

Grant Proposal

MultiTroph: Multi-trophic interactions in a forest biodiversity experiment in China

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Abstract

Biodiversity-ecosystem functioning (BEF) research has shown that ecosystem functioning and stability are closely linked to biodiversity. A cornerstone of this field is the BEF-China research platform, i.e. the world's largest forest biodiversity experiment in subtropical China. It has demonstrated that tree diversity enhances productivity, carbon

sequestration and ecosystem stability. However, the strength of these positive tree diversity effects varies widely across forests, possibly because higher trophic levels (such as herbivores and predators) mediate how biodiversity influences ecosystem functioning.

To better understand how tree diversity influences higher trophic levels and their contributions to forest functioning, the German Research Foundation (DFG) is funding the project *MultiTroph*. *MultiTroph* quantifies species interactions and integrates them into food webs to understand when and why ecosystem functions change or destabilise with species loss. We expect that trophic interaction networks reveal how species share or separate their ecological roles, with more niche overlap in species-rich forests and more niche specialisation in species-poor forests.

Here, we outline our conceptual framework and research goals. We are convinced that *MultiTroph* will expand existing BEF research and provide a more holistic understanding of the role of multi-trophic food webs in forest ecosystems.

Keywords

Biodiversity-ecosystem functioning (BEF), multi-trophic interactions, forest ecosystems, multi-trophic networks, BEF-China, DNA barcoding

Authors' note

This publication is derived from a grant proposal and contains selected portions of the original document with certain parts condensed for brevity or slightly modified to improve clarity. The proposal was submitted to the German Research Foundation (DFG) in September 2021 and we received the positive decision in April 2022. The DFG Research Unit FOR 5281 “Multi-Trophic Interactions in a Forest Biodiversity Experiment in China” secured funding for a four-year period and commenced in October 2022. The project is coordinated by Prof. Dr. Alexandra-Maria Klein, Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Germany. Prof. Dr. Chao-Dong Zhu, Institute of Zoology, Chinese Academy of Sciences, is responsible for coordinating the associated research activities at the Chinese site. The activities of the Chinese researchers are not funded by the DFG.

Introduction

Forests are crucial for the provision of essential ecosystem services and provide habitats for the largest share of global terrestrial biodiversity (Brockerhoff et al. 2017, van der Plas et al. 2018, Watson et al. 2018, Barlow et al. 2018). Recent research highlights their role in mitigating global environmental change through diversification and reforestation (Hua et al. 2016, Huang et al. 2018, Ammer 2019, Baeten et al. 2019, Messier et al. 2021), influencing policy recommendations (Verdone and Seidl 2017, IPCC 2018, IUCN 2019, UNEP 2019). However, the best approaches for restoring degraded forests and planting

new ones are still debated (Antonelli 2019, Chazdon and Brancalion 2019, Lewis et al. 2019).

Biodiversity-ecosystem functioning (BEF) research can provide insights into this question. BEF studies have shown that biodiverse communities enhance biomass production, carbon sequestration and ecosystem stability (Hooper et al. 2005, Cardinale et al. 2012, Tilman et al. 2014, van der Plas 2019). Recent work incorporates higher trophic levels (herbivores, pollinators etc.) into BEF research (Hillebrand and Matthiessen 2009, Thébault and Fontaine 2010, Petermann et al. 2010, Haddad et al. 2011, Pufal and Klein 2013, Hines et al. 2015, Gossner et al. 2016, Seabloom et al. 2017, Schuldt et al. 2018, Guo et al. 2021), but understanding their mechanisms and interactions requires further investigation (Wang and Brose 2018, Fornoff et al. 2019, Penone et al. 2019, Schuldt et al. 2019, Fornoff et al. 2021).

An integrative research perspective is essential due to drastic declines in higher trophic level organisms that maintain key ecosystem functions (Hallmann et al. 2017, Vogel 2017, Leather 2018, Eisenhauer et al. 2019, Seibold et al. 2019, Didham et al. 2020). For forests, trophic interactions depend on tree diversity (Staab et al. 2016, Leles et al. 2017, Nell et al. 2018, Fornoff et al. 2019), which, in turn, have repercussions on tree growth (Schuldt et al. 2017). Therefore, BEF research must comprise ecological niche properties and species interactions across multiple trophic levels (Thébault et al. 2007, Thébault and Fontaine 2010, Hines et al. 2015, Wang and Brose 2018, Seibold et al. 2018). The *MultiTroph* Research Unit integrates BEF relationships across trophic levels using the well-established experiment *BEF-China* in southeast China (Bruehlheide et al. 2014). The goals include understanding how primary producer biodiversity influences multiple trophic levels, how interaction networks respond along diversity gradients and how these interactions affect the stability of consumer communities and overall ecosystem functioning (Ebeling et al. 2012, Staab et al. 2015, Soliveres et al. 2016, Seabloom et al. 2017, Simons and Weisser 2017, Peters et al. 2019).

The BEF-China experiment

The BEF-China experiment is currently the largest forest BEF experiment worldwide (Bruehlheide et al. 2014) and located in the Chinese subtropics in the Jiangxi Province, near the village of Xingangshan (29°06' N/117°55' E). The climate of the region is subtropical (Köppen classification: Cfa) and characterised by hot and humid summers contrasting cool and relatively dry winters (mean annual temperature 16.7°C, mean annual precipitation 1821 mm; see Yang et al. (2013)). The potential natural vegetation of the region is a diverse mixed evergreen broad-leaved forest with roughly equal contributions of deciduous and evergreen tree species. Old growth forest is numerically dominated by evergreen tree species, such as *Castanopsis eyrei* (Fagaceae) and *Schima superba* (Theaceae) (Bruehlheide et al. 2011). Today, natural secondary forests are mostly restricted to steeper slopes and remote sites; land use is dominated by housing, smallholder agriculture and plantations of *Pinus massoniana* (Pinaceae) and *Cunninghamia lanceolata* (Cupressaceae).

The BEF-China experiment aims to determine how tree species diversity impacts ecosystem functioning. Established during the DFG-funded research unit FOR 891 (2008-2016), it includes 566 plots of 25.8 x 25.8 m, each containing 400 trees planted 1.29 m apart. The experiment uses 42 local tree species, with plots featuring 1, 2, 4, 8, 16 or 24 species, including monocultures of key conifers. Species composition follows random or trait-based extinction scenarios (Bruehlheide et al. 2014, Chen et al. 2020).

The plots are spread across two sites (A and B, 4.5 km apart), planted in 2009 and 2010, with independent species pools. A subset of 300 "core plots" (150 per site) excludes shrub-only plots, commercial conifer monocultures, free succession plots and genetic diversity plots. On these 300 plots, many long-term variables of functions related to trophic interactions have been measured (e.g. herbivory, trophobioses, fungal pathogens) in the past years. *MultiTroph* therefore carries out all main research activities on these core plots and closely collaborates with the Sino-German International Research Training Group TreeDi (林地 DFG GRK 2324 "Tree Diversity Interactions: The role of tree-tree interactions in local neighbourhoods in Chinese subtropical forests") to cover a subset of 505 out of the total of 566 plots of the whole BEF-China experimental platform.

While the general strategy within BEF-China is to conduct all measurements on all core plots, 32 plots per site (64 in total) are treated as so-called VIPs (very intensively studied plots), which have been particularly intensively studied in the past. The VIP plots are representatives of the central design and constitute a diversity gradient from 1 - 24 tree species per plot.

Within the plant ecological focus of FOR 891, first studies on trophic interactions and their dependency on tree diversity were conducted. Preliminary evidence indicates that tree diversity can stabilise trophic interaction networks (Staab et al. 2015, Fornoff et al. 2019). In the early successional stage of the BEF-China experiment, generalist herbivores feeding on several tree species were dominant (Zhang et al. 2017), which could explain the positive relationship between tree diversity and leaf damage (Schuldt et al. 2015), indicating associational susceptibility. Damage caused by herbivores and by leaf pathogenic fungi was positively related and additive, but had contrasting effects on tree growth. Trees (over)compensated growth in response to herbivore, but not to fungal pathogen damage, which was attenuated by tree diversity (Schuldt et al. 2017a). Leaf damage was also positively related to infestations with sap-sucking insects, such as aphids tended by ants (so called trophobiosis), indicating lower per tree resistance against one herbivore guild when trees are investing in defence against a different herbivore guild (Schuldt et al. 2017c). Interestingly, leaf damage on trees infested with trophobioses was higher when tree diversity was low, but decreased under high diversity, suggesting a net positive effect of Hemiptera-ant interactions when tree diversity is high. In this regard, single behaviourally dominant predatory ant species that benefit from high tree diversity may have particularly pronounced effects on herbivore suppression (Schuldt et al. 2017c). Likely, tree diversity effects on higher trophic levels are strongest at the plot level, as various components of leaf litter ant diversity (abundance, species

richness, phylogenetic diversity) increase only with plot level, but not with local neighbourhood tree species richness (Skarbek et al. 2020).

