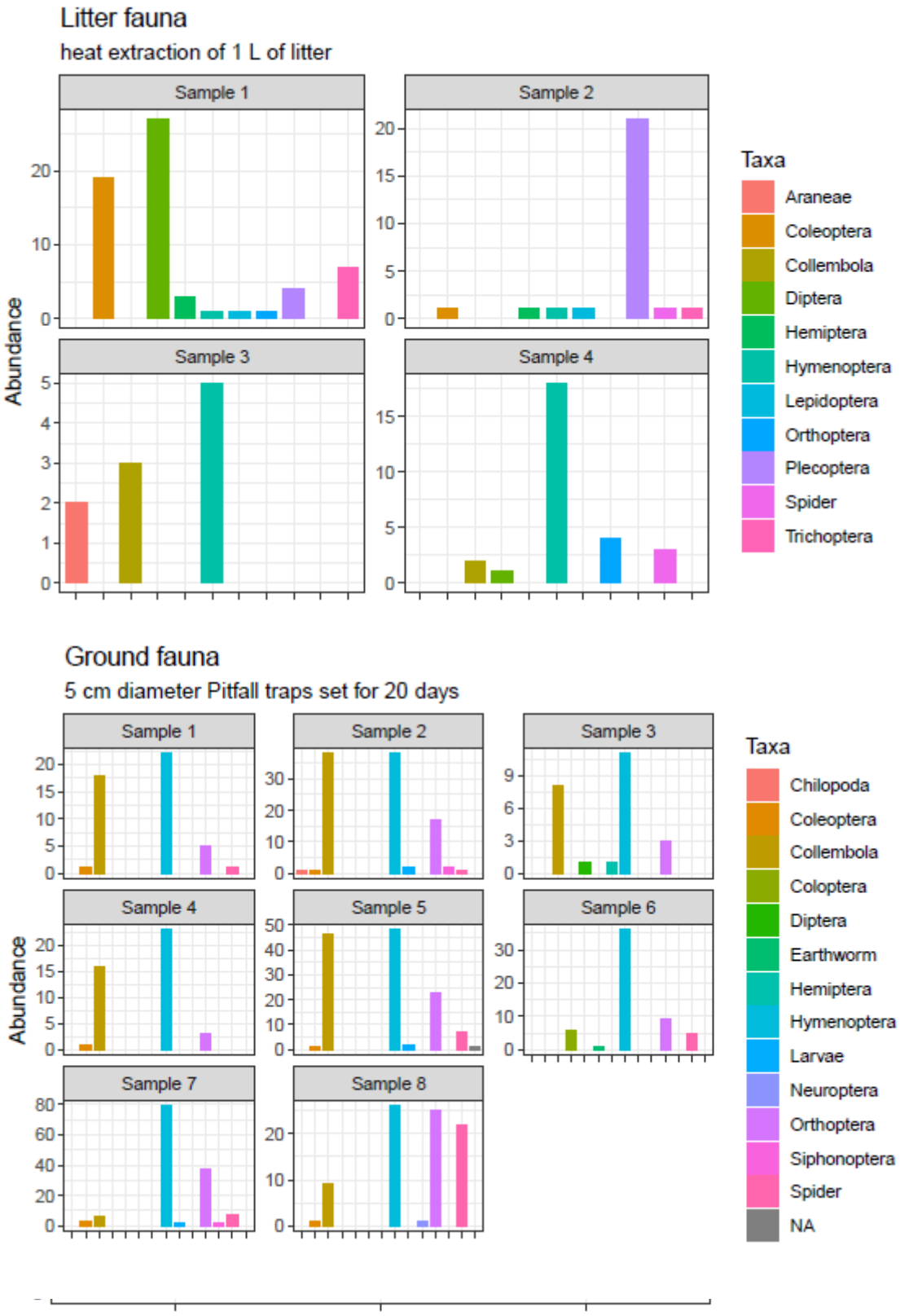
Macrofauna was collected by hand on 50 x 50 cm square during the 10 minutes after litter removal near the Common Garden experiment.

Litter fauna

Litter fauna was collected by heat extraction from 2 L of litter collected near the Common Garden experiment.

Pitfall trap collected

Four pitfall traps of 5 cm diameter filled with Glycerol were set for 20 days in 4 locations across BEF China.


Litter fauna
heat extraction of 1 L of litter
Sample 1
Sample 2
Sample 3
Sample 4
Abundance
Taxa
Araneae
Coleoptera
Collembola
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Orthoptera
Plecoptera
Spider
Trichoptera
Ground fauna
5 cm diameter Pitfall traps set for 20 days
Sample 1
Sample 2
Sample 3
Sample 4
Sample 5
Sample 6
Sample 7
Sample 8
Abundance
Taxa
Chilopoda
Coleoptera
Collembola
Coloptera
Diptera
Earthworm
Hemiptera
Hymenoptera
Larvae
Neuroptera
Orthoptera
Siphonoptera
Spider
NA

Supplementary material: Chapter II - Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning

Supplementary material II – S1 Material and methods

Study site, study design, and sampling

Our study site was located in south-east China in the Jiangxi province (29.08-29.11° N, 117.90-117.93° E). The region is characterized by a subtropical climate with warm, rainy summers and cold, dry winters (mean temperature of 16.7°C and mean rainfall of 1821 mm) (Yang et al. 2013). Soils in the region are Cambisols and Cambisol derivatives, with Regosol on ridges and crests (Geißler et al. 2012). The natural vegetation consists of species-rich broad-leaved forests dominated by *Quercus glauca, Castanopsis eyrei, Daphniphyllum oldhamii,* and *Lithocarpus glaber* (Bruelheide et al. 2011; Bruelheide et al. 2014). Sampling took place in BEF China, a tree diversity experiment, including tree species mixture plots (1, 2, 4, 8, and 16 tree species per plot), was planted in 2009 after clear-cutting the original forest (Fig. 1) (Bruelheide et al. 2014). To account for the role of tree diversity and soil quality, we collected 150 soil samples across different levels of tree diversity randomly distributed in the landscape (Fig. 1, Suppl. S2). We sampled from mid-August to late-September 2018, before the litterfall season. To avoid spatio-temporal autocorrelation, the daily sample location was chosen randomly, and to control for the distance to the trees, each sample was extracted on the transect between two trees. For each pair of trees, we extracted four soil cores (5 cm diameter; 10 cm depth), 5 cm and 20 cm away from the centerpoint between the tree pair (Fig. 1). A composite sample was built from these four cores by homogenizing with a 2 mm sieve.

Soil quality analyses

Soil moisture was measured from 25 g of soil by drying at 40°C for two days. A subsample was used to measure soil pH in a 1:2.5 soil-water solution. Soil total organic carbon (TOC) was measured by a TOC Analyzer (Liqui TOC II; Elementar Analysensysteme GmbH, Hanau, Germany). Soil total nitrogen (TN) was measured on an auto-analyzer (SEAL Analytical GmbH, Norderstedt, Germany) using the Kjeldahl method (Bradstreet 1954). Soil total phosphorus (TP) concentration was measured after wet digestion with H_2SO_4 and $HClO_4$ by a UV-VIS spectrophotometer (UV2700, SHIMADZU, Japan). Carbon to nitrogen and carbon to phosphorus ratios were calculated as TOC:TN and TOC:TP, respectively.

Soil microbial biomass

Microbial biomass was measured using phospholipid fatty acid (PLFA) analysis. PLFAs were extracted from 5 g of frozen soil following Frostegård et al. (1991) (Frostegård et al. 1991). Biomarkers were assigned to microbial functional groups according to Ruess et al. (2010) (Ruess and Chamberlain 2010). These markers targeted bacteria (gram-positive bacteria: i15:0, a15:0, i16:0, i17:0; gram-negative bacteria: cy17:0, cy19:0; general bacterial markers: 16:1ω5; 16:1ω7), arbuscular mycorrhizal fungi (20:1ω9), and saprophytic and ectomycorrhizal association fungi (18:1ω9 and 18:2ω6,9, see Suppl. S3). Total microbial biomass was calculated as the sum of biomasses of all microbial groups. The ratio of bacteria to fungi (B:F) was calculated as the ratio of the sum of all bacterial biomasses to the sum of all fungal biomasses.

Active microbial biomass was measured using the substrate-induced respiration method (Scheu 1992). About 6 g of soil was used to determine soil active microbial biomass, and 8 mg of glucose per gram of dry soil was added to saturated the soil micro-organism catabolism enzymes. O_2 respiration was measured based on electrolyte O_2 micro-compensation using an automated respirometer. Active

microbial biomass was calculated from the maximum initial respiratory response after induction (MIRR).

Soil microbial taxonomic profile

Microbial DNA was extracted from freeze-dried soil samples using a PowerSoil DNA Isolation Kit (MO BIO Laboratories Inc., Carlsbad, CA, United States). DNA concentrations were checked with a NanoDrop spectrophotometer (Thermo Fisher Scientific, Dreieich, Germany), and the extracts were adjusted to 10–15 ng/ul. The bacterial and fungal amplicon libraries were prepared following Schöps et al. (2018) (Schöps et al. 2018) and Nawaz et al. (2019) (Nawaz et al. 2019). Briefly, bacterial and fungal amplicon libraries were built separately using 16S rRNA gene and ITS2 rDNA regions, respectively. The bacterial 16S rRNA gene was amplified with universal primers 515f and 806r (Caporaso et al. 2011) with Illumina adapter sequence overhangs. The fungal ITS2 rDNA region was amplified by performing a semi-nested PCR using the initial primer combination of ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990)hr followed by the primer pair fITS7 (Ihrmark et al. 2012) and ITS4 containing the Illumina adapter sequences. The amplicon libraries were indexed, purified, quantified, and pooled equimolarly to a final concentration of 4nM which was then mixed in 1:3 ratio to make the final sequencing library. Paired-end sequencing of 2x300 bp was performed on an Illumina MiSeq platform (Illumina Inc., San Diego, CA, United States) using the MiSeq Reagent kit v3 at the Department of Environmental Microbiology, UFZ.

Bioinformatic analysis was performed using the Quantitative Insights into Microbial Ecology – QIIME 2 2020.2 (Bolyen et al. 2019). The forward and reverse reads were demultiplexed, primer sequences were trimmed, denoised, and grouped into Amplicon Sequence Variants (ASVs) using cut-adapt for chimeria removal (q2-cutadapt) (Martin 2011) and DADA2 for non-target taxa removal (via q2-dada2) (Callahan et al. 2016). ASV tables were imported into R with the 'phyloseq' package (McMurdie and Holmes 2013). The fungal and bacterial ASVs were rarefied to 16,542 and 28,897 reads per sample respectively. OTU richness, Shannon diversity, and Pielou evenness were calculated using the 'microbiome' package (Lahti et al. 2017). We inspected the correlations between these indices and focused our analyses on Shannon diversity index (Suppl. S4).

Soil microbial functional profile

DNA was extracted with the FastDNA Spin Kit for Soil (MP Biomedicals, USA) following the manufacturer's instructions. DNA concentrations were checked with a NanoDrop spectrophotometer (Thermo Fisher Scientific, Dreieich, Germany), and DNA concentrations were quantified with the QuantiFluor dsDNA kit (Promega, USA) and a microplate reader (SpectraMax M5, Molecular Devices). DNA was diluted to 50 ng μl^{-1} with sterile water and stored at −20 °C.

Microbial functional genes coding for enzymes involved in carbon anabolism and catabolism processes, which are central to soil carbon cycling (complete list in Suppl. S5) (Liang et al. 2017), were quantified using a high-throughput quantitative-PCR-based chip (HT-qPCR; SmartChip Real-time PCR system, WaferGen Biosystems, Fremont, USA). This chip contained 72 primer pairs: 36 designed pairs, 35 published pairs, and the bacterial 16S rRNA gene, which allows to quantify 72 DNA genes in parallel (Zheng et al. 2018). PCR reaction conditions were as follows: initial denaturation of 10 min at 95°C, and 40 cycles of denaturation at 95°C for 30 s, annealing 30 s at 58°C and extension at 72°C for another 30 s. The melting curve was automatically generated by the WaferGen software. Three replicates for each sample were analyzed. Results with multiple melting peaks or with amplification efficiencies less than 80% and over 120% were excluded. Only results with a threshold cycle (C_T) less than 31 (the detection limit for this method) were used for further analysis. The relative copy number of each functional gene was calculated as shown in eq. 1 (Looft et al. 2012). Then, the relative abundance of a

given functional gene was defined as the proportion of the relative copy number of a functional gene to the relative copy number of the 16S rRNA gene.

Gene relative copy number (GR): $GR = (31\text{-}C_T) \times (10/3) / GR_{16S}$ (1)

To compare abundance patterns across functional genes, we scaled each functional gene abundance between 0 and 1 across all samples using the z-transformation, and we summed the scaled abundance of functional genes related to carbon catabolism (i.e. "Cata", Suppl. S5). To quantify the evenness of the functional gene abundances, the functional gene Pielou evenness was calculated using the R 'diversity' from the 'vegan' package ("FG evenness", respectively).

Soil microbial physiological potential

Microbial physiological potential indices were calculated from substrate-induced respiration assays using the Microresp.® method (Campbell et al. 2003). Fourteen substrates from three chemical classes (i.e. saccharides, amino-acid, and carboxylic acids) were selected to create a gradient of molecular weights (ranging from 89 to 221 $g.mol^{-1}$), and a gradient of carbon oxidation states (ranging from -2 to 3 e^- , Suppl. S5). Ten g of soil was evenly distributed on the half of 96 deep-well plate and incubated at 25°C for five days. For each substrate, 30 mg of substrate per gram of soil water was added to three wells. CO_2 production of the wells was fixed in agar – cresol red gel during the six following hours. Total CO_2 production of the wells was measured by colorimetry using a photo-spectrometer. Two indices were calculated from these CO_2 measurements: substrate-use efficiency and substrate-use range. Substrate-use efficiency was calculated as the Pielou evenness (from R 'diversity' function package 'vegan') of the CO_2 production of all substrates. Substrate-use range was defined as the difference in CO2 production between oxalic acid and alanine, the two substrates on the upper and lower extremes of carbon oxidation. We performed sensitivity analyses to explore the effects of substrate selection on these indices, which showed that substrate selection did not alter our results and conclusions (Suppl. S6).

Soil microbial respiration

Soil microbial respiration was measured on 6 g of fresh soil following Scheu *et al*. (1992) (Scheu 1992) without adding any substrate or water, thereby reflecting the actual respiration at the site. During 24 hours, O_2 consumption was continuously measured using an automated respirometer based on electrolytic O_2 micro-compensation (Scheu 1992). Soil microbial respiration was calculated as the mean of O_2 consumption between the 14 to 24 hours after starting the measurement. Active microbial biomass (with substrate addition) and microbial respiration (without substrate addition) were measured on the same sample and machine. To test the robustness of our results, all following analyses were run with and without active microbial biomass.

Statistical analyses

All data handling and statistical analyses were performed using the R statistical software version 4.0.3, and all R scripts used for this study can be found in our GitHub repository (https://github.com/remybeugnon/Beugnon-Du_et_al_2021_Microbial_community_and_functions). All metrics inferred from soil measurements are summarized in the Suppl. S4. In order to avoid any model-fit deviation due to scale differences between variables, all explanatory variables were centered and divided by two standard deviations for our analyses using the R 'rescale' function from the 'arm' package. For each analysis, we compared the

drivers' effect sizes defined as the standardized estimate of a given variable in the model where the response variable was centered and divided by two standard deviations.

Tree diversity effects on soil microbial community facets and functions

We used linear multivariate models and normal distribution assumptions to test the effects of tree species richness on soil microbial biomass (total and active microbial biomass), taxonomic profile (B:F ratio and Shannon diversity of bacteria and fungi), functional profile (catabolic functional gene abundance and evenness), physiological potential (substrate-use efficiency and range), and microbial respiration. All previous linear multivariate models were tested in R using the 'lm' function and statistical hypotheses of the following linear models were tested in Suppl. S7 using the 'model_check' function from the 'performance' package in R.

Effects of soil microbial facets on microbial functions

We tested the correlation between the microbial facets – soil microbial biomass, taxonomic and functional profiles – using Pearson correlation tests. We used linear multivariate models and normal distribution assumptions to test the effects of microbial biomass (total and active microbial biomass), taxonomic profile (B:F ratio and Shannon diversity of bacteria and fungi) and functional profile (catabolic functional gene abundance, and evenness) on soil microbial physiological potential (substrate-use efficiency and range), and soil microbial respiration. Explanatory variables (microbial biomasses, taxonomic and functional profile indices) were selected using forward and backward step selection based on AIC (i.e., R 'step' function from 'stats' package). A variance partitioning analysis was performed on the final set of variables to disentangle the effects of microbial biomass and taxonomic profile using the R 'varpart' function from the 'vegan' package. All previous linear multivariate models were tested in R using the 'lm' function and statistical hypotheses of the following linear models were tested in Suppl. S8 using the 'model_check' function from the 'performance' package in R

Cascading effects of the different soil microbial community facets on microbial physiological potential and microbial respiration

We tested the relationships between soil microbial biomass, taxonomic and functional profiles, physiological potential, and respiration using a Structural Equation Modeling (SEM) framework. Microbial biomass, taxonomic and functional profiles were linked to each other by correlations, and their effects on physiological potential indices and soil microbial respiration were modeled with causal relations (directed paths). Our SEM was fitted using the R 'sem' function from the 'lavaan' package (Rosseel 2012). The model fit to our data, and model quality were estimated using three complementary indices: (i) the root mean square error of approximation (RMSEA), (ii) the comparative fit index (CFI), and (iii) the standardized root mean squared residuals (SRMR). Model fits were considered acceptable when RMSEA < 0.10, CFI > 0.9 and SRMR < 0.08. All statistical hypotheses and complete outputs can be found in Suppl. S9.

Effects of tree species richness and soil quality on relationships between the soil microbial community and their functions

To test the effects of tree species richness and soil quality on the relationship between the soil microbial community facets and microbial respiration, we added the causal effects of soil quality indices and tree species richness onto the variables of our previous SEM model. To assess which group of response variables was the most affected by soil quality and tree species richness, the effects of soil quality and tree species richness were summarized by a group of response variables (soil microbial biomass, taxonomic profile, functional profile, physiological potential, and microbial respiration). For each group of response variables, we summed all the absolute standardized effects of soil quality or tree species

richness on each of the response variables. Additionally, to assess the importance of soil quality indices and tree species richness for microbial community facets and microbial functions, we summed the absolute standardized effects of each soil quality index and tree species richness. All statistical hypotheses and complete outputs can be found in Suppl. S10.

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Supplementary material II -S2: tree selection

List of tree species building the pairs of tree species in the different plots of Site A (BEF China experiment)

Species	Leaf persistence
Castanea henryi	deciduous
Castanopsis sclerophylla	evergreen
Choerospondias axillaris	deciduous
Cyclobalanopsis glauca	evergreen
Koelreuteria bipinnata	deciduous
Liquidambar formosana	deciduous
Lithocarpus glaber	evergreen
Nyssa sinensis	deciduous
Quercus fabri	deciduous
Quercus serrata	deciduous
Sapindus mukorossi	deciduous
Sapium sebiferum	deciduous

Sampling point description and attributes (paragraphs were added for readability)

Code	Site	Plot	Diversity level	Species 1	Species 2
26-E24	A	E24	1	*Liquidambar formosana*	*Liquidambar formosana*
33-E31	A	E31	1	*Quercus fabri*	*Quercus fabri*
34-E31	A	E31	1	*Quercus fabri*	*Quercus fabri*
27-E33	A	E33	1	*Lithocarpus glaber*	*Lithocarpus glaber*
28-E33	A	E33	1	*Lithocarpus glaber*	*Lithocarpus glaber*
1-E34	A	E34	1	*Castanea henryi*	*Castanea henryi*
2-E34	A	E34	1	*Castanea henryi*	*Castanea henryi*
37-F21	A	F21	1	*Quercus serrata*	*Quercus serrata*
38-F21	A	F21	1	*Quercus serrata*	*Quercus serrata*
10-G17	A	G17	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
29-G22	A	G22	1	*Lithocarpus glaber*	*Lithocarpus glaber*
22-G24	A	G24	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
23-G24	A	G24	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
36-G33	A	G33	1	*Quercus serrata*	*Quercus serrata*
30-H25	A	H25	1	*Nyssa sinensis*	*Nyssa sinensis*
3-I12	A	I12	1	*Castanea henryi*	*Castanea henryi*
24-I28	A	I28	1	*Liquidambar formosana*	*Liquidambar formosana*
25-I28	A	I28	1	*Liquidambar formosana*	*Liquidambar formosana*
14-K9	A	K9	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
8-L11	A	L11	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
9-L11	A	L11	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
13-L23	A	L23	1	*Choerospondias axillaris*	*Choerospondias axillaris*
43-N11	A	N11	1	*Sapindus mukorossi*	*Sapindus mukorossi*
46-N13	A	N13	1	*Sapium sebiferum*	*Sapium sebiferum*

Code	Site	Plot	Diversity level	Species 1	Species 2
47-N13	A	N13	1	*Sapium sebiferum*	*Sapium sebiferum*
11-O27	A	O27	1	*Choerospondias axillaris*	*Choerospondias axillaris*
21-Q13	A	Q13	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
r-21-Q13	A	Q13	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
35-Q16	A	Q16	1	*Quercus fabri*	*Quercus fabri*
15-R14	A	R14	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
16-R14	A	R14	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
44-R17	A	R17	1	*Sapindus mukorossi*	*Sapindus mukorossi*
45-W13	A	W13	1	*Sapium sebiferum*	*Sapium sebiferum*
32-W14	A	W14	1	*Nyssa sinensis*	*Nyssa sinensis*
51-C32	A	C32	2	*Castanea henryi*	*Castanea henryi*
52-C32	A	C32	2	*Castanea henryi*	*Nyssa sinensis*
96-C32	A	C32	2	*Castanea henryi*	*Nyssa sinensis*
95-C32	A	C32	2	*Nyssa sinensis*	*Nyssa sinensis*
97-C32	A	C32	2	*Nyssa sinensis*	*Nyssa sinensis*
53-F22	A	F22	2	*Castanea henryi*	*Castanea henryi*
54-F22	A	F22	2	*Castanea henryi*	*Castanea henryi*
55-F22	A	F22	2	*Castanea henryi*	*Nyssa sinensis*
98-F22	A	F22	2	*Nyssa sinensis*	*Nyssa sinensis*
87-H31	A	H31	2	*Liquidambar formosana*	*Liquidambar formosana*
86-H31	A	H31	2	*Liquidambar formosana*	*Sapindus mukorossi*
113-H31	A	H31	2	*Sapindus mukorossi*	*Liquidambar formosana*
112-H31	A	H31	2	*Sapindus mukorossi*	*Sapindus mukorossi*
118-I27	A	I27	2	*Sapium sebiferum*	*Sapium sebiferum*
81-J21	A	J21	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
82-J21	A	J21	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
83-J21	A	J21	2	*Koelreuteria bipinnata*	*Lithocarpus glaber*
92-J21	A	J21	2	*Lithocarpus glaber*	*Lithocarpus glaber*
72-K3	A	K3	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
73-K3	A	K3	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
75-K3	A	K3	2	*Cyclobalanopsis glauca*	*Quercus fabri*
64-O6	A	O6	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
65-O6	A	O6	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
66-O6	A	O6	2	*Castanopsis sclerophylla*	*Quercus serrata*
105-O6	A	O6	2	*Quercus serrata*	*Quercus serrata*
63-P26	A	P26	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
62-P26	A	P26	2	*Castanopsis sclerophylla*	*Quercus serrata*
102-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
103-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
104-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
74-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
76-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Quercus fabri*
77-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Quercus fabri*
100-Q21	A	Q21	2	*Quercus fabri*	*Quercus fabri*
101-Q21	A	Q21	2	*Quercus fabri*	*Quercus fabri*
84-Q7	A	Q7	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
85-Q7	A	Q7	2	*Koelreuteria bipinnata*	*Lithocarpus glaber*

Supplementary material: Chapter II - Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning

Code	Site	Plot	Diversity level	Species 1	Species 2
93-Q7	A	Q7	2	*Lithocarpus glaber*	*Lithocarpus glaber*
94-Q7	A	Q7	2	*Lithocarpus glaber*	*Lithocarpus glaber*
69-S18	A	S18	2	*Choerospondias axillaris*	*Choerospondias axillaris*
70-S18	A	S18	2	*Choerospondias axillaris*	*Sapium sebiferum*
71-S18	A	S18	2	*Choerospondias axillaris*	*Sapium sebiferum*
119-S18	A	S18	2	*Sapium sebiferum*	*Sapium sebiferum*
r-120-S18	A	S18	2	*Sapium sebiferum*	*Sapium sebiferum*
88-T17	A	T17	2	*Liquidambar formosana*	*Liquidambar formosana*
89-T17	A	T17	2	*Liquidambar formosana*	*Liquidambar formosana*
90-T17	A	T17	2	*Liquidambar formosana*	*Sapindus mukorossi*
115-T17	A	T17	2	*Sapindus mukorossi*	*Sapindus mukorossi*
130-F27	A	F27	4	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
131-F27	A	F27	4	*Choerospondias axillaris*	*Castanopsis sclerophylla*
153-F27	A	F27	4	*Quercus serrata*	*Choerospondias axillaris*
161-F27	A	F27	4	*Sapium sebiferum*	*Choerospondias axillaris*
162-F27	A	F27	4	*Sapium sebiferum*	*Sapium sebiferum*
139-F28	A	F28	4	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
132-N20	A	N20	4	*Choerospondias axillaris*	*Choerospondias axillaris*
154-N20	A	N20	4	*Quercus serrata*	*Castanopsis sclerophylla*
155-N20	A	N20	4	*Quercus serrata*	*Quercus serrata*
156-N20	A	N20	4	*Quercus serrata*	*Sapium sebiferum*
163-N20	A	N20	4	*Sapium sebiferum*	*Castanopsis sclerophylla*
133-N8	A	N8	4	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
149-N8	A	N8	4	*Quercus fabri*	*Cyclobalanopsis glauca*
125-P19	A	P19	4	*Castanea henryi*	*Castanea henryi*
126-P19	A	P19	4	*Castanea henryi*	*Nyssa sinensis*
143-P19	A	P19	4	*Liquidambar formosana*	*Sapindus mukorossi*
148-P19	A	P19	4	*Nyssa sinensis*	*Sapindus mukorossi*
160-P19	A	P19	4	*Sapindus mukorossi*	*Sapindus mukorossi*
141-P29	A	P29	4	*Liquidambar formosana*	*Liquidambar formosana*
142-P29	A	P29	4	*Liquidambar formosana*	*Nyssa sinensis*
147-P29	A	P29	4	*Nyssa sinensis*	*Castanea henryi*
159-P29	A	P29	4	*Sapindus mukorossi*	*Castanea henryi*
146-W12/X12	A	W12/X12	4	*Lithocarpus glaber*	*Lithocarpus glaber*
176-P27	A	P27	8	*Cyclobalanopsis glauca*	*Quercus fabri*
181-P27	A	P27	8	*Koelreuteria bipinnata*	*Lithocarpus glaber*
166-R16	A	R16	8	*Castanea henryi*	*Liquidambar formosana*
171-R16	A	R16	8	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
175-R16	A	R16	8	*Choerospondias axillaris*	*Sapium sebiferum*
190-R16	A	R16	8	*Nyssa sinensis*	*Castanea henryi*
193-R16	A	R16	8	*Quercus serrata*	*Castanopsis sclerophylla*
194-R16	A	R16	8	*Quercus serrata*	*Quercus serrata*
198-R16	A	R16	8	*Sapindus mukorossi*	*Sapindus mukorossi*
199-R16	A	R16	8	*Sapindus mukorossi*	*Sapindus mukorossi*
200-R16	A	R16	8	*Sapium sebiferum*	*Quercus serrata*
201-R16	A	R16	8	*Sapium sebiferum*	*Sapium sebiferum*
165-S10	A	S10	8	*Castanea henryi*	*Castanea henryi*
170-S10	A	S10	8	*Castanopsis sclerophylla*	*Sapium sebiferum*

Code	Site	Plot	Diversity level	Species 1	Species 2
173-S10	A	S10	8	*Choerospondias axillaris*	*Castanopsis sclerophylla*
174-S10	A	S10	8	*Choerospondias axillaris*	*Choerospondias axillaris*
186-S10	A	S10	8	*Liquidambar formosana*	*Liquidambar formosana*
185-S10	A	S10	8	*Liquidambar formosana*	*Nyssa sinensis*
188-S10	A	S10	8	*Nyssa sinensis*	*Nyssa sinensis*
189-S10	A	S10	8	*Nyssa sinensis*	*Sapindus mukorossi*
197-S10	A	S10	8	*Sapindus mukorossi*	*Castanea henryi*
178-S14	A	S14	8	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
183-S15	A	S15	8	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
r-216-S15	A	S15	8	*Koelreuteria bipinnata*	*Lithocarpus glaber*
184-S15	A	S15	8	*Koelreuteria bipinnata*	*Quercus fabri*
191-T15	A	T15	8	*Quercus fabri*	*Quercus fabri*
220-L21	A	L21	16	*Liquidambar formosana*	*Choerospondias axillaris*
203-L22	A	L22	16	*Castanea henryi*	*Nyssa sinensis*
204-L22	A	L22	16	*Castanea henryi*	*Sapindus mukorossi*
217-L22	A	L22	16	*Liquidambar formosana*	*Castanea henryi*
219-L22	A	L22	16	*Liquidambar formosana*	*Liquidambar formosana*
218-L22	A	L22	16	*Liquidambar formosana*	*Nyssa sinensis*
221-L22	A	L22	16	*Lithocarpus glaber*	*Lithocarpus glaber*
222-L22	A	L22	16	*Quercus fabri*	*Quercus fabri*
230-L22	A	L22	16	*Sapium sebiferum*	*Castanopsis sclerophylla*
226-M21	A	M21	16	*Quercus serrata*	*Sapium sebiferum*
r-213-U10	A	U10	16	*Cyclobalanopsis glauca*	*Quercus fabri*
225-U10	A	U10	16	*Quercus serrata*	*Quercus serrata*
229-U10	A	U10	16	*Sapindus mukorossi*	*Sapindus mukorossi*
231-U10	A	U10	16	*Sapium sebiferum*	*Sapium sebiferum*
232-N9	A	N9	24	*Castanea henryi*	*Castanea henryi*
236-N9	A	N9	24	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
238-N9	A	N9	24	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
241-N9	A	N9	24	*Sapindus mukorossi*	*Nyssa sinensis*
234-R18	A	R18	24	*Castanopsis sclerophylla*	*Quercus serrata*
235-R18	A	R18	24	*Choerospondias axillaris*	*Quercus serrata*
239-R18	A	R18	24	*Nyssa sinensis*	*Nyssa sinensis*

Supplementary material II – S3: PLFA biomarkers

PLFA biomarkers used to identify soil microbes' functional groups

Fatty acid	Lipid fraction	Predominant origin	Literature
i15:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
a15:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
i16:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
i17:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
16:1n7	PLFA	Bacteria widespread	Guckert et al. (1991), Zelles (1999)
16:1n-5	PLFA	General bacteria	Nichols et al. (1986), Zelles (1997)
cy17:0	PLFA	Gram-negative bacteria	Zelles (1997, 1999)
18:1n9	PLFA	Fungi (saprophytic, EM)	Bååth (2003), Vestal and White (1989),Zelles (1999), Harwood and Russell (1984), Ruess et al. (2007)
cy19:0	PLFA	Gram-negative bacteria	Zelles (1997, 1999)
18:2n6c	PLFA	Fungi (saprophytic, EM)	Frostegård and Bååth (1996), Zelles (1999)
20:1	PLFA	AM fungi (Gigaspora)	Sakamoto et al. (2004)

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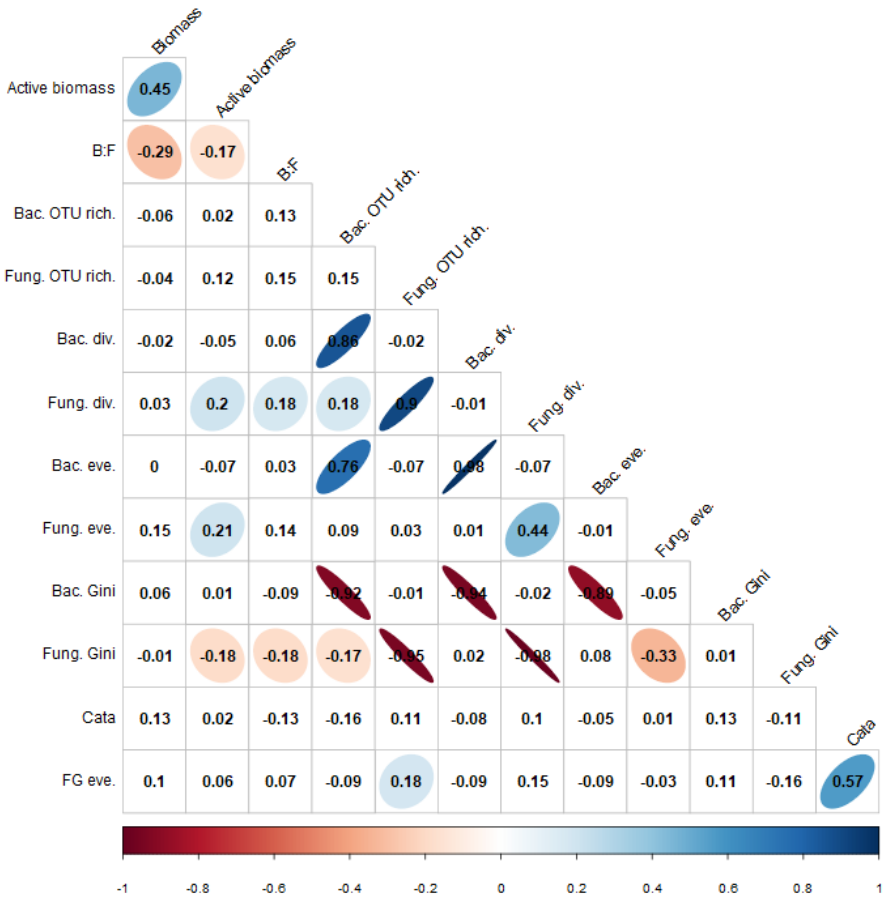
microbial communities in soil: a review. Biology and fertility of soils, 29(2), 111-129.

