



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 *abiotic¹* 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 CO₂ and its effects on climate change are responsible for species extinctions (IPBES 2019). Likewise, increasing atmospheric CO₂ is increasing seawater acidity

and leads to species extinctions in marine ecosystems (Bindoff al. 2019). et 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 2008; et al.



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 microclimatic 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 biodiversityecosystem 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. of tree-tree interactions on ecosystem



2021). This design aims to study the effect **Fig. 5: BEF-China Site A**: elevation plot and diversity treatments (Bruelheide *et al.* 2014). The plot elevation ranging from 105 to 280 m.

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. 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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