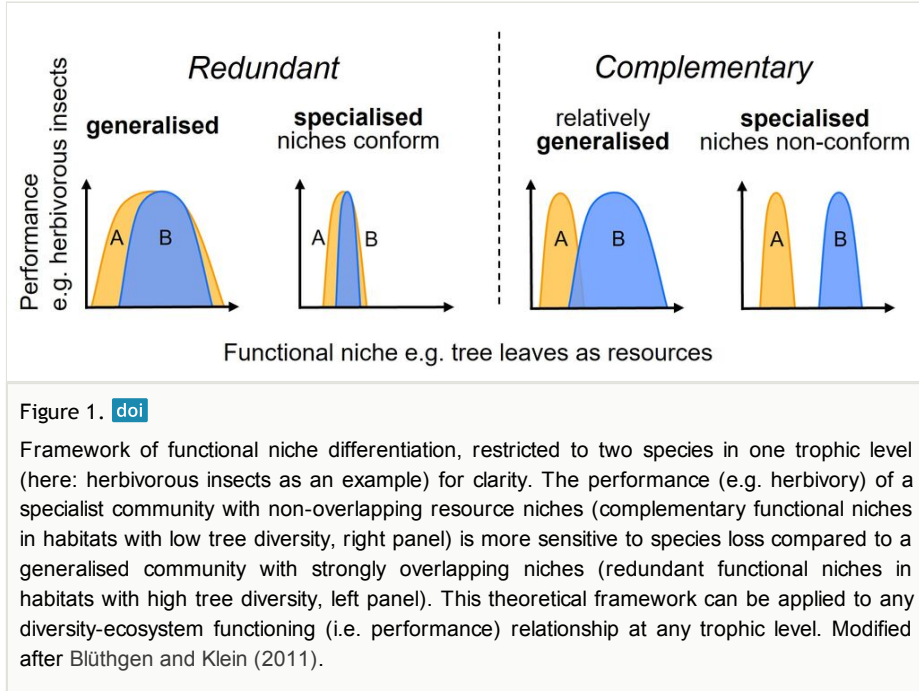
Research in other forest biodiversity experiments confirmed the general importance of combining all trophic levels and their trophic interactions (including nutrients) that mediate biodiversity-ecosystem functioning relationships (e.g. Oelmann et al. (2010), Plath et al. (2011), Haase et al. (2015), Muiruri et al. (2016), Nell et al. (2018)). However, the results on trophic interactions, their relationship with tree diversity and our understanding of their consequence for tree performance and growth are still rudimentary and, so far, restricted to a few rather specific study systems (see also Grossman et al. (2018)). A central aim of the Research Unit *MultiTroph* is to comprehensively investigate interactions at the plot level involving all important trophic and functional groups of primary producers and aboveground consumers.

Objectives

The overall objective of *MultiTroph* is to identify mechanisms underlying the relationships of biodiversity with ecosystem functions across trophic levels. *MultiTroph* quantifies species interactions between primary producers and different trophic and functional groups of consumers and ultimately connects the different interaction types to large food webs to increase our understanding of how, why and when ecosystem functions are destabilised with species loss. The studied interactions focus on functional redundancy and complementarity identified via specific interaction modules including key trophic levels. Our guiding principle is the expectation that quantitative trophic interaction networks help to identify niche overlaps within producer-consumer interactions (e.g. tree niches for herbivorous insects and their performance in herbivory) in generalised/redundant communities with overlapping niches in habitats with high tree diversity compared to specialised/complementary communities with separated niches in specialised/complementary communities with separated niches in habitats with low tree diversity (resource, for example, tree resource use, Fig. 1).

Identifying functional niches across multiple trophic levels, therefore, helps to understand the performance of the respective function. In general, it is assumed that a specialised community shows a linear relationship with the performed function while, in a generalised community, functional performance saturates with increasing species richness (Blüthgen and Klein 2011, Fig. 2). The functional performance of specialised trophic interactions is, therefore, expected to be less stable with respect to species loss than that of generalised interactions (Thébault and Fontaine 2010), but can reach higher performance levels at high diversity, since specialists typically have a higher per capita performance (Dunne et al. 2002a, Srinivasan et al. 2007). Nevertheless, a specialised network with clearly separated niches may involve more species at the consumer level because of reduced inter-specific competition and this may buffer the expected lower functional redundancy. The trade-offs between different specialisation-performance/functioning mechanisms (e.g. complementarity/low redundancy versus competition) are, to the best of our knowledge, not yet studied in the context of plant diversity, but are

essential to increase our knowledge in BEF research and can only be assessed with quantitative trophic interaction networks.



Traditionally, consumer responses to changes in plant diversity (and thus, primary producers) have been assessed in the field by measuring the presence/absence or abundance of particular taxa across a diversity gradient, while ignoring the presence and strength of trophic interactions between taxa (e.g. Haddad et al. (2009), Mumme et al. (2015)). However, it is the trophic interactions between species that influence the consumer communities (McCann 2000). Therefore, examining the strength and patterns of trophic interactions in species interaction networks is important to understand mechanisms driving the relationship between diversity and stability of consumer communities (Tylianakis et al. 2010, Poisot et al. 2013, Fornoff et al. 2019). There are at least three pathways that describe how plant diversity (primary producers) can influence higher trophic level (consumer) communities. Firstly, the abundance and diversity of consumers at each trophic level can influence the number of possible interaction partners in the associated trophic levels (Haddad et al. 2009, Scherber et al. 2010, Guo et al. 2021). Second, the number and strength of connections and the degree of specialisation influence the stability of the food web (McCann et al. 1998, Ebeling et al. 2011, Staab et al. 2015). Third, modularity of food webs caused by subsets of species that interact more with each other than with other species in the network can limit the propagating effects of trophic interactions to more localised modules within the network (Newman 2006, Dormann et al. 2017). Empirical evidence supports the existence of each of these pathways, suggesting that they are not mutually exclusive and operate concurrently. Linking the interaction network modules of all consumer groups to the experimental tree

diversity gradients (based on both random and non-random, trait-based extinction scenarios) of the BEF-China experiment (Bruehlheide et al. 2014) lead to specific predictions of which traits, species or trophic guilds are most affected by the loss of tree diversity and specific tree species. By:

1. measuring the abundance and diversity and
2. quantifying the interaction modules of multiple trophic groups, we are able to construct comprehensive food webs that allow us to
3. understand the functional consequences of tree species loss for forest ecosystem functionality.

Subprojects (SP)

The project includes six sub-projects (SP1-SP6) and two central projects (coordination; data management and synthesis) to collectively sample and analyse data on the BEF-China platform:

- SP1 focuses on decomposition and deadwood interactions (PIs: Prof. Dr. Heike Feldhaar, University of Bayreuth / Prof. Dr. Simon Thorn, University of Marburg);
- SP2 studies soil-plant element flow and stoichiometry (PIs: Prof. Dr. Yvonne Oelmann, Prof. Dr. Thomas Scholten, Dr. Steffen Seitz, University of Tübingen);
- SP3 investigates plant-herbivore-predator food webs and functions (PIs: Assoc. Prof. Dr. Jana S. Petermann, University of Salzburg / Prof. Dr. Andreas Schuldt, University of Göttingen);
- SP4 analyses cavity-nesting bees, wasps and related trophic interactions (PIs: Prof. Dr. Alexandra-Maria Klein, Dr. Felix Fornoff, University of Freiburg / Dr. Manuela Sann, Museum of Natural History Bern);
- SP5 examines seed-predating invertebrates (PIs: Prof. Dr. Alexandra Erfmeier, Prof. Dr. Tim Diekötter, Kiel University);
- SP6 studies ant trophic interactions and functions (PIs: Prof. Dr. Michael Staab, University of Lüneburg / Prof. Dr. Heike Feldhaar, University of Bayreuth).

The central projects handle administration, fieldwork coordination (Z1), data management and synthesis of multi-functionality (Z2). Data are collected from 300 core BEF-China plots, targeting diversity, biomass and function across the tree diversity gradient. For some interactions, data are focused on the 64 VIP plots. Various methods, including DNA sequencing and stable isotope analysis, quantify trophic interactions within each SP. *MultiTroph* models multi-trophic interaction networks linked to a large food web, predicting niche shifts when tree species are lost. The project synthesises diversity and function data to understand species richness drivers and uses long-term data to study how multi-diversity and ecosystem functioning evolve through succession stages.

In the following section, we provide a detailed description of the objectives and methods for each subproject as well as the central project Z2.

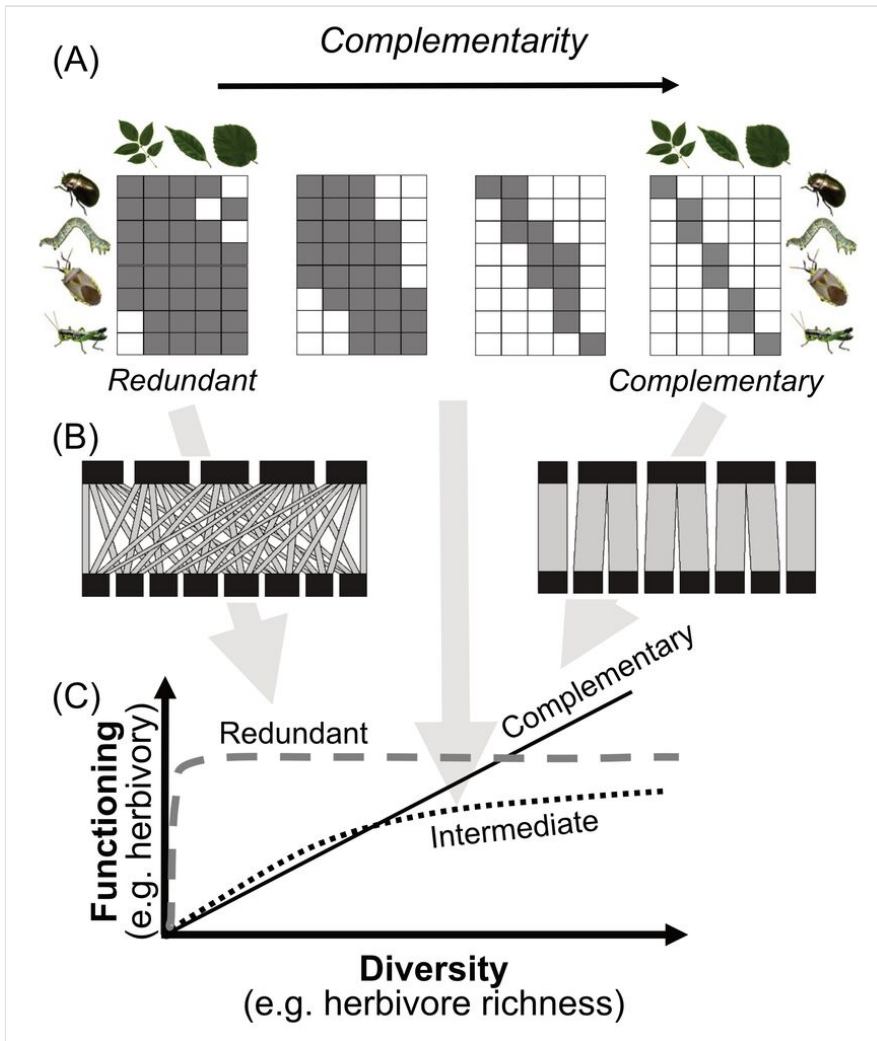


Figure 2. [doi](#)