Supplementary material II – S4: measurements summary

A. Correlations between the microbial variable



B. The structured list of variables used in the analyses.

Variable group	Variable name (acronyms)		Definition and measurement method	Hypotheses and analyses referring to it
Soil chemical properties	Soil carbon content (TOC)		Measured on top soil (0-10 cm) using TOC analyzer	Hypothesis 4, Fig. 5, Suppl. S10
	Soil carbon to nitrogen ratio (C:N)		Calculated on top soil (0-10 cm) measurements	Hypothesis 4, Fig. 5, Suppl. S10
	Soil carbon to nitrogen ratio (C:P)		Calculated on top soil (0-10 cm) measurements	Hypothesis 4, Fig. 5, Suppl. S10
	Soil pH (pH)		Measured on top soil (0-10 cm) using 1:2.5 soil - water solution	Hypothesis 4, Fig. 5, Suppl. S10
	Soil water content (RH)		Measured on 25 g of top soil (0-10 cm) air-dryed at 40 °C	Hypothesis 4, Fig. 5, Suppl. S10
Tree Species Richness	Tree species richness		Number of tree species per plot	Hypothesis 1&4, Fig. 1&5, Suppl. S7&10
Soil microbial community facets	Microbial biomass	Total microbial biomass (Biomass)	Total microbial biomass calculated from PLFA markers measurements	Hypotheses 1-4, Fig. 1-5, Suppl. S3, S7-10
		Active microbial biomass (Active biomass)	The active fraction of the total microbial biomass calculated from substrate-induced respiration (SIR, Scheu 1992)	Hypotheses 1-4, Fig. 1-5, Suppl. S3, S7-S10
	Taxonomic profile	Bacteria to fungi ratio (B:F)	Bacteria to fungi ratio was calculated using microbial functional groups biomass measured by PLFA analyses	Hypotheses 1-4, Fig. 1-5, Suppl. S3, S6-S10
		Bacteria Shannon diversity (Bac. div.)	Baterial community Shannon diversity calculated from 16S sequencing data	Hypotheses 1-4, Fig. 1-5, Suppl. S3, S6-S10
		Fungi Shannon diversity (Fung. div.)	Fungi community Shannon diversity calculated from ITS sequencing data	Hypotheses 1-4, Fig. 1-5, Suppl. S3, S6-10
	Functional profile	FG evenness	The absolute or relative abundance of functional genes measured by qPCR. See Suppl. S5 for a complete list of measured functional genes	Hypotheses 1-4, Fig. 1-4, Suppl. S5 & S7-9

		Catabolism functional genes (Cata)	Sum of the abundance of functional genes involved in carbon catabolism. The variables can be calculated on the absolute or relative abundance of the functional genes and will be specified.	Hypotheses 1-4, Fig. 1-4, Suppl. S5 & S7-9
Soil physiological potential	Substrate induced-respiration (SIR)		Substrate-induced respiration (i.e. CO_2 production during six hours after substrate addition) of fourteen substrates (i.e. 5 saccharides, 4 amino-acids, and 5 carboxylic-acids) measured with the Microresp® method.	Hypotheses 1-4, Fig. 1-5, Suppl. S5 & S7-9
	Substrate-induced respiration efficiency (SIR efficiency)		Pielou evenness of the substrate-induced respiration (i.e. CO_2 production during six hours after substrate addition) of fourteen substrates (i.e. complete list in Suppl. S3)	Hypotheses 1-4, Fig. 1-5, Suppl. S5 & S7-9
	Substrate-induced respiration response range (SIR range)		The absolute difference of CO_2 production between alamine induced respiration and oxalic-acid induced respiration measured with the Microresp® method.	Hypotheses 1-4, Fig. 1-5, Suppl. S5 & S7-9
Ecosystem function	Microbial respiration (M. resp.)		Soil basal respiration measured (SIR, Scheu 1992)	Hypotheses 1-4, Fig. 1-5, Suppl. S7-9

Supplementary material II – S5: Functional genes

List of functional genes and their functional attributes

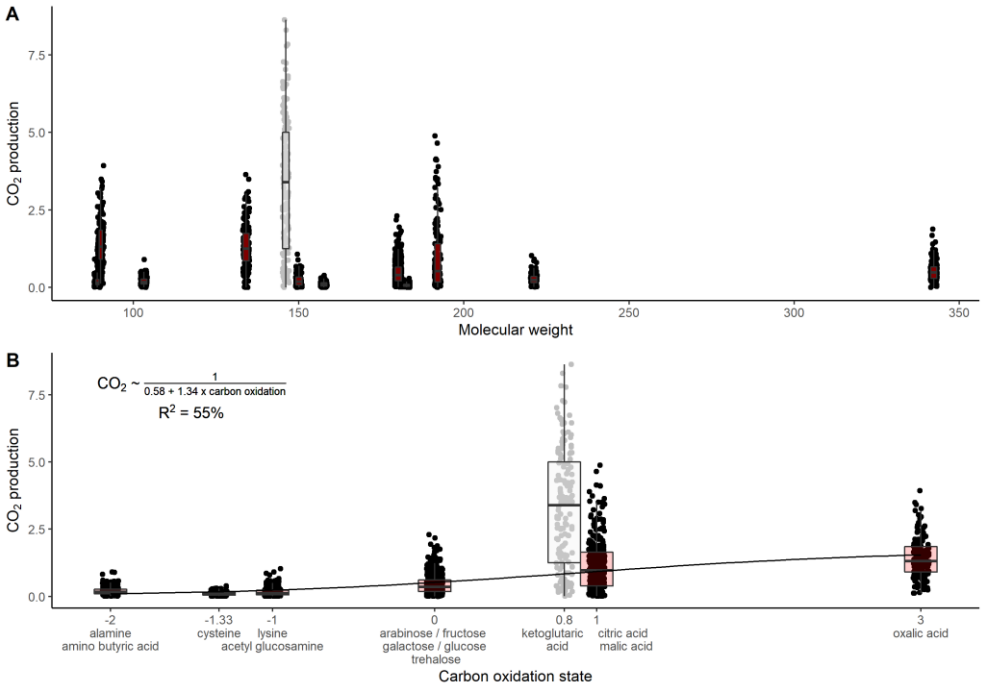
Function in the carbon cycle	Functional gene name	Specific functional gene function
Carbon catabolism	abfA	Hemicellulose
	apu	Starch
	cex	Cellulose
	chiA	Chitin
	ipu	Starch
	lig	Lignin
	manB	Hemicellulose
	mnp	Lignin
	mxaF	Methane production
	naglu	Cellulose
	pox	Lignin
	pqq-mdh	Methane production
	sga	Starch
	xylA	Hemicellulose

Supplementary material II – S6: MicroResp. ® measurements

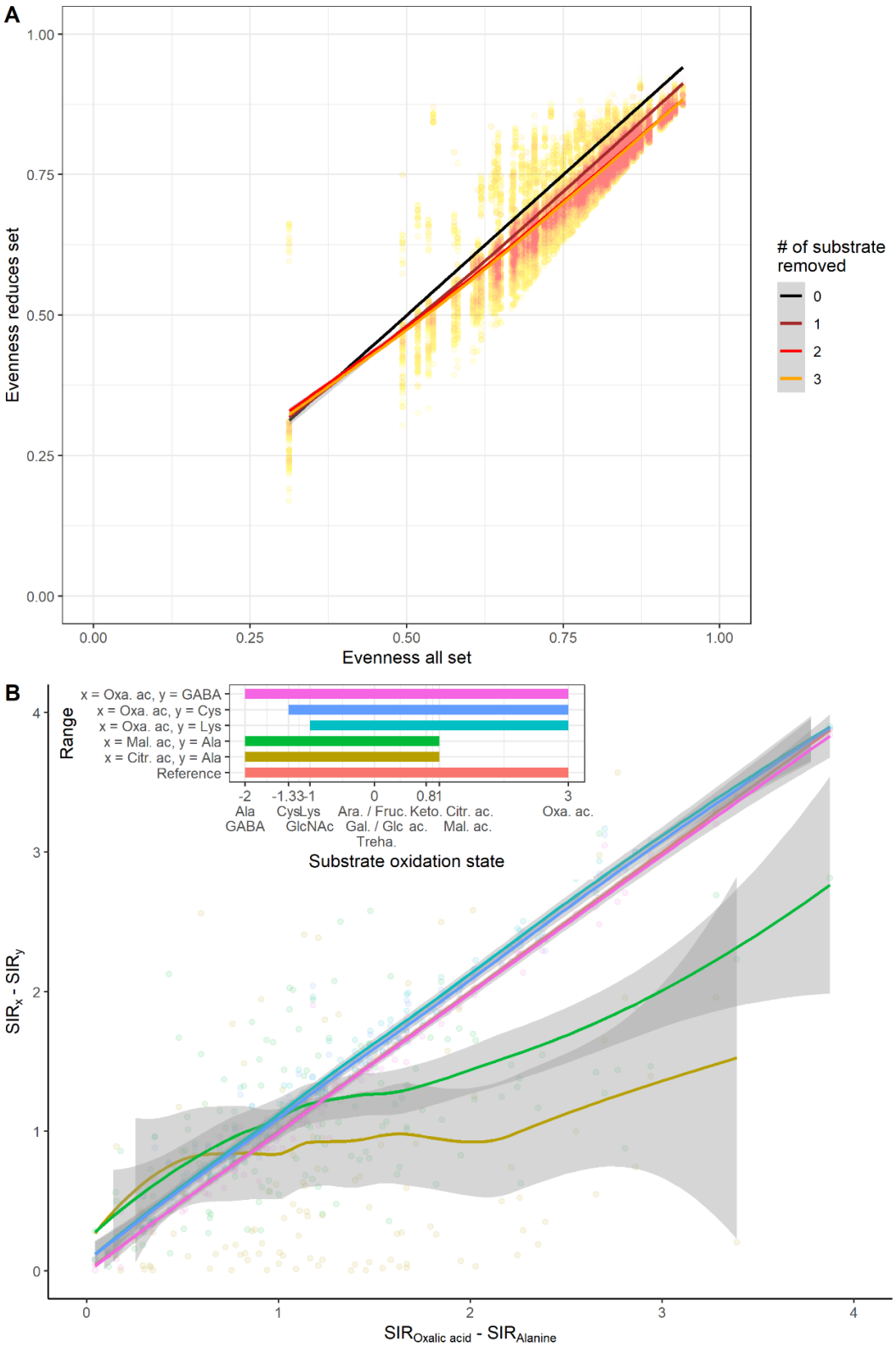
I. List of substrates used in substrate-induced respiration measurements (i.e. Microresp® method) and chemical attributes.

Full name	Chemical group	Formula	Molecular Weight	Mean carbon oxidation state
L-Alamine	Amino acid	$C_3H_7NO_2$	89.094	-2
γ-Aminobutyric acid	Amino acid	$C_4H_9NO_2$	103.121	-2
L-Cysteine-HCl	Amino acid	$C_3H_8ClNO_2S$	157.612	-1.33
L-Arginine	Amino acid	$C_6H_{14}N_4O_2$	174.204	-1
L-Lysine-HCl	Amino acid	$C_6H_{15}ClN_2O_2$	182.648	-1
Oxalic acid	Carboxylic acid	$(COOH)_2$	90.034	3
L-Malic acid	Carboxylic acid	$C_4H_6O_5$	134.087	1
α-Ketoglutaric acid	Carboxylic acid	$C_5H_6O_5$	146.11	0.8
Citric acid	Carboxylic acid	$C_6H_8O_7$	192.123	1
L-(+)-Arabinose	Sugar	$C_5H_{10}O_5$	150.13	0
D-(-)-Fructose	Sugar	$C_6H_{12}O_6$	180.156	0
D-(+)-Galactose	Sugar	$C_6H_{12}O_6$	180.156	0
D-(+)-Glucose	Sugar	$C_6H_{12}O_6$	180.156	0
N-Acetyl glucosamine	Sugar	$C_8H_{15}NO_6$	221.209	-1

II. **CO_2 production during the six hours following the substrate addition in the Microresp. ® measurements.** CO_2 production against substrate molecular weight (**A.**) or against mean carbon oxidation state (**B.**).



III. Effect of (A.) substrate removal and (B.) change of induction range definition on indices values



Supplementary material II – S7: R output Fig. 2

A. Model shape selection

Tree species richness effect on soil microbial facets and functions. For each soil microbial facets and functions, we tested the shape of the relationship using the 'lm' function and the following relations: linear (i.e. y ~ x), quadratic (i.e. y ~ x^2), polynomial (i.e. y ~ x + x^2 + x^3) and logarithmic (i.e. y ~ log(x)). The models were ordered by AIC and considered different when the difference of AIC was higher than 4. When several models had a comparable fit (difference of AIC below 4) the simplest model was chosen (i.e. linear < logarithmic < quadratic < polynomial).

Microbial biomass

Total microbial biomass

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
polynomial	y ~ poly(x, degree = 3)	2886	2901	0.098	0.079	4013.930	4069.297
linear	y ~ x	2889	2898	0.056	0.050	4105.131	4133.153
quadratic	y ~ x^2	2889	2898	0.056	0.050	4105.131	4133.153
log	y ~ log(x)	2893	2902	0.027	0.021	4167.715	4196.163

Active microbial biomass

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
polynomial	y ~ poly(x, degree = 3)	1768	1783	0.049	0.029	91.784	93.050
linear	y ~ x	1770	1779	0.010	0.003	93.621	94.260
quadratic	y ~ x^2	1770	1779	0.010	0.003	93.621	94.260
log	y ~ log(x)	1771	1780	0.001	-0.006	94.060	94.702

Microbial taxonomic profile

Bacteria to fungi ratio

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
log	y ~ log(x)	207	216	0.016	0.010	0.477	0.480
linear	y ~ x	207	216	0.015	0.008	0.477	0.480
quadratic	y ~ x^2	207	216	0.015	0.008	0.477	0.480
polynomial	y ~ poly(x, degree = 3)	211	226	0.017	-0.004	0.476	0.483

Bacterial Shannon diversity

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
log	y ~ log(x)	388	397	0.060	0.053	0.881	0.887
polynomial	y ~ poly(x, degree = 3)	391	406	0.069	0.050	0.876	0.888
linear	y ~ x	391	400	0.044	0.037	0.888	0.894
quadratic	y ~ x^2	391	400	0.044	0.037	0.888	0.894

Fungal Shannon diversity

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
log	y ~ log(x)	-98	-89	0.000	-0.006	0.170	0.171
linear	y ~ x	-98	-89	0.000	-0.007	0.170	0.171
quadratic	y ~ x^2	-98	-89	0.000	-0.007	0.170	0.171
polynomial	y ~ poly(x, degree = 3)	-97	-82	0.014	-0.006	0.169	0.171

Microbial functional profile

Catabolism functional genes

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
log	y ~ log(x)	566	575	0.010	0.003	1.604	1.615
linear	y ~ x	566	575	0.007	0.000	1.607	1.618
quadratic	y ~ x^2	566	575	0.007	0.000	1.607	1.618
polynomial	y ~ poly(x, degree = 3)	569	584	0.014	-0.007	1.601	1.624

Functional genes evenness

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
log	y ~ log(x)	-455	-446	0.003	-0.003	0.051	0.051
linear	y ~ x	-455	-446	0.003	-0.004	0.051	0.051
quadratic	y ~ x^2	-455	-446	0.003	-0.004	0.051	0.051
polynomial	y ~ poly(x, degree = 3)	-452	-437	0.011	-0.010	0.051	0.051

Microbial physiological potential

Substrate-induced respiration efficiency

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
linear	y ~ x	41	50	0.071	0.064	0.272	0.274
quadratic	y ~ x^2	41	50	0.071	0.064	0.272	0.274
log	y ~ log(x)	42	51	0.063	0.057	0.274	0.275
polynomial	y ~ poly(x, degree = 3)	45	60	0.072	0.053	0.272	0.276

Substrate-induced respiration response range

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
log	y ~ log(x)	340	349	0.005	-0.002	0.749	0.754
linear	y ~ x	341	350	0.003	-0.003	0.750	0.755
quadratic	y ~ x^2	341	350	0.003	-0.003	0.750	0.755
polynomial	y ~ poly(x, degree = 3)	345	360	0.004	-0.017	0.749	0.760

Microbial respiration

Name	Model	AIC	BIC	R2	R2_adjusted	RMSE	Sigma
linear	y ~ x	149	157	0.023	0.017	0.392	0.394
quadratic	y ~ x^2	149	157	0.023	0.017	0.392	0.394
log	y ~ log(x)	150	159	0.015	0.009	0.393	0.396
polynomial	y ~ poly(x, degree = 3)	151	166	0.035	0.015	0.389	0.395

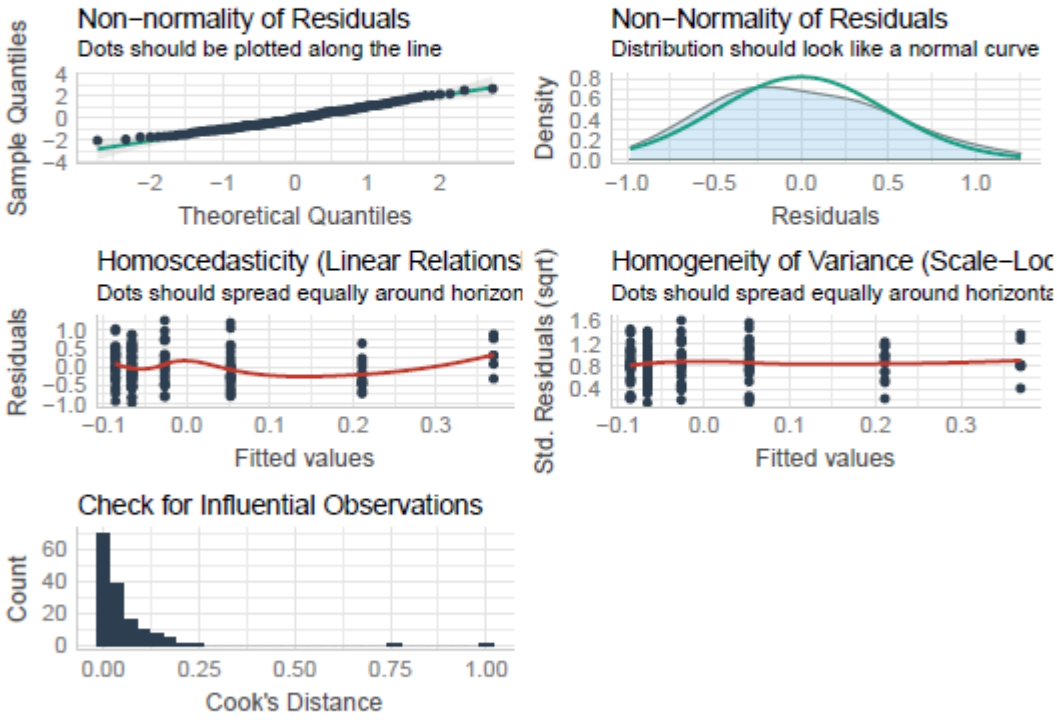
B. Model quality check

Tree species richness effect on soil microbial facets and functions. The relation was tested using the "lm" function in R. Model statistical assumptions were tested using the "check_model" function from the R package "performance".

Microbial biomass

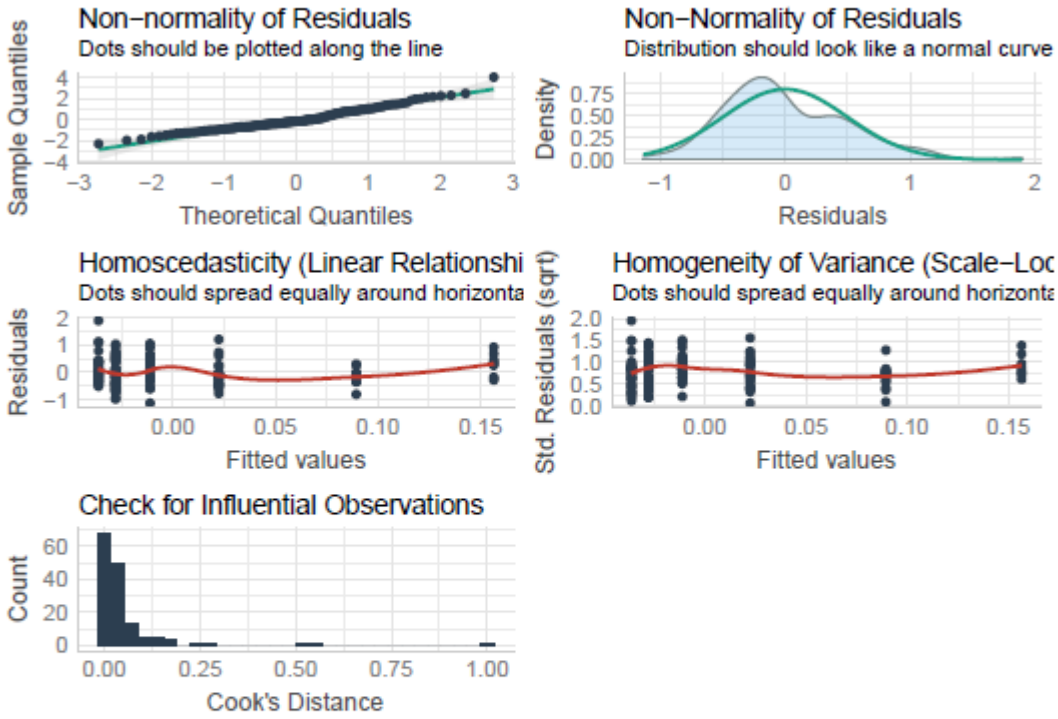
Total microbial biomass

.



Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.106	0.054	-1.96	0.051
Tree species richness	0.02	0.007	2.95	0.004

Active microbial biomass

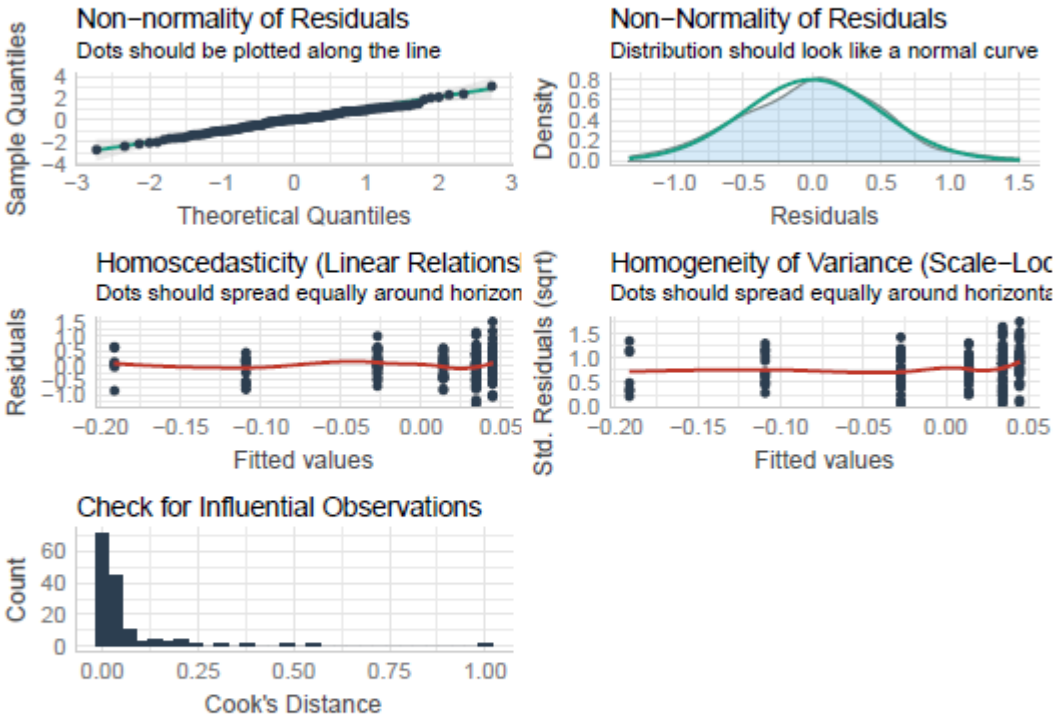


Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.045	0.055	-0.81	0.417
Tree species richness	0.008	0.007	1.22	0.224

Microbial taxonomic profile

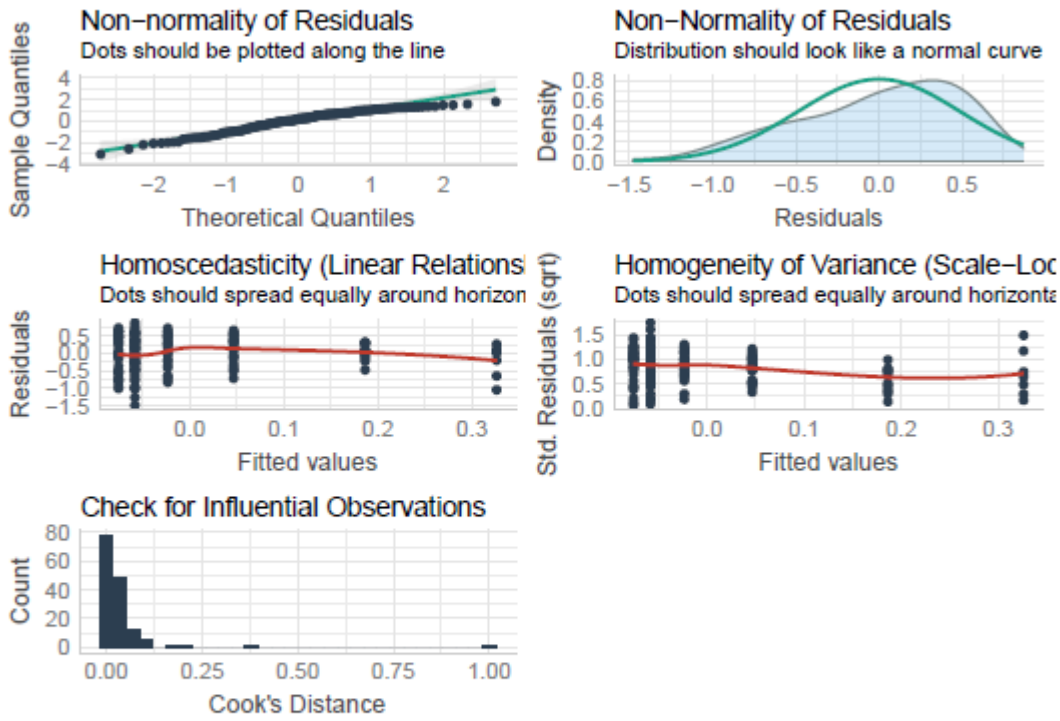
Bacteria to fungi ratio

.



Explanatory	Estimate	SE	t.value	p.value
(Intercept)	0.055	0.055	1	0.32
Tree species richness	-0.01	0.007	-1.5	0.137

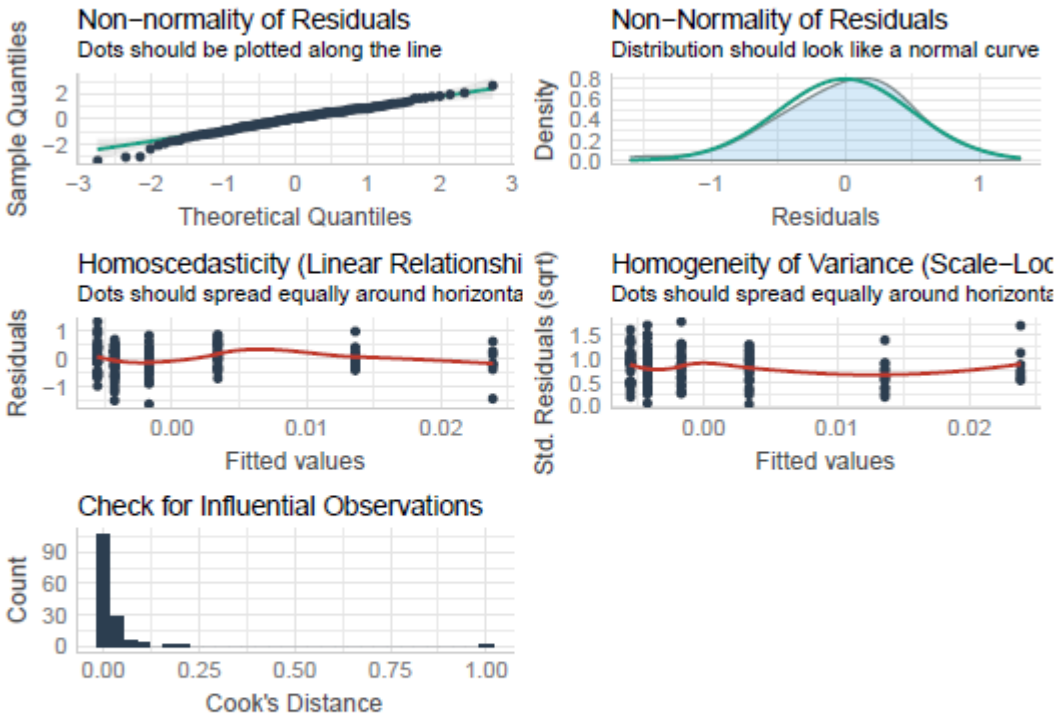
Bacterial Shannon diversity



Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.093	0.054	-1.72	0.087
Tree species richness	0.017	0.007	2.59	0.011

Fungal Shannon diversity

.

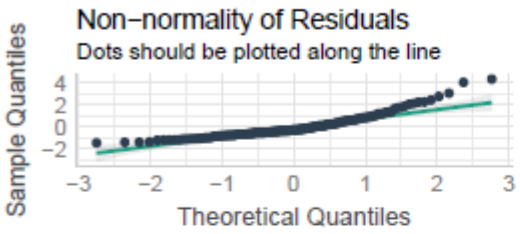


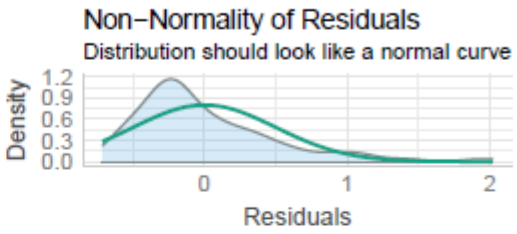
Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.007	0.055	-0.12	0.902
Tree species richness	0.001	0.007	0.18	0.854

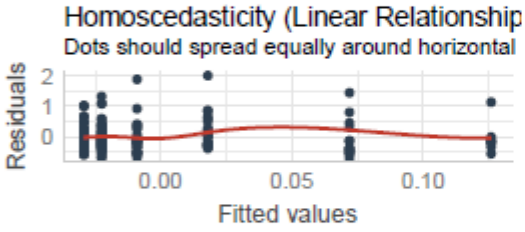
Microbial functional profile

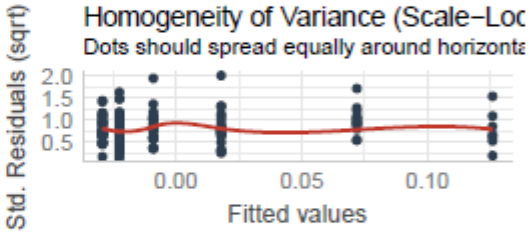
Catabolism functional genes

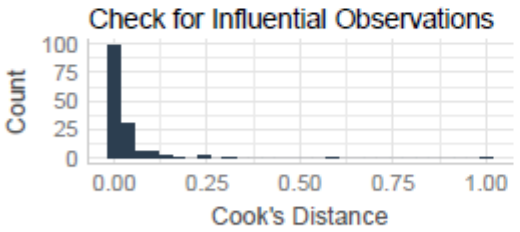
.





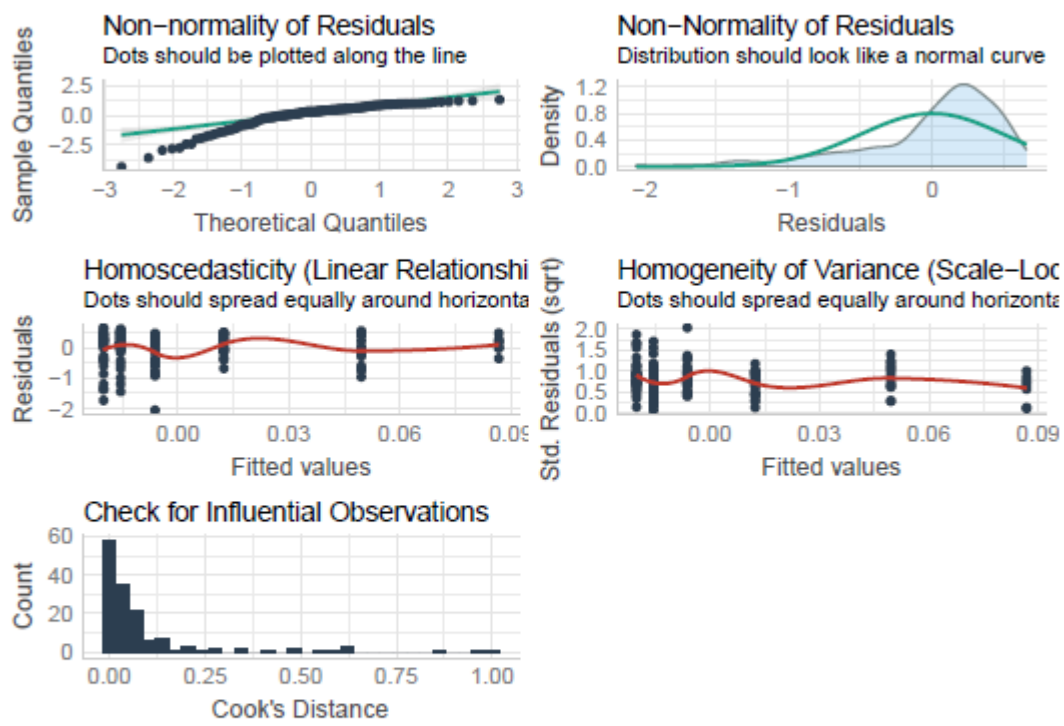






Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.036	0.055	-0.65	0.515
Tree species richness	0.007	0.007	0.98	0.329

Functional genes evenness

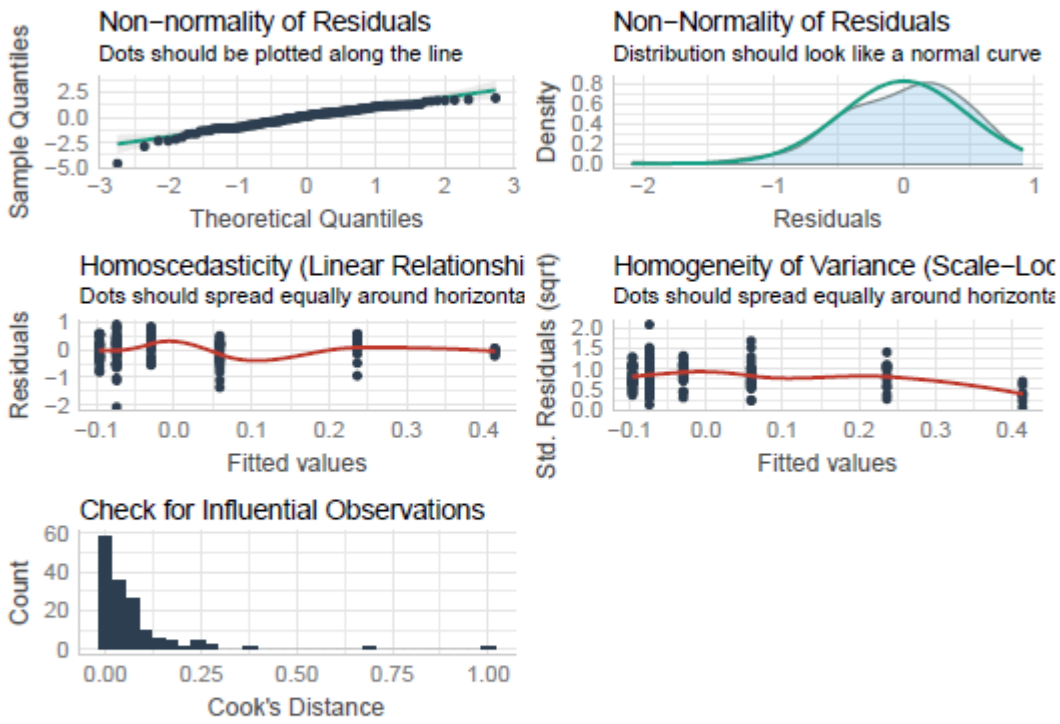


Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.025	0.055	-0.45	0.654
Tree species richness	0.005	0.007	0.67	0.501

Microbial physiological potential

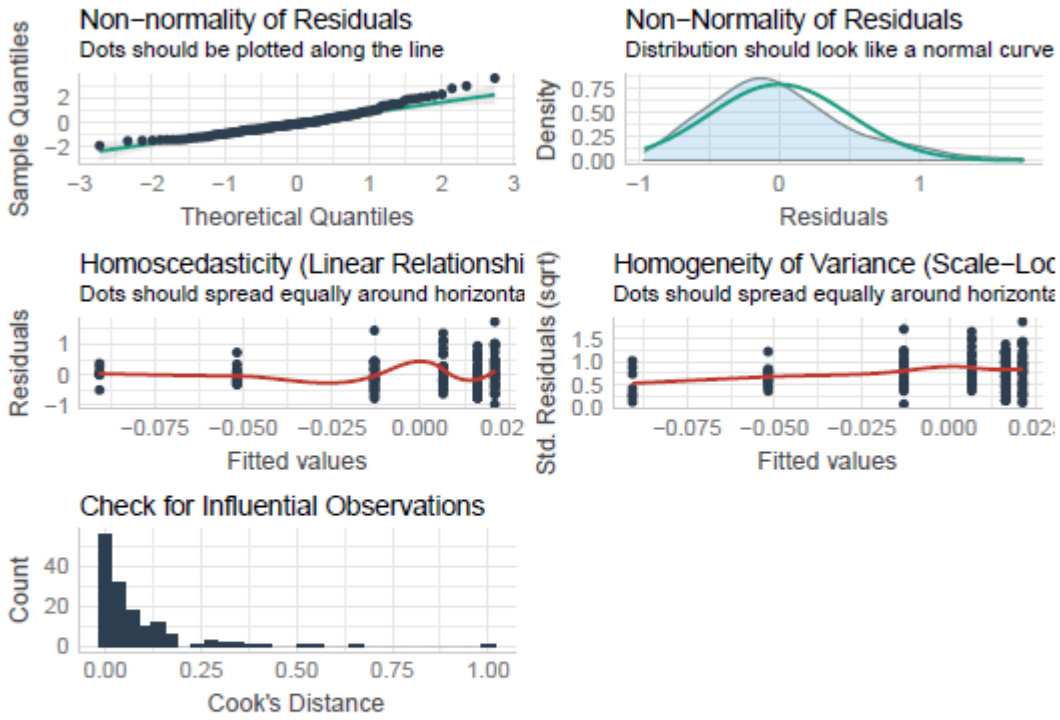
Substrate-induced respiration efficiency

.



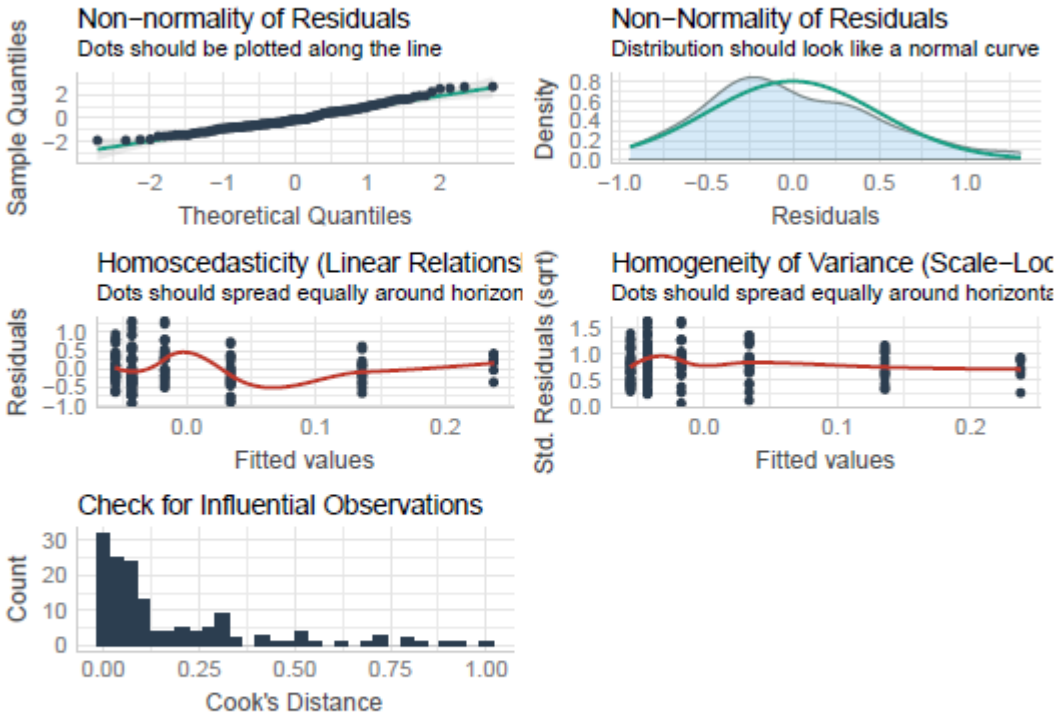
Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.118	0.053	-2.22	0.028
Tree species richness	0.022	0.007	3.33	0.001

Substrate-induced respiration response range



Explanatory	Estimate	SE	t.value	p.value
(Intercept)	0.026	0.055	0.47	0.639
Tree species richness	-0.005	0.007	-0.7	0.482

Microbial respiration



Explanatory	Estimate	SE	t.value	p.value
(Intercept)	-0.068	0.055	-1.24	0.216
Tree species richness	0.013	0.007	1.86	0.064

Supplementary material II – S8: R output Fig. 3

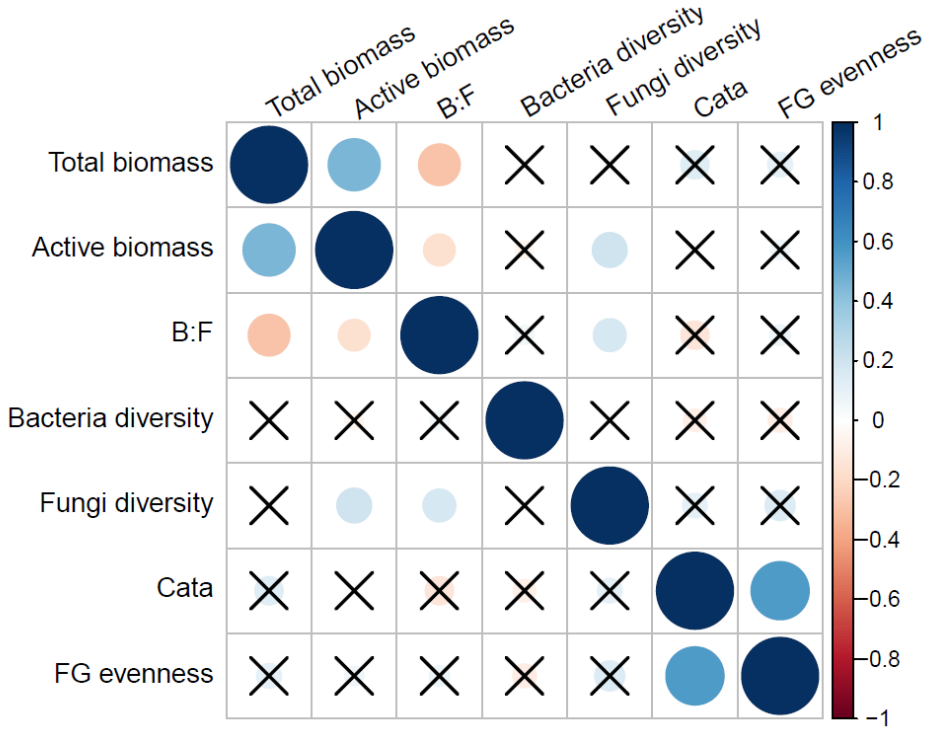
Correlation matrix between microbial facets

Pearson correlation coefficients

	Total biomass	Active biomass	B:F	Bacteria diversity	Fungi diversity	Cata	FG evenness
Total biomass	1.000	0.455	-0.290	-0.016	0.029	0.132	0.102
Active biomass	0.455	1.000	-0.167	-0.055	0.201	0.019	0.062
B:F	-0.290	-0.167	1.000	0.059	0.179	-0.133	0.070
Bacteria diversity	-0.016	-0.055	0.059	1.000	-0.014	-0.083	-0.093
Fungi diversity	0.029	0.201	0.179	-0.014	1.000	0.100	0.150
Cata	0.132	0.019	-0.133	-0.083	0.100	1.000	0.569
FG evenness	0.102	0.062	0.070	-0.093	0.150	0.569	1.000

Pearson correlation p-value

	Total biomass	Active biomass	B:F	Bacteria diversity	Fungi diversity	Cata	FG evenness
Total biomass	0.00e+00	6.46e-09	3.48e-04	8.49e-01	7.27e-01	1.09e-01	2.18e-01
Active biomass	6.46e-09	0.00e+00	4.24e-02	5.07e-01	1.45e-02	8.22e-01	4.56e-01
B:F	3.48e-04	4.24e-02	0.00e+00	4.79e-01	2.92e-02	1.07e-01	3.96e-01
Bacteria diversity	8.49e-01	5.07e-01	4.79e-01	0.00e+00	8.71e-01	3.19e-01	2.61e-01
Fungi diversity	7.27e-01	1.45e-02	2.92e-02	8.71e-01	0.00e+00	2.27e-01	6.97e-02
Cata	1.09e-01	8.22e-01	1.07e-01	3.19e-01	2.27e-01	0.00e+00	4.42e-14
FG evenness	2.18e-01	4.56e-01	3.96e-01	2.61e-01	6.97e-02	4.42e-14	0.00e+00

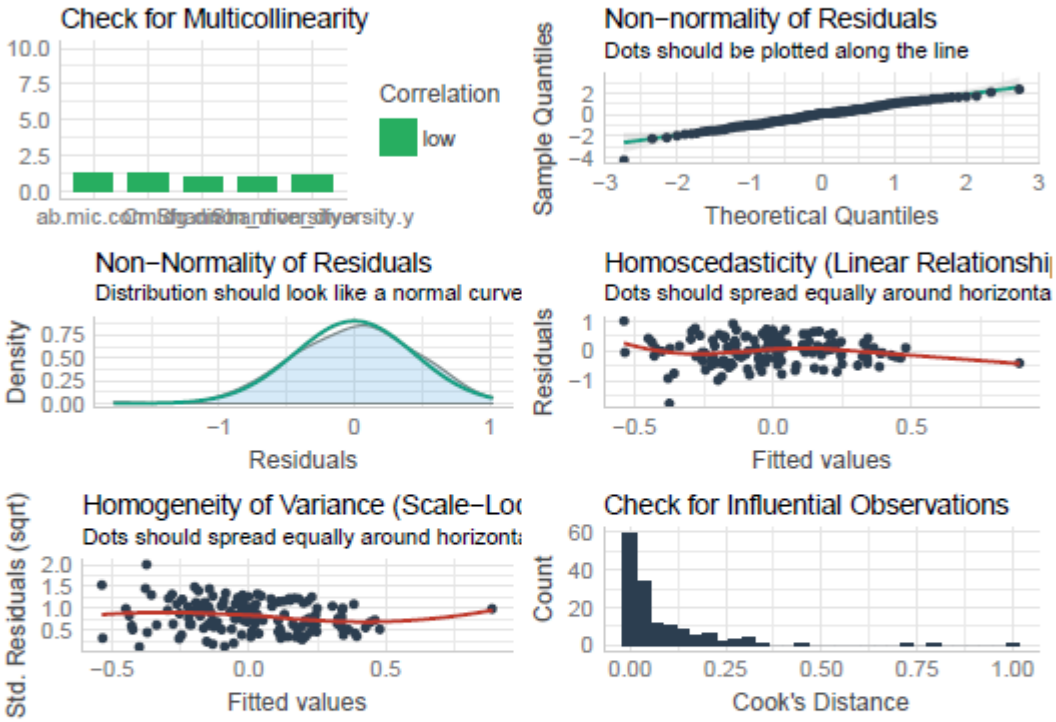


Effect of soil microbial facets on microbial function

Microbial physiological potential

Substrate-induces respiration efficiency

Model statistical assumptions .



.

Model fit .

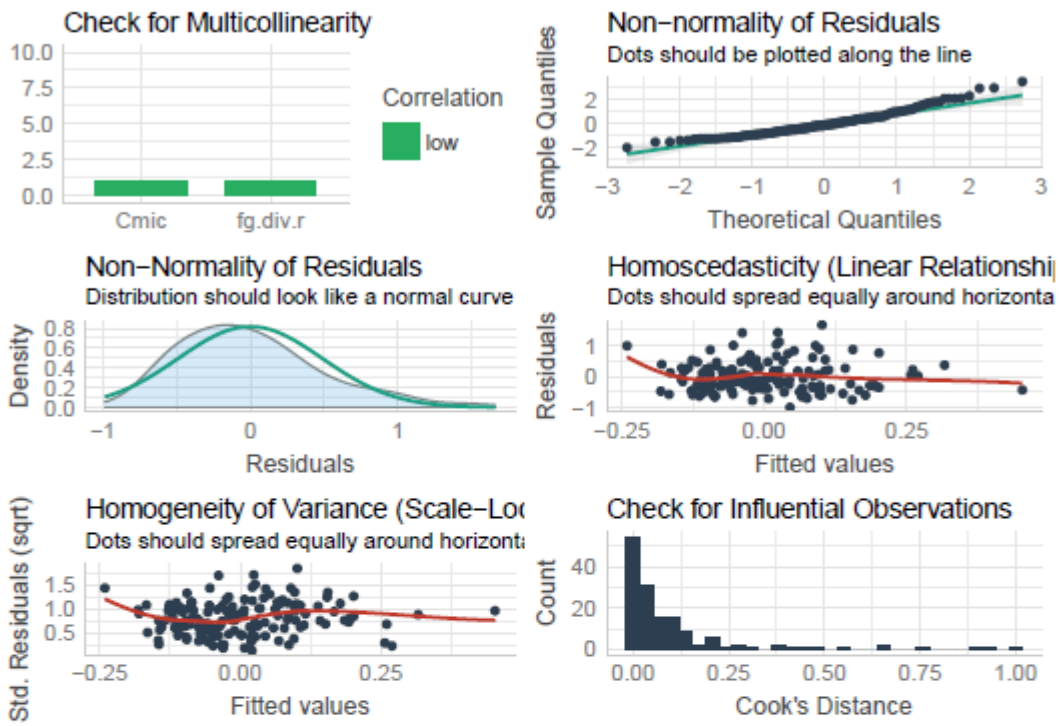
Explanatory	Estimate	SE	t.value	p.value
(Intercept)	0	0.037	0	1
Total biomass	0.238	0.084	2.84	0.005
Active biomass	0.264	0.085	3.09	0.002
Bacteria diversity	0.108	0.074	1.46	0.147
Fungi diversity	-0.152	0.077	-1.98	0.05
FG evenness	-0.166	0.076	-2.2	0.029

Variance partitioning .

Explanatory	Df	R squared	Ajusted R squared
Microbial biomass	2	0.150	0.138
Taxonomic profile	2	0.025	0.012
Functional profile	1	0.025	0.018
Microbial biomass + Taxonomic profile	4	0.195	0.172
Microbial biomass + Functional profile	3	0.189	0.172
Taxonomic profile + Functional profile	3	0.043	0.023
All	5	0.221	0.194

Substrate-induced respiration response range

Model statistical assumptions .



.

Model fit .

Explanatory	Estimate	SE	t.value	p.value
(Intercept)	0	0.04	0	1
Active biomass	0.175	0.081	2.16	0.033
FG evenness	-0.143	0.081	-1.77	0.079

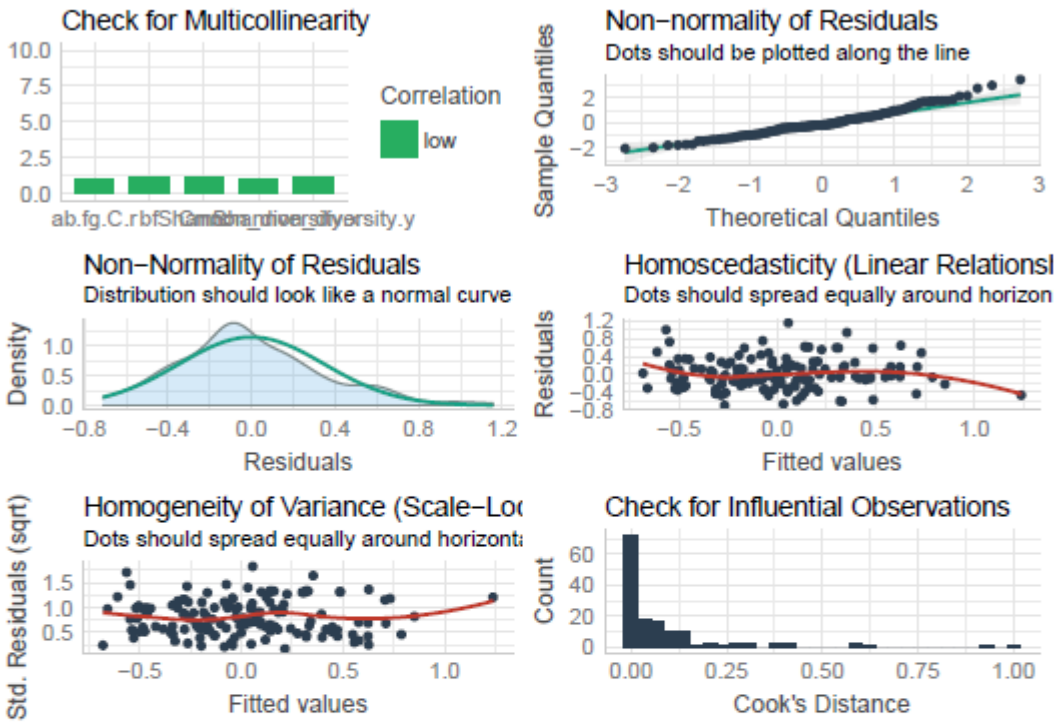
.

Variance partitioning .

Explanatory	Df	R squared	Ajusted R squared
Microbial biomass	1	0.028	0.021
Functional profile	1	0.018	0.011
All	2	0.048	0.035

Microbial respiration

Model statistical assumptions .



.

Model fit .

Explanatory	Estimate	SE	t.value	p.value
(Intercept)	0	0.029	0	1
Active biomass	0.675	0.061	11.07	0
B:F	-0.146	0.061	-2.37	0.019
Bacteria diversity	0.092	0.059	1.57	0.12
Fungi diversity	-0.175	0.062	-2.85	0.005
Cata	-0.132	0.059	-2.21	0.029

.

Variance partitioning .

Explanatory	Df	R squared	Ajusted R squared
Microbial biomass	1	0.431	0.427
Taxonomic profile	3	0.078	0.059
Functional profile	1	0.016	0.009
Microbial biomass + Taxonomic profile	4	0.501	0.487
Microbial biomass + Functional profile	2	0.450	0.442
Taxonomic profile + Functional profile	4	0.101	0.076
All	5	0.518	0.501

.

VIF analysis

Active microbial biomass	B:F	Bacteria diversity
1.09	1.11	1.01
Fungi diversity	Cata	
1.11	1.04	

Supplementary material II – S9: SEM hypotheses

Expected causal relationships

Response variable	Explanatory variable	Hypothesis [Reference from the main text]
Basal respiration	Total microbial biomass	Increasing soil microbial biomass should increase basal respiration [19]
Basal respiration	Active microbial biomass	Increasing active soil microbial biomass should increase basal respiration [19]
Basal respiration	B:F	Increasing B:F is expected to increase microbial community activity and thereafter, respiration [7-10]
Basal respiration	Bacteria diversity	Bacteria diversity should increase microbial respiration by increasing resource use [7-10]
Basal respiration	Fungi diversity	Fungi diversity should increase microbial respiration by increasing resource use [7-10]
Basal respiration	Cata	Increasing catabolism functional genes abundance (i.e. Cata) should increase microbial respiration by increasing the genetic material supporting the catabolism processes [30, 36]
Basal respiration	FG evenness	Increasing catabolism functional gene evenness should increase microbial respiration by increasing the physiological pathways supported by the genetic material [30, 36]
Basal respiration	SIR efficiency	Increasing microbial SIR efficiency should increase microbial respiration due to a higher number of physiological pathways supported [40 - 41]
Basal respiration	SIR range	Increasing microbial SIR range should increase microbial respiration due to a stronger response of the microbial community to complex substrates with longer pathways [40 - 41]
Basal respiration	TOC	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26, 46]
Basal respiration	C:N	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26, 46]
Basal respiration	C:P	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26, 46]

Basal respiration	pH	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26, 46]
Basal respiration	RH	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26, 46]
Basal respiration	Tree species richness	Increasing tree species richness should increase microbial respiration by providing a higher amount and diversity of substrates [11, 21-22, 24]
SIR efficiency	Biomass	Increasing microbial biomass should increase SIR efficiency by reducing microbial lag time before the exponential growth [19, 45]
SIR efficiency	Active microbial biomass	Increasing microbial biomass should increase SIR efficiency by reducing microbial lag time before the exponential growth [19, 45]
SIR efficiency	B:F	Changes in microbial community composition are expected to affect microbial processes [42 - 44]
SIR efficiency	Bacteria diversity	Changes in microbial community composition are expected to affect microbial processes [42 - 44]
SIR efficiency	Fungi diversity	Changes in microbial community composition are expected to affect microbial processes [42 - 44]
SIR efficiency	Cata	Increasing catabolism functional genes should increase SIR efficiency by reducing microbial lag time before the exponential growth [37, 39]
SIR efficiency	FG evenness	Increasing catabolism functional gene evenness should increase SIR efficiency by optimizing all physiological pathways [37, 39]
SIR efficiency	TOC	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26, 27]
SIR efficiency	C:N	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26]
SIR efficiency	C:P	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26]
SIR efficiency	pH	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26]

SIR efficiency	RH	Soil chemical properties affect soil functions by changing resource limitations and physiological processes [12, 13, 25, 26]
SIR efficiency	Tree species richness	Increasing tree species richness should increase microbial physiological potential by providing a higher amount and diversity of substrates [11, 21-22, 24]
SIR range	Biomass	Increasing microbial biomass should increase SIR range by reducing microbial lag time before the exponential growth and favor long physiological pathways [19, 45]
SIR range	Active microbial biomass	Increasing microbial biomass should increase SIR efficiency by reducing microbial lag time before the exponential growth [19, 45]
SIR range	B:F	Changes in microbial community composition are expected to affect microbial processes [42 - 44]
SIR range	Bacteria diversity	Changes in microbial community composition are expected to affect microbial processes [42 - 44]
SIR range	Fungi diversity	Changes in microbial community composition are expected to affect microbial processes [42 - 44]
SIR range	Cata	Increasing catabolism functional genes should increase SIR range by reducing microbial lag before the exponential growth and favor long physiological pathways [37, 39]
SIR range	FG evenness	Increasing catabolism functional gene evenness should increase SIR range by optimizing all physiological pathways [37, 39]
SIR range	TOC	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
SIR range	C:N	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
SIR range	C:P	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
SIR range	pH	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
SIR range	RH	Soil chemical properties affect soil microbial functions (such as microbial

		growth) by changing resource limitations and physiological processes [13]
SIR range	Tree species richness	Increasing tree species richness should increase microbial physiological potential by providing a higher amount and diversity of substrates [11, 21-22, 24]
Biomass	TOC	Soil chemical properties affect soil microbial functions (such as microbial growth) by affecting resource limitations and physiological processes [13]
Biomass	C:N	Soil chemical properties affect soil microbial functions (such as microbial growth) by affecting resource limitations and physiological processes [13]
Biomass	C:P	Soil chemical properties affect soil microbial functions (such as microbial growth) by affecting resource limitations and physiological processes [13]
Biomass	pH	Soil chemical properties affect soil microbial functions (such as microbial growth) by affecting resource limitations and physiological processes [13]
Biomass	RH	Soil chemical properties affect soil microbial functions (such as microbial growth) by affecting resource limitations and physiological processes [13]
Biomass	Tree species richness	Increase of tree species richness should increase substrate abundance and therefore the system's carrying capacity [16, 21-22, 24]
Active microbial biomass	TOC	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
Active microbial biomass	C:N	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
Active microbial biomass	C:P	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
Active microbial biomass	pH	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]
Active microbial biomass	RH	Soil chemical properties affect soil microbial functions (such as microbial growth) by changing resource limitations and physiological processes [13]

Active microbial biomass	Tree species richness	Increase of tree species richness increases substrate abundance and therefore the system's carrying capacity [21-22]
B:F	TOC	Soil chemical properties shape microbial community structure [13, 16]
B:F	C:N	Soil chemical properties shape microbial community structure [13, 16]
B:F	C:P	Soil chemical properties shape microbial community structure [13, 16]
B:F	pH	Soil chemical properties shape microbial community structure [13, 16]
B:F	RH	Soil chemical properties shape microbial community structure [13, 16]
B:F	Tree species richness	Tree species richness should increase bacteria to fungi ratio [21]
Bacteria diversity	TOC	Soil chemical properties shape microbial community structure [13, 16]
Bacteria diversity	C:N	Soil chemical properties shape microbial community structure [13, 16]
Bacteria diversity	C:P	Soil chemical properties shape microbial community structure [13, 16]
Bacteria diversity	pH	Soil chemical properties shape microbial community structure [13, 16]
Bacteria diversity	RH	Soil chemical properties shape microbial community structure [13, 16]
Bacteria diversity	Tree species richness	Increase of tree species richness increases substrate diversity and therefore functional niche complementarity [21-22]
Fungi diversity	TOC	Soil chemical properties shape microbial community structure [13, 16]
Fungi diversity	C:N	Soil chemical properties shape microbial community structure [13, 16]
Fungi diversity	C:P	Soil chemical properties shape microbial community structure [13, 16]
Fungi diversity	pH	Soil chemical properties shape microbial community structure [13, 16]
Fungi diversity	RH	Soil chemical properties shape microbial community structure [13, 16]
Fungi diversity	Tree species richness	Increase of tree species richness increases substrate diversity and therefore functional niche complementarity [21-22]
Cata	TOC	Soil chemical properties shape microbial community structure [12, 13, 25, 26, 30-32]
Cata	C:N	Soil chemical properties shape microbial community structure [12, 13, 25, 26, 30-32]
Cata	C:P	Soil chemical properties shape microbial community structure [12, 13, 25, 26, 30-32]
Cata	pH	Soil chemical properties shape microbial community structure [12, 13, 25, 26, 30-32]
Cata	RH	Soil chemical properties shape microbial community structure [12, 13, 25, 26, 30-32]

Cata	Tree species richness	Increase of tree species richness increases substrate diversity and therefore functional niche complementarity [21-22]
FG evenness	TOC	Soil chemical properties affect soil microbial community composition by changing resource limitations and therefore species selection [12, 13, 25, 26, 30-32]
FG evenness	C:N	Soil chemical properties affect soil microbial community composition by changing resource limitations and therefore species selection [12, 13, 25, 26, 30-32]
FG evenness	C:P	Soil chemical properties affect soil microbial community composition by changing resource limitations and therefore species selection [12, 13, 25, 26, 30-32]
FG evenness	pH	Soil chemical properties affect soil microbial community composition by changing resource limitations and therefore species selection [12, 13, 25, 26, 30-32]
FG evenness	RH	Soil chemical properties affect soil microbial community composition by changing resource limitations and therefore species selection [12, 13, 25, 26, 30-32]
FG evenness	Tree species richness	Increasing tree species richness increases substrate diversity and therefore functional niche complementarity [21-22]

Correlations (relationships where directionality of effects is not clear from the literature)

First variable	Second variable	Hypothesis [Reference from the main text]
Biomass	Active microbial biomass	We expect the biomass of active microbes to increase with increasing total microbial biomass
Biomass	B:F	We expect the B:F ratio to positively correlate with the microbial biomass
Biomass	Bacteria diversity	We expect a positive biomass ~ diversity relationship
Biomass	Fungi diversity	We expect a positive biomass ~ diversity relationship
Biomass	Cata	The number of genes copies is expected to increase with the number of cells
Biomass	FG evenness	We expect a positive biomass ~ diversity relationship
Active microbial biomass	B:F	We expect the B:F ratio to positively correlate with the microbial biomass
Active microbial biomass	Bacteria diversity	We expect a positive biomass ~ diversity relationship
Active microbial biomass	Fungi diversity	We expect a positive biomass ~ diversity relationship
Active microbial biomass	Cata	The number of genes copies is expected to increase with the number of cells
Active microbial biomass	FG evenness	We expect a positive biomass ~ diversity relationship
B:F	Bacteria diversity	We expect a positive biomass ~ diversity relationship, which also implies a positive B:F ~ bacteria diversity relationship
B:F	Fungi diversity	We expect a positive biomass ~ diversity relationship, which also implies a positive B:F ~ bacteria diversity relationship
B:F	Cata	We expect a positive relationship, as most of the measured genes are bacterial
B:F	FG evenness	We expect a positive relationship, as most of the measured genes are bacterial
Bacteria diversity	Fungi diversity	We expect bacteria and fungi diversity to be positively correlated to each another as driven by similar processes
Bacteria diversity	Cata	We expect a positive biomass ~ diversity relationship [33]
Bacteria diversity	FG evenness	We expect taxonomic and functional diversity to be strongly positively correlated to each another as driven by similar processes [33]
Fungi diversity	Cata	We expect a positive biomass ~ diversity relationship [33]

Fungi diversity	FG evenness	We expect taxonomic and functional diversity to be strongly correlated to each another as driven by similar processes [33]
Cata	FG evenness	We expect a positive biomass ~ diversity relationship
SIR efficiency	SIR range	We expect SIR range and efficiency to be positively correlated
TOC	C:N	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
TOC	C:P	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
TOC	pH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
TOC	RH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
TOC	Tree species richness	We expect soil chemical properties and tree species richness may be correlated; while significant tree diversity effects on soil properties can be expected, initial plot selection could also have caused non-causal relationships
C:N	C:P	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
C:N	pH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
C:N	RH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
C:N	Tree species richness	We expect soil chemical properties and tree species richness may be correlated; while significant tree diversity effects on soil properties can be expected, initial plot selection could also have caused non-causal relationships
C:P	pH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
C:P	RH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
C:P	Tree species richness	We expect soil chemical properties and tree species richness may be correlated; while significant tree diversity effects on soil properties can be expected, initial plot selection could also have caused non-causal relationships
pH	RH	We expect soil chemical properties to be correlated [see Scholten et al. 2017]
pH	Tree species richness	We expect soil chemical properties and tree species richness may be correlated; while significant tree diversity effects on soil properties can be expected, initial plot selection could also have caused non-causal relationships
RH	Tree species richness	We expect soil chemical properties and tree species richness may be correlated; while significant tree diversity effects on soil properties can be expected, initial plot selection could also have caused non-causal relationships

Supplementary material II – S10: R outputs Fig. 4

Contents

1 Introduction

The following document will display the R summary after fitting the structural equation model displayed in figure Fig. 4. The model was fitted using the "lavaan" package. (See all hypotheses rational and references in S9)

2 Model structure

```
form =
'
# Causal relations

Basal respiration ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    SIR efficiency + SIR range

SIR efficiency ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness

SIR range ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness

# Correlations

Biomass ~~ Active biomass
Biomass ~~ B:F
Biomass ~~ Bacteria diversity
Biomass ~~ Fungi diversity
Biomass ~~ Cata
Biomass ~~ FG evenness

Active biomass ~~ B:F
Active biomass ~~ Bacteria diversity
Active biomass ~~ Fungi diversity
Active biomass ~~ Cata
Active biomass ~~ FG evenness

B:F ~~ Bacteria diversity
B:F ~~ Fungi diversity
B:F ~~ Cata
B:F ~~ FG evenness

Bacteria diversity ~~ Fungi diversity
Bacteria diversity ~~ Cata
Bacteria diversity ~~ FG evenness

Fungi diversity ~~ Cata
Fungi diversity ~~ FG evenness

Cata ~~ FG evenness

SIR range ~~ SIR efficiency'
```

3 Model fit

3.1 Fit quality

.

Fit index	Value
cfi	1
rmsea	0
srmr	0

3.2 Explained variance

.

Variable	R.squared
Basal respiration	0.573
SIR eff.	0.232
SIR range	0.084

3.3 Model output

Response	Relation	Explanatory	Estimate	SE	p value
Basal respiration	~	Total biomass	-0.034	0.065	0.595
Basal respiration	~	Active biomass	0.590	0.060	< 0.001***
Basal respiration	~	B:F	-0.109	0.060	0.067
Basal respiration	~	Bacteria diversity	0.046	0.055	0.409
Basal respiration	~	Fungi diversity	-0.128	0.058	0.027 *
Basal respiration	~	Cata	-0.113	0.067	0.094
Basal respiration	~	FG evenness	0.020	0.068	0.771
Basal respiration	~	SIR eff.	0.176	0.062	0.005 **
Basal respiration	~	SIR range	0.213	0.057	< 0.001***
SIR eff.	~	Total biomass	0.209	0.083	0.012 *
SIR eff.	~	Active biomass	0.258	0.082	0.002 **
SIR eff.	~	B:F	-0.096	0.079	0.222
SIR eff.	~	Bacteria diversity	0.115	0.072	0.11
SIR eff.	~	Fungi diversity	-0.134	0.076	0.077
SIR eff.	~	Cata	0.037	0.090	0.685
SIR eff.	~	FG evenness	-0.179	0.089	0.045 *
SIR range	~	Total biomass	0.096	0.092	0.295
SIR range	~	Active biomass	0.148	0.091	0.103
SIR range	~	B:F	-0.047	0.086	0.586
SIR range	~	Bacteria diversity	0.111	0.079	0.16
SIR range	~	Fungi diversity	-0.099	0.083	0.233
SIR range	~	Cata	-0.039	0.099	0.694
SIR range	~	FG evenness	-0.101	0.098	0.302
Total biomass	~~	Active biomass	0.455	0.065	< 0.001***
Total biomass	~~	B:F	-0.290	0.075	< 0.001***
Total biomass	~~	Bacteria diversity	-0.016	0.082	0.847
Total biomass	~~	Fungi diversity	0.029	0.082	0.725
Total biomass	~~	Cata	0.132	0.081	0.101
Total biomass	~~	FG evenness	0.102	0.081	0.211
Active biomass	~~	B:F	-0.167	0.080	0.037 *
Active biomass	~~	Bacteria diversity	-0.055	0.082	0.503
Active biomass	~~	Fungi diversity	0.201	0.079	0.011 *
Active biomass	~~	Cata	0.019	0.082	0.82
Active biomass	~~	FG evenness	0.062	0.082	0.451
B:F	~~	Bacteria diversity	0.059	0.082	0.474
B:F	~~	Fungi diversity	0.179	0.080	0.024 *
B:F	~~	Cata	-0.133	0.081	0.1
B:F	~~	FG evenness	0.070	0.082	0.39
Bacteria diversity	~~	Fungi diversity	-0.014	0.082	0.869
Bacteria diversity	~~	Cata	-0.083	0.082	0.312
Bacteria diversity	~~	FG evenness	-0.093	0.081	0.254
Fungi diversity	~~	Cata	0.100	0.081	0.22
Fungi diversity	~~	FG evenness	0.150	0.080	0.063
Cata	~~	FG evenness	0.569	0.056	< 0.001***
SIR eff.	~~	SIR range	-0.185	0.079	0.02 *
Basal respiration	~~	Basal respiration	0.427	0.053	< 0.001***

(continued)

Response	Relation	Explanatory	Estimate	SE	p value
SIR eff.	~~	SIR eff.	0.768	0.061	$< 0.001^{***}$
SIR range	~~	SIR range	0.916	0.044	$< 0.001^{***}$

4 Model inflation by measurement methods

Active microbial biomass and microbial respiration were measured using the same machine and subsample. Therefore, we are testing the stability of our observation and results when removing microbial biomass.