Conceptual representation of niche complementarity in trophic interaction networks, (A) illustrated as a matrix with the example of herbivore species as rows, tree species as columns and realised interactions as grey cells. Specialisation increases from left to right; (B) Exemplary quantitative trophic interaction networks (left: generalised; right: specialised); (C) The shape of the biodiversity-functioning relationship depends on the extent of functional complementarity (redundant/generalised, intermediate and complementary/specialised). Modified after Blüthgen and Klein (2011).

SP1: Wood decomposition and decomposer interactions

The overall objective of SP1 is to characterise the bottom-up effects of tree diversity on: (i) the amount and diversity of naturally occurring deadwood to assess resource availability

and quality for saproxylic insects and nutrient input into soil along this decomposition pathway; (ii) the (functional trait) diversity of saproxylic insect communities in naturally occurring deadwood and how these are shaped indirectly by tree diversity through changes in biotic interactions that may influence community assembly; (iii) functional traits of saproxylic insects in deadwood and their effect on wood decomposition rate using experimentally exposed deadwood with and without insect exclusion; and (iv) comparison of deadwood colonisation and decomposition rate of suspended deadwood with deadwood on the ground. Our work is organised accordingly into four work packages (WP) following the main aims.

Workpackage 1: Natural deadwood diversity and abundance related to tree diversity

WP1 characterises the amount and diversity of deadwood along the tree diversity gradient. Deadwood diversity and amounts should increase with tree functional diversity through initial variation in traits (wood and bark traits, diameter, standing or lying) and the entailing differences in decomposability and range of decay stages within a plot (Guo et al. 2021). In low-diversity plots, the amount of deadwood strongly depends on tree species identity. In such plots with a single tree species with relatively slow growth and high wood density, only comparatively little deadwood should be available at this relatively young area of the forest stand since high-density wood is associated with low mortality rates (at least in tropical forests). In contrast, fast-growing tree species that tend to have low-density wood (Chave et al. 2009, Pietsch et al. 2014) should have lower mechanic stability and may, thus, be more susceptible to disturbances and breakage. Fast growing tree species may also have reached a growth stage where branches start to break off. Plots with such fast growing tree species should, therefore, contain more deadwood. We expect that the identity effect (variance of deadwood abundance) is very strong between plots comprised of different monocultures or only very few species. The variance in deadwood amounts should decrease with higher tree diversity. As increasing tree species richness can increase productivity and carbon storage in forests (Fichtner et al. 2018, Hildebrand et al. 2021), including increased carbon stocks in deadwood (Liu et al. 2018), we expect the mean amount of deadwood per plot to be positively correlated with tree diversity.

Deadwood volume and diversity are determined in all 300 core plots to obtain information on the natural abundance and diversity of deadwood along the tree diversity gradient. We measure deadwood according to type (standing or lying), tree species, decay stage, diameter and length for objects in two size classes (> 2 cm to 7 cm diameter and > 7 cm diameter) within a 10 x 10 m subplot in all plots. Additionally, we assess deadwood-related microhabitats on living trees, such as tree hollows and other structures as described by Larrieu et al. (2018). We use linear mixed models to test the relationship between tree diversity and the amount as well as diversity of dead wood.

Workpackage 2: Impacts of tree diversity on diversity and functional traits of saproxylic insect communities in naturally occurring deadwood

WP2 disentangles the direct effects of tree diversity on saproxylic insect communities through the amount and quality of deadwood generated, from the indirect effects mediated by structural heterogeneity influencing microclimate or by altering biotic interactions, for example, through changes in abundance and functional traits of potential competitors or predators. Abundance and diversity of saproxylic insects is expected to be positively correlated with the amount and diversity of deadwood (Seibold and Thorn 2018, Thorn et al. 2020). In boreal and temperate forests, the enrichment of deadwood amount generally resulted in an increased abundance and diversity of saproxylic insects (Seibold et al. 2017, Sandström et al. 2019). In a global-scale study, the retention of larger proportions of deadwood in forests after disturbances was positively correlated with the diversity of saproxylic taxa (Thorn et al. 2020). Although data on subtropical and tropical forests are scarce, studies suggest that higher amounts (Lachat et al. 2006) or deadwood of larger diameter (Grove 2002) have positive effects on saproxylic insect diversity. With higher tree diversity the diversity of deadwood (lying/standing, diameter, decay stage) also increases with respect to wood traits. Studies in tropical cloud forests identified tree species identity and decay stage as the most important parameters influencing saproxylic beetle communities in deadwood (Ramírez-Hernández et al. 2019). Likewise, macroinvertebrate communities differed between deadwood of different tree species (Pietsch et al. 2019) and attractiveness of deadwood strongly related to wood traits, such as wood density, C:N ratio or the content of lignins and phenolics (Pietsch et al. 2019, Guo et al. 2021, Wu et al. 2021).

Tree diversity affects structural heterogeneity within forest stands and consequently also the microclimate. For saproxylic beetles, microclimatic conditions and, of lesser importance, host tree identity have been identified as important determinants for local communities (Seibold et al. 2016, Schauer et al. 2018). In tropical forests, termites react more strongly to differences in canopy openness due to forest disturbance or degradation than ants with decreasing abundances and species richness (Luke et al. 2014, Ewers et al. 2015). We, therefore, expect that termite species richness and abundance increases with tree diversity, while ant species richness and abundance remain at approximately similar levels along the tree diversity gradient. However, ants may interfere more strongly with termites with higher tree diversity as predatory ants have been shown to increase with tree diversity (Staab et al. 2014).

To characterise the local species pool of saproxylic insects, we sample insects from five deadwood objects covering the natural range of deadwood types at each plot. This yields data on the regional species pool over all 300 core plots. For the selected deadwood objects, we search the surface, the area under bark and the inner part of the wood as described in Müller et al. (2016). Ant species are determined in collaboration with SP6. Termites and adult beetles are identified to genus or, if possible, species level, using taxonomic keys supported by DNA barcoding. For beetles, we expect to find mainly larvae within the deadwood objects, thus requiring the use of DNA barcoding for identification. Morphometric measurements are taken for ant workers of social insects

and adult beetles for functional trait analyses (Donovan et al. 2001, Davies et al. 2003, Parr et al. 2017, Hagge et al. 2019). While saproxylic beetles are often highly dependent on deadwood, ants and termites may use deadwood as nest site only or use it as shelter above their soil nests while foraging elsewhere (Blüthgen and Feldhaar 2010, Dossa et al. 2020). To capture the proportion of deadwood nesting (and feeding) ants and termites within the ground-living community, we compare ant and termite communities sampled from leaf litter within the 300 core plots (data for ants and samples of termites are provided by SP6) and determine the subset of species using deadwood as nest site or nutritional resource. In addition to the samples from pitfall traps and flight interception traps in SP3 and from leaf litter from SP6, we search for signs of termites above ground in two 5 x 5 m quadrats (searched for 20 min each) and search soil cores (five cores per plot 12 x 12 cm for 10 min each) to capture soil-dwelling termites. This allows us to test whether the presence of dominant and/or more predatory ant colonies in the surroundings of deadwood potentially influences colonisation of the deadwood objects by other saproxylic insects. Especially, termites may be preyed upon by ants (Tuma et al. 2020) and may, thus, avoid exposed deadwood in areas with high ant activity (but see Basset et al. (2020)).

The taxonomic diversity of communities is compared over the tree diversity gradient using a unified statistical framework, based on Hill numbers (Hsieh et al. 2016). This framework provides coverage-based standardisations of diversity, including taxonomic, phylogenetic and functional diversity (Chao et al. 2020). These measures are tested against tree diversity. Based on the DNA barcoding data of saproxylic insects, we analyse the interaction between deadwood and the insects using network analysis (with R package *bipartite*). We expect an increasing complexity of the plot-level interaction networks along the tree diversity gradient due to a stronger specialisation towards deadwood with a particular quality (e.g. tree species or decay stage) with increasing deadwood diversity. Biotic interactions amongst saproxylic insects cannot be captured well using a bipartite network, since interactions may be competitive, predatory and facilitative. In addition, interaction networks can only capture saproxylic insects co-occurring within the same deadwood object (i.e. established links in a network), while the absence of a link (e.g. through competitive exclusion) cannot be captured or explained. We, therefore, also analyse co-occurrence patterns, based on co-occurrence of species within the same piece of deadwood as well as co-occurrence within the same plot using presence/absence data and calculate the C-score (Gotelli 2000). We subsequently follow the approach of Ellwood et al. (2016), which is similar to the C-score on the community level, but is able to test for segregation (i.e. competitive exclusion) as well as aggregation simultaneously. Pairwise occurrence of species is also tested using a probabilistic approach implemented in the R-package *cooccur* (Griffith et al. 2016). We additionally use piecewise structural equation modelling (pSEM; Lefcheck (2016)) to test the direct and indirect effects of abiotic factors (temperature, humidity, elevation; measured in Zproject) as well as tree species diversity, deadwood amount, ant abundance (and functional traits) and termite abundance on the decomposer community.

Workpackage 3: Impacts of tree diversity, wood traits and saproxylic insects on decomposition of lying deadwood

WP3 disentangles the contribution of wood traits and saproxylic insect communities as well as their biotic interactions (facilitation, competition, predation) to wood decomposition along the tree diversity gradient. Wood traits (Liu et al. 2015, Pietsch et al. 2019, Guo et al. 2021, Wu et al. 2021) as well as decomposer communities (Pietsch et al. 2019, Wu et al. 2021) influence deadwood decomposition rate, with decomposer communities differing between wood types, suggesting specialisation of at least some saproxylic species (Pietsch et al. 2019). Only one study (Wu et al. 2021) tested the effects of tree diversity on wood decomposition within BEF-China (in 2015/2016, six to seven years after trees were planted). Here, the authors used fine woody debris (FWD) of seven different tree species and estimated the respective contribution of insects and fungi to the decomposition process. Results of Wu et al. (2021) were ambiguous, with positive effects of tree species diversity for the mass-loss rate of FWD of *Cunninghamia lanceolata*, but negative effects on that of *Schima superba* after one year. After two years, FWD in plots with higher tree species diversity showed increased fungal hyphal growth. Except for *C. lanceolata*, biotic factors explained more variation in mass loss than abiotic factors, underscoring their importance. The volume of a piece of deadwood (Grove 2002) as well as wood traits (Pietsch et al. 2019, Guo et al. 2021) influence the decomposer communities and the decomposition rate. Larger insects (or larger colonies), such as cerambycid beetles or some *Camponotus* ant species, are only be attracted to larger pieces of leaf litter and dead wood (coarse woody debris, CWD). We generally expect a faster colonisation of CWD in plots with higher tree diversity since saproxylic insects should be locally more abundant and more diverse due to the higher diversity of naturally occurring deadwood (see WP1). Due to the importance of insects and especially termites in wood decomposition (Griffiths et al. 2019, Guo et al. 2021, Wu et al. 2021), the decomposition rate should be significantly lower when insects are excluded from CWD. When insects have access to CWD, we expect that high-quality CWD (e.g. with lower C:N-ratio, low levels of phenolic compounds or lignin and low wood density (Guo et al. 2021, Wu et al. 2021) is more attractive to insects, especially termites and are colonised first, resulting in a higher mass loss of this CWD in the first year. We furthermore expect lower decomposition rates of deadwood when CWD is colonised by ants due to an inhibitory effect of antimicrobial secretions on fungi (Brinker et al. 2019, Tragust et al. 2020) and potential exclusion of or predation on other saproxylic insects.

To disentangle the contribution of insects on wood decomposition and their biotic interactions along the tree diversity gradient, we set up an insect exclusion experiment in the 64 VIP plots using CWD from four focal tree species differing in wood traits (*Pinus massoniana* as a gymnosperm, *Schima superba* with intermediate wood quality; both have been used before in wood decomposition experiments in subtropical China, *S. superba* is also used in SP4; *Alniphyllum fortunei* which is softer and for decomposers of higher quality than *S. superba* due to its lower C:N-ratio, as well as *Quercus serrata*, whose wood contains high levels of phenolics (Guo et al. 2021, Wu et al. 2021)). We place four pieces of CWD per species into each plot: two where macroinvertebrates

(termites, ants, beetles) are excluded and two with access of macroinvertebrates. One set (excluded vs. access) is retrieved after 12 months and the second set after 18 months. Thus, we lay out 16 pieces of CWD in each of the 64 VIP plots (4 tree species x 2 insects excluded x 2 with insect access). We cut logs (~ 10 cm in diameter and 50 cm in length) from stems of young healthy trees without visible signs of insect or fungal activity. Before the CWD is exposed, we cut off a slice of 5 cm from both ends of the log for measurements of wood density. Initial wood density (and that after retrieval from the field) is calculated as dry mass per volume. The volume of the 5 cm sections is measured by water displacement. The sections are then dried at 60°C for 72 h and weighed to enable the calculation of dry mass per volume. Wood decomposition is measured as mass loss. All pieces of CWD are enclosed in nylon mesh bags (material available locally). For samples where insects are excluded, we use a mesh size of 0.25 mm and for those with insect access a mesh size of 7 mm. After retrieval of the CWD, we collect surface-active ants and termites. Fungal hyphal growth or fruiting bodies are examined visually. Then a slice of 5 cm is again cut off from both ends of the log for measurements of mass loss. The remaining 30 cm of CWD is transferred to emergence chambers for insect rearing (see Pietsch et al. (2019)). Morphometric measurements of all adult saproxylic insects are taken for functional trait analyses (see WP2). Individuals are determined to species level using taxonomic keys, aided by barcoding. Deadwood-nesting bees from our rearing samples are transferred to SP4 for determination. Communities of saproxylic insects are analysed, based on their functional traits. To test the effect of different factors on wood decomposition (measured as mass loss), we use linear mixed effects models, with insect treatment (access or exclusion), wood type, tree diversity of the plots, harvest time, as well as their interactions as fixed factors. We use variance partitioning to examine the variance explained per fixed factor. The community composition of the saproxylic insects in the different wood types is tested using permutational MANOVA and non-metric multidimensional scaling (using the vegan package in R). To capture fungal communities, we take drill cores per log before logs are placed into plots as well as directly after removal from the field.

Workpackage 4: Impacts of tree diversity and saproxylic insects on decomposition of suspended deadwood

WP4 compares decomposition and colonisation by saproxylic insects of deadwood on the ground to suspended deadwood, with the latter potentially comprising a substantial proportion of total deadwood within a forest stand (Gora et al. 2019). Decomposition rates have been shown to be higher in CWD with contact to the ground (Gora et al. 2019a, Law et al. 2019, Wu et al. 2021). With the drier and hotter microclimate with increasing height above ground (Gora et al. 2019a), wood decomposition by termites becomes less important in comparison to the ground level, while microbial decomposition becomes relatively more important (Gora et al. 2019a, Law et al. 2019). Microbes and saproxylic insects both show a vertical stratification (Roisin et al. 2006, Law et al. 2019). Aside from decomposers, many arthropods and birds use cavities in deadwood above ground as nest sites (Stokland et al. 2012, van der Hoek et al. 2017). Nest site limitation is stronger aboveground than on the ground for several groups. For instance, the occupancy of

artificial bamboo nests by cavity-nesting ants was ~ 75% aboveground, but only ~ 25% on the ground after 10 weeks (Mottl et al. 2020). Cavities made by wood-boring beetles are readily colonised by many different arthropod species, including ants, other Hymenoptera and beetles (Novais et al. 2018). Abundance and species richness were higher in experimental deadwood above ground. We expect that the decomposition rate of suspended deadwood (without contact to the ground) is slower than of deadwood with contact to the ground since termites are less abundant in this higher stratum. Biotic interactions amongst different decomposer groups and groups using the deadwood as nesting space should occur more frequently in suspended deadwood due to the stronger nest site limitation above ground. However, many arthropods may require wood-boring organisms as ecosystem engineers to facilitate their access to deadwood, which may result in much slower colonisation of suspended deadwood without preformed cavities. Biotic interactions should be very strong between ants and other cavity-nesting insects, such as bees and wasps due to the abundance of ants above ground in subtropical and tropical forests (Novais et al. 2018, Mottl et al. 2020), potentially preventing the access of decomposers, which should, in turn, reduce decomposition (see WP2).

In close collaboration with SP4, we expose CWD of freshly cut *Schima superba* (approximate dimensions 15 x 30 cm (diameter x length); same size as in SP4) without preformed cavities or holes drilled into the wood on the 64 VIP plots for one year. One piece of CWD is laid out on the ground close to the stem of a tree (same or neighbouring tree as used in SP4) and two pairs of CWD are attached to a tree. The first pair is close to the ground and the second pair higher up in the tree attached to branches of similar height. Similar to SP4, ants are excluded from one piece of CWD from each pair without contact to the ground using insect glue. To ensure comparability with WP3, we also lay out one piece each on the ground using the mesh bags with 0.25 or 7 mm mesh size, respectively. After one year, we measure mass loss (see WP3) of CWD with contact to the ground versus suspended CWD. The remaining CWD is searched for surface-active ants and termites and subsequently placed into emergence chambers to rear emerging insects and compare insect species and functional diversity (trophic guilds) of CWD with and without access of ants. Together with SP4, this allows us to assess the importance of wood-boring insects as ecosystem engineers facilitating cavity-nesting of other functional groups, such as hymenopteran pollinators or predatory wasps. Analysis of wood decomposition in relation to location of deadwood (ground vs. to different heights above ground) and insect treatment (access vs. excluded with glue/mesh) is conducted as described in WP3.