4.1 Fit quality

.

Fit index	Value
cfi	1
rmsea	0
srmr	0

4.2 Explained variance

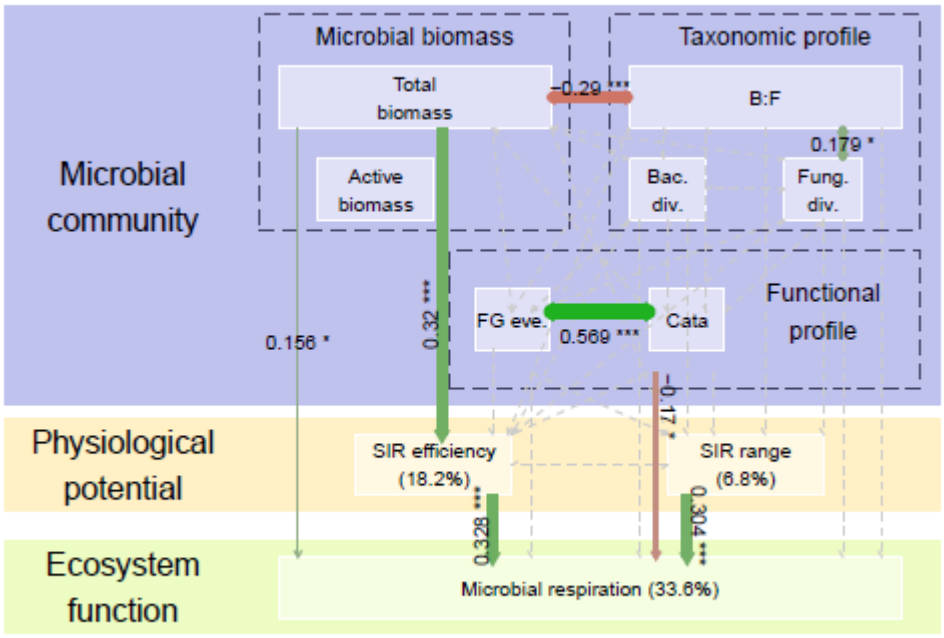
.

Variable	R.squared
Basal respiration	0.336
SIR eff.	0.182
SIR range	0.068

4.3 Model output

Response	Relation	Explanatory	Estimate	SE	p value
Basal respiration	~	Total biomass	0.156	0.076	0.039 *
Basal respiration	~	B:F	-0.141	0.074	0.056
Basal respiration	~	Bacteria diversity	-0.006	0.068	0.935
Basal respiration	~	Fungi diversity	0.013	0.070	0.855
Basal respiration	~	Cata	-0.170	0.083	0.041 *
Basal respiration	~	FG evenness	0.082	0.085	0.333
Basal respiration	~	SIR eff.	0.328	0.072	< 0.001***
Basal respiration	~	SIR range	0.304	0.068	< 0.001***
SIR eff.	~	Total biomass	0.320	0.075	< 0.001***
SIR eff.	~	B:F	-0.121	0.081	0.135
SIR eff.	~	Bacteria diversity	0.104	0.075	0.162
SIR eff.	~	Fungi diversity	-0.081	0.076	0.292
SIR eff.	~	Cata	0.010	0.093	0.911
SIR eff.	~	FG evenness	-0.167	0.092	0.07
SIR range	~	Total biomass	0.159	0.083	0.055
SIR range	~	B:F	-0.061	0.087	0.482
SIR range	~	Bacteria diversity	0.104	0.080	0.189
SIR range	~	Fungi diversity	-0.068	0.082	0.404
SIR range	~	Cata	-0.054	0.099	0.586
SIR range	~	FG evenness	-0.094	0.099	0.341
Total biomass	~~	B:F	-0.290	0.075	< 0.001***
Total biomass	~~	Bacteria diversity	-0.016	0.082	0.847
Total biomass	~~	Fungi diversity	0.029	0.082	0.725
Total biomass	~~	Cata	0.132	0.081	0.101
Total biomass	~~	FG evenness	0.102	0.081	0.211
B:F	~~	Bacteria diversity	0.059	0.082	0.474
B:F	~~	Fungi diversity	0.179	0.080	0.024 *
B:F	~~	Cata	-0.133	0.081	0.1
B:F	~~	FG evenness	0.070	0.082	0.39
Bacteria diversity	~~	Fungi diversity	-0.014	0.082	0.869
Bacteria diversity	~~	Cata	-0.083	0.082	0.312
Bacteria diversity	~~	FG evenness	-0.093	0.081	0.254
Fungi diversity	~~	Cata	0.100	0.081	0.22
Fungi diversity	~~	FG evenness	0.150	0.080	0.063
Cata	~~	FG evenness	0.569	0.056	< 0.001***
SIR eff.	~~	SIR range	-0.145	0.080	0.071
Basal respiration	~~	Basal respiration	0.664	0.063	< 0.001***
SIR eff.	~~	SIR eff.	0.818	0.057	< 0.001***
SIR range	~~	SIR range	0.932	0.040	< 0.001***

```
## Warning: package 'readxl' was built under R version 4.0.3
```


Microbial community
Microbial biomass
Total biomass
Active biomass
Taxonomic profile
B:F
Bac. div.
Fung. div.
Functional profile
FG eve.
Cata
Physiological potential
SIR efficiency (18.2%)
SIR range (6.8%)
Ecosystem function
Microbial respiration (33.6%)
−0.29 ***
0.179 *
0.156 *
0.32 ***
0.569 ***
−0.17 *
0.328 ***
0.304 ***

Supplementary material II – S11: R outputs Fig. 5

Contents

1 Introduction

The following document will display the R summary after fitting the structural equation model displayed in figure Fig. 5. The model was fitted using the "lavaan" package.(See all hypotheses rational and references in S9)

2 Model structure

```
form =
'
# Causal relations
## Ecosystem function
Basal respiration ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    SIR efficiency + SIR range +
                    TOC + C:N + C:P + pH + RH + Tree.species.richness

## Physiological potentiel
SIR efficiency ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    TOC + C:N + C:P + pH + RH + Tree.species.richness

SIR range ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    TOC + C:N + C:P + pH + RH + Tree.species.richness

## Genetic potential
Cata ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

FG evenness ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

## Community structure
B:F ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

Bacteria diversity ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

Fungi diversity ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

## Microbial biomass
Biomass ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

Active biomass ~ TOC + C:N + C:P + pH + RH + Tree.species.richness

# Correlations
## Microbial community

Biomass ~~ Active biomass
Biomass ~~ B:F
Biomass ~~ Bacteria diversity
Biomass ~~ Fungi diversity
Biomass ~~ Cata
Biomass ~~ FG evenness

Active biomass ~~ B:F
Active biomass ~~ Bacteria diversity
Active biomass ~~ Fungi diversity
```

```
Active biomass -- Cata
Active biomass -- FG evenness

B:F -- Bacteria diversity
B:F -- Fungi diversity
B:F -- Cata
B:F -- FG evenness

Bacteria diversity -- Fungi diversity
Bacteria diversity -- Cata
Bacteria diversity -- FG evenness

Fungi diversity -- Cata
Fungi diversity -- FG evenness

Cata -- FG evenness

# Physiological potential
SIR range -- SIR efficiency

# Soil chemical properties & tree species richness
Tree.species.richness -- TOC
Tree.species.richness -- C:P
Tree.species.richness -- C:N
Tree.species.richness -- pH
Tree.species.richness -- RH

TOC -- C:P
TOC -- C:N
TOC -- pH
TOC -- RH

C:P -- C:N
C:P -- pH
C:P -- RH

C:N -- pH
C:N -- RH

pH -- RH'
```

3 Model fit

3.1 Fit quality

.

Fit index	Value
cfi	1
rmsea	0
srmr	0

4 Model output

4.1 Explained variance

.

Variable	R.squared
Basal respiration	0.68
SIR eff.	0.335
SIR range	0.172
Cata	0.037
FG evenness	0.045
Fungi diversity	0.055
Bacteria diversity	0.079
B:F	0.053
Active biomass	0.166
Total biomass	0.465

4.2 Summarized effects

4.2.1 Effect of soil and tree species richness

Total effects of soil chemical properties and tree species richness on microbial community facets and functions.

Variable	Total.effect
TOC	1.384
C:N	0.000
C:P	0.269
RH	0.546
pH	0.585
TreeD.	0.489

4.2.2 Link between the groups

Response	Relation	Explanatory	Total.effect
Microbial biomass	~	Soil chemical properties	1.474
Taxonomic profile	~	Soil chemical properties	0.199
Functional profile	~	Soil chemical properties	0.000
Physiological potential	~	Soil chemical properties	0.799
Microbial respiration	~	Soil chemical properties	0.312
Microbial biomass	~	Tree species richness	0.173
Taxonomic profile	~	Tree species richness	0.164
Functional profile	~	Tree species richness	0.000
Physiological potential	~	Tree species richness	0.152
Microbial respiration	~	Tree species richness	0.000
Taxonomic profile	~~	Microbial biomass	0.568
Functional profile	~~	Microbial biomass	0.000
Physiological potential	~	Microbial biomass	0.543
Microbial respiration	~	Microbial biomass	0.567
Functional profile	~~	Taxonomic profile	0.000
Physiological potential	~	Taxonomic profile	0.182
Microbial respiration	~	Taxonomic profile	0.138
Physiological potential	~	Functional profile	0.186
Microbial respiration	~	Functional profile	0.000
Microbial respiration	~	Physiological potential	0.175
Soil chemical properties	~~	Soil chemical properties	1.440
Microbial biomass	~~	Microbial biomass	0.334
Taxonomic profile	~~	Taxonomic profile	0.188
Functional profile	~~	Functional profile	0.554
Physiological potential	~~	Physiological potential	0.000

4.3 Complete R summary

Response	Relation	Explanatory	Estimate	SE	p value
Basal respiration	~	Total biomass	0.085	0.072	0.236
Basal respiration	~	Active biomass	0.567	0.057	< 0.001***
Basal respiration	~	B:F	-0.138	0.053	0.009 **
Basal respiration	~	Bacteria diversity	0.025	0.051	0.619
Basal respiration	~	Fungi diversity	-0.094	0.051	0.067
Basal respiration	~	Cata	-0.094	0.059	0.11
Basal respiration	~	FG evenness	0.011	0.060	0.859
Basal respiration	~	SIR eff.	0.090	0.058	0.12
Basal respiration	~	SIR range	0.175	0.052	< 0.001***
Basal respiration	~	TOC	-0.113	0.077	0.14
Basal respiration	~	C:P	0.096	0.064	0.134
Basal respiration	~	C:N	-0.046	0.049	0.348
Basal respiration	~	pH	-0.078	0.057	0.169
Basal respiration	~	RH	0.312	0.054	< 0.001***
Basal respiration	~	TreeD.	0.019	0.052	0.718
SIR eff.	~	Total biomass	0.093	0.101	0.356
SIR eff.	~	Active biomass	0.258	0.079	0.001 **
SIR eff.	~	B:F	-0.078	0.075	0.295
SIR eff.	~	Bacteria diversity	0.024	0.072	0.737
SIR eff.	~	Fungi diversity	-0.094	0.072	0.193
SIR eff.	~	Cata	0.044	0.084	0.603
SIR eff.	~	FG evenness	-0.186	0.085	0.028 *
SIR eff.	~	TOC	0.038	0.108	0.725
SIR eff.	~	C:P	0.113	0.089	0.204
SIR eff.	~	C:N	0.076	0.070	0.282
SIR eff.	~	pH	-0.205	0.078	0.009 **
SIR eff.	~	RH	0.042	0.075	0.578
SIR eff.	~	TreeD.	0.152	0.073	0.038 *
SIR range	~	Total biomass	0.285	0.111	0.01 *
SIR range	~	Active biomass	0.129	0.089	0.147
SIR range	~	B:F	-0.057	0.083	0.494
SIR range	~	Bacteria diversity	0.182	0.079	0.021 *
SIR range	~	Fungi diversity	-0.086	0.081	0.287
SIR range	~	Cata	-0.023	0.094	0.808
SIR range	~	FG evenness	-0.079	0.095	0.406
SIR range	~	TOC	-0.325	0.118	0.006 **
SIR range	~	C:P	0.269	0.098	0.006 **
SIR range	~	C:N	-0.051	0.078	0.518
SIR range	~	pH	0.168	0.088	0.056
SIR range	~	RH	0.151	0.083	0.069
SIR range	~	TreeD.	-0.104	0.082	0.207
Cata	~	TOC	0.089	0.103	0.391
Cata	~	C:P	-0.130	0.105	0.217
Cata	~	C:N	0.092	0.082	0.259
Cata	~	pH	-0.017	0.092	0.855
Cata	~	RH	-0.106	0.084	0.205

(continued)

Response	Relation	Explanatory	Estimate	SE	p value
Cata	~	TreeD.	0.073	0.084	0.388
FG evenness	~	TOC	0.058	0.103	0.57
FG evenness	~	C:P	-0.166	0.105	0.113
FG evenness	~	C:N	0.138	0.081	0.088
FG evenness	~	pH	-0.053	0.091	0.565
FG evenness	~	RH	-0.070	0.084	0.403
FG evenness	~	TreeD.	0.039	0.084	0.639
Fungi diversity	~	TOC	0.171	0.102	0.092
Fungi diversity	~	C:P	-0.110	0.104	0.292
Fungi diversity	~	C:N	-0.006	0.081	0.944
Fungi diversity	~	pH	0.199	0.090	0.026 *
Fungi diversity	~	RH	-0.017	0.083	0.839
Fungi diversity	~	TreeD.	0.043	0.084	0.607
Bacteria diversity	~	TOC	0.089	0.101	0.379
Bacteria diversity	~	C:P	-0.026	0.103	0.799
Bacteria diversity	~	C:N	0.100	0.080	0.212
Bacteria diversity	~	pH	-0.112	0.089	0.209
Bacteria diversity	~	RH	0.068	0.082	0.41
Bacteria diversity	~	TreeD.	0.164	0.082	0.045 *
B:F	~	TOC	-0.058	0.102	0.574
B:F	~	C:P	-0.042	0.105	0.69
B:F	~	C:N	-0.097	0.081	0.232
B:F	~	pH	0.068	0.091	0.451
B:F	~	RH	0.132	0.083	0.112
B:F	~	TreeD.	-0.108	0.083	0.194
Active biomass	~	TOC	0.407	0.092	< 0.001***
Active biomass	~	C:P	-0.033	0.098	0.74
Active biomass	~	C:N	0.037	0.076	0.631
Active biomass	~	pH	0.181	0.085	0.032 *
Active biomass	~	RH	0.067	0.078	0.391
Active biomass	~	TreeD.	0.086	0.078	0.275
Total biomass	~	TOC	0.652	0.069	< 0.001***
Total biomass	~	C:P	-0.072	0.079	0.36
Total biomass	~	C:N	0.106	0.061	0.082
Total biomass	~	pH	0.018	0.068	0.797
Total biomass	~	RH	-0.234	0.063	< 0.001***
Total biomass	~	TreeD.	0.173	0.063	0.006 **
Active biomass	~~	Total biomass	0.334	0.073	< 0.001***
B:F	~~	Total biomass	-0.244	0.077	0.002 **
Bacteria diversity	~~	Total biomass	-0.163	0.080	0.041 *
Fungi diversity	~~	Total biomass	-0.046	0.082	0.577
Cata	~~	Total biomass	0.095	0.081	0.242
FG evenness	~~	Total biomass	0.099	0.081	0.226
B:F	~~	Active biomass	-0.153	0.080	0.057
Bacteria diversity	~~	Active biomass	-0.119	0.081	0.143
Fungi diversity	~~	Active biomass	0.161	0.080	0.045 *
Cata	~~	Active biomass	0.002	0.082	0.977
FG evenness	~~	Active biomass	0.069	0.082	0.401

(continued)

Response	Relation	Explanatory	Estimate	SE	p value
Bacteria diversity	~~	B:F	0.104	0.081	0.202
Fungi diversity	~~	B:F	0.188	0.079	0.018 *
Cata	~~	B:F	-0.109	0.081	0.178
FG evenness	~~	B:F	0.097	0.081	0.235
Fungi diversity	~~	Bacteria diversity	-0.003	0.082	0.975
Cata	~~	Bacteria diversity	-0.107	0.081	0.189
FG evenness	~~	Bacteria diversity	-0.119	0.081	0.143
Cata	~~	Fungi diversity	0.084	0.082	0.305
FG evenness	~~	Fungi diversity	0.143	0.081	0.076
Cata	~~	FG evenness	0.554	0.057	< 0.001***
SIR eff.	~~	SIR range	-0.161	0.080	0.044 *
C:P	~~	TreeD.	-0.001	0.082	0.993
C:N	~~	TreeD.	0.008	0.082	0.922
pH	~~	TreeD.	-0.246	0.077	0.001 **
RH	~~	TreeD.	0.081	0.082	0.324
TOC	~~	TreeD.	0.132	0.081	0.102
TOC	~~	C:P	0.603	0.052	< 0.001***
TOC	~~	C:N	0.012	0.082	0.883
TOC	~~	pH	-0.263	0.077	< 0.001***
TOC	~~	RH	0.108	0.081	0.182
C:P	~~	C:N	-0.038	0.082	0.642
C:P	~~	pH	-0.328	0.073	< 0.001***
C:P	~~	RH	0.016	0.082	0.848
C:N	~~	pH	0.142	0.081	0.078
C:N	~~	RH	-0.123	0.081	0.129
pH	~~	RH	-0.246	0.077	0.001 **
Basal respiration	~~	Basal respiration	0.320	0.043	< 0.001***
SIR eff.	~~	SIR eff.	0.665	0.063	< 0.001***
SIR range	~~	SIR range	0.828	0.056	< 0.001***
Cata	~~	Cata	0.963	0.031	< 0.001***
FG evenness	~~	FG evenness	0.955	0.033	< 0.001***
Fungi diversity	~~	Fungi diversity	0.945	0.037	< 0.001***
Bacteria diversity	~~	Bacteria diversity	0.921	0.042	< 0.001***
B:F	~~	B:F	0.947	0.036	< 0.001***
Active biomass	~~	Active biomass	0.834	0.056	< 0.001***
Total biomass	~~	Total biomass	0.535	0.060	< 0.001***

5 Model simplification

In order to simplify our model, soil parameter have been added into a latent variable. The model fit was tested and the estimates were compared to the full model. The difference between the model output been neglectable, we favored the full model in our manuscript to leave the reader the opportunity to explore the different mechanisms. Below the simplified model and its outputs

```
form =
'
# Latent variable
```

```
fert =~ TOC + C:N + C:P + pH + RH

# Causal relations
## Ecosystem function
Basal respiration ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    SIR efficiency + SIR range +
                    fert + Tree.species.richness

## Physiological potentiel
SIR efficiency ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    fert + Tree.species.richness

SIR range ~ Biomass + Active biomass +
                    B:F + Bacteria diversity + Fungi diversity +
                    Cata + FG evenness +
                    fert + Tree.species.richness

## Genetic potential
Cata ~ fert + Tree.species.richness

FG evenness ~ fert + Tree.species.richness

## Community structure
B:F ~ fert + Tree.species.richness

Bacteria diversity ~ fert + Tree.species.richness

Fungi diversity ~ fert + Tree.species.richness

## Microbial biomass
Biomass ~ fert + Tree.species.richness

Active biomass ~ fert + Tree.species.richness

# Correlations
## Microbial community

Biomass ~~ Active biomass
Biomass ~~ B:F
Biomass ~~ Bacteria diversity
Biomass ~~ Fungi diversity
Biomass ~~ Cata
Biomass ~~ FG evenness

Active biomass ~~ B:F
Active biomass ~~ Bacteria diversity
Active biomass ~~ Fungi diversity
Active biomass ~~ Cata
Active biomass ~~ FG evenness
```

```
B:F ~~ Bacteria diversity
B:F ~~ Fungi diversity
B:F ~~ Cata
B:F ~~ FG evenness

Bacteria diversity ~~ Fungi diversity
Bacteria diversity ~~ Cata
Bacteria diversity ~~ FG evenness

Fungi diversity ~~ Cata
Fungi diversity ~~ FG evenness

Cata ~~ FG evenness

# Physiological potential
SIR range ~~ SIR efficiency

# Soil chemical properties & tree species richness
Tree.species.richness ~~ fert
'
```

5.1 Fit quality

.

Fit index	Value
cfi	0.82251
rmsea	0.11403
srmr	0.07261

5.2 Complete R summary

Response	Relation	Explanatory	Estimate	SE	p value
Basal respiration	~	Total biomass	-0.078	0.075	0.3
Basal respiration	~	Active biomass	0.587	0.060	< 0.001***
Basal respiration	~	B:F	-0.110	0.060	0.065
Basal respiration	~	Bacteria diversity	0.024	0.057	0.674
Basal respiration	~	Fungi diversity	-0.132	0.058	0.022 *
Basal respiration	~	Cata	-0.115	0.067	0.086
Basal respiration	~	FG evenness	0.020	0.068	0.765
Basal respiration	~	SIR eff.	0.156	0.063	0.014 *
Basal respiration	~	SIR range	0.224	0.057	< 0.001***
Basal respiration	~	fert	0.057	0.067	0.394
Basal respiration	~	TreeD.	0.068	0.058	0.245
SIR eff.	~	Total biomass	0.076	0.098	0.437
SIR eff.	~	Active biomass	0.239	0.080	0.003 **
SIR eff.	~	B:F	-0.096	0.077	0.214
SIR eff.	~	Bacteria diversity	0.052	0.073	0.479

(continued)

Response	Relation	Explanatory	Estimate	SE	p value
SIR eff.	~	Fungi diversity	-0.141	0.073	0.055
SIR eff.	~	Cata	0.027	0.087	0.757
SIR eff.	~	FG evenness	-0.171	0.087	0.05
SIR eff.	~	fert	0.162	0.088	0.065
SIR eff.	~	TreeD.	0.189	0.073	0.01 *
SIR range	~	Total biomass	0.212	0.107	0.049 *
SIR range	~	Active biomass	0.165	0.090	0.065
SIR range	~	B:F	-0.044	0.086	0.604
SIR range	~	Bacteria diversity	0.161	0.080	0.045 *
SIR range	~	Fungi diversity	-0.093	0.082	0.254
SIR range	~	Cata	-0.031	0.097	0.746
SIR range	~	FG evenness	-0.110	0.097	0.254
SIR range	~	fert	-0.153	0.097	0.112
SIR range	~	TreeD.	-0.134	0.082	0.1
Cata	~	fert	0.008	0.080	0.921
Cata	~	TreeD.	0.080	0.082	0.332
FG evenness	~	fert	-0.030	0.080	0.709
FG evenness	~	TreeD.	0.060	0.083	0.471
Fungi diversity	~	fert	0.062	0.080	0.443
Fungi diversity	~	TreeD.	0.007	0.083	0.929
Bacteria diversity	~	fert	0.102	0.078	0.193
Bacteria diversity	~	TreeD.	0.196	0.079	0.013 *
B:F	~	fert	-0.083	0.080	0.297
B:F	~	TreeD.	-0.112	0.081	0.168
Active biomass	~	fert	0.346	0.074	< 0.001***
Active biomass	~	TreeD.	0.056	0.077	0.469
Total biomass	~	fert	0.569	0.064	< 0.001***
Total biomass	~	TreeD.	0.164	0.065	0.012 *
Active biomass	~~	Total biomass	0.321	0.075	< 0.001***
B:F	~~	Total biomass	-0.274	0.075	< 0.001***
Bacteria diversity	~~	Total biomass	-0.159	0.080	0.047 *
Fungi diversity	~~	Total biomass	-0.012	0.081	0.885
Cata	~~	Total biomass	0.138	0.080	0.083
FG evenness	~~	Total biomass	0.134	0.080	0.094
B:F	~~	Active biomass	-0.137	0.080	0.089
Bacteria diversity	~~	Active biomass	-0.122	0.081	0.132
Fungi diversity	~~	Active biomass	0.191	0.079	0.016 *
Cata	~~	Active biomass	0.008	0.082	0.918
FG evenness	~~	Active biomass	0.071	0.081	0.382
Bacteria diversity	~~	B:F	0.096	0.081	0.236
Fungi diversity	~~	B:F	0.189	0.079	0.017 *
Cata	~~	B:F	-0.124	0.081	0.125
FG evenness	~~	B:F	0.076	0.082	0.354
Fungi diversity	~~	Bacteria diversity	-0.024	0.082	0.774
Cata	~~	Bacteria diversity	-0.103	0.081	0.203
FG evenness	~~	Bacteria diversity	-0.105	0.081	0.198
Cata	~~	Fungi diversity	0.099	0.081	0.225

(continued)

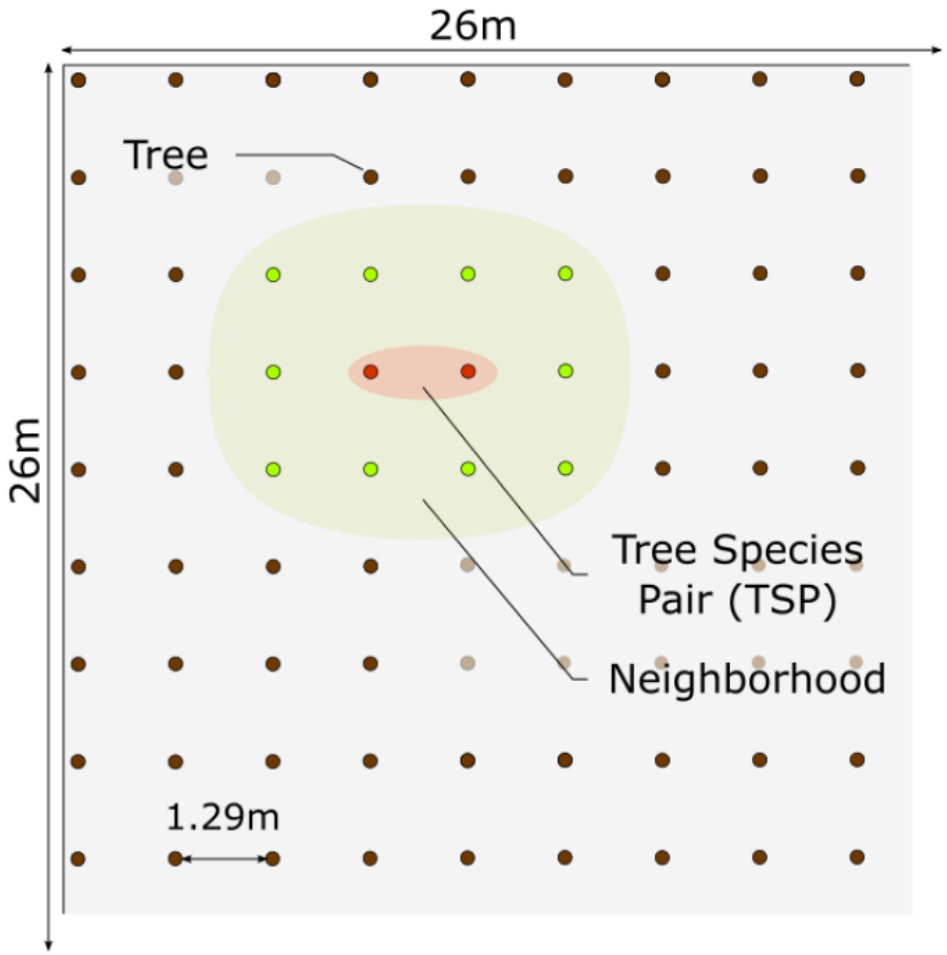
Response	Relation	Explanatory	Estimate	SE	p value
FG evenness	~~	Fungi diversity	0.151	0.080	0.06
Cata	~~	FG evenness	0.568	0.056	< 0.001***
SIR eff.	~~	SIR range	-0.148	0.080	0.065
fert	~~	TreeD.	0.129	0.079	0.103
TOC	~~	TOC	-0.054	0.122	0.656
C:P	~~	C:P	0.655	0.074	< 0.001***
C:N	~~	C:N	1.000	0.002	< 0.001***
pH	~~	pH	0.939	0.038	< 0.001***
RH	~~	RH	0.987	0.018	< 0.001***
Basal respiration	~~	Basal respiration	0.422	0.053	< 0.001***
SIR eff.	~~	SIR eff.	0.722	0.062	< 0.001***
SIR range	~~	SIR range	0.887	0.049	< 0.001***
Cata	~~	Cata	0.993	0.013	< 0.001***
FG evenness	~~	FG evenness	0.996	0.010	< 0.001***
Fungi diversity	~~	Fungi diversity	0.996	0.010	< 0.001***
Bacteria diversity	~~	Bacteria diversity	0.946	0.036	< 0.001***
B:F	~~	B:F	0.978	0.024	< 0.001***
Active biomass	~~	Active biomass	0.872	0.052	< 0.001***
Total biomass	~~	Total biomass	0.625	0.073	< 0.001***
fert	=~	TOC	1.027	0.059	< 0.001***
fert	=~	C:P	0.587	0.063	< 0.001***
fert	=~	C:N	0.009	0.080	0.905
fert	=~	pH	-0.246	0.077	0.001 **
fert	=~	RH	0.112	0.079	0.156

Supplementary material: Chapter III - Abiotic and biotic drivers of scale-dependent tree trait effects on soil microbial biomass and soil carbon concentration

Supplementary material III – S1: design

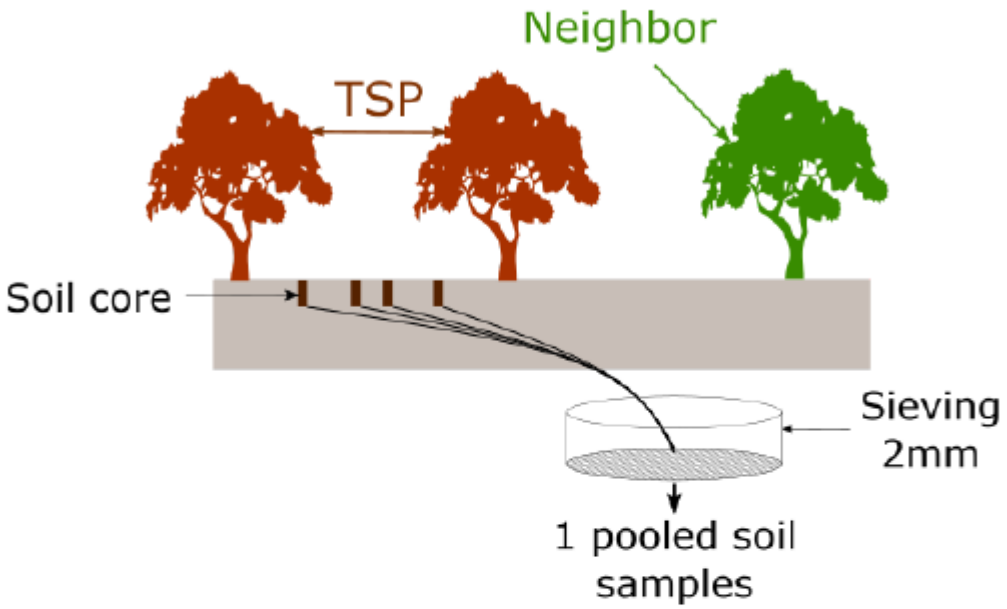
A. Plot design

Plantation design in BEF China plot with example of tree species pair (i.e. TSP in red) and its neighborhood (in green).



B. Tree Species pair sampling design

Soil sampling design between the tree species pairs, where four soil cores were taken and pooled together.