SP2: Trophic-interaction, tree-diversity and soil-erosion effects on soil-plant stoichiometry

The subproject tests interrelations between trophic interactions, tree diversity and soil erosion with multi-element stoichiometry of resources and different trophic levels (plants as primary producers and soil microorganisms as consumers). Additionally, we conduct a full soil data baseline (all major plant nutrients and soil properties) as a courtesy to all subprojects.

Our hypotheses are:

1. Soil erosion redistributes nutrients along slopes and differentiates the nutrient pattern in soils available to soil microorganisms and trees. Since C and N are transported in the liquid phase and P bonds to soil particles, the stoichiometry of the eroded material changes during transport and can translate into higher trophic levels via soil microorganisms and tree roots;
2. Eroded parts show lower nutrient availability and foster nutrient recycling, while deposition areas are dominated by nutrient overyielding and nutrient uptake. In contrast, diverse tree mixtures mitigate soil erosion and offset topographic differences along slopes and balance the trade-off between nutrient uptake and nutrient recycling;
3. Soil microorganisms both recycle and take up nutrients more efficiently (= 'nutrient overyielding') in soil of diverse tree mixtures. However, nutrient overyielding is the dominant underlying mechanism and controls microbial stoichiometry;
4. Similarly, trees both recycle and take up nutrients more efficiently in diverse tree mixtures. In contrast to soil microorganisms, nutrient recycling dominates as the underlying mechanism and, thus, drives tree litter stoichiometry. Consequently, tree diversity effects on the stoichiometry of different trophic levels are decoupled.

Workpackage 1: Joint sampling strategy and soil data baseline (StS, TS)

A major task of SP2 is the collection of soil samples on the core plots of both sites and the provision of soil data for all subprojects. Therefore, we follow a joint sampling strategy to manage necessary fieldwork in a team effort of all subproject participants from the Chinese and German sides and together with SP3. For mycorrhizal, microbiology and soil chemistry, we jointly take soil samples and share aliquots to maximise synergies and optimise joint data analyses. The main sampling campaign takes place when all baseline soil samples together with herbivory data (SP3) are collected. Further collection of herbivory data is jointly conducted during the rainy season together with runoff plot measurements.

First soil data are already available from the previous BEF-China project in two time steps (2010, 2014, cf. Scholten et al. (2017)). This time series is supplemented with the newly-acquired data points. With reference to the existing sampling design from BEF-China, a pooled soil sample for each time five depth increments is taken for every core plot, leading to a total of 1500 samples (150 core plots x 2 sites x 5 depth increments). They are collected using Eijkelpamp 7 cm sampling augers to a depth of 0.5 m. The samples are dried, sieved (< 2 mm) and transported to the Laboratory for Soil Science and Geocology, Tübingen, via transport routes already established within the BEF-China platform, to conduct corresponding soil analyses. The transport to Germany comprises mineral soil samples excluding animal and plant material and is carried out in strict compliance with all regulations established in the current version of the Nagoya Protocol on Access and Benefit Sharing (ABS). The soil baseline is recorded once; sample transport would not be necessary in a potential second phase of the project. Contents of

C, N and sulphur (S) is measured with an elemental analysis (Vario EL III, Elementar, Hanau, Germany) and pH is determined in H₂O and KCl (WTW pH meter with Sentix electrodes, Weilheim, Germany). Additionally, bulk soil density in the topsoil (0-5 cm) is determined gravimetrically after drying in cooperation with our Chinese research partners in the Xingangshan field lab. Accordingly, similar lab analyses on C, N, P and K are conducted on herbivore samples of the VIPs in the Laboratory for Soil Science and Geocology, Tübingen, in cooperation with SP3. If by chance we encounter termites during sampling/sample processing, we hand over the individuals to SP1. Furthermore, soil properties obtained in this WP serve as a potential predictor for termite abundance in SP1.

Workpackage 2: Differentiation of nutrient patterns by erosion and transport related processes (StS, TS)

This work package investigates the redistribution and differentiation of nutrients by soil erosion processes and adjunct changes in stoichiometry according to Hypothesis (i).

Sediment and nutrient discharge within surface runoff is measured with small-scale runoff plots (ROPs) under natural rainfall at different positions within the experimental plots, based on methods developed in BEF-China (Seitz et al. 2016, Trogisch et al. 2017). Following the work of Goebes et al. (2015) on the kinetic energy of throughfall in relation to species identity and richness, these are the areas close to the trunk and the overlap area between adjacent trees. Stem runoff is added as a third major area, which, to our knowledge, has not been considered in erosion research to date. Further, bulk precipitation is collected at both sites with the already established BEF-China climate stations and measured for the same components as throughfall.

A first set of ROPs (0.4 m × 0.4 m) is installed on every VIP at each study site with five replications (32 ROPs × 2 sites × 3 repetitions = 192). They consist of stainless-steel panels that are connected to covered runoff gutters and 20 l reservoirs. By their specific size, they capture initial interrill processes and are highly suitable to study basic aspects of initial soil erosion since self-energising processes of rill formation and sheet wash are excluded (Thomaz and Vestena 2012). This aspect makes them particularly appropriate for interplot comparisons, for example, to define impacts of vegetation with a high number of replication (Seitz et al. 2016). At every ROP, surrounding tree composition is recorded and leaf area index, soil surface cover and slope are determined with a fisheye single-lens camera system (Nikon D7200 with Nikkor AF DX 10.5 mm 180°, Tokyo, Japan) and HemiView V8 (Delta-T devices, Cambridge, UK), the photogrammetric grid quadrat method and an inclinometer, respectively. A second set of larger ROPs (1.3 m × 1.3 m, according to the experimental planting distance) is installed around one selected tree individual at every investigated VIP and used to measure stemflow and initial erosion directly at the stem base (32 ROPs × 2 sites = 64). To be able to scale stemflow observations, selected individual trees represent the full range of species and canopy structural characteristics for research site A and its replicate site B. Additionally, direct measurements of stemflow and allocated nutrients are accomplished using flexible

gutters mounted at breast height (1.3 m) around the stem (Sadeghi et al. 2020). Flexible tubing is installed for larger stems (> 0.2 m) and collar-like plastic cups are used for smaller stems (< 0.2 m; Levia and Germer (2015)). ROPs and stemflow gutters are installed in early summer 2022 and are tested directly in a first trial run. Subsequent measurement time steps are May to July 2023 and 2024 during the monsoon season, in which up to $\frac{3}{4}$ of the annual rainfall is occurring in this region. This period of the year is also most suitable for field fauna collections, so that we conduct field campaigns together with SP3 at that time.

Since soil erosion is especially caused by high-intensity precipitation occurring during monsoon time in the study area, we measure rainfall events between May and July classified as erosive ($> 12.7 \text{ mm h}^{-1}$) following Wischmeier and Smith (1978). Climate stations covering all relevant meteorological parameters are at service on every research site providing data on precipitation amount, intensity, temperature and wind. Measured soil and sediment variables are the amount of runoff, infiltration and discharge, C, N and P contained in it, pollen and remains of leaves and branches as well as living and dead organisms. The preparatory on-site analysis is carried out in close cooperation with our Chinese colleagues. This concerns, in particular, the extraction and determination of the constituents in the runoff. The subsequent chemical analysis is carried out centrally in Tübingen, together with other measurements on C:N:P stoichiometry and the soil baseline. The main workload is to operate and maintain erosion measurement plots and to prepare the solutions obtained and the substances they contain, which requires a technician on site to closely monitor and maintain the measurement setup. Statistical analysis is performed using linear mixed effects models and generalised additive models to finally test the stoichiometry and redistribution of nutrients along the slopes and how they translate into higher trophic levels.

Workpackage 3: Nutrient availability and recycling at hillslope scale with changing tree diversity (StS, TS)

This work package examines the entire slope length for differences in nutrient availability between eroded areas and depositional areas, according to Hypothesis (ii).

For this purpose, the data obtained on sediment and nutrient transport are processed into a uniform dataset. Here, the datasets are combined into downslope transects through monocultures or species mixtures, so that the erosion process on the slope can be reconstructed. These transects cover slopes mainly characterised by different monocultures as well as by more diverse mixtures. Therefore, end member mixing analysis (EMMA), based on multi-flow algorithms, is applied to differentiate the origin of discharge and matter transport between plots (Chaves et al. 2008, Ali et al. 2010, Penna and van Meerveld 2019). EMMA is conducted with R and the adjunct EMMAgeo package and differences of nutrient availability between eroded and deposited areas, as well as the influence of tree diversity on erosional processes and the trade-off between nutrient uptake and nutrient recycling, are investigated.

Workpackage 4: Productivity- vs. recycling-driven tree diversity effects on nutrients in soil microorganisms (YO)

In this work package, we assess tree diversity effects on the multielement stoichiometry of soil microorganisms and the underlying mechanisms (Hypothesis iii).

In order to assess multielement stoichiometry of soil microorganisms, we measure element concentrations in soil microorganisms. To this end, we take ten replicate soil samples at 0-5 cm during the joint sampling campaign (see WP1) that are combined to one composite sample per plot (all core plots; $n = 300$). We measure C_{mic} and N_{mic} concentrations following the fumigation method of Vance et al. (1987). TOC and TN concentration in the resulting K_2SO_4 extracts are measured. An aliquot of the fumigated soil aliquot (and the non-fumigated control) are also used to assess microbial potassium (K_{mic}) concentrations, but we use ammonium acetate (CH_3COONH_4) as extraction solution (Lorenz et al. 2010). In these extracts, we also measure the other elements (calcium (Ca), magnesium (Mg), sodium (Na), manganese (Mn) and iron (Fe)) determined for foliar multielement-stoichiometry of trees. We use the hexanol fumigation method to assess P_{mic} (Bünemann et al. 2008, Sorkau et al. 2018). Phosphate concentrations in solutions are measured photometrically by means of a CFA.