C. Tree species selection

List of tree species building the tree species pairs (TSPs) in the different plots of Site A (BEF China experiment)

Species	Leaf persistence
Castanea henryi	deciduous
Castanopsis sclerophylla	evergreen
Choerospondias axillaris	deciduous
Cyclobalanopsis glauca	evergreen
Koelreuteria bipinnata	deciduous
Liquidambar formosana	deciduous
Lithocarpus glaber	evergreen
Nyssa sinensis	deciduous
Quercus fabri	deciduous
Quercus serrata	deciduous
Sapindus mukorossi	deciduous
Sapium sebiferum	deciduous

D. Tree Species Pairs (TSPs) selection

Tree species pairs description and attributes (paragraphs were added for readability)

TSP code	Site	Plot	Diversity level	Species 1	Species 2
26-E24	A	E24	1	*Liquidambar formosana*	*Liquidambar formosana*
33-E31	A	E31	1	*Quercus fabri*	*Quercus fabri*
34-E31	A	E31	1	*Quercus fabri*	*Quercus fabri*
27-E33	A	E33	1	*Lithocarpus glaber*	*Lithocarpus glaber*
28-E33	A	E33	1	*Lithocarpus glaber*	*Lithocarpus glaber*
1-E34	A	E34	1	*Castanea henryi*	*Castanea henryi*
2-E34	A	E34	1	*Castanea henryi*	*Castanea henryi*
37-F21	A	F21	1	*Quercus serrata*	*Quercus serrata*
38-F21	A	F21	1	*Quercus serrata*	*Quercus serrata*
10-G17	A	G17	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
29-G22	A	G22	1	*Lithocarpus glaber*	*Lithocarpus glaber*
22-G24	A	G24	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
23-G24	A	G24	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
36-G33	A	G33	1	*Quercus serrata*	*Quercus serrata*
30-H25	A	H25	1	*Nyssa sinensis*	*Nyssa sinensis*
3-I12	A	I12	1	*Castanea henryi*	*Castanea henryi*
24-I28	A	I28	1	*Liquidambar formosana*	*Liquidambar formosana*
25-I28	A	I28	1	*Liquidambar formosana*	*Liquidambar formosana*
14-K9	A	K9	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
8-L11	A	L11	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
9-L11	A	L11	1	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
13-L23	A	L23	1	*Choerospondias axillaris*	*Choerospondias axillaris*
42-N11	A	N11	1	*Sapindus mukorossi*	*Sapindus mukorossi*
43-N11	A	N11	1	*Sapindus mukorossi*	*Sapindus mukorossi*
46-N13	A	N13	1	*Sapium sebiferum*	*Sapium sebiferum*
47-N13	A	N13	1	*Sapium sebiferum*	*Sapium sebiferum*
11-O27	A	O27	1	*Choerospondias axillaris*	*Choerospondias axillaris*
12-O27	A	O27	1	*Choerospondias axillaris*	*Choerospondias axillaris*
21-Q13	A	Q13	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
r-21-Q13	A	Q13	1	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
35-Q16	A	Q16	1	*Quercus fabri*	*Quercus fabri*
15-R14	A	R14	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
16-R14	A	R14	1	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
44-R17	A	R17	1	*Sapindus mukorossi*	*Sapindus mukorossi*
45-W13	A	W13	1	*Sapium sebiferum*	*Sapium sebiferum*
31-W14	A	W14	1	*Nyssa sinensis*	*Nyssa sinensis*
32-W14	A	W14	1	*Nyssa sinensis*	*Nyssa sinensis*
51-C32	A	C32	2	*Castanea henryi*	*Castanea henryi*
52-C32	A	C32	2	*Castanea henryi*	*Nyssa sinensis*
96-C32	A	C32	2	*Castanea henryi*	*Nyssa sinensis*
95-C32	A	C32	2	*Nyssa sinensis*	*Nyssa sinensis*
97-C32	A	C32	2	*Nyssa sinensis*	*Nyssa sinensis*
53-F22	A	F22	2	*Castanea henryi*	*Castanea henryi*
54-F22	A	F22	2	*Castanea henryi*	*Castanea henryi*
55-F22	A	F22	2	*Castanea henryi*	*Nyssa sinensis*

(continued)

TSP code	Site	Plot	Diversity level	Species 1	Species 2
98-F22	A	F22	2	*Nyssa sinensis*	*Nyssa sinensis*
87-H31	A	H31	2	*Liquidambar formosana*	*Liquidambar formosana*
86-H31	A	H31	2	*Liquidambar formosana*	*Sapindus mukorossi*
113-H31	A	H31	2	*Sapindus mukorossi*	*Liquidambar formosana*
112-H31	A	H31	2	*Sapindus mukorossi*	*Sapindus mukorossi*
114-H31	A	H31	2	*Sapindus mukorossi*	*Sapindus mukorossi*
67-I27	A	I27	2	*Choerospondias axillaris*	*Choerospondias axillaris*
68-I27	A	I27	2	*Choerospondias axillaris*	*Choerospondias axillaris*
116-I27	A	I27	2	*Sapium sebiferum*	*Choerospondias axillaris*
117-I27	A	I27	2	*Sapium sebiferum*	*Choerospondias axillaris*
118-I27	A	I27	2	*Sapium sebiferum*	*Sapium sebiferum*
81-J21	A	J21	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
82-J21	A	J21	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
83-J21	A	J21	2	*Koelreuteria bipinnata*	*Lithocarpus glaber*
91-J21	A	J21	2	*Lithocarpus glaber*	*Koelreuteria bipinnata*
r-91-J21	A	J21	2	*Lithocarpus glaber*	*Koelreuteria bipinnata*
92-J21	A	J21	2	*Lithocarpus glaber*	*Lithocarpus glaber*
72-K3	A	K3	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
73-K3	A	K3	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
75-K3	A	K3	2	*Cyclobalanopsis glauca*	*Quercus fabri*
99-K3	A	K3	2	*Quercus fabri*	*Quercus fabri*
64-O6	A	O6	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
65-O6	A	O6	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
66-O6	A	O6	2	*Castanopsis sclerophylla*	*Quercus serrata*
105-O6	A	O6	2	*Quercus serrata*	*Quercus serrata*
63-P26	A	P26	2	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
62-P26	A	P26	2	*Castanopsis sclerophylla*	*Quercus serrata*
w-104-P26	A	P26	2	*Quercus serrata*	*Castanopsis sclerophylla*
102-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
103-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
104-P26	A	P26	2	*Quercus serrata*	*Quercus serrata*
74-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
76-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Quercus fabri*
77-Q21	A	Q21	2	*Cyclobalanopsis glauca*	*Quercus fabri*
100-Q21	A	Q21	2	*Quercus fabri*	*Quercus fabri*
101-Q21	A	Q21	2	*Quercus fabri*	*Quercus fabri*
84-Q7	A	Q7	2	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
85-Q7	A	Q7	2	*Koelreuteria bipinnata*	*Lithocarpus glaber*
93-Q7	A	Q7	2	*Lithocarpus glaber*	*Lithocarpus glaber*
94-Q7	A	Q7	2	*Lithocarpus glaber*	*Lithocarpus glaber*
69-S18	A	S18	2	*Choerospondias axillaris*	*Choerospondias axillaris*
70-S18	A	S18	2	*Choerospondias axillaris*	*Sapium sebiferum*
71-S18	A	S18	2	*Choerospondias axillaris*	*Sapium sebiferum*
119-S18	A	S18	2	*Sapium sebiferum*	*Sapium sebiferum*
r-120-S18	A	S18	2	*Sapium sebiferum*	*Sapium sebiferum*
88-T17	A	T17	2	*Liquidambar formosana*	*Liquidambar formosana*
89-T17	A	T17	2	*Liquidambar formosana*	*Liquidambar formosana*

(continued)

TSP code	Site	Plot	Diversity level	Species 1	Species 2
90-T17	A	T17	2	*Liquidambar formosana*	*Sapindus mukorossi*
115-T17	A	T17	2	*Sapindus mukorossi*	*Sapindus mukorossi*
130-F27	A	F27	4	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
131-F27	A	F27	4	*Choerospondias axillaris*	*Castanopsis sclerophylla*
153-F27	A	F27	4	*Quercus serrata*	*Choerospondias axillaris*
161-F27	A	F27	4	*Sapium sebiferum*	*Choerospondias axillaris*
162-F27	A	F27	4	*Sapium sebiferum*	*Sapium sebiferum*
139-F28	A	F28	4	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
132-N20	A	N20	4	*Choerospondias axillaris*	*Choerospondias axillaris*
154-N20	A	N20	4	*Quercus serrata*	*Castanopsis sclerophylla*
155-N20	A	N20	4	*Quercus serrata*	*Quercus serrata*
156-N20	A	N20	4	*Quercus serrata*	*Sapium sebiferum*
163-N20	A	N20	4	*Sapium sebiferum*	*Castanopsis sclerophylla*
133-N8	A	N8	4	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
149-N8	A	N8	4	*Quercus fabri*	*Cyclobalanopsis glauca*
125-P19	A	P19	4	*Castanea henryi*	*Castanea henryi*
126-P19	A	P19	4	*Castanea henryi*	*Nyssa sinensis*
143-P19	A	P19	4	*Liquidambar formosana*	*Sapindus mukorossi*
148-P19	A	P19	4	*Nyssa sinensis*	*Sapindus mukorossi*
160-P19	A	P19	4	*Sapindus mukorossi*	*Sapindus mukorossi*
124-P29	A	P29	4	*Castanea henryi*	*Liquidambar formosana*
141-P29	A	P29	4	*Liquidambar formosana*	*Liquidambar formosana*
142-P29	A	P29	4	*Liquidambar formosana*	*Nyssa sinensis*
147-P29	A	P29	4	*Nyssa sinensis*	*Castanea henryi*
159-P29	A	P29	4	*Sapindus mukorossi*	*Castanea henryi*
150-U15	A	U15	4	*Quercus fabri*	*Quercus fabri*
140-V12/W12	A	V12/**W**12	4	*Koelreuteria bipinnata*	*Lithocarpus glaber*
146-W12/X12	A	**W**12/X12	4	*Lithocarpus glaber*	*Lithocarpus glaber*
176-P27	A	P27	8	*Cyclobalanopsis glauca*	*Quercus fabri*
181-P27	A	P27	8	*Koelreuteria bipinnata*	*Lithocarpus glaber*
187-P27	A	P27	8	*Lithocarpus glaber*	*Lithocarpus glaber*
166-R16	A	R16	8	*Castanea henryi*	*Liquidambar formosana*
171-R16	A	R16	8	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
175-R16	A	R16	8	*Choerospondias axillaris*	*Sapium sebiferum*
190-R16	A	R16	8	*Nyssa sinensis*	*Castanea henryi*
193-R16	A	R16	8	*Quercus serrata*	*Castanopsis sclerophylla*
194-R16	A	R16	8	*Quercus serrata*	*Quercus serrata*
198-R16	A	R16	8	*Sapindus mukorossi*	*Sapindus mukorossi*
199-R16	A	R16	8	*Sapindus mukorossi*	*Sapindus mukorossi*
200-R16	A	R16	8	*Sapium sebiferum*	*Quercus serrata*
201-R16	A	R16	8	*Sapium sebiferum*	*Sapium sebiferum*
165-S10	A	S10	8	*Castanea henryi*	*Castanea henryi*
170-S10	A	S10	8	*Castanopsis sclerophylla*	*Sapium sebiferum*
173-S10	A	S10	8	*Choerospondias axillaris*	*Castanopsis sclerophylla*
174-S10	A	S10	8	*Choerospondias axillaris*	*Choerospondias axillaris*
172-S10	A	S10	8	*Choerospondias axillaris*	*Quercus serrata*
186-S10	A	S10	8	*Liquidambar formosana*	*Liquidambar formosana*
185-S10	A	S10	8	*Liquidambar formosana*	*Nyssa sinensis*

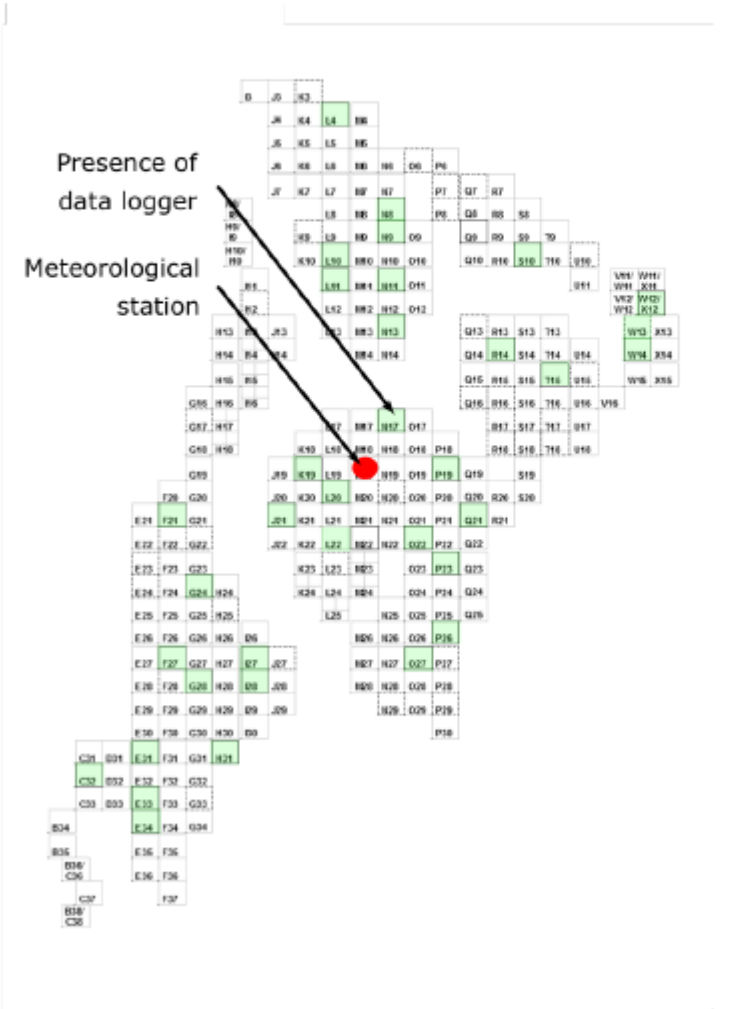
(continued)

TSP code	Site	Plot	Diversity level	Species 1	Species 2
188-S10	A	S10	8	*Nyssa sinensis*	*Nyssa sinensis*
189-S10	A	S10	8	*Nyssa sinensis*	*Sapindus mukorossi*
197-S10	A	S10	8	*Sapindus mukorossi*	*Castanea henryi*
178-S14	A	S14	8	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
183-S15	A	S15	8	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
r-216-S15	A	S15	8	*Koelreuteria bipinnata*	*Lithocarpus glaber*
184-S15	A	S15	8	*Koelreuteria bipinnata*	*Quercus fabri*
191-T15	A	T15	8	*Quercus fabri*	*Quercus fabri*
220-L21	A	L21	16	*Liquidambar formosana*	*Choerospondias axillaris*
216-L21	A	L21	16	*Sapindus mukorossi*	*Lithocarpus glaber*
203-L22	A	L22	16	*Castanea henryi*	*Nyssa sinensis*
204-L22	A	L22	16	*Castanea henryi*	*Sapindus mukorossi*
209-L22	A	L22	16	*Choerospondias axillaris*	*Castanopsis sclerophylla*
210-L22	A	L22	16	*Choerospondias axillaris*	*Choerospondias axillaris*
r-213-L22	A	L22	16	*Cyclobalanopsis glauca*	*Quercus fabri*
217-L22	A	L22	16	*Liquidambar formosana*	*Castanea henryi*
219-L22	A	L22	16	*Liquidambar formosana*	*Liquidambar formosana*
218-L22	A	L22	16	*Liquidambar formosana*	*Nyssa sinensis*
221-L22	A	L22	16	*Lithocarpus glaber*	*Lithocarpus glaber*
222-L22	A	L22	16	*Quercus fabri*	*Quercus fabri*
230-L22	A	L22	16	*Sapium sebiferum*	*Castanopsis sclerophylla*
r-220-M21	A	M21	16	*Liquidambar formosana*	*Sapindus mukorossi*
226-M21	A	M21	16	*Quercus serrata*	*Sapium sebiferum*
208-M22	A	M22	16	*Castanopsis sclerophylla*	*Castanopsis sclerophylla*
211-M22	A	M22	16	*Choerospondias axillaris*	*Sapium sebiferum*
213-U10	A	U10	16	*Cyclobalanopsis glauca*	*Quercus fabri*
r-213-U10	A	U10	16	*Cyclobalanopsis glauca*	*Quercus fabri*
225-U10	A	U10	16	*Quercus serrata*	*Quercus serrata*
229-U10	A	U10	16	*Sapindus mukorossi*	*Sapindus mukorossi*
231-U10	A	U10	16	*Sapium sebiferum*	*Sapium sebiferum*
232-N9	A	N9	24	*Castanea henryi*	*Castanea henryi*
236-N9	A	N9	24	*Cyclobalanopsis glauca*	*Cyclobalanopsis glauca*
238-N9	A	N9	24	*Koelreuteria bipinnata*	*Koelreuteria bipinnata*
241-N9	A	N9	24	*Sapindus mukorossi*	*Nyssa sinensis*
234-R18	A	R18	24	*Castanopsis sclerophylla*	*Quercus serrata*
235-R18	A	R18	24	*Choerospondias axillaris*	*Quercus serrata*
239-R18	A	R18	24	*Nyssa sinensis*	*Nyssa sinensis*

Supplementary material III – S2: temperature modeling

A. Temperature and humidity data logger distribution

Spatial distribution of temperature and humidity data logger and position of the meteorological station in BEF China Site A



B. Variables

Description of the variables used to predict air temprature at the plot level.

Variables	Name	Usage	Units
Logger daily minimum temperature	T.min	Response	Celsius
Logger daily average temperature	T.mean	Response	Celsius
Logger daily maximum temperature	T.max	Response	Celsius
Station daily minimum temperature	T.station.min	Explanatory	Celsius
Station daily minimum temperature	T.station.mean	Explanatory	Celsius
Station daily minimum temperature	T.station.max	Explanatory	Celsius
Daily solar radiation	Radiation	Explanatory	W/qm
Rainfall	Rain	Explanatory	mm
Latitudinal position	X	Explanatory	No unit
Longitudinal position	Y	Explanatory	No unit
Gaussian radial basis vectors	B1 - B12	Explanatory	No unit
Date	date	Explanatory	dd.mm.yyyy hh:mm
Altitude	Alt	Explanatory	m
Eastness	East	Explanatory	Celsius
Northness	North	Explanatory	Celsius
Slope	Slope	Explanatory	Celsius
Plot profile curvature	Curve.Pr	Explanatory	%
Plot plan curvature	Curve.Pl	Explanatory	%
Annual solar radiation	Solar.radiation	Explanatory	W/qm
Tree Species Richness	Sp.Rich	Explanatory	No unit
Forest vertical stratification	ENL	Explanatory	No unit

C. Model structure

Structure of the model used to predict air temperature.

$$\begin{aligned} min.T \sim (X + Y + date)^2 \\ +poly(T.station.min, 3) + poly(T.station.mean, 3) + poly(T.station.max, 3) \\ +Solar * Radiation + Rainfall + Rainfall.week \\ +ENL + Spe.Rich \\ +Alt + East + North + Slope + Curve.Pr + Curve.Pl \\ +B1 + B2 + B3 + B4 + B5 + B6 + B7 + B8 + B9 + B10 + B11 + B12 \end{aligned} \quad (1)$$

$$\begin{aligned} mean.T \sim (X + Y + date)^2 \\ +poly(T.station.min, 3) + poly(T.station.mean, 3) + poly(T.station.max, 3) \\ +Solar * Radiation + Rainfall + Rainfall.week \\ +ENL + Spe.Rich \\ +Alt + East + North + Slope + Curve.Pr + Curve.Pl \\ +B1 + B2 + B3 + B4 + B5 + B6 + B7 + B8 + B9 + B10 + B11 + B12 \end{aligned} \quad (2)$$

$$\begin{aligned} max.T \sim (X + Y + date)^2 \\ + poly(T.station.min, 3) + poly(T.station.mean, 3) + poly(T.station.max, 3) \\ + Solar * Radiation + Rainfall + Rainfall.week \\ + ENL + Spe.Rich \\ + Alt + East + North + Slope + Curve.Pr + Curve.Pl \\ + B1 + B2 + B3 + B4 + B5 + B6 + B7 + B8 + B9 + B10 + B11 + B12 \end{aligned} \quad (3)$$

D. Model fit

Model fit output of each response variable.

Minimum temperature

```
Call:
lm(formula = min.T ~ X_DD + poly(mean.T.station, degree = 3) +
    poly(min.T.station, degree = 3) + poly(max.T.station, degree = 3) +
    ENL + East + Slope + Curve.Pr + Rain.day + Rain.week + B1 +
    B4 + B5 + B7 + B8 + B9 + B10 + B11 + B12, data = df.comp2.mod)

Residuals:
     Min       1Q   Median       3Q      Max
-3.07162 -0.75806  0.04286  0.75880  2.45860

Coefficients:
                                  Estimate Std. Error t value Pr(>|t|)
(Intercept)                      1.283e+05  3.684e+04   3.481 0.000513 ***
X_DD                            -1.088e+03  3.124e+02  -3.481 0.000514 ***
poly(mean.T.station, degree = 3)1 -4.309e+02  3.512e+01 -12.269  < 2e-16 ***
poly(mean.T.station, degree = 3)2  1.578e+02  1.562e+01  10.108  < 2e-16 ***
poly(mean.T.station, degree = 3)3  1.744e+00  5.514e+00   0.316 0.751776
poly(min.T.station, degree = 3)1   3.895e+02  2.158e+01  18.048  < 2e-16 ***
poly(min.T.station, degree = 3)2  -1.153e+02  9.136e+00 -12.624  < 2e-16 ***
poly(min.T.station, degree = 3)3   2.222e+00  3.991e+00   0.557 0.577733
poly(max.T.station, degree = 3)1   1.561e+02  1.494e+01  10.452  < 2e-16 ***
poly(max.T.station, degree = 3)2  -7.778e+01  7.647e+00 -10.172  < 2e-16 ***
poly(max.T.station, degree = 3)3   8.440e+00  3.512e+00   2.403 0.016386 *
ENL                               9.234e-03  1.165e-03   7.926 4.36e-15 ***
East                             -1.711e-01  8.767e-02  -1.951 0.051208 .
Slope                            -2.317e-02  8.658e-03  -2.677 0.007515 **
Curve.Pr                         -3.246e-03  9.069e-04  -3.579 0.000356 ***
Rain.day                         -1.006e-01  8.358e-03 -12.033  < 2e-16 ***
Rain.week                        -6.798e-02  3.920e-03 -17.341  < 2e-16 ***
B1                                3.001e+00  1.706e+00   1.759 0.078740 .
B4                               -4.969e+00  1.635e+00  -3.039 0.002416 **
B5                                7.599e+00  1.578e+00   4.814 1.63e-06 ***
B7                                1.194e+01  3.418e+00   3.492 0.000493 ***
B8                               -1.210e+01  2.034e+00  -5.948 3.38e-09 ***
B9                                1.294e+01  2.045e+00   6.328 3.26e-10 ***
```

```
B10                              -1.030e+01  4.591e+00  -2.245 0.024941 *
B11                               1.631e+01  3.432e+00   4.751 2.21e-06 ***
B12                              -9.278e+00  2.230e+00  -4.160 3.36e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.9883 on 1511 degrees of freedom
  (232 observations deleted due to missingness)
Multiple R-squared:  0.8833,    Adjusted R-squared:  0.8813
F-statistic: 457.3 on 25 and 1511 DF,  p-value: < 2.2e-16
```

Average temperature

```
Call:
lm(formula = mean.T ~ X_DD + date + poly(mean.T.station, degree = 3) +
    poly(min.T.station, degree = 3) + poly(max.T.station, degree = 3) +
    Solar.radiation + Radiation + ENL + Sp.Rich + Alt + North +
    Slope + Curve.Pr + Curve.Pl + Rain.day + Rain.week + B1 +
    B2 + B3 + B4 + B5 + B6 + B7 + B8 + B9 + B10 + B11 + B12,
    data = df.comp2.mod)

Residuals:
    Min      1Q  Median      3Q     Max
-3.2275 -0.6104 -0.0125  0.5653  3.2355

Coefficients:
                                  Estimate Std. Error t value Pr(>|t|)
(Intercept)                       1.973e+05  5.839e+04   3.379 0.000747 ***
X_DD                             -1.677e+03  4.952e+02  -3.386 0.000728 ***
date                              2.820e-02  2.958e-03   9.533  < 2e-16 ***
poly(mean.T.station, degree = 3)1 -4.432e+01  3.269e+01  -1.356 0.175356
poly(mean.T.station, degree = 3)2  6.870e+01  1.534e+01   4.478 8.10e-06 ***
poly(mean.T.station, degree = 3)3 -2.283e+01  4.994e+00  -4.572 5.24e-06 ***
poly(min.T.station, degree = 3)1   8.654e+01  1.984e+01   4.363 1.37e-05 ***
poly(min.T.station, degree = 3)2  -5.637e+01  9.049e+00  -6.229 6.07e-10 ***
poly(min.T.station, degree = 3)3   1.998e+01  3.690e+00   5.415 7.11e-08 ***
poly(max.T.station, degree = 3)1   7.204e+01  1.413e+01   5.098 3.86e-07 ***
poly(max.T.station, degree = 3)2  -4.363e+01  7.576e+00  -5.759 1.02e-08 ***
poly(max.T.station, degree = 3)3   1.352e+01  3.129e+00   4.322 1.65e-05 ***
Solar.radiation                  -1.681e-05  2.673e-06  -6.288 4.20e-10 ***
Radiation                         5.556e-04  2.815e-05  19.736  < 2e-16 ***
ENL                              -2.099e-02  1.480e-03 -14.181  < 2e-16 ***
Sp.Rich                          -2.372e-02  7.208e-03  -3.291 0.001023 **
Alt                               3.373e-02  6.170e-03   5.466 5.39e-08 ***
North                            -4.303e+00  6.038e-01  -7.127 1.59e-12 ***
Slope                            -1.013e-01  2.008e-02  -5.046 5.06e-07 ***
Curve.Pr                          9.134e-03  1.350e-03   6.764 1.91e-11 ***
Curve.Pl                          6.286e-03  1.421e-03   4.425 1.03e-05 ***
Rain.day                         -1.142e-01  7.552e-03 -15.117  < 2e-16 ***
Rain.week                        -5.896e-02  3.699e-03 -15.940  < 2e-16 ***
B1                               -7.099e+01  4.995e+00 -14.212  < 2e-16 ***
B2                                2.340e+01  2.285e+00  10.240  < 2e-16 ***
```

```
B3                                -3.943e+01  4.178e+00  -9.438  < 2e-16 ***
B4                                 4.069e+01  2.434e+00  16.716  < 2e-16 ***
B5                                -5.834e+01  3.737e+00 -15.612  < 2e-16 ***
B6                                 1.583e+01  2.988e+00   5.297 1.36e-07 ***
B7                                -9.252e+01  6.319e+00 -14.642  < 2e-16 ***
B8                                 5.345e+01  3.705e+00  14.427  < 2e-16 ***
B9                                -6.078e+01  4.586e+00 -13.253  < 2e-16 ***
B10                                2.737e+01  5.692e+00   4.809 1.67e-06 ***
B11                               -6.597e+01  6.047e+00 -10.909  < 2e-16 ***
B12                                1.885e+01  3.752e+00   5.024 5.67e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.8796 on 1502 degrees of freedom
  (232 observations deleted due to missingness)
Multiple R-squared:  0.9143,    Adjusted R-squared:  0.9124
F-statistic: 471.5 on 34 and 1502 DF,  p-value: < 2.2e-16
```

Maximum temperature

```
Call:
lm(formula = max.T ~ Y_DD + date + poly(mean.T.station, degree = 3) +
    poly(min.T.station, degree = 3) + poly(max.T.station, degree = 3) +
    Solar.radiation + Radiation + ENL + Sp.Rich + Alt + North +
    Curve.Pr + Curve.Pl + Rain.day + Rain.week + B1 + B2 + B3 +
    B4 + B5 + B6 + B7 + B8 + B9 + B10 + B11 + B12, data = df.comp2.mod)

Residuals:
    Min      1Q  Median      3Q     Max
-7.2717 -1.1448 -0.0354  1.1209  6.3630

Coefficients:
                                    Estimate Std. Error t value Pr(>|t|)
(Intercept)                       -1.031e+05  5.531e+04  -1.864  0.06256 .
Y_DD                               3.488e+03  1.899e+03   1.837  0.06645 .
date                               9.851e-02  6.316e-03  15.598  < 2e-16 ***
poly(mean.T.station, degree = 3)1 -1.154e+02  6.980e+01  -1.654  0.09833 .
poly(mean.T.station, degree = 3)2  6.833e+00  3.276e+01   0.209  0.83479
poly(mean.T.station, degree = 3)3 -7.794e+01  1.066e+01  -7.309 4.35e-13 ***
poly(min.T.station, degree = 3)1   5.100e+01  4.235e+01   1.204  0.22872
poly(min.T.station, degree = 3)2   6.042e+00  1.932e+01   0.313  0.75452
poly(min.T.station, degree = 3)3   6.303e+01  7.879e+00   8.000 2.46e-15 ***
poly(max.T.station, degree = 3)1   2.174e+02  3.017e+01   7.206 9.08e-13 ***
poly(max.T.station, degree = 3)2  -3.558e+01  1.618e+01  -2.200  0.02797 *
poly(max.T.station, degree = 3)3   3.403e+01  6.681e+00   5.094 3.96e-07 ***
Solar.radiation                   -1.989e-05  3.090e-06  -6.437 1.63e-10 ***
Radiation                          1.505e-03  6.011e-05  25.035  < 2e-16 ***
ENL                               -1.180e-01  2.766e-03 -42.656  < 2e-16 ***
Sp.Rich                           -5.137e-02  1.634e-02  -3.143  0.00170 **
Alt                                3.165e-02  1.173e-02   2.699  0.00704 **
North                             -6.390e+00  7.255e-01  -8.808  < 2e-16 ***
Curve.Pr                           4.041e-02  2.958e-03  13.659  < 2e-16 ***
```

```
Curve.P1                          1.757e-02  2.924e-03   6.010 2.32e-09 ***
Rain.day                         -1.492e-01  1.613e-02  -9.254  < 2e-16 ***
Rain.week                        -7.077e-02  7.898e-03  -8.960  < 2e-16 ***
B1                               -2.250e+02  1.078e+01 -20.865  < 2e-16 ***
B2                                6.613e+01  3.865e+00  17.113  < 2e-16 ***
B3                               -1.278e+02  9.322e+00 -13.705  < 2e-16 ***
B4                                1.354e+02  7.032e+00  19.251  < 2e-16 ***
B5                               -1.960e+02  7.642e+00 -25.642  < 2e-16 ***
B6                                4.253e+01  6.425e+00   6.619 5.02e-11 ***
B7                               -3.138e+02  1.275e+01 -24.600  < 2e-16 ***
B8                                1.852e+02  7.700e+00  24.047  < 2e-16 ***
B9                               -2.249e+02  9.658e+00 -23.284  < 2e-16 ***
B10                               6.914e+01  1.631e+01   4.239 2.38e-05 ***
B11                              -2.324e+02  1.141e+01 -20.358  < 2e-16 ***
B12                               5.648e+01  1.007e+01   5.611 2.39e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.878 on 1503 degrees of freedom
  (232 observations deleted due to missingness)
Multiple R-squared:  0.8818,    Adjusted R-squared:  0.8792
F-statistic: 339.7 on 33 and 1503 DF,  p-value: < 2.2e-16
```

Supplementary material III – S3: PLFA biomarkers

PLFA biomarkers used to identify soil microbes' functional groups

Fatty acid	Lipid fraction	Predominant origin	Literature
i15:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
a15:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
i16:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
i17:0	PLFA	Gram-positive bacteria	Zelles (1997, 1999)
16:1n7	PLFA	Bacteria widespread	Guckert et al. (1991), Zelles (1999)
16:1n-5	PLFA	General bacteria	Nichols et al. (1986), Zelles (1997)
cy17:0	PLFA	Gram-negative bacteria	Zelles (1997, 1999)
18:1n9	PLFA	Fungi (saprophytic, EM)	Bååth (2003), Vestal and White (1989),Zelles (1999), Harwood and Russell (1984), Ruess et al. (2007)
cy19:0	PLFA	Gram-negative bacteria	Zelles (1997, 1999)
18:2n6c	PLFA	Fungi (saprophytic, EM)	Frostegård and Bååth (1996), Zelles (1999)
20:1	PLFA	AM fungi (Gigaspora)	Sakamoto et al. (2004)

References

Baath, E., & Anderson, T. H. (2003). Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. Soil Biology and Biochemistry, 35(7), 955-963.

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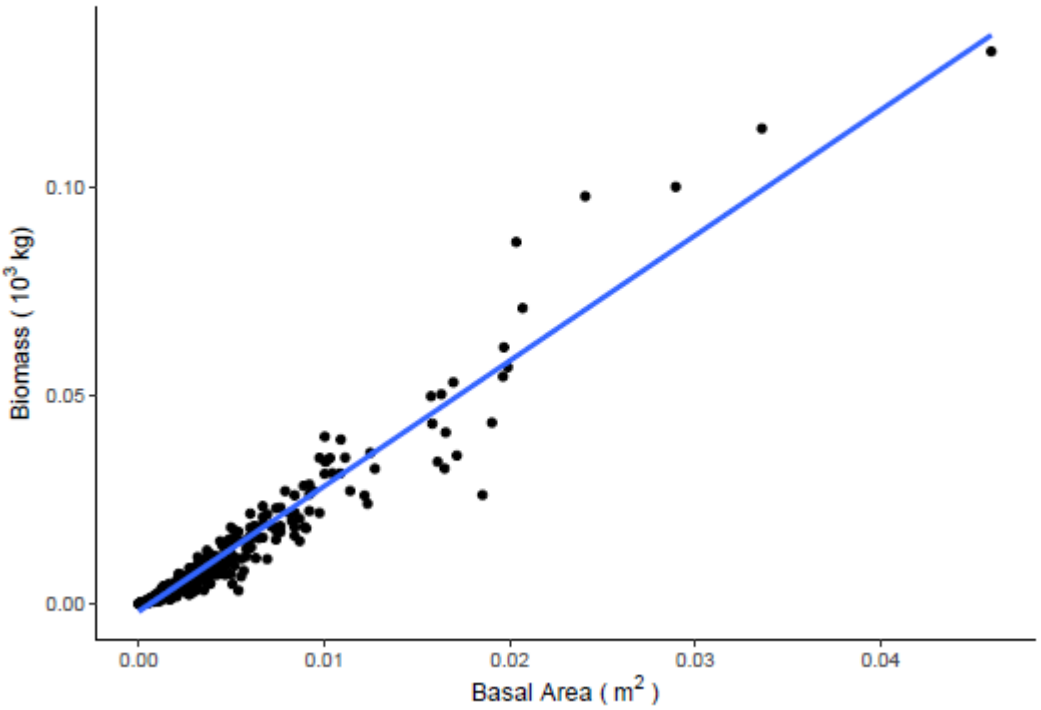
microbial communities in soil: a review. Biology and fertility of soils, 29(2), 111-129.