We assess microbial nutrient overyielding as a potential mechanism underlying tree diversity effects on multielement stoichiometry of soil microorganisms. Microbial nutrient stocks are calculated by multiplication of the soil mass in the rooting depth volume (considering bulk soil density) and $Nutrient_{mic}$ concentrations. We calculate microbial nutrient overyielding as the deviation of the observed microbial nutrient stocks of mixed stands from the expected microbial nutrient stocks, based on the corresponding monoculture stands. This approach has been established already for nutrient overyielding of trees (Oelmann et al. 2010).

The determination of nutrient recycling within soil microorganisms is challenging and the outcome is difficult to interpret (Spohn and Widdig 2017). Therefore, we tackle microbial nutrient recycling from another angle by considering the nutrients of microbial origin leached from soil as an indication of less efficient microbial nutrient cycling. To this end, we indirectly label nutrients of microbial origin (NO_3^- , PO_4^{3-}) by applying ^{18}O -enriched water (+100‰) in a laboratory soil incubation experiment (Mayer et al. 2001, Hacker et al. 2019). Subsequently, the ^{18}O label are introduced into NO_3^- and PO_4^{3-} because of metabolic processing of N and P (Kendall and McDonnell 1998, Blake 2005). During 14 days, we percolate the soil every other day with ^{18}O -enriched water by applying a vacuum of 300 mbar (Oelmann et al. 2007). In this way, we also extract NO_3^- and PO_4^{3-} in the percolation solution. The resulting percolation solutions are merged for the whole incubation period to yield sufficient mass of NO_3^- and PO_4^{3-} for isotope analysis. We use the purification procedure according to Silva et al. (2000) for NO_3^- and according to Weiner et al. (2011) for PO_4^{3-} . The final steps of the procedures are the precipitation of NO_3^- and PO_4^{3-} as $AgNO_3$ and Ag_3PO_4 , by the addition of Ag_2O and Ag-ammine solution, respectively. In $AgNO_3$ and Ag_3PO_4 , the O isotope ratios of NO_3^- ($\delta^{18}O_{NO_3}$) and PO_4^{3-} ($\delta^{18}O_{PO_4}$) are measured by means of a TC/EA-IRMS. Due to the labour- and cost-intensive

isotope approach, the incubation experiment comprises only soil samples from the VIP plots ($n = 70$).

Tree diversity effects on bivariate element ratios, nutrient overyielding and nutrient recycling of soil microorganisms are assessed by linear mixed models, based on the design variables of the experiment. We use structural equation modelling to pinpoint the contribution of the two underlying mechanisms to multielement stoichiometry of soil microorganisms. To account for effects of the microbial community composition in soil, we use data kindly provided by our Chinese cooperation partner Prof. Dr. Naili Zhang. We use multivariate approaches (e.g. canonical correspondence analysis) to reveal links between microbial stoichiometry and microbial community composition. The ultimate goal is the assessment of species/species groups that have a strong influence on microbial stoichiometry. These species/species groups provide an estimate of the importance of community vs. species-specific effects on microbial stoichiometry. In addition to the inclusion of potential species-specific effects, the SEM comprises $C_{mic}:Nutrient_{mic}$ ratios, microbial nutrient overyielding and microbial nutrient recycling.

Following our hypothesis (iii), we expect that $C_{mic}:Nutrient_{mic}$ ratios decrease with increasing tree diversity. Second, the deviation between observed and expected microbial nutrient stocks are positive (= nutrient overyielding) and increase with increasing tree diversity. Third, we expect that $\delta^{18}O_{NO_3}$ and $\delta^{18}O_{PO_4}$ values decrease with increasing tree species richness. This is caused by a reduced ^{18}O -label recovery due to a smaller contribution of microbially cycled NO_3^- and PO_4^{3-} under high as compared to low tree diversity. In other words, the inverse of the $\delta^{18}O_{NO_3}$ and $\delta^{18}O_{PO_4}$ values depict the retention of ^{18}O -labelled NO_3^- and PO_4^{3-} in the microbial biomass and, thus, the extent of nutrient recycling. Finally, microbial $C_{mic}:N_{mic}$ and $C_{mic}:P_{mic}$ ratios decrease with increasing tree diversity and this is more closely related to more efficient nutrient uptake, i.e. nutrient overyielding, than to nutrient recycling.

As microbial biomass/nutrients in soil might represent a potential food source for termites, SP1 also makes use of the data gathered in this WP.

SP3: Plant-herbivore-predator food webs, stoichiometry and functions

By collecting data on community composition, consumption rates, body mass and elemental contents of arthropods, as well as direct feeding links at higher trophic levels, we aim at predicting the responses of the multitrophic plant-herbivore-predator system to tree diversity loss. We specifically extend previous work by including three trophic levels (trees, herbivorous arthropods and predatory arthropods) and by linking multitrophic communities and their interactions with biomass distributions and stoichiometry to enable the analysis of trophic pyramids and energy-based networks. We also record tritrophic species-level networks for selected tree species. We use novel methods in the BEF-China experiment (stoichiometry, gut content barcoding in collaboration with our Chinese collaborators) and collect additional arthropod groups from other vegetation strata using multiple collection methods.

Based on the results of previous studies, we expect that tree diversity strongly affects consumer communities in various ways and hypothesise that:

1. tree diversity effects on abundance and species richness decrease with increasing trophic level and this leads - together with changes in intra- and interspecific body size distributions of herbivores and predators - to shifts in trophic pyramids along the tree diversity gradient. We further hypothesise that;
2. intraspecific changes in carbon:nutrient ratios of herbivores and predators can be observed with increasing tree diversity, reflecting increased nutrient availability in plant tissues (within and across species) in more diverse plant communities;
3. Multitrophic plant-herbivore-predator energy networks are expected to show higher stocks (standing biomass) and fluxes (herbivory, predation) across trophic levels at higher tree diversity. In addition, we hypothesise that;
4. structural properties of highly resolved plant-herbivore-predator networks provide more detailed mechanistic explanations of how changes in plant diversity affect ecosystem functioning.

Workpackage 1: Trophic community composition of arthropods

In this work package, we test the following specific hypotheses that:

- there is a positive effect of tree diversity on the abundance and diversity of consumer levels, but with diminishing effects at higher trophic levels;
- tree diversity shifts intra- and interspecific body size distributions;
- as a result, (biomass-based) trophic pyramids change;
- increasing tree diversity allows arthropods to achieve more ideal elemental ratios, potentially contributing to the change in trophic pyramids.

To address these hypotheses, we use two sampling methods for important groups of arthropods living on the forest floor (pitfall traps) and flying in the canopy (flight interception traps). Data from those methods are, so far, limited in the experimental sites of BEF-China, where previous efforts were mostly directed towards foliage-dwelling arthropods on young trees (e.g. Zhang et al. (2017)) and selected tree species pairs (as part of TreeDi). We set up one trap of each type near the centre of all core plots of site A in year 1 and of site B in year 2. The collections are conducted at peak arthropod activity in May-June for two times two weeks (resulting in a total of 300 pooled samples per trap type across two years). Collected specimens are identified to (morpho)species level and assigned to trophic groups (herbivores, predators, parasitoids, detritivores, pollinators, omnivores), based on information retrieved from relevant literature (see, for example, *Zhu (1995)*, *Zhang et al. (2017)*). Species identification is facilitated by previous data and by current and future barcoding efforts in TreeDi and by our Chinese collaborators. Briefly, there are existing DNA barcode libraries for the site including for spiders, ants, cavity-nesting Hymenoptera and other bees and Lepidoptera (e.g. Wang et al. (2020)). These are expanded by our Chinese partners with new collections and integrated with other publicly available data, within a system under development for DNA-based assignment of taxon and traits and a phylogenetic framework. Species in trophic groups other than

herbivores and predators (e.g. detritivores, SP1) or in specific species groups (e.g. ants, SP6) are collaboratively analysed with the respective subprojects to complement their diversity data from specific collection methods (e.g. wood emergence traps in SP1 and Winkler extraction in SP6, respectively) with our information from ground and canopy collections. These additional data allow an evaluation of the diversity of these specific groups (based on the collection methods in other SPs) against their regional species pools (general area and plot-level).

To assess tree-diversity related shifts in a functional trait across species, we measure the body length of 10 adult individuals per plot of the most abundant arthropod species (for the herbivore and predator level, respectively). For the less abundant species, these measurements are complemented by literature data relating to the lowest taxonomic level possible. From this body-size data, we are able to determine biomass through allometric equations (see, for example, Petermann et al. (2015)) and calculate biomass-based predator:prey ratios and trophic pyramids. Carbon and nitrogen contents are measured in collaboration with SP2 for one abundant and representative species of herbivore (e.g. *Phyllolytus variabilis*, Curculionidae, Coleoptera) and one species of predator (e.g. a common species of the Salticidae, Araneae) to assess shifts of elemental contents within species. We use subsamples of dried and ground bulk samples of 10 individuals of each species per plot where possible. Carbon and nitrogen contents are measured with an elemental analyser (Vario EL III, Elementar, Hanau, Germany) at the University of Tübingen.