Supplementary material III – S4: tree biomass estimations

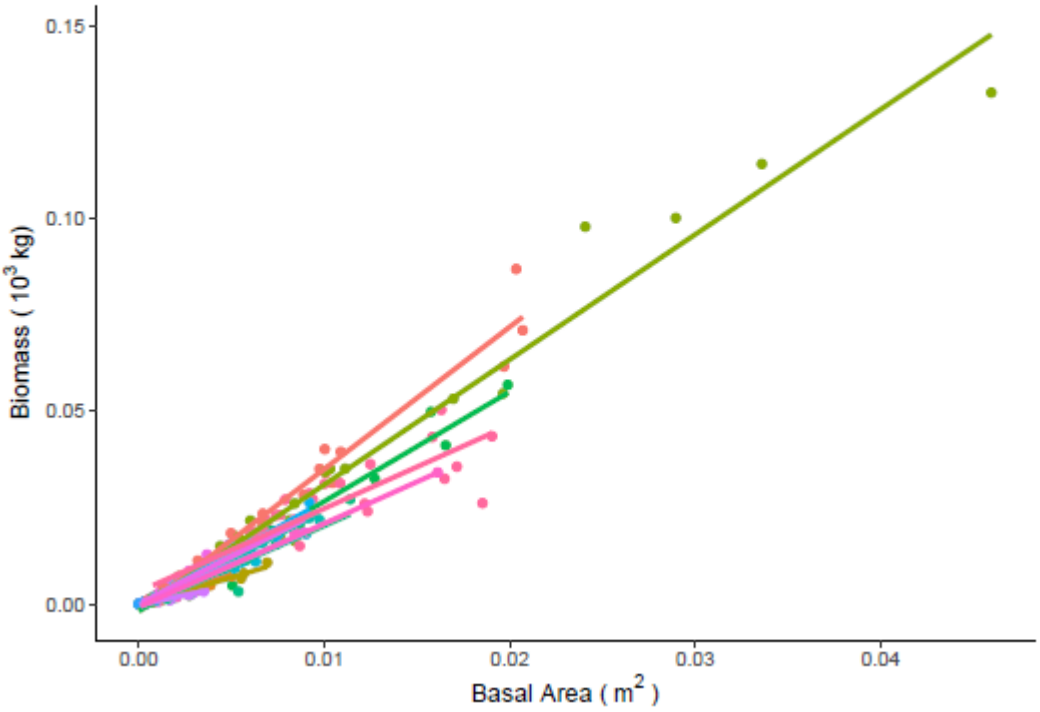
Tree allometric relationships

```
## `geom_smooth()` using formula 'y ~ x'
```



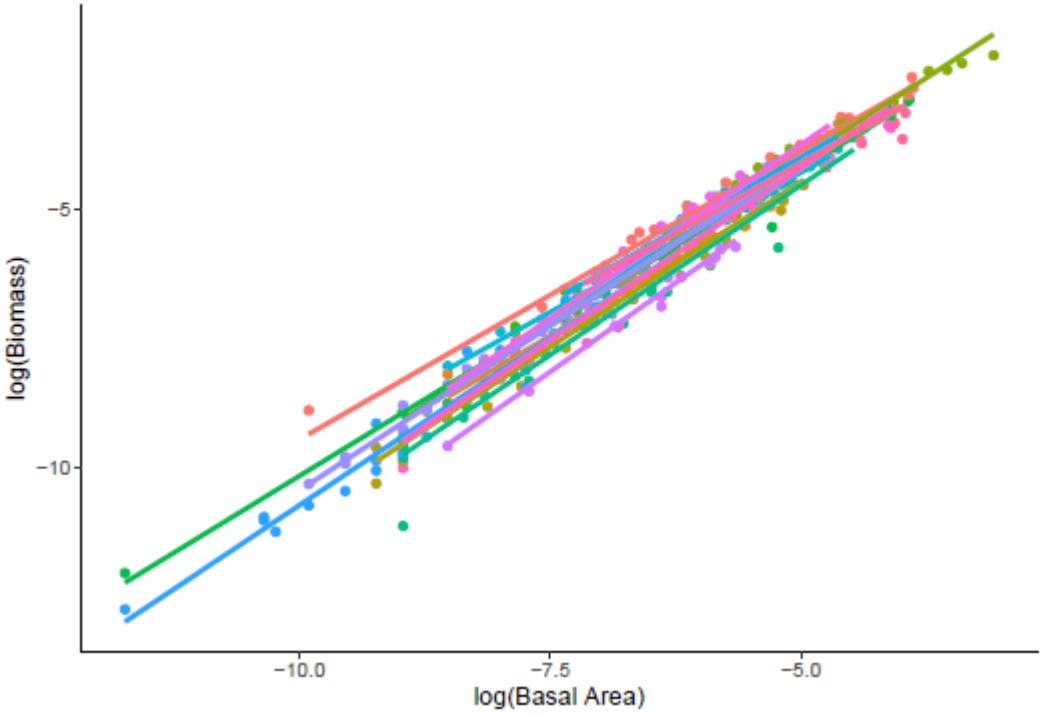
Tree species-specific allometric relationship

```
## `geom_smooth()` using formula 'y ~ x'
```



Tree species-specific allometric relationship log - log transformed

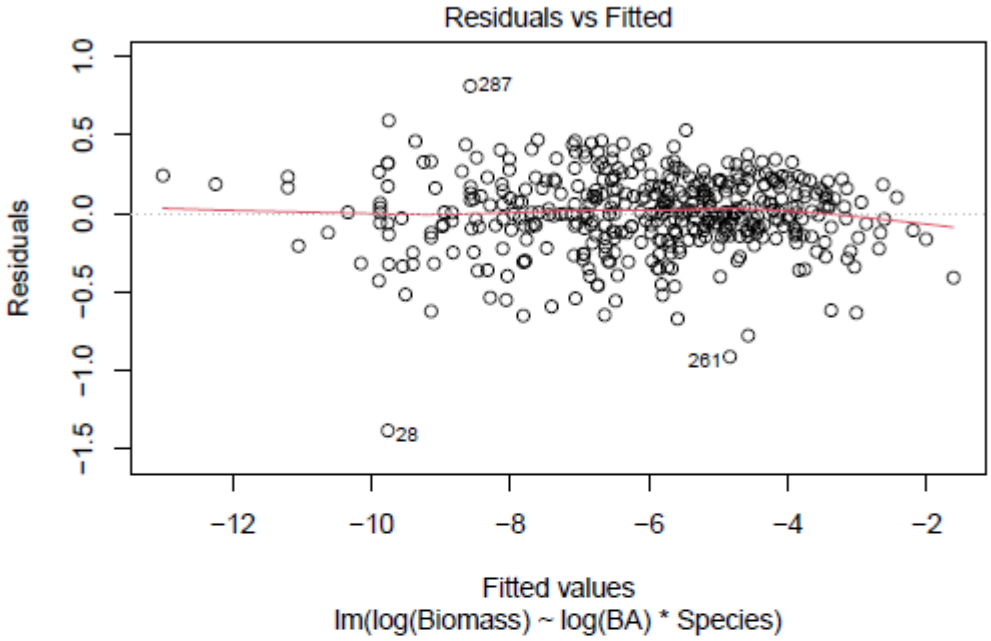
```
## `geom_smooth()` using formula 'y ~ x'
```

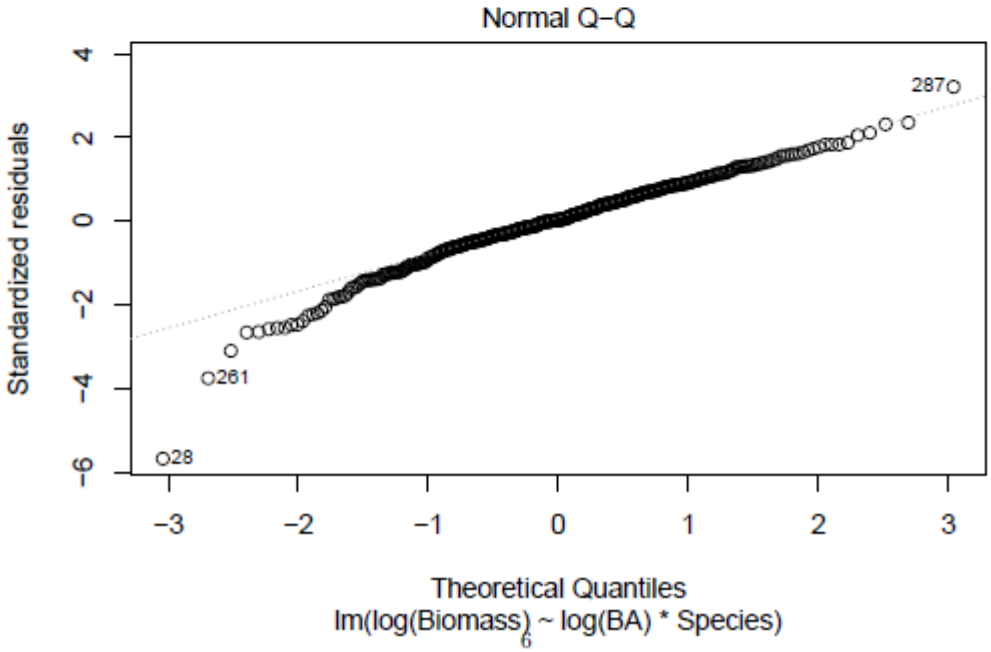


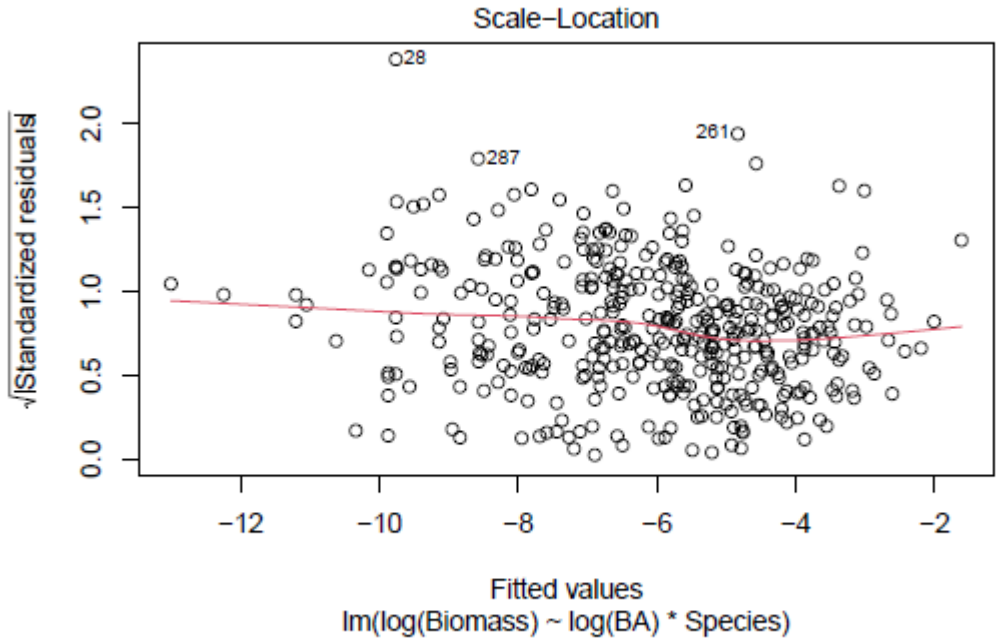
Model summary

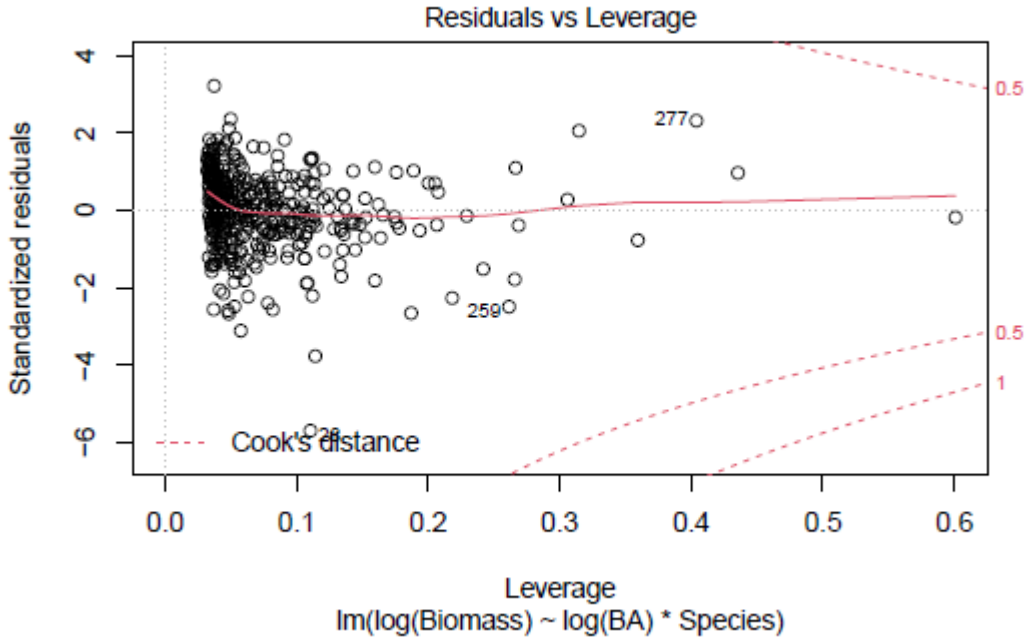
	Estimate	Std Error	t-value	p-value
(Intercept)	1.736	0.220	7.904	0.000
log(BA)	1.120	0.037	29.895	0.000
SpeciesCastanopsis eyrei	-0.505	0.534	-0.946	0.345
SpeciesCastanopsis fargesii	-0.694	0.263	-2.641	0.009
SpeciesCastanopsis sclerophylla	0.196	0.345	0.566	0.571
SpeciesChoerospondias axillaris	0.540	0.300	1.802	0.072
SpeciesCyclobalanopsis glauca	0.321	0.424	0.757	0.449
SpeciesCyclobalanopsis myrsinaefolia	-0.018	0.294	-0.061	0.952
SpeciesKoelreuteria bipinnata	0.309	0.353	0.875	0.382
SpeciesLiquidambar formosana	0.556	0.423	1.315	0.189
SpeciesLithocarpus glaber	-0.613	0.394	-1.556	0.120
SpeciesNyssa sinensis	-0.127	0.523	-0.243	0.808
SpeciesQuercus fabri	0.510	0.390	1.307	0.192
SpeciesQuercus serrata	0.571	0.384	1.486	0.138
SpeciesRhus chinensis	0.445	0.652	0.683	0.495
SpeciesSapindus mukorossi	1.237	0.414	2.991	0.003
SpeciesSapium sebiferum	0.743	0.384	1.933	0.054
SpeciesSchima superba	-0.418	0.363	-1.151	0.250
log(BA):SpeciesCastanopsis eyrei	0.038	0.081	0.470	0.639
log(BA):SpeciesCastanopsis sclerophylla	0.160	0.054	2.977	0.003
log(BA):SpeciesChoerospondias axillaris	0.142	0.053	2.664	0.008
log(BA):SpeciesCyclobalanopsis glauca	0.121	0.064	1.894	0.059
log(BA):SpeciesCyclobalanopsis myrsinaefolia	0.069	0.048	1.435	0.152
log(BA):SpeciesKoelreuteria bipinnata	0.196	0.054	3.662	0.000
log(BA):SpeciesLiquidambar formosana	0.148	0.070	2.122	0.034
log(BA):SpeciesLithocarpus glaber	-0.038	0.065	-0.577	0.564
log(BA):SpeciesNyssa sinensis	0.002	0.092	0.019	0.985
log(BA):SpeciesQuercus fabri	0.178	0.053	3.356	0.001
log(BA):SpeciesQuercus serrata	0.156	0.054	2.888	0.004
log(BA):SpeciesRhus chinensis	0.258	0.100	2.568	0.011
log(BA):SpeciesSapindus mukorossi	0.225	0.064	3.504	0.001
log(BA):SpeciesSapium sebiferum	0.216	0.060	3.592	0.000
log(BA):SpeciesSchima superba	-0.035	0.068	-0.510	0.611

Model fit


Residuals vs Fitted
Residuals
Fitted values
lm(log(Biomass) ~ log(BA) * Species)
287
261
28


Normal Q−Q
Standardized residuals
Theoretical Quantiles
lm(log(Biomass) ~ log(BA) * Species)
287
261
28


Scale−Location
√|Standardized residuals|
0.0
0.5
1.0
1.5
2.0
28
261
287
−12
−10
−8
−6
−4
−2
Fitted values
lm(log(Biomass) ~ log(BA) * Species)


Residuals vs Leverage
Standardized residuals
−6
−4
−2
0
2
4
277
259
28
Cook's distance
0.5
0.5
1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Leverage
lm(log(Biomass) ~ log(BA) * Species)

Supplementary material III – S5: variables

A. List of variables

Variables	Code	Unit	Calculation	Hypothesis ◌ used for calculation ①explanatory ❶response
Tree variables				
Plot diversity level	Diversity_level	none	Treatment	①②③
Forest vertical stratification	ENL	none	Calculated from laser scanning measurements (Perles-Garcia et al. 2021 *under review*)	①②③
Diameter at Breast Height	DBH	m	Measured	◌
Basal Area	BA	m^2	$BA = \frac{(DBH)^2}{4\pi}$	◌
TSP biomass	$TSP_{biomass}$	m^2	Calculated from BA (Appendix S4)	①②③
Surrounding trees biomass	$tree_{biomass}$	m^2	Calculated from BA (Appendix S4)	①②③
Specific Root Length	SRL	$m.g^{-1}$	Measured	◌
Root Diameter	RD	m	Measured	◌
Fungal association	AM or EM	none	Estimated from literature	◌
Root diameter community weighted mean at TSP level	$TSP_{CWM\ RD}$	m	$\text{TSP CWM RD} = \sum_{i\ \epsilon\ TSP\ species} \frac{RD_i \times BA_i}{TSP_{biomass}}$	①②③
Specific root length community weighted mean at TSP level	$TSP_{CWM\ SRL}$	$m.g^{-1}$	$\text{TSP CWM SRL} = \sum_{i\ \epsilon\ TSP\ species} \frac{SRL_i \times BA_i}{TSP_{biomass}}$	①②③
Fugal association ratio at TSP level	$TSP_{AM/EM}$	none	$\text{TSP}\frac{\text{AM}}{\text{EM}} = \sum_{i\ \epsilon\ TSP\ species} \frac{a_i \times BA_i}{TSP_{biomass}}$ $a_i = -1\ or\ 1\ if\ EM\ or\ AM\ association$	①②③
Root Diameter community weighted mean at neighborhood level	CWM_{RD}	m	$\text{CWM RD} = \sum_{i\ \epsilon\ species} \frac{RD_i \times BA_i}{tree_{biomass}}$	①②③
Specific Root Length community weighted mean at neighborhood level	CWM_{SRL}	$m.g^{-1}$	$\text{CWM SRL} = \sum_{i\ \epsilon\ species} \frac{SRL_i \times BA_i}{tree_{biomass}}$	①②③
Fugal association ratio at neighborhood level	AM/EM	none	$\text{TSP}\frac{\text{AM}}{\text{EM}} = \sum_{i\ \epsilon\ species} \frac{a_i \times BA_i}{tree_{biomass}}$ $a_i = -1\ or\ 1\ if\ EM\ or\ AM\ association$	①②③
Root diameter functional richness at TSP level	$TSP_{FRic\ RD}$	m	$TPS\ FRic\ RD = f(RD)_{TSP}$, 'FD' package	①②③
Specific root length functional richness at TSP level	$TSP_{FRic\ SRL}$	$m.g^{-1}$	$TPS\ FRic\ SRL = f(SRL)_{TSP}$, 'FD' package	①②③
Root diameter functional	$FDis_{RD}$	m	$FDis\ RD = f(RD, BA)$, 'FD' package	①②③

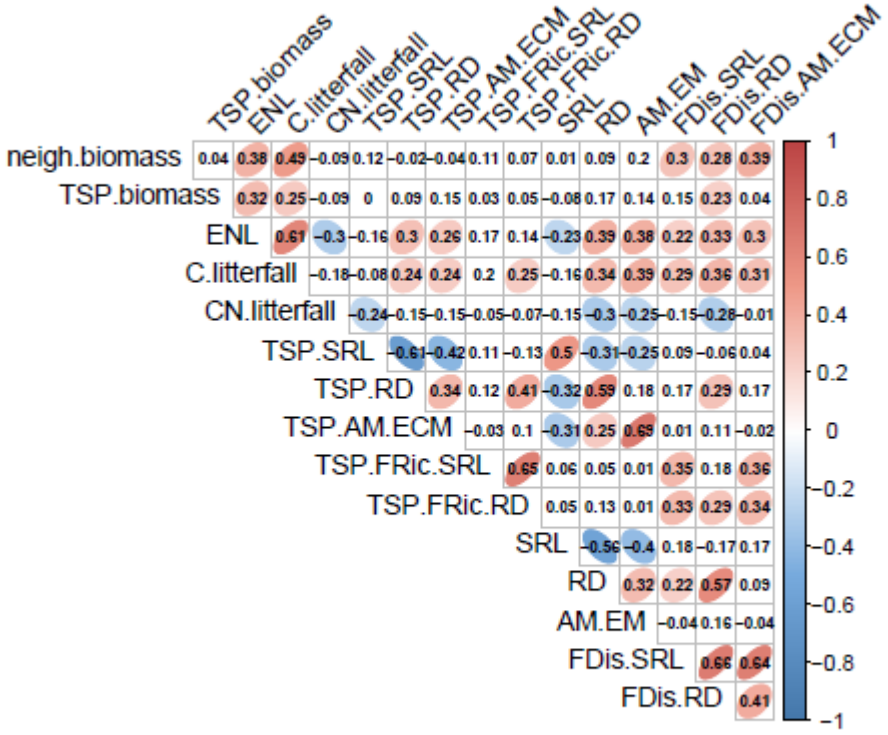
dissimilarity at neighborhood level				
Specific root length functional dissimilarity at neighborhood level	$FDis_{SRL}$	$m.g^{-1}$	$FDis\ SRL = f(SRL, BA)$, 'FD' package	①②③
Specific root length functional dissimilarity at neighborhood level	$FDis_{AM/EM}$	none	$FDis\frac{AM}{EM} = f(\frac{AM}{EM}, BA)$, 'FD' package	①②③
Tree community root functional dissimilarity	FDis	none	$FDis = f(\frac{AM}{EM}, RD, SRL, BA)$, 'FD' package	①②③
Leaf carbon content	$[C]_{leaf}$	$g.g^{-1}$	Measured	◌
Leaf nitrogen content	$[N]_{leaf}$	$g.g^{-1}$	Measured	◌
Annual litter productivity	$m_{litterfall}$	g	Measured	◌
Annual litter carbon deposition	$C_{litterfall}$	g	$C_{litterfall} = m_{litterfall} \times [C]_{leaf}$	①②③
Annual litter nitrogen deposition	$N_{litterfall}$	g	$N_{litterfall} = m_{litterfall} \times [N]_{leaf}$	①②③
Soil microbial community				
Soil microbial biomass	mic.bio	$mg.g^{-1}$	Measured	②❷③❸
MICRO-ENVIRONMENTAL VARIABLES				
Biotic environmental variables				
Litter abundance observed om the ground	Litter.ab	none	Estimated	③
Litter carbon content	$[C]_{litter}$	$g.g^{-1}$	Measured	③
Litter nitrogen content	$[N]_{litter}$	$g.g^{-1}$	Measured	③
Root biomass	root.biomass	$g.m^{-3}$	Measured from soil cores	③
Understory plant abundance	plant.ab	none	Estimated	③
Soil chemistry variables				
Soil carbon stock 2010	$Soil_C^{2010}$	$g.g^{-1}$	Measured	①②③
Soil carbon stock 2018	$Soil_C^{2018}$	$g.g^{-1}$	Measured	❶❷❸
Soil nitrogen content in 2018	TN	$g.g^{-1}$	Measured	③
Soil phosphorus content in 2018	TP	$g.g^{-1}$	Measured	③
Soil C:N ratio	C:N	none	$C:N = \frac{Soil_C^{2018}}{TN}$	③
Soil C:P ratio	C:P	none	$C:P = \frac{Soil_C^{2018}}{TP}$	③
Micro-climatic variables				
Soil water content	RH	$g.g^{-1}$	Measured	③
Minimum, average and maximum air temperature of the sampling day and	T.min, T.mean, T.max, T.min.wee	°C	Estimated from climatic models (Supplementary S2)	◌

week before sampling	k, T.mean.week, T.max.week			
Temperature conditions	Temperature	none	First PCA axis of climatic variables	③
Plot topography				
Slope	Slope	°	Design (Scholten *et al*. 2017)	①②③
Plan curvature	Curv. PL	°	Design (Scholten *et al*. 2017)	①②③
Profile curvature	Curv. PR	°	Design (Scholten *et al*. 2017)	①②③
Altitude	Altitude	m	Design (Scholten *et al*. 2017)	①②③

B. Hypotheses

Hypothesis	Response variable	Explanatory variable
H1	$Soil_C^{2018}$	$Soil_C^{2010}$, $TSP_{biomass}$, $tree_{biomass}$, $C_{litterfall}$, $N_{litterfall}$, $TSP_{CWM\ RD}$, $TSP_{CWM\ SRL}$, $TSP_{AM/EM}$, $TSP_{FRic\ RD}$, $TSP_{FRic\ SRL}$, CWM_{RD}, CWM_{SRL}, AM/EM, $FDis_{RD}$, $FDis_{SRL}$, $FDis_{AM/EM}$, FDis
H2.1	$Soil_C^{2018}$	mic.bio
H2.2	$mic.bio$	$Soil_C^{2010}$, $TSP_{biomass}$, $tree_{biomass}$, $C_{litterfall}$, $N_{litterfall}$, $TSP_{CWM\ RD}$, $TSP_{CWM\ SRL}$, $TSP_{AM/EM}$, $TSP_{FRic\ RD}$, $TSP_{FRic\ SRL}$, CWM_{RD}, CWM_{SRL}, AM/EM, $FDis_{RD}$, $FDis_{SRL}$, $FDis_{AM/EM}$, FDis
H3.1	$mic.bio$	$env.var \in$ [Temperature, RH, TN, TP, C.N, C.P, $root.biomass, plant.ab, litter.ab, [C]_{litter}, [N]_{litter}$]
H3.2	$env.var \in$ [RH, TN, TP, C.N, C.P, $root.biomass, plant.ab, litter.ab, [C]_{litter}, [N]_{litter}$]	$Soil_C^{2010}$, $TSP_{biomass}$, $tree_{biomass}$, $C_{litterfall}$, $N_{litterfall}$, $TSP_{CWM\ RD}$, $TSP_{CWM\ SRL}$, $TSP_{AM/EM}$, $TSP_{FRic\ RD}$, $TSP_{FRic\ SRL}$, CWM_{RD}, CWM_{SRL}, AM/EM, $FDis_{RD}$, $FDis_{SRL}$, $FDis_{AM/EM}$, FDis
	$Temperature$	$TSP_{biomass}$, $tree_{biomass}$, $C_{litterfall}$, $N_{litterfall}$,

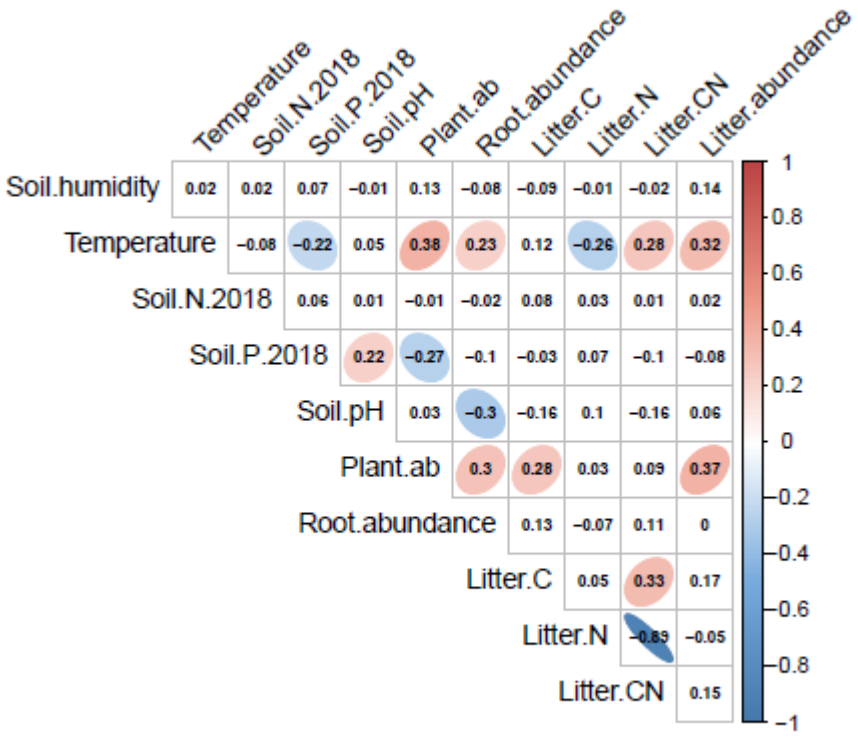
Supplementary material III – S6: correlation between traits



Correlation between root functional traits indices. Ellips were only diplayed when the correlation was significant, and, were sized, colored and oriented by correlation strengh and direction.

Supplementary material III – S7: climate variables

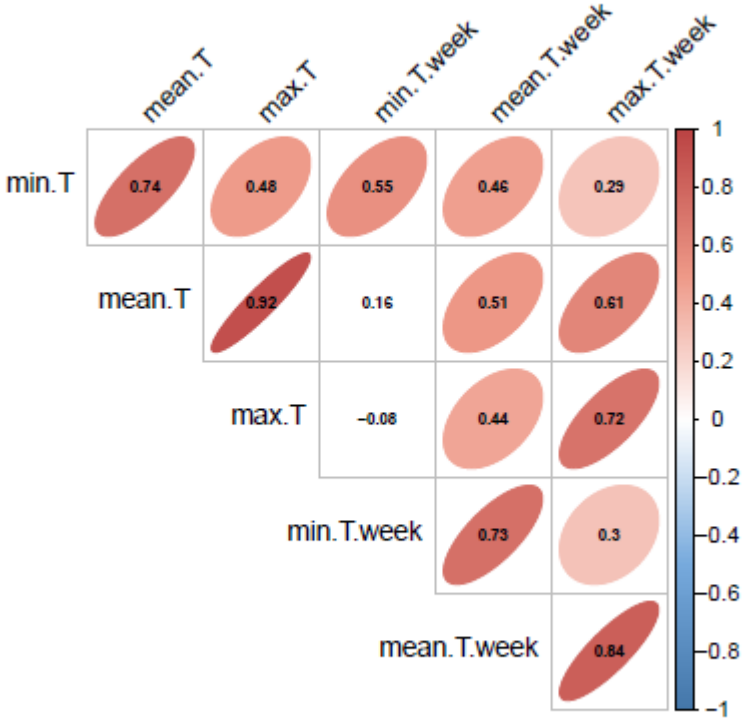
A. Correlation between micro-environmental variables



Correlation between micro-environmental variables. Ellips were only diplayed when the correlation was significant, and, were sized, colored and oriented by correlation strengh and direction.

B. Microclimate primary component analyses

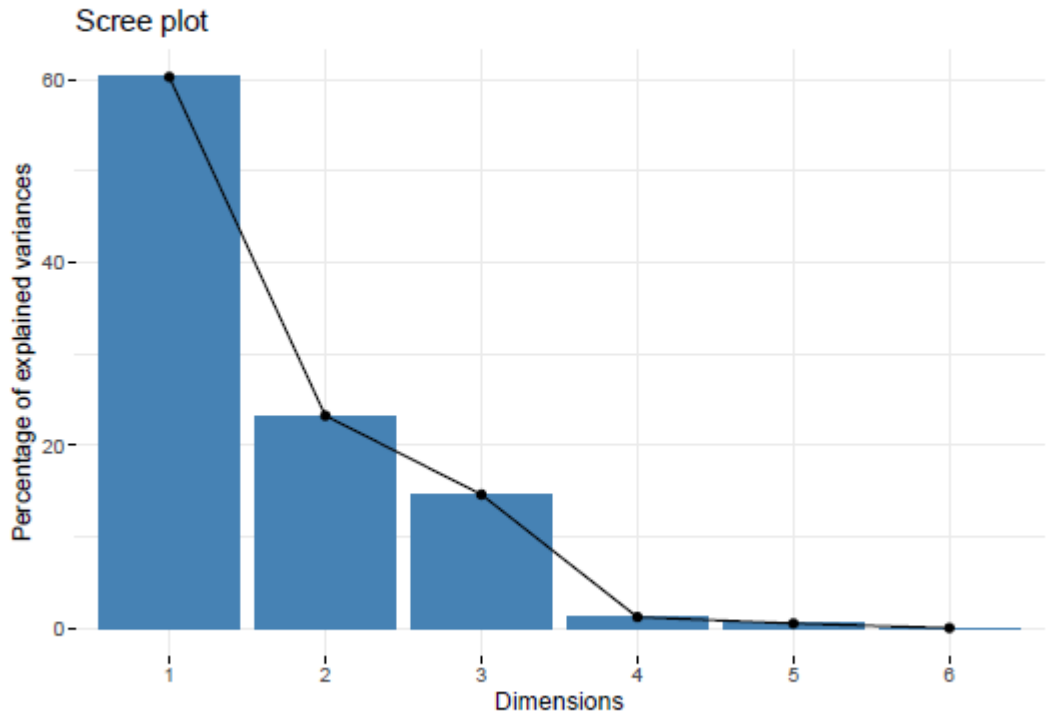
B.1. Correlation between micro-climatic variables



Correlation between micro-climatic variables. Ellips were only diplayed when the correlation was significant, and, were sized, colored and oriented by correlation strengh and direction.

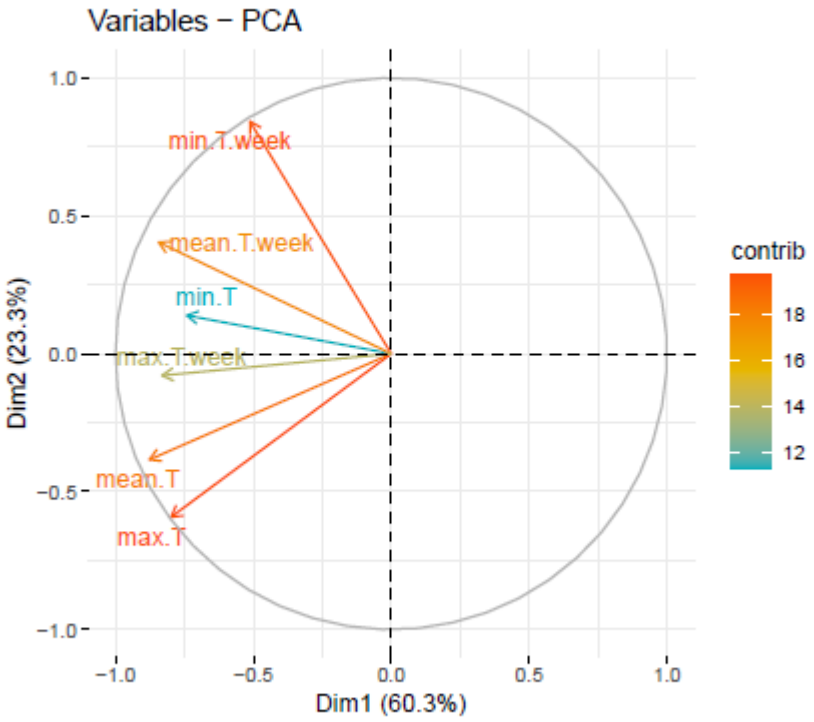
B.2. Primary component analysis of micro-climatic variables

B.2.1. PCA Scree plot



Part of variance explained by each dimension of the PCA projection.

B.2.2. Micro-climatic variables projection on the two first axes of the PCA projection



Supplementary material III – S8: model assumptions

The assumptions of the linear models fitted in our analyses were tested using the "check_model" function from the R package performance.

Models Hypothesis H1

Soil historical carbon concentration model

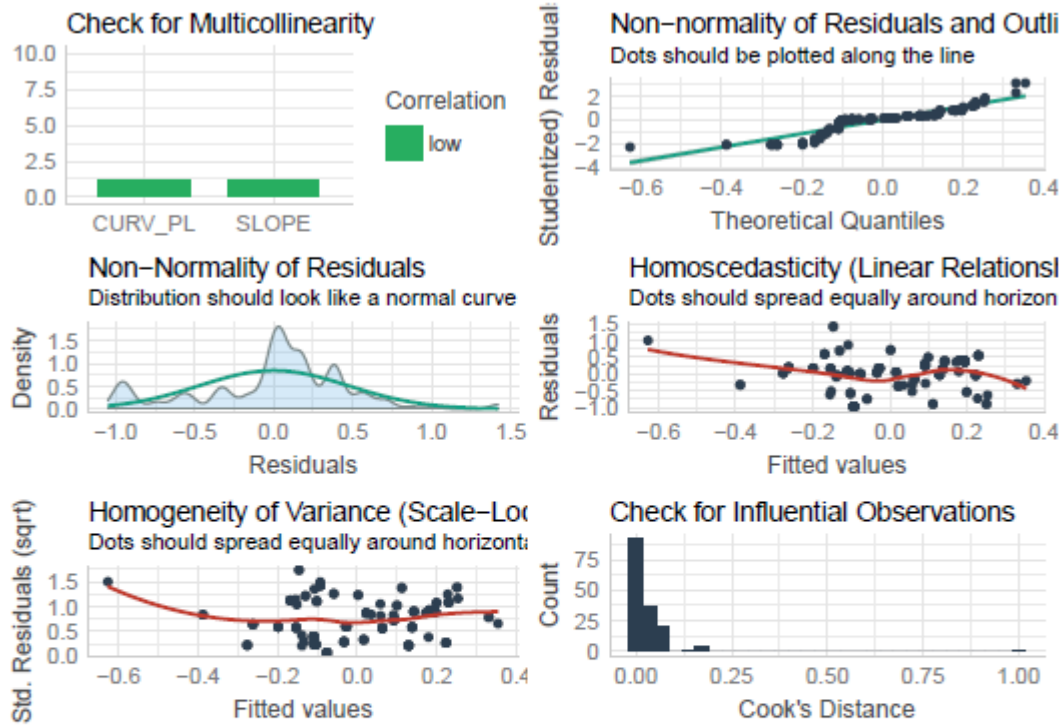
Summary

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.038	0.000	1.000
CURV_PL	0.357	0.084	4.258	0.000
SLOPE	0.175	0.084	2.090	0.038

Model statistical hypotheses

```
## `geom_smooth()` using formula 'y ~ x'
## `geom_smooth()` using formula 'y ~ x'
## `geom_smooth()` using formula 'y ~ x'

## `stat_bin()` using `bins = 30`. Pick better value with `binwidth`.
```

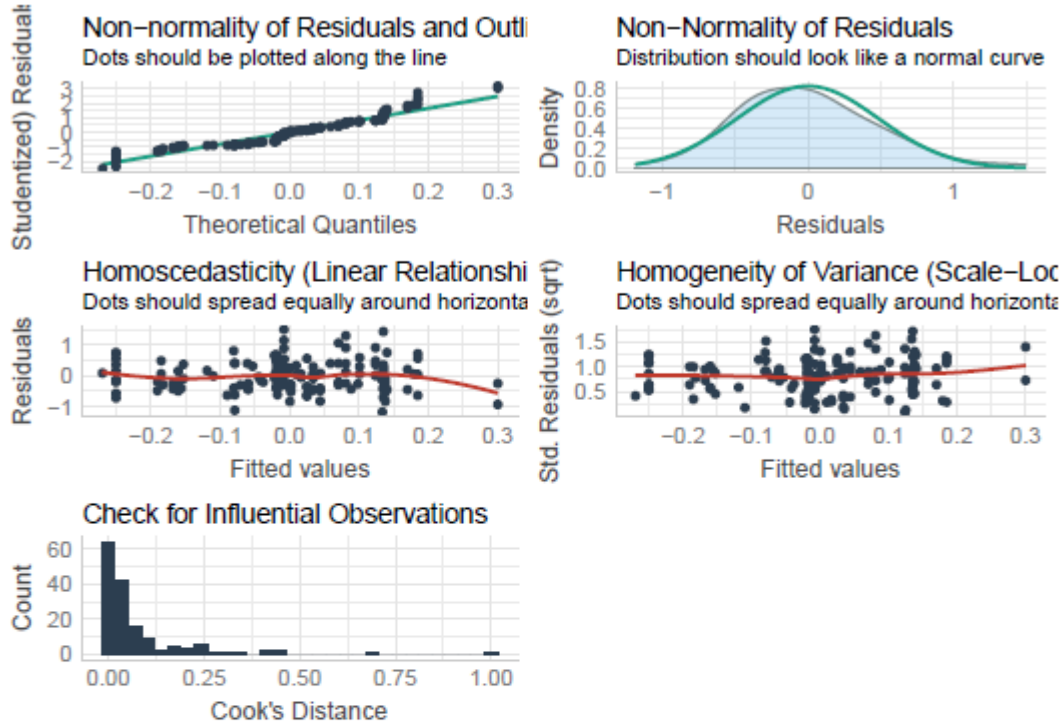


Tree diversity effects on carbon concentration model

Summary

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.039	0.00	1.000
Soil.C.2010	0.236	0.079	2.99	0.003

Model statistical hypotheses

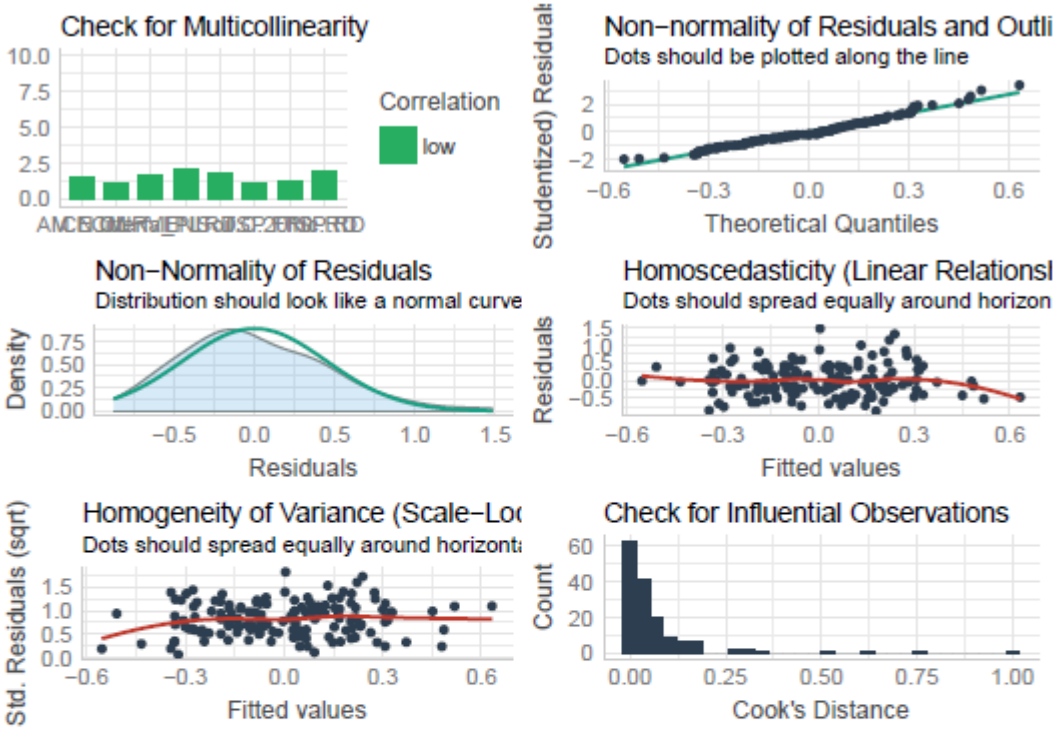


Tree functional traits effects on carbon concentration model

Summary

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.037	0.000	1.000
CURV_PL	0.236	0.095	2.482	0.014
CN.litterfall	-0.218	0.081	-2.701	0.008
ENL	0.344	0.106	3.228	0.002
TSP.RD	0.206	0.103	2.010	0.046
TSP.FRic.RD	-0.135	0.084	-1.613	0.109
RD	-0.286	0.101	-2.829	0.005
AM.ECM	-0.155	0.093	-1.659	0.099
Soil.C.2010	0.294	0.080	3.673	0.000

Model statistical hypotheses



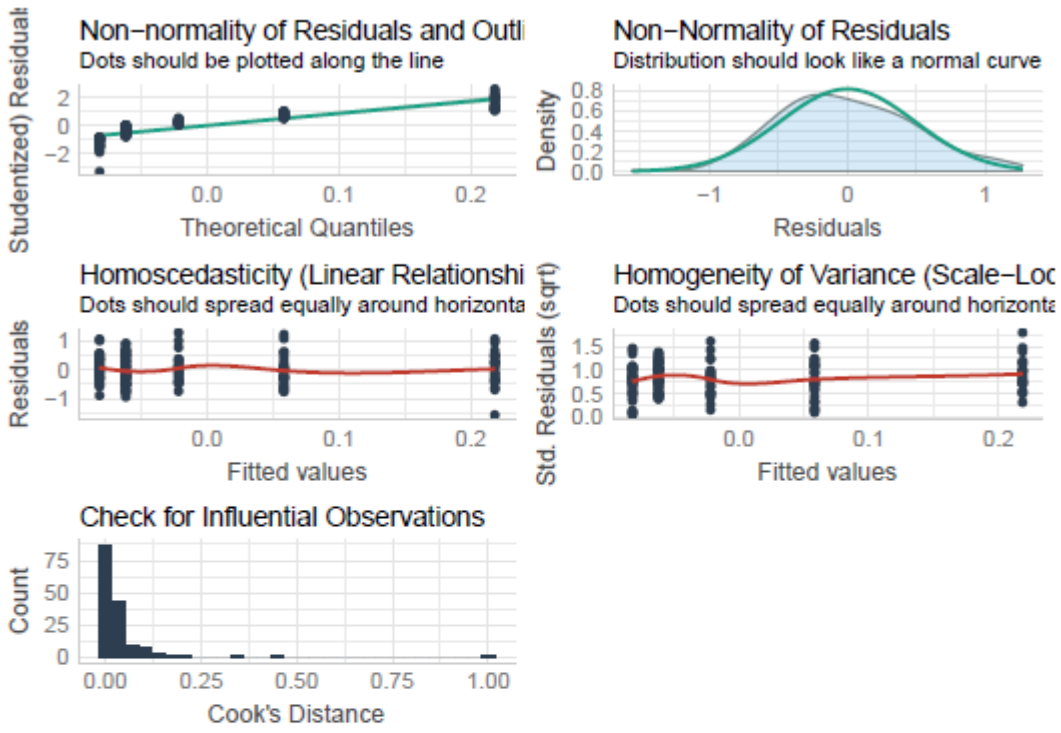
Models Hypothesis H2

Tree diversity effects on microbial biomass

Summary

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.040	0.000	1.000
Sp.rich	0.202	0.079	2.544	0.012

Model statistical hypotheses

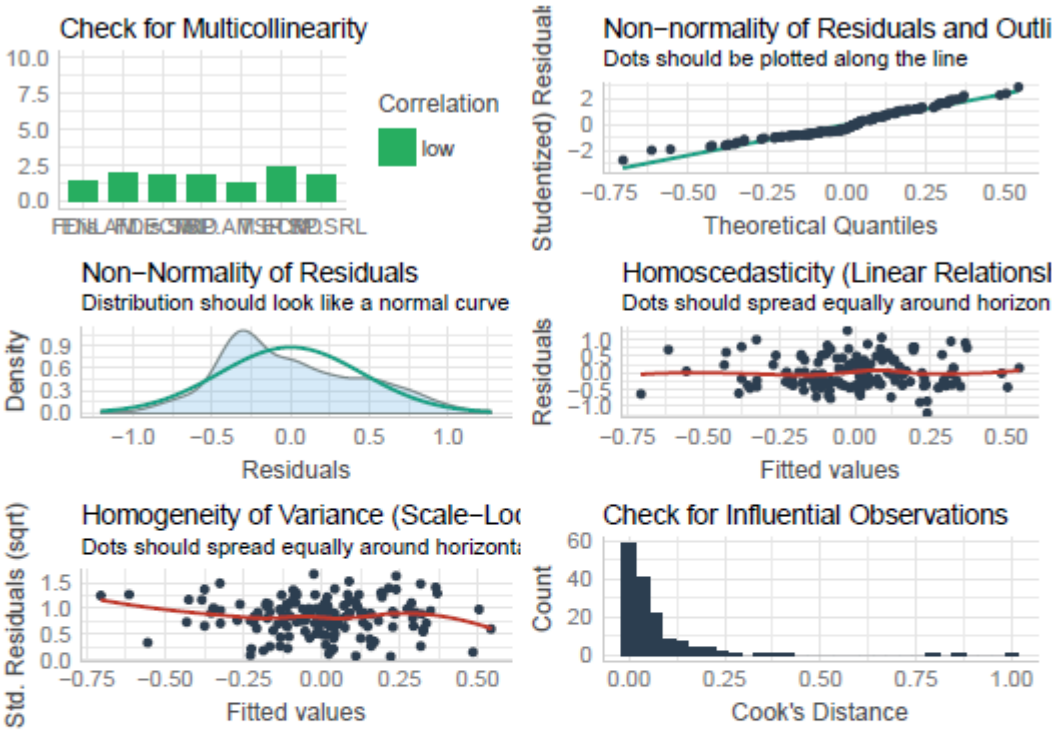


Tree functional traits effects on microbial biomass

Summary

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.037	0.000	1.000
ENL	0.177	0.087	2.037	0.043
TSP.SRL	0.223	0.103	2.176	0.031
TSP.RD	0.308	0.116	2.643	0.009
TSP.AM.ECM	-0.145	0.085	-1.695	0.092
FDis.SRL	-0.216	0.102	-2.124	0.035
FDis.AM.ECM	0.153	0.103	1.488	0.139
RD	-0.349	0.100	-3.494	0.001

Model statistical hypotheses



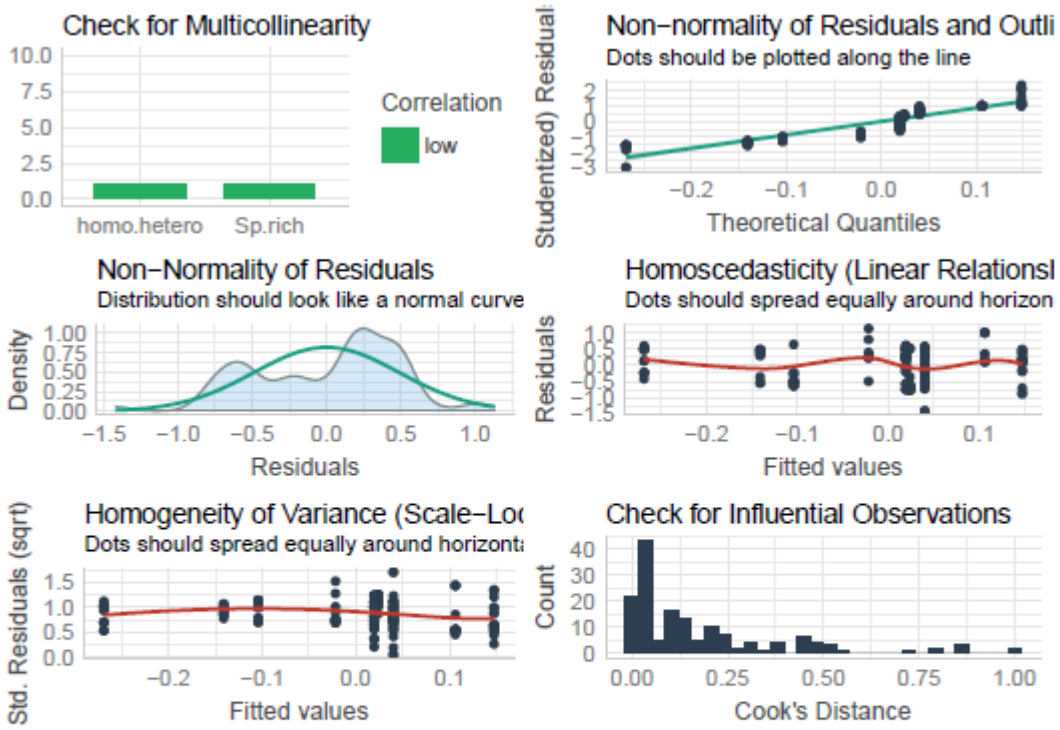
Models Hypothesis H3

Tree diversity and traits effects on environmental conditions

Temperature

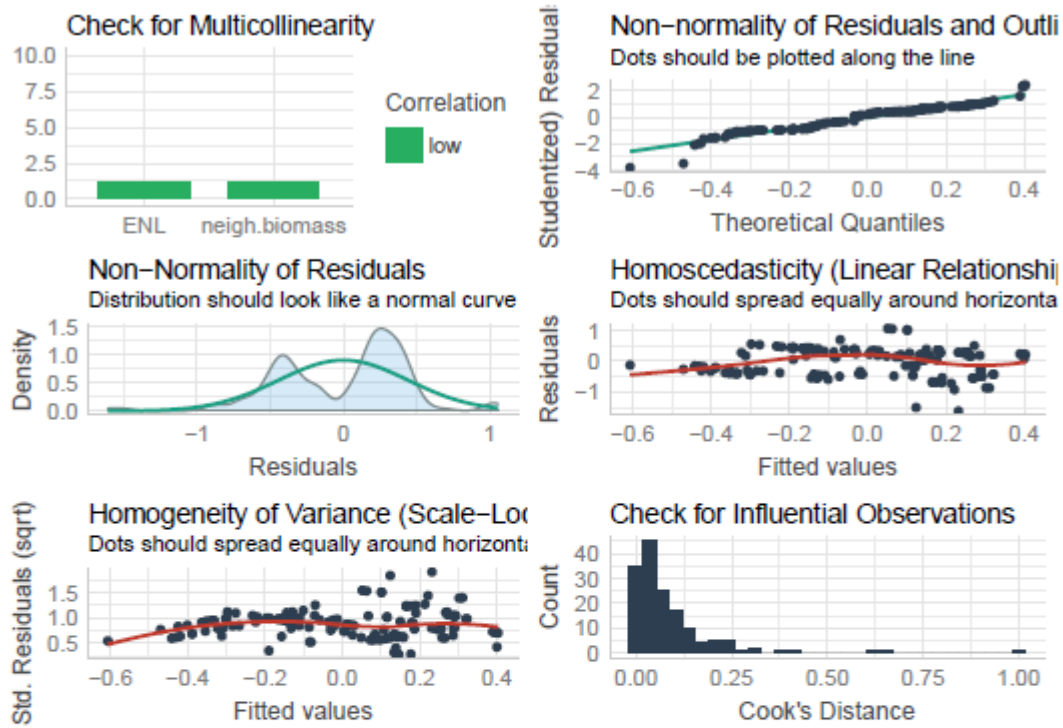
Species richness model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.040	0.000	1.000
Sp.rich	-0.208	0.082	-2.534	0.012
homo.hetero	0.128	0.086	1.484	0.140



Trait model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.036	0.000	1.000
neigh.biomass	-0.113	0.078	-1.452	0.149
ENL	-0.406	0.078	-5.207	0.000



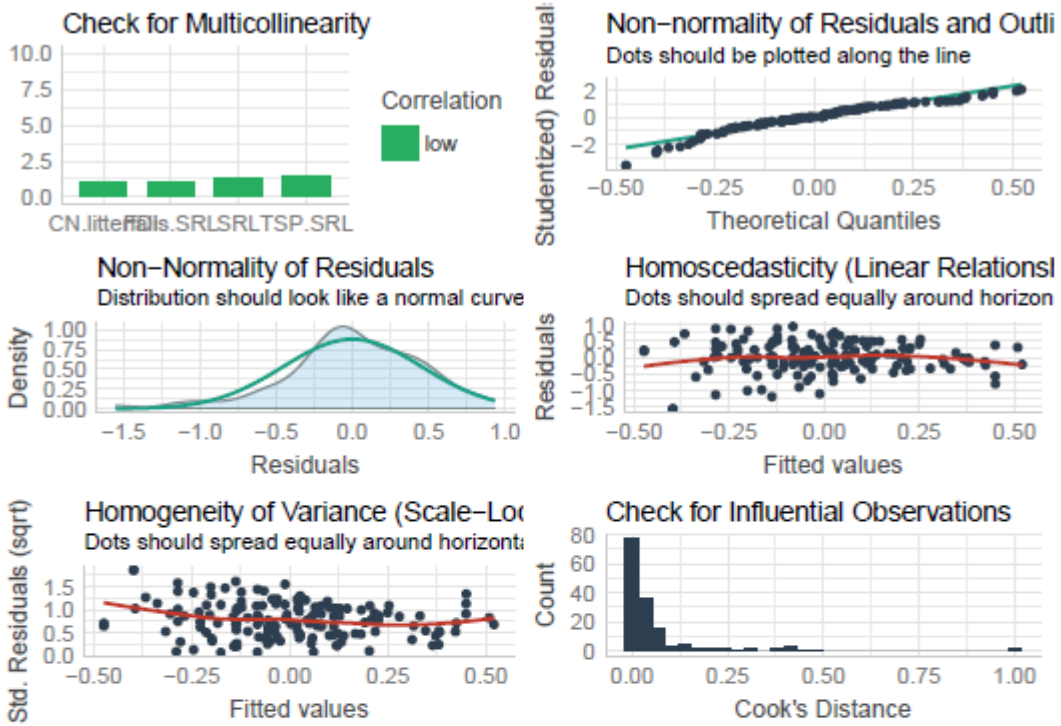
Soil relative humidity

Species richness model

(No variable selected)

Trait model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.037	0.000	1.000
CN.litterfall	-0.247	0.077	-3.192	0.002
TSP.SRL	-0.290	0.088	-3.301	0.001
FDis.SRL	0.111	0.076	1.454	0.148
SRL	-0.145	0.087	-1.656	0.100



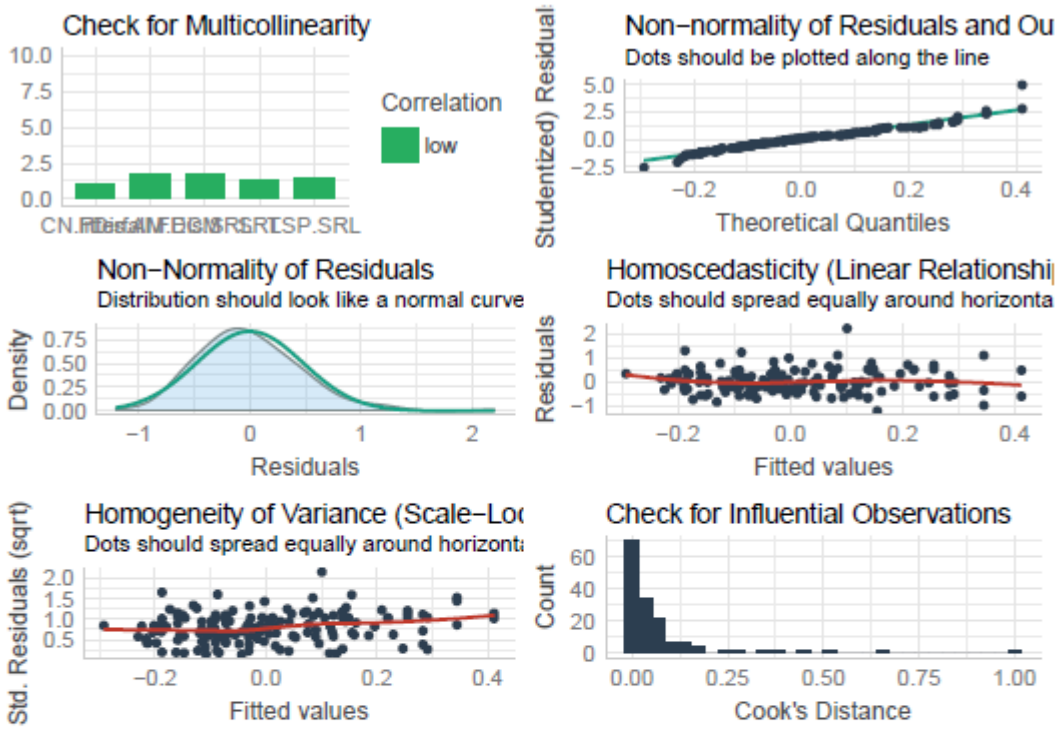
Soil nitrogen

Species richness model

(No variable selected)

Trait model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.039	0.000	1.000
CN.litterfall	-0.189	0.082	-2.300	0.023
TSP.SRL	-0.135	0.093	-1.460	0.146
FDis.SRL	-0.253	0.104	-2.422	0.017
FDis.AM.ECM	0.149	0.104	1.442	0.151
SRL	0.214	0.092	2.318	0.022



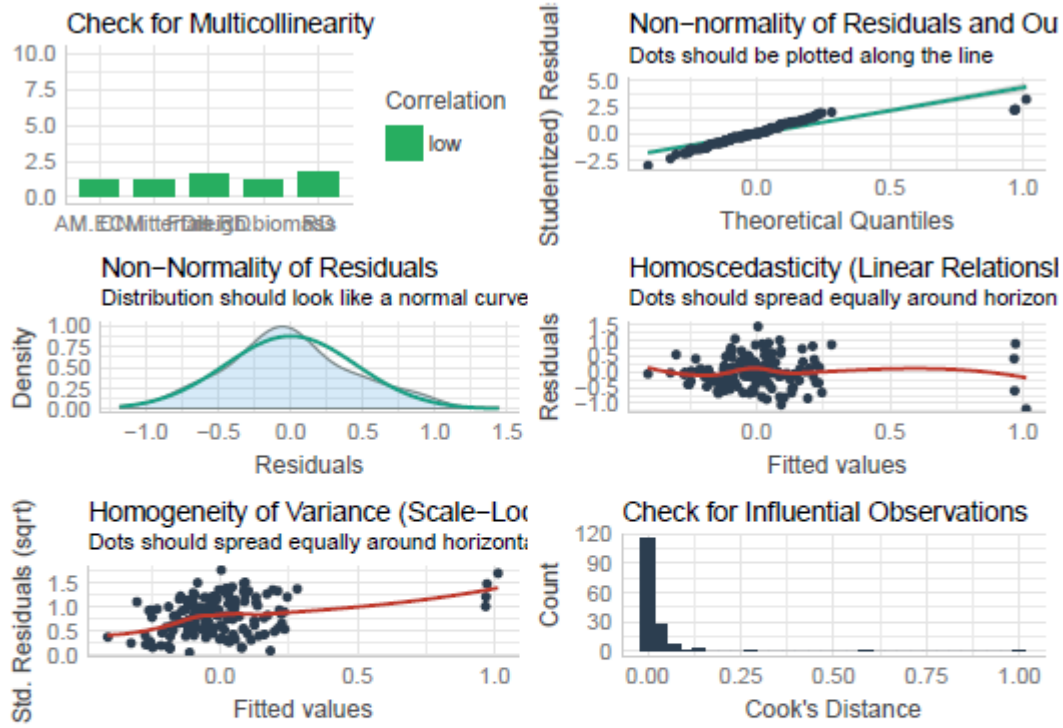
Soil phosphorus

Species richness model

(No variable selected)

Trait model

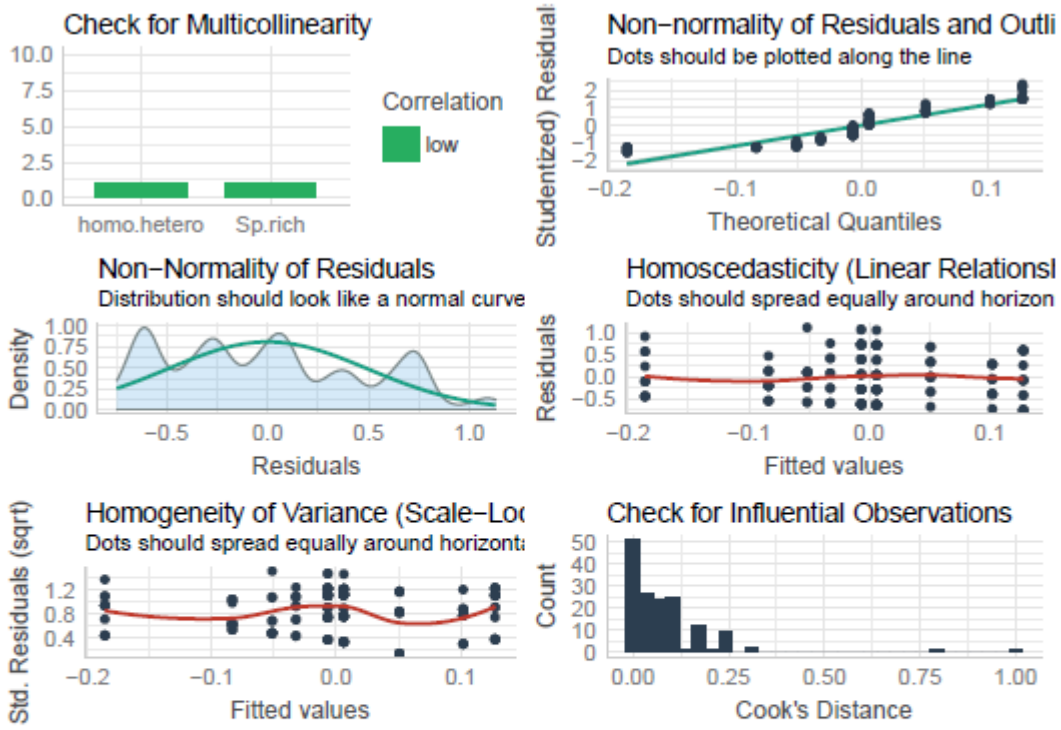
	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.037	0.000	1.000
CN.litterfall	-0.186	0.080	-2.309	0.022
neigh.biomass	0.149	0.080	1.866	0.064
FDis.RD	-0.446	0.096	-4.622	0.000
RD	0.408	0.097	4.214	0.000
AM.ECM	-0.127	0.082	-1.552	0.123



Plant abundance

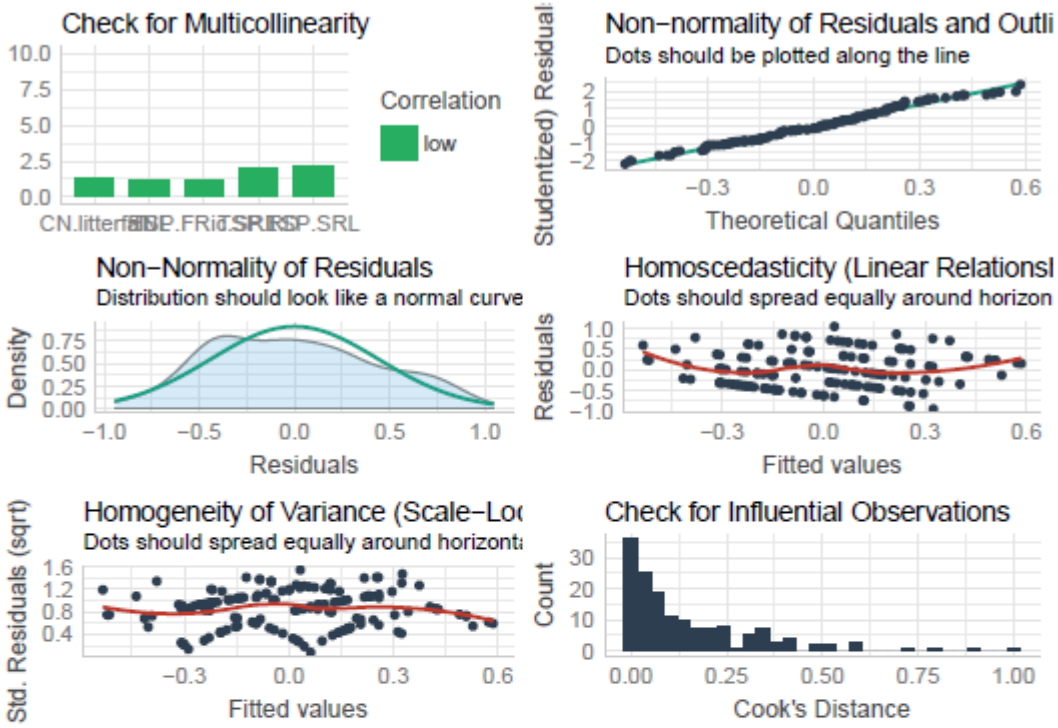
Species richness model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.040	0.000	1.000
Sp.rich	-0.129	0.083	-1.559	0.121
homo.hetero	0.135	0.087	1.545	0.124



Trait model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.036	0.000	1.000
CN.litterfall	-0.305	0.085	-3.591	0.000
ENL	-0.472	0.080	-5.909	0.000
TSP.SRL	-0.262	0.105	-2.488	0.014
TSP.RD	-0.212	0.103	-2.055	0.042
TSP.FRic.SRL	0.181	0.076	2.376	0.019



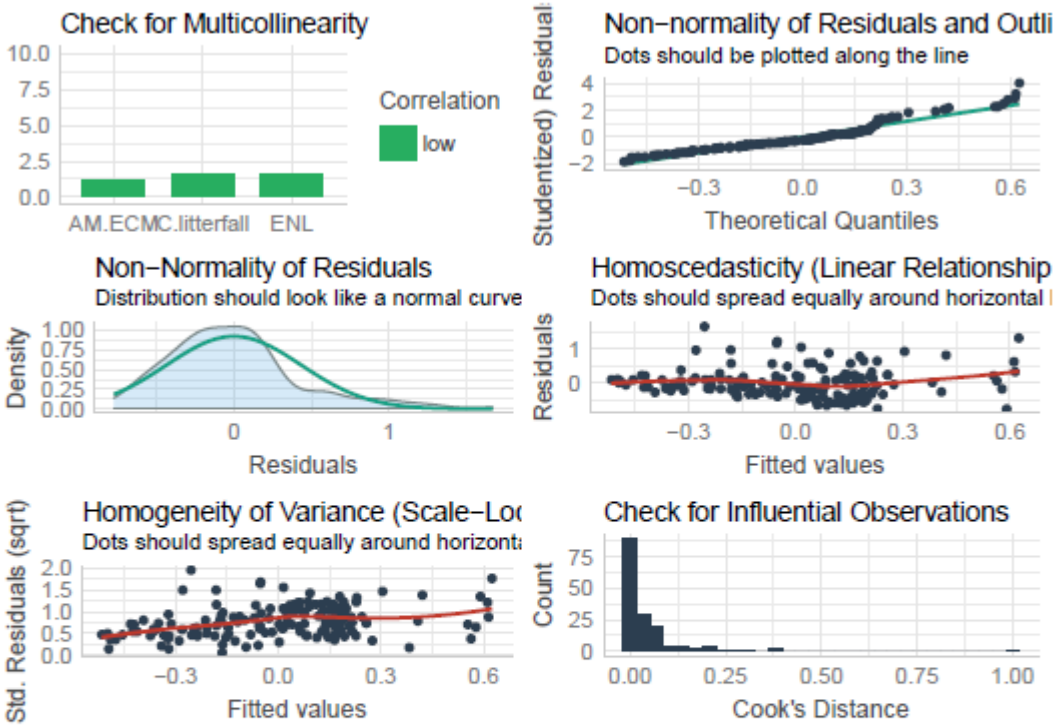
Root biomass

Species richness model

(No variable selected)