We statistically analyse the effect of tree diversity (taxonomic, functional and phylogenetic diversity, tree species composition) on the abundance, diversity and community composition of the two arthropod groups (living on the forest-floor and flying in the canopy) using linear or generalised linear models. In addition, trait and phylogenetic information of the arthropods accumulated by our Chinese partners are used to facilitate collaborative trait-based and phylogenetic analyses. Biomass-based predator-prey ratios are a response variable that allows a more complete analysis of the effect of tree diversity on trophic network structure. The shift in body size distributions with increasing tree diversity is analysed as a community-weighted mean (complementing the community-level analyses above), as well as at an intraspecific level for the most abundant species. Intraspecific measurements of C and N contents of one abundant herbivore and one predator species allows for a more mechanistic interpretation of these effects. Arthropod C:N ratios are related to plot-level plant C:N ratios (SP2), as well as to tree diversity. In addition, we use C:N ratios of the herbivore and the predator as predictors for their abundance and biomass (Jochum et al. 2017) along the tree diversity gradient.

Workpackage 2: Trophic functions of arthropods

In this work package, we test the following specific hypotheses:

- herbivory and pathogen infestation rates decrease with tree diversity in established tree communities;
- predation rates increase with tree diversity;

- energy networks generally show higher stocks and fluxes across trophic levels in higher tree diversity (despite decreases in herbivory rates), but with higher top-down effects of predators (i.e. stronger herbivore control) in plots with higher tree diversity.

We measure rates of herbivory and pathogen infestation in all 300 core plots. These data complement herbivory data collected in 2011/12 and 2014/15 (Schuldt et al. 2015, Schuldt et al. 2017b) and enable an analysis of herbivory over time during forest development (see Z2 for details), as well as a first assessment of herbivory in relatively well-established plots. To record herbivory, we visit all core plots of site A in August-October in year 1 and of site B in year 2. Specifically, we visually scan seven leaves per each of three branches for each of the central tree individuals of each plot and assess damage for each leaf, precisely following previous data collection methods for better comparability. Damage is classified into different types inflicted by different herbivore groups (chewing, skeletonising, mining, sucking, galling) or different pathogens (mildew fungi, rust fungi, necrotic lesions, spots). All tree species on all plots are assessed, with replicated individuals of each species per plot. We measure predation rates using artificial clay caterpillars on the same plots during the same time, focusing on tree species with low and high herbivory rates (based on previous assessments), respectively, to cover a wide range of herbivory scenarios and to be able to relate herbivory measurements to predation rates analytically. We place six artificial caterpillars per tree on two tree individuals of different species (with the lowest and highest recorded herbivory) in each plot following previously used methods (Yang et al. 2018). The caterpillars are left in the field for one week and then screened for damage by predators (Low et al. 2014).

Sums of herbivory and pathogen damage across the different groups are used as the tree species and plot-specific herbivory and pathogen rates and are analysed as a response variable in terms of changes in tree diversity, as well as across time using previous data (in collaboration with Z2, see Z2 project proposal for details). Herbivory rates are also related to plant C:N ratios measured in SP2. Artificial caterpillar damage incidences are analysed as predation rates, separately for bird and arthropod (and possibly mammal or reptile) predators. Predation rates are related to herbivory of the respective tree species in a plot to assess potential top-down effects of predators on herbivores and damage caused by them (also vs. plant pathogens). The data collected here, as well as previously collected data and certain information from literature, enable us to construct energy flux networks (Buzhdygan et al. 2020) for the plant-herbivore-predator networks of each plot to assess shifts in energy dynamics with changes in tree diversity.

Workpackage 3: Resolved plant-herbivore-predator food webs

In this work package, we test the following specific hypotheses:

- network properties of species-level plant-herbivore-predator networks change along the tree diversity gradient, for example, in terms of increasing connectance;

- changes in network properties can be related to increased ecosystem functioning (e.g. energy fluxes between trophic levels) along the tree diversity gradient;
- inter- and intraspecific shifts in elemental contents of plants can be linked to similar shifts in herbivores with increasing tree diversity.

Highly resolved plant-herbivore-predator food webs are assembled for the VIP plots. For up to five tree species (three deciduous and two evergreen species to assess a range of species with different leaf traits), we collect all tree-associated arthropods during one campaign in year 3 using fogging with insecticides, pending final approval of the BEF-China Steering Committee (committee members have already expressed support at this stage). In case of organisational difficulties, we switch to traditional branch-beating techniques. Collected arthropods are separated into trophic groups and identified as in WP1. Identification, especially of caterpillars and spiders, is supported by data from previous and future barcoding by our Chinese collaborators. These taxa are also a major focus as they provide feeding links to cavity-nesting bees and wasps in SP4. Predators and parasitoids collected here are used to establish co-occurrence links as basic information. More centrally, however, direct predation links are recorded using gut-content metabarcoding of abundant predator species (spiders of different species, for example, from the families Salticidae and Araneidae) in collaboration with our Chinese partners to be able to assemble species-specific plant-herbivore-predator food webs. Three abundant herbivore species and one abundant predator species from these collections are analysed for C contents as well as other elements (e.g. N, P, Ca, K, Mg, Na, Mn, Fe) to follow effects of tree diversity on organism stoichiometry through the food web in collaboration with SP2 (from soil via trees to herbivores and predators). We use subsamples of bulk samples of 10 individuals per tree species where possible. Carbon and nutrient contents are measured at the University of Tübingen by SP2, using an elemental analyser (Vario EL III, Elementar, Hanau, Germany). Other elemental concentrations will be determined using an ICP-OES after acid- and pressure-assisted digestion of dried and crushed samples (Orłowski et al. 2020, see SP2 for more details on methods).

We construct highly resolved (species-specific) plant-herbivore food webs for selected tree species for all VIP plots in which these species occur. The predator level of these food webs is added for the most abundant predator species, specifically also those that occur as prey in the hymenopteran nests investigated by SP4. Using these species-specific data, we are able to assess effects of tree diversity on food-web characteristics, such as connectance and linkage density (Dunne et al. 2002b). We assess the risk of missing important interactions by taking into account the abundance of additional (less common) species of predators in the fogging samples and setting up co-occurrence webs resolved to tree species level, based on literature and body size information of the collected arthropod predators. Our tree-specific herbivore-predator networks can then be linked (in collaboration with Z2) to other resolved parts of the entire trophic network (e.g. cavity-nesting bees and wasps and their prey in SP4). Carbon:nutrient ratios of herbivores and the predator are analytically related to the elemental ratios in the herbivores' individual host trees. We are able to assess if consumers track food elemental

contents and if this relationship is stronger in plots with higher tree diversity. Shifts in nutrient contents are also analysed in multidimensional space (*González et al. 2017*) and related to tree diversity. Information on elemental contents can furthermore be used to corroborate pathways of energy and nutrient flows (WP2) through the networks and we relate these pathways to tree diversity.

SP4: Linking cavity-nesting bee and wasp food webs to other trophic interactions

This subproject distinguishes tree diversity-driven bottom-up functions, acting on quantitative interaction networks of cavity-nesting Hymenoptera across trophic levels, including their food resources and natural enemies. Drivers of cavity-nesting community establishment under natural conditions in deadwood as alternative nests are tested. We focus on separated overarching objectives in three workpackages (WP):

WP1 addresses how tree diversity alters multi-trophic cavity-nesting Hymenoptera communities and their interactions with parasitoids. In WP1, we study, for the first time, the influences of tree diversity along temporal changes of forest succession over a period of 10 years (2013-2024) at the 64 VIP plots. We additionally analyse the relative importance of the different tree diversity components (taxonomic, functional and phylogenetic tree diversity) on cavity-nesting bees, wasps and their natural enemies in a controlled diversity gradient, installing, for the first time, reed nests at all 300 core plots. WP1 tests two hypotheses:

1. Tree diversity changes cavity-nesting communities, but only starting at the point after canopy closure with forest succession. This assumption is based on our comparison of cavity-nesting communities at the experimental sites during the first years of plot establishment with established old-growth forest plots (*Fornoff et al. 2021*);
2. Tree functional diversity explains higher complementarity of resources than taxonomic and phylogenetic tree diversity and should, therefore, be a strong predictor of the diversity of bee/wasp-parasitoid interactions. Traits affecting functions are not only related to bee and wasp feeding, but also to nesting such as tree resin, which is beneficial for some bees (*Drescher et al. 2017*).

WP2 extends the parasitoid-host interactions so far studied with reed nests to prey and food resources of hosts. This provides the unique opportunity to establish a mechanistic interaction link to the experimentally controlled trophic level of forest trees. Observed multi-trophic interactions of more than two trophic levels involving primary producers are lacking across forest BEF-studies worldwide (except for investigations on trophobiotic tree-ant-Hemiptera interactions at the BEF-China sites when trees were small and leaves accessible; see *Staab et al. (2014)*, *Cao et al. (2018)*, *Fornoff et al. (2019)*). With the identification of herbivorous prey, we aim to establish the feeding links between herbivore-hunting wasps with trees (together with SP3). Additionally, bee pollen is directly attributed to flowering trees. We establish the methodology of continuous prey

identifications using DNA barcoding and ultimately metabarcoding. As this is methodologically challenging, we establish a DNA barcoding approach combined with high-throughput sequencing to study samples taken only at the subset of VIP-plots. Given the challenging analyses of Next Generation Sequencing (NGS) data, we rely on and refine already approved data analysis pipelines (Sann et al. 2018, Yang et al. 2020, Sann et al. 2021) and develop a reference database comprising newly-generated DNA libraries of pollen ITS sequences and COI barcodes. WP2 tests two hypotheses:

1. Traditional DNA barcoding leads to high taxonomic resolution and is needed to establish a reliable metabarcoding approach that leads to identifications at family, genus and species levels;
2. Tree diversity explains the degree of specialisation of bees and wasps, but this pattern dampens with trophic distance to the tree food resources.

WP3 uses a new cavity-nesting model (already tested in forest and shaded garden plots in Germany) to link the trophic interactions of Hymenoptera to deadwood (coarse woody debris) and, therefore, to decomposers and ants. At each VIP plot of both study sites, we install deadwood with cavities to simulate natural conditions for cavity-nesting Hymenoptera and deadwood decomposers. By comparing exclusion of ants to ant accessible deadwood and comparing deadwood with drilled cavities to non-prepared deadwood (SP1), we study the competition and synergies between bees, wasps, ants (SP6) and decomposers across the tree diversity gradient (SP1). WP3 tests the hypothesis that nests closer to the ground and nests allowing access for ants have low bee and wasp occupancy with low parasitism rates. This is because solitary bees seem to accept unfavourable microclimatic nest-site conditions in a trade-off for lower parasitism rates (Hranitz et al. 2009). How the presence of decomposers influence the presence of bees, wasps and their parasitoids (e.g. through ecological engineering of wood-boring beetles), with and without ants, along the tree diversity gradient, is part of SP1.

Three different monitoring methods are applied to different subsets of the BEF-China study plots. One continues the standard reed-filled cavity-nest monitoring plastic tubes at VIP plots and extends the monitoring to all 300 core plots. We add two further monitoring methods to the VIP plots providing new insights to further trophic and non-trophic interactions and links to sub-projects: Layer nests allow non-destructive access even to freshly established brood cells to collect prey objects for molecular identification and wood with drilled holes emulates naturally occurring nests in deadwood at different locations (forest ground, trunk, canopy).

Additionally, we offer student projects, which are complementary to the main focus of this subproject. For example, we identify shared aphid species tended by ants and hunted by cavity-nesting wasps. To achieve this, we use our available data on tree-ant-Hemiptera, particularly aphids, interactions (trophobiosis; Staab et al. (2014), Fornoff et al. (2019)) and combine the data with our identifications of aphids hunted by cavity-nesting wasps using DNA barcoding from WP2. This is done as part of a B.Sc. thesis. The data are

provided to Z2 to enlarge our multi-trophic data of the *MultiTroph* project with direct feeding links starting at the tree level.

Workpackage 1: Tree diversity effects on trophic interactions with increasing forest succession

We continue the long-term, monthly monitoring of cavity-nesting bee and wasp interactions by using standardised cavity nests at VIP plots (32 plots per site) (Staab et al. 2016, Staab et al. 2018a, Fornoff et al. 2021, Guo et al. 2021). We sampled cavity-nesting Hymenoptera from 2011 (site A) and from 2012 (site B) until 2017 at the VIP plots. Afterwards, our Chinese counterparts continued until today using the same sampling protocols. With this research group, we have the possibility to continue this long-term sampling. At the VIP plots, we newly install two poles with two common reed nests each (4 reed nests at each of the 64 plots). We collect occupied reed internodes and replace them with unoccupied internodes every month from March to October at site A and at site B. Nests occupied by bee and wasp larvae are opened in the laboratory to count dead nest cells, while the vital bee and wasp larvae are reared to determine bee, wasp and natural enemy species morphologically with the reference cavity-nesting Hymenoptera collection of the Institute of Zoology, Chinese Academy of Sciences in Beijing. As we aim to link our long-term cavity-nesting Hymenoptera data to forest succession, we measure canopy cover above each of the two cavity-nesting poles by using hemispherical pictures taken at 1.3 m above ground (i.e. nest height) with a 140 mm fish eye lens. Canopy cover is calculated as the percentage of black area of total image size using image J (www.imagej.net), based on the mean of both data points per plot. Canopy cover increases continuously with forest establishment and is, therefore, a suitable predictor for increasing forest succession to study tree diversity effects with increasing forest succession.

We further extend our nest sampling to all 300 core plots. As this is extremely labour-intensive, we reduce the sampling effort and use two nests installed at one pole per plot, instead of using two poles with two nets each. These two nests can be considered as a subset of the nest exposure design of the VIP plots. We conduct this monitoring at site A and at site B in two consecutive years to balance the workload between years. With this approach, we assess the functional groups of spider-hunting and herbivore-hunting wasps, as well as pollen-collecting bees as pollinators and, if possible, for each individual their specific parasitoids (if parasitism takes place) on a monthly basis. The full tree diversity gradient with 300 plots allows us to disentangle the effects of the different components of tree diversity (mainly species richness, functional and phylogenetic diversity or distance) on diversity and network specialisation. We do this with structural equation models (SEM), with 'site' as predictor variable and with generalised mixed effect models. Additionally, the labour-intensive enlarged sample size is fundamental for the evaluation of tree diversity effects on multidiversity and multifunctionality across multi-trophic levels for synthesis in Z2.

Workpackage 2: Multitrophic network extension facilitated by DNA barcoding to link bees and wasps to their food resources

To extend the individual-based interactions to the food resources of bees and wasps, namely herbivorous insects, spiders and pollen, we need to collect fresh pollen and recently hunted and paralysed insects from the bee and wasp nests at the 64 VIP sites. As the bee and wasp larvae are consuming their food generally within one month, we need to have easy access to food resources in nests. For this, we use a cavity nest model, which we name 'layer nest'. To test the model, we have built and installed layer nests in spring 2021 and exposed them in forest and shaded gardens in Germany to prove they work for our research purpose in *MultiTroph*. Similar cavity-nesting models are used by commercial wild bee rearing companies or farmers in Europe and the USA. Our layer nests consist of ten layers of artificial, water-resistant wood boards. Each board provides ten holes of the same diameter with different diameters between boards, ranging between 2-12 mm. The layer nests provide an even more standardised sampling than the reed nests we have used so far at the BEF-China plots. This is because we can offer pre-defined numbers of the most occupied diameters (known from our existing data from China) as nesting possibilities. The cavities for nesting are carved as grooves into wood boards with one open side, which are covered by a transparent plastic foil glued to the wood. This prohibits pathogen and natural enemy spread between nests, whilst allowing natural gas exchange with the wood. The layers can be separated in the field and grooves can be checked at any time for freshly-established bee and wasp brood cells. This gives us the possibility to easily access the bee or wasp larvae including their food items for the subsequent DNA barcoding approach. The layer nests make the sampling of fresh food and prey resources practicable compared to using reed nests where we have to cut the reed for examinations, with many nests with no food resources left.

One layer nest is placed in each of the 64 VIP plots for one season. The layer nests are installed 1.5 m above ground, orientated SE-NW, protected from rain by a transparent roof and protected from crawling arthropods like ants by insect glue at the pole below the layer nest. From our previous samplings, we expect about 50 to 100 spider-hunting wasp nests, 200 to 400 herbivore-hunting wasp nests and 150 to 300 bee nests. Five to ten nests per study plot are sampled three times across the vegetation period in April, June and August. According to our experience with cavity nests, DNA barcoding will be performed for around 4,000 individuals.

For each wasp nest, one larva and several prey individuals are collected in 80% ethanol and separated into morphotypes for the subsequent DNA barcoding approach. Several samples are taken as duplicates to simultaneously apply a DNA metabarcoding approach. This allows us to compare the barcoding success of separated samples with bulk samples. Given that bees tend to collect a mixture of pollen as larval provision, we use a DNA metabarcoding approach to identify the species origin of pollen together with our Mercator fellow Christina Grozinger, as she is experienced in conducting DNA metabarcoding of pollen collected by bees (*Sponsler et al. 2020a, Sponsler et al. 2020b*). Pollen balls from the nests are pooled and homogenised using Omni Bead Ruptor 24

Elite (Omni International). DNA is extracted using Phire Direct PCR reagents (Thermo Fisher). Nested PCR is performed to amplify the plastid intron *trnL* and the nuclear ribosomal spacer regions ITS1 and ITS2. Libraries are cleaned and normalised using a SequelPrep normalisation kit (Thermo Fisher). Libraries are sequenced in China using Illumina Miseq. The Grozinger lab assists with data interpretation and has also developed a Pollen Diagnostics Data Management Platform for managing samples and associated sequence information and an automated pipeline for analysing high throughput sequencing data from pollen samples to identify the plant families, genera or species in the samples (Crone et al. 2024). Tree sequences from the experiment are available and we additionally collect common plant species in the surrounding area and obtain the specific sequence from these plants to build up a local plant library to use for analysing pollen of cavity-nesting bees.

Voucher insect specimens are taken for each barcode sample to be stored at the zoological collection of the Institute of Zoology, Chinese Academy of Science. The DNA extraction, COI amplification with standard primers and high throughput sequencing on an Illumina platform are performed at a selected sequencing facility in Beijing, China. Post-processing of the generated raw sequencing data follows already approved Next-Generation-Sequencing data analysis pipelines by further developing optimised methods to establish reference DNA libraries and barcodes. This greatly improves the data analysis and resolution on the parallel established metabarcoding approach with bees and herbivore-hunting wasps using 400 mixed samples each. All generated sequence data are provided and uploaded to the National Center for Biotechnology Information (NCBI) Barcode of Life Data System (BOLD).

Workpackage 3: Linking cavity-nesting Hymenoptera to deadwood and decomposers

Deadwood pieces (approximate dimensions 15 x 30 cm (diameter x length)) of the locally occurring tree species, *Schima superba* (Theaceae) are used to attract cavity-nesting bees and wasps and other wood-dwelling organisms (beetles, ants, termites (