Trait model

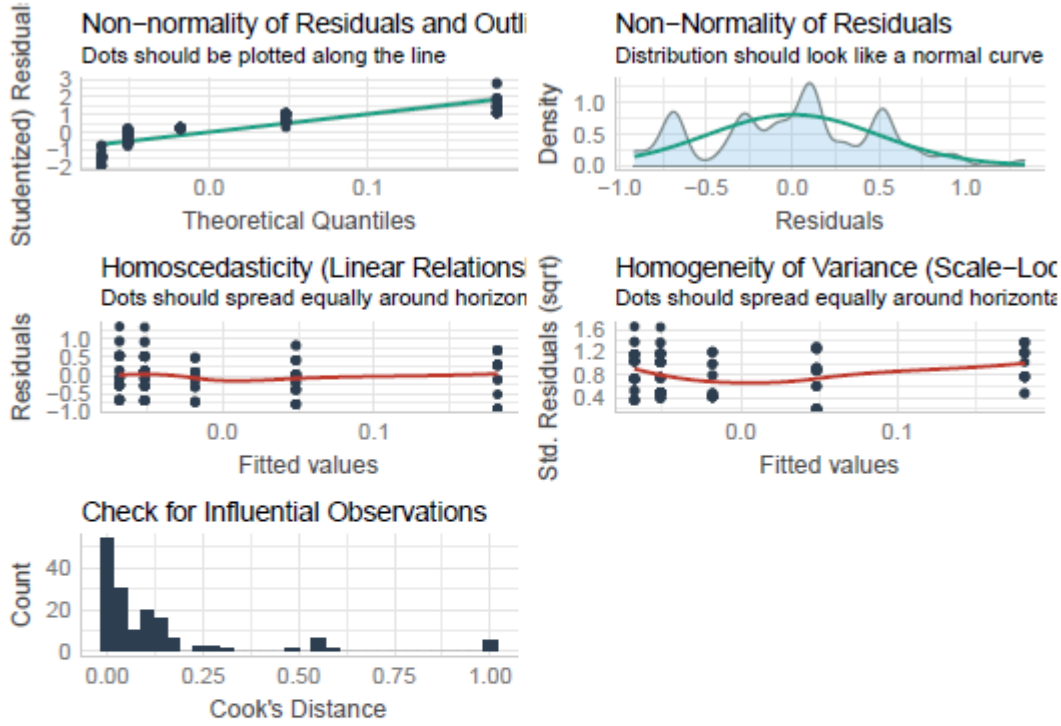
	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.035	0.000	1.000
C.litterfall	-0.218	0.091	-2.393	0.018
ENL	-0.389	0.091	-4.275	0.000
AM.ECM	0.237	0.079	3.022	0.003



Litter abundance

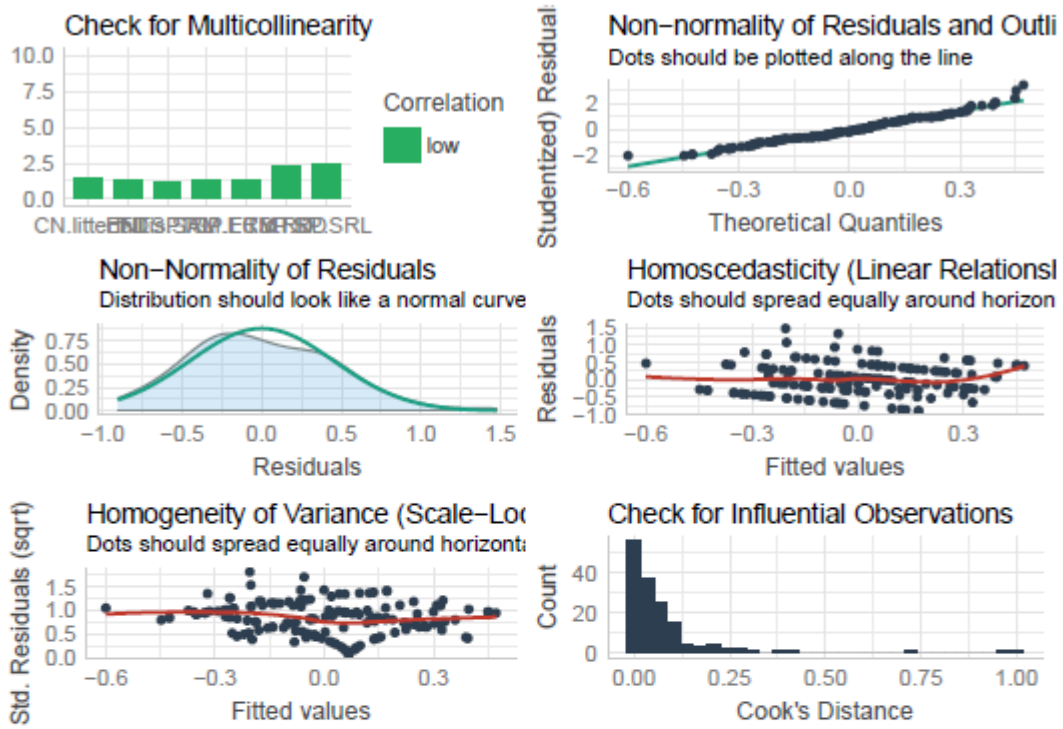
Species richness model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.04	0.000	1.000
Sp.rich	0.168	0.08	2.098	0.038



Trait model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.037	0.000	1.000
CN.litterfall	-0.153	0.090	-1.698	0.092
ENL	-0.294	0.084	-3.502	0.001
TSP.SRL	-0.365	0.116	-3.135	0.002
TSP.RD	-0.254	0.115	-2.206	0.029
TSP.AM.ECM	-0.205	0.087	-2.358	0.020
TSP.FRic.RD	0.120	0.087	1.391	0.166
FDis.SRL	0.217	0.083	2.620	0.010



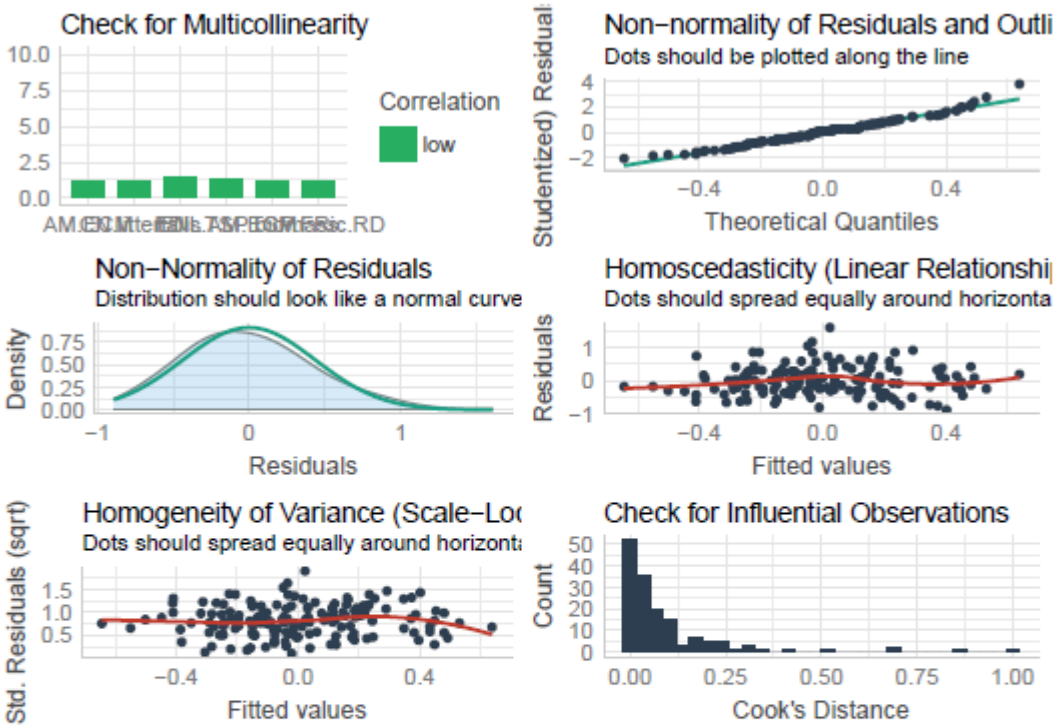
Litter CN

Species richness model

(No variable selected)

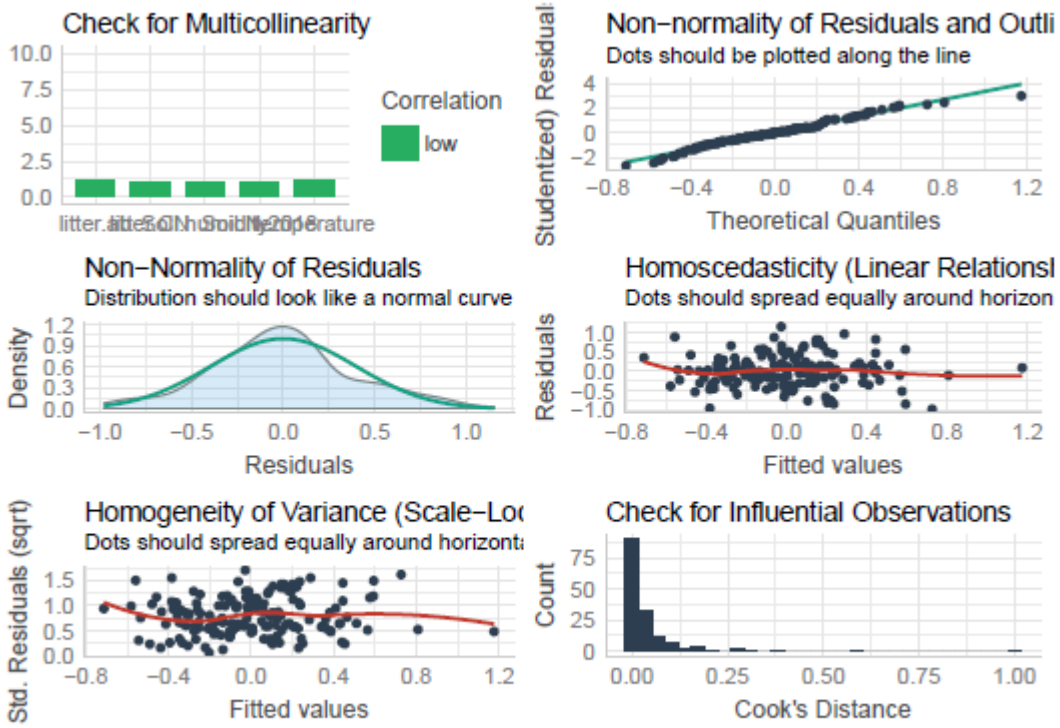
Trait model

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.036	0.000	1.000
CN.litterfall	0.233	0.077	3.046	0.003
TSP.biomass	-0.116	0.076	-1.523	0.130
ENL	-0.306	0.089	-3.440	0.001
TSP.FRic.RD	0.159	0.077	2.065	0.041
FDis.AM.ECM	0.133	0.081	1.641	0.103
AM.ECM	0.369	0.080	4.612	0.000



Environmental effects on microbial biomass

	Estimate	Std Error	t-value	p-value
(Intercept)	0.000	0.033	0.000	1.000
Soil.humidity	-0.221	0.066	-3.334	0.001
temperature	-0.379	0.072	-5.282	0.000
Soil.N.2018	0.385	0.066	5.846	0.000
litter.CN	0.239	0.068	3.494	0.001
litter.ab	0.117	0.070	1.669	0.097


Check for Multicollinearity
Correlation
low
Non−normality of Residuals and Outli
Dots should be plotted along the line
Studentized) Residual
Theoretical Quantiles
Non−Normality of Residuals
Distribution should look like a normal curve
Density
Residuals
Homoscedasticity (Linear Relationsl
Dots should spread equally around horizon
Residuals
Fitted values
Homogeneity of Variance (Scale−Loc
Dots should spread equally around horizonta
Std. Residuals (sqrt)
Fitted values
Check for Influential Observations
Count
Cook's Distance

Supplementary material III – S9: hypothesis 1 – model and complete output

Model

```
model = '
Soil.C.2018 ~ Soil.C.2010 +
              CURV_PR +
              CN.litterfall + ENL +
              TSP.RD + RD

Soil.C.2010 ~ SLOPE + CURV_PL

ENL ~ Sp.rich + SLOPE + CURV_PL + CURV_PR
'
```

Results

Explained variance

Variable	R-squared (%)
Soil.C.2018	18.9
Soil.C.2010	10.8
ENL	34.5

Grouped summary

Relation	Effect size
Neighbors aboveground productivity & traits ~ Topography	0.5162866
Neighbors aboveground productivity & traits ~ Tree species richness	0.2479653
Neighbors aboveground productivity & traits ~~ Neighbors aboveground productivity & traits	0.1626817
Soil C 2010 ~ Topography	0.5325655
Soil C 2010 ~~ Soil C 2010	0.2215195
Soil C 2018 ~ Neighbors aboveground productivity & traits	0.4486591
Soil C 2018 ~ Neighbors root traits	0.2840925
Soil C 2018 ~ Soil C 2010	0.2632744
Soil C 2018 ~~ Soil C 2018	0.2063895

Full summary

Response	Operator	Explanatory	Estimate	SE	p-value
Soil.C.2018	~	Soil.C.2010	0.2632744	0.0767597	0.0006039
Soil.C.2018	~	CURV_PL	0.1635409	0.0873078	0.0610472
Soil.C.2018	~	CN.litterfall	-0.1999060	0.0771914	0.0096047
Soil.C.2018	~	ENL	0.2487531	0.0835579	0.0029107
Soil.C.2018	~	TSP.RD	0.1402681	0.0916951	0.1260854
Soil.C.2018	~	RD	-0.2840925	0.0949800	0.0027800
Soil.C.2010	~	SLOPE	0.1753615	0.0830657	0.0347621
Soil.C.2010	~	CURV_PL	0.3572040	0.0830657	0.0000171
ENL	~	Sp.rich	0.2479653	0.0687963	0.0003129
ENL	~	SLOPE	0.2151081	0.0723778	0.0029585
ENL	~	CURV_PL	-0.1897751	0.0971164	0.0506896
ENL	~	CURV_PR	0.3011785	0.1008265	0.0028164
Soil.C.2018	~~	Soil.C.2018	0.2063895	0.0235203	0.0000000
Soil.C.2010	~~	Soil.C.2010	0.2215195	0.0252445	0.0000000
ENL	~~	ENL	0.1626817	0.0185393	0.0000000
CURV_PL	~~	CURV_PL	0.2483766	0.0000000	NA
CURV_PL	~~	CN.litterfall	0.0176342	0.0000000	NA
CURV_PL	~~	TSP.RD	-0.0364343	0.0000000	NA
CURV_PL	~~	RD	-0.0332459	0.0000000	NA
CURV_PL	~~	SLOPE	-0.0995559	0.0000000	NA
CURV_PL	~~	Sp.rich	0.0228885	0.0000000	NA
CURV_PL	~~	CURV_PR	-0.1797195	0.0000000	NA
CN.litterfall	~~	CN.litterfall	0.2483766	0.0000000	NA
CN.litterfall	~~	TSP.RD	-0.0382589	0.0000000	NA
CN.litterfall	~~	RD	-0.0754086	0.0000000	NA
CN.litterfall	~~	SLOPE	0.0082185	0.0000000	NA
CN.litterfall	~~	Sp.rich	-0.0201507	0.0000000	NA
CN.litterfall	~~	CURV_PR	-0.0147584	0.0000000	NA
TSP.RD	~~	TSP.RD	0.2483766	0.0000000	NA
TSP.RD	~~	RD	0.1472590	0.0000000	NA
TSP.RD	~~	SLOPE	0.0013656	0.0000000	NA
TSP.RD	~~	Sp.rich	0.0031850	0.0000000	NA
TSP.RD	~~	CURV_PR	0.0277585	0.0000000	NA
RD	~~	RD	0.2483766	0.0000000	NA
RD	~~	SLOPE	0.0009270	0.0000000	NA
RD	~~	Sp.rich	0.0146583	0.0000000	NA
RD	~~	CURV_PR	0.0575185	0.0000000	NA
SLOPE	~~	SLOPE	0.2483766	0.0000000	NA
SLOPE	~~	Sp.rich	-0.0167863	0.0000000	NA
SLOPE	~~	CURV_PR	0.1002248	0.0000000	NA
Sp.rich	~~	Sp.rich	0.2483766	0.0000000	NA
Sp.rich	~~	CURV_PR	-0.0686821	0.0000000	NA
CURV_PR	~~	CURV_PR	0.2483766	0.0000000	NA

Supplementary material III – S10: hypothesis 2 – model and complete output

Model

```
model = '
Soil.C.2018 ~ Soil.C.2010 +
              CURV_PR +
              CN.litterfall + ENL +
              TSP.RD + RD + mic.bio

Soil.C.2010 ~ SLOPE + CURV_PL

ENL ~ Sp.rich + SLOPE + CURV_PL + CURV_PR

mic.bio ~ ENL + TSP.SRL + TSP.RD + FDis.SRL + RD + Soil.C.2018
'
```

Results

Explained variance

Variable	R-squared (%)
Soil.C.2018	28.9
Soil.C.2010	10.8
ENL	34.5
mic.bio	47.7

Grouped summary

Relation	Effect size
Mic. biomass ~ Neighbors root traits	0.2847093
Mic. biomass ~ Soil C 2018	0.5058328
Mic. biomass ~ TSP root traits	0.4384361
Mic. biomass ~~ Mic. biomass	0.1346658
Neighbors aboveground productivity & traits ~ Topography	0.5162879
Neighbors aboveground productivity & traits ~ Tree species richness	0.2479654
Neighbors aboveground productivity & traits ~~ Neighbors aboveground productivity & traits	0.1626817
Soil C 2010 ~ Topography	0.5325641
Soil C 2010 ~~ Soil C 2010	0.2215195
Soil C 2018 ~ Neighbors aboveground productivity & traits	0.4067151
Soil C 2018 ~ Soil C 2010	0.2474918
Soil C 2018 ~~ Soil C 2018	0.1807433

Full summary

Response	Operator	Explanatory	Estimate	SE	p-value
Soil.C.2018	~	Soil.C.2010	0.2474918	0.0770108	0.0013102
Soil.C.2018	~	CURV_PL	0.1434109	0.0833647	0.0853808
Soil.C.2018	~	CN.litterfall	-0.1886355	0.0801345	0.0185733
Soil.C.2018	~	ENL	0.2180795	0.0910763	0.0166444
Soil.C.2018	~	TSP.RD	0.1215180	0.0916470	0.1848610
Soil.C.2018	~	RD	-0.2336665	0.1279800	0.0678796
Soil.C.2018	~	mic.bio	0.1170902	0.2045576	0.5670461
Soil.C.2010	~	SLOPE	0.1753612	0.0830657	0.0347624
Soil.C.2010	~	CURV_PL	0.3572028	0.0830657	0.0000171
ENL	~	Sp.rich	0.2479654	0.0687963	0.0003129
ENL	~	SLOPE	0.2151080	0.0723778	0.0029585
ENL	~	CURV_PL	-0.1897739	0.0971164	0.0506911
ENL	~	CURV_PR	0.3011799	0.1008265	0.0028163
mic.bio	~	ENL	0.1037488	0.0636897	0.1033191
mic.bio	~	TSP.SRL	0.2098794	0.0797900	0.0085285
mic.bio	~	TSP.RD	0.2285567	0.0947419	0.0158473
mic.bio	~	FDis.SRL	-0.0949518	0.0629932	0.1317253
mic.bio	~	RD	-0.2847093	0.0819990	0.0005164
mic.bio	~	Soil.C.2018	0.5058328	0.1446843	0.0004721
Soil.C.2018	~~	Soil.C.2018	0.1807433	0.0447773	0.0000543
Soil.C.2010	~~	Soil.C.2010	0.2215195	0.0252445	0.0000000
ENL	~~	ENL	0.1626817	0.0185393	0.0000000
mic.bio	~~	mic.bio	0.1346658	0.0160947	0.0000000
CURV_PL	~~	CURV_PL	0.2483766	0.0000000	NA
CURV_PL	~~	CN.litterfall	0.0176342	0.0000000	NA
CURV_PL	~~	TSP.RD	-0.0364343	0.0000000	NA
CURV_PL	~~	RD	-0.0332459	0.0000000	NA
CURV_PL	~~	SLOPE	-0.0995559	0.0000000	NA
CURV_PL	~~	Sp.rich	0.0228885	0.0000000	NA
CURV_PL	~~	CURV_PR	-0.1797195	0.0000000	NA
CURV_PL	~~	TSP.SRL	0.0113570	0.0000000	NA
CURV_PL	~~	FDis.SRL	-0.0351465	0.0000000	NA
CN.litterfall	~~	CN.litterfall	0.2483766	0.0000000	NA
CN.litterfall	~~	TSP.RD	-0.0382589	0.0000000	NA
CN.litterfall	~~	RD	-0.0754086	0.0000000	NA
CN.litterfall	~~	SLOPE	0.0082185	0.0000000	NA
CN.litterfall	~~	Sp.rich	-0.0201507	0.0000000	NA
CN.litterfall	~~	CURV_PR	-0.0147584	0.0000000	NA
CN.litterfall	~~	TSP.SRL	-0.0594828	0.0000000	NA
CN.litterfall	~~	FDis.SRL	-0.0380842	0.0000000	NA
TSP.RD	~~	TSP.RD	0.2483766	0.0000000	NA
TSP.RD	~~	RD	0.1472590	0.0000000	NA
TSP.RD	~~	SLOPE	0.0013656	0.0000000	NA
TSP.RD	~~	Sp.rich	0.0031850	0.0000000	NA
TSP.RD	~~	CURV_PR	0.0277585	0.0000000	NA
TSP.RD	~~	TSP.SRL	-0.1526118	0.0000000	NA

(continued)

Response	Operator	Explanatory	Estimate	SE	p-value
TSP.RD	~~	FDis.SRL	0.0417814	0.0000000	NA
RD	~~	RD	0.2483766	0.0000000	NA
RD	~~	SLOPE	0.0009270	0.0000000	NA
RD	~~	Sp.rich	0.0146583	0.0000000	NA
RD	~~	CURV_PR	0.0575185	0.0000000	NA
RD	~~	TSP.SRL	-0.0763342	0.0000000	NA
RD	~~	FDis.SRL	0.0557553	0.0000000	NA
SLOPE	~~	SLOPE	0.2483766	0.0000000	NA
SLOPE	~~	Sp.rich	-0.0167863	0.0000000	NA
SLOPE	~~	CURV_PR	0.1002248	0.0000000	NA
SLOPE	~~	TSP.SRL	0.0101562	0.0000000	NA
SLOPE	~~	FDis.SRL	-0.0000568	0.0000000	NA
Sp.rich	~~	Sp.rich	0.2483766	0.0000000	NA
Sp.rich	~~	CURV_PR	-0.0686821	0.0000000	NA
Sp.rich	~~	TSP.SRL	0.0098234	0.0000000	NA
Sp.rich	~~	FDis.SRL	0.0794879	0.0000000	NA
CURV_PR	~~	CURV_PR	0.2483766	0.0000000	NA
CURV_PR	~~	TSP.SRL	-0.0123199	0.0000000	NA
CURV_PR	~~	FDis.SRL	-0.0095466	0.0000000	NA
TSP.SRL	~~	TSP.SRL	0.2483766	0.0000000	NA
TSP.SRL	~~	FDis.SRL	0.0212875	0.0000000	NA
FDis.SRL	~~	FDis.SRL	0.2483766	0.0000000	NA

Supplementary material III – S11: hypothesis 3 – model and complete output

Model

```
model = '
Soil.C.2018 ~ Soil.C.2010 +
              CURV_PR +
              CN.litterfall + ENL +
              TSP.RD + RD

Soil.C.2010 ~ SLOPE + CURV_PL

ENL ~ Sp.rich + SLOPE + CURV_PL + CURV_PR

mic.bio ~ ENL +
          TSP.SRL + TSP.RD + FDis.SRL + RD +
          Soil.C.2018 +
          temperature + Soil.humidity +
          Soil.N.2018 +
          litter.CN

temperature ~ ENL
Soil.humidity ~ CN.litterfall + TSP.SRL
Soil.N.2018 ~ CN.litterfall + FDis.SRL + SRL
litter.CN ~ CN.litterfall + ENL + TSP.FRic.RD + AM.ECM
'
```

Results

Explained variance

Variable	R-squared (%)
Soil.C.2018	18.9
Soil.C.2010	10.8
ENL	34.5
mic.bio	54.2
temperature	20.2
Soil.humidity	15.0
Soil.N.2018	6.3
litter.CN	26.1

Grouped summary

Relation	Effect size
Environment ~ Neighbors aboveground productivity & traits	1.2486435
Environment ~ Neighbors root traits	0.5059349
Environment ~ TSP root traits	0.5529788
Environment ~~ Environment	0.8391214
Mic. biomass ~ Environment	0.6101499
Mic. biomass ~ Neighbors root traits	0.1750829
Mic. biomass ~ Soil C 2018	0.5616956
Mic. biomass ~ TSP root traits	0.3851936
Mic. biomass ~~ Mic. biomass	0.1101626
Neighbors aboveground productivity & traits ~ Topography	0.5162855
Neighbors aboveground productivity & traits ~ Tree species richness	0.2479654
Neighbors aboveground productivity & traits ~~ Neighbors aboveground productivity & traits	0.1626816
Soil C 2010 ~ Topography	0.5325651
Soil C 2010 ~~ Soil C 2010	0.2215193
Soil C 2018 ~ Neighbors aboveground productivity & traits	0.4486605
Soil C 2018 ~ Neighbors root traits	0.2840931
Soil C 2018 ~ Soil C 2010	0.2632743
Soil C 2018 ~~ Soil C 2018	0.2063896

Full summary

Response	Operator	Explanatory	Estimate	SE	p-value
Soil.C.2018	~	Soil.C.2010	0.2632743	0.0767598	0.0006039
Soil.C.2018	~	CURV_PL	0.1635416	0.0873079	0.0610464
Soil.C.2018	~	CN.litterfall	-0.1999060	0.0771914	0.0096047
Soil.C.2018	~	ENL	0.2487545	0.0835580	0.0029106
Soil.C.2018	~	TSP.RD	0.1402688	0.0916951	0.1260836
Soil.C.2018	~	RD	-0.2840931	0.0949800	0.0027799
Soil.C.2010	~	SLOPE	0.1753616	0.0830657	0.0347620
Soil.C.2010	~	CURV_PL	0.3572036	0.0830657	0.0000171
ENL	~	Sp.rich	0.2479654	0.0687963	0.0003129
ENL	~	SLOPE	0.2151084	0.0723778	0.0029585
ENL	~	CURV_PL	-0.1897770	0.0971164	0.0506872
ENL	~	CURV_PR	0.3011770	0.1008265	0.0028165
mic.bio	~	ENL	-0.0058516	0.0638538	0.9269837
mic.bio	~	TSP.SRL	0.1962537	0.0728819	0.0070863
mic.bio	~	TSP.RD	0.1889399	0.0827128	0.0223546
mic.bio	~	FDis.SRL	-0.0425622	0.0571996	0.4568165
mic.bio	~	RD	-0.1750829	0.0691727	0.0113706
mic.bio	~	Soil.C.2018	0.5616956	0.0546386	0.0000000
mic.bio	~	temperature	-0.2864916	0.0600708	0.0000018
mic.bio	~	Soil.humidity	-0.1118651	0.0566677	0.0483756
mic.bio	~	Soil.N.2018	-0.0257387	0.0545010	0.6367402
mic.bio	~	litter.CN	0.2117932	0.0556415	0.0001410
temperature	~	ENL	-0.4492955	0.0719909	0.0000000
Soil.humidity	~	CN.litterfall	-0.2589748	0.0765287	0.0007143
Soil.humidity	~	TSP.SRL	-0.3562751	0.0765287	0.0000032
Soil.N.2018	~	CN.litterfall	-0.1512382	0.0795412	0.0572520
Soil.N.2018	~	FDis.SRL	-0.1530869	0.0799635	0.0555616
Soil.N.2018	~	SRL	0.1590020	0.0798791	0.0465322
litter.CN	~	CN.litterfall	0.2412895	0.0743530	0.0011737
litter.CN	~	ENL	-0.2990837	0.0720974	0.0000335
litter.CN	~	TSP.FRic.RD	0.1967037	0.0719495	0.0062586
litter.CN	~	AM.ECM	0.3469329	0.0742888	0.0000030
Soil.C.2018	~~	Soil.C.2018	0.2063896	0.0235203	0.0000000
Soil.C.2010	~~	Soil.C.2010	0.2215193	0.0252445	0.0000000
ENL	~~	ENL	0.1626816	0.0185393	0.0000000
mic.bio	~~	mic.bio	0.1101626	0.0125542	0.0000000
temperature	~~	temperature	0.1982378	0.0225913	0.0000000
Soil.humidity	~~	Soil.humidity	0.2111682	0.0240649	0.0000000
Soil.N.2018	~~	Soil.N.2018	0.2327641	0.0265259	0.0000000
litter.CN	~~	litter.CN	0.1969512	0.0224447	0.0000000
CURV_PL	~~	CURV_PL	0.2483766	0.0000000	NA
CURV_PL	~~	CN.litterfall	0.0176342	0.0000000	NA
CURV_PL	~~	TSP.RD	-0.0364343	0.0000000	NA
CURV_PL	~~	RD	-0.0332459	0.0000000	NA
CURV_PL	~~	SLOPE	-0.0995559	0.0000000	NA
CURV_PL	~~	Sp.rich	0.0228885	0.0000000	NA

(continued)

Response	Operator	Explanatory	Estimate	SE	p-value
CURV_PL	~~	CURV_PR	-0.1797195	0.0000000	NA
CURV_PL	~~	TSP.SRL	0.0113570	0.0000000	NA
CURV_PL	~~	FDis.SRL	-0.0351465	0.0000000	NA
CURV_PL	~~	SRL	0.0121095	0.0000000	NA
CURV_PL	~~	TSP.FRic.RD	-0.0020780	0.0000000	NA
CURV_PL	~~	AM.ECM	0.0430630	0.0000000	NA
CN.litterfall	~~	CN.litterfall	0.2483766	0.0000000	NA
CN.litterfall	~~	TSP.RD	-0.0382589	0.0000000	NA
CN.litterfall	~~	RD	-0.0754086	0.0000000	NA
CN.litterfall	~~	SLOPE	0.0082185	0.0000000	NA
CN.litterfall	~~	Sp.rich	-0.0201507	0.0000000	NA
CN.litterfall	~~	CURV_PR	-0.0147584	0.0000000	NA
CN.litterfall	~~	TSP.SRL	-0.0594828	0.0000000	NA
CN.litterfall	~~	FDis.SRL	-0.0380842	0.0000000	NA
CN.litterfall	~~	SRL	-0.0363731	0.0000000	NA
CN.litterfall	~~	TSP.FRic.RD	-0.0178646	0.0000000	NA
CN.litterfall	~~	AM.ECM	-0.0608569	0.0000000	NA
TSP.RD	~~	TSP.RD	0.2483766	0.0000000	NA
TSP.RD	~~	RD	0.1472590	0.0000000	NA
TSP.RD	~~	SLOPE	0.0013656	0.0000000	NA
TSP.RD	~~	Sp.rich	0.0031850	0.0000000	NA
TSP.RD	~~	CURV_PR	0.0277585	0.0000000	NA
TSP.RD	~~	TSP.SRL	-0.1526118	0.0000000	NA
TSP.RD	~~	FDis.SRL	0.0417814	0.0000000	NA
TSP.RD	~~	SRL	-0.0784069	0.0000000	NA
TSP.RD	~~	TSP.FRic.RD	0.1007104	0.0000000	NA
TSP.RD	~~	AM.ECM	0.0438371	0.0000000	NA
RD	~~	RD	0.2483766	0.0000000	NA
RD	~~	SLOPE	0.0009270	0.0000000	NA
RD	~~	Sp.rich	0.0146583	0.0000000	NA
RD	~~	CURV_PR	0.0575185	0.0000000	NA
RD	~~	TSP.SRL	-0.0763342	0.0000000	NA
RD	~~	FDis.SRL	0.0557553	0.0000000	NA
RD	~~	SRL	-0.1397787	0.0000000	NA
RD	~~	TSP.FRic.RD	0.0324377	0.0000000	NA
RD	~~	AM.ECM	0.0800884	0.0000000	NA
SLOPE	~~	SLOPE	0.2483766	0.0000000	NA
SLOPE	~~	Sp.rich	-0.0167863	0.0000000	NA
SLOPE	~~	CURV_PR	0.1002248	0.0000000	NA
SLOPE	~~	TSP.SRL	0.0101562	0.0000000	NA
SLOPE	~~	FDis.SRL	-0.0000568	0.0000000	NA
SLOPE	~~	SRL	0.0014794	0.0000000	NA
SLOPE	~~	TSP.FRic.RD	-0.0252828	0.0000000	NA
SLOPE	~~	AM.ECM	-0.0436689	0.0000000	NA
Sp.rich	~~	Sp.rich	0.2483766	0.0000000	NA
Sp.rich	~~	CURV_PR	-0.0686821	0.0000000	NA
Sp.rich	~~	TSP.SRL	0.0098234	0.0000000	NA
Sp.rich	~~	FDis.SRL	0.0794879	0.0000000	NA

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Response	Operator	Explanatory	Estimate	SE	p-value
Sp.rich	~~	SRL	0.0135911	0.0000000	NA
Sp.rich	~~	TSP.FRic.RD	0.0419447	0.0000000	NA
Sp.rich	~~	AM.ECM	0.0171725	0.0000000	NA
CURV_PR	~~	CURV_PR	0.2483766	0.0000000	NA
CURV_PR	~~	TSP.SRL	-0.0123199	0.0000000	NA
CURV_PR	~~	FDis.SRL	-0.0095466	0.0000000	NA
CURV_PR	~~	SRL	-0.0384493	0.0000000	NA
CURV_PR	~~	TSP.FRic.RD	-0.0060808	0.0000000	NA
CURV_PR	~~	AM.ECM	-0.0153894	0.0000000	NA
TSP.SRL	~~	TSP.SRL	0.2483766	0.0000000	NA
TSP.SRL	~~	FDis.SRL	0.0212875	0.0000000	NA
TSP.SRL	~~	SRL	0.1250474	0.0000000	NA
TSP.SRL	~~	TSP.FRic.RD	-0.0318750	0.0000000	NA
TSP.SRL	~~	AM.ECM	-0.0632655	0.0000000	NA
FDis.SRL	~~	FDis.SRL	0.2483766	0.0000000	NA
FDis.SRL	~~	SRL	0.0442603	0.0000000	NA
FDis.SRL	~~	TSP.FRic.RD	0.0825569	0.0000000	NA
FDis.SRL	~~	AM.ECM	-0.0094878	0.0000000	NA
SRL	~~	SRL	0.2483766	0.0000000	NA
SRL	~~	TSP.FRic.RD	0.0121057	0.0000000	NA
SRL	~~	AM.ECM	-0.0982008	0.0000000	NA
TSP.FRic.RD	~~	TSP.FRic.RD	0.2483766	0.0000000	NA
TSP.FRic.RD	~~	AM.ECM	0.0024365	0.0000000	NA
AM.ECM	~~	AM.ECM	0.2483766	0.0000000	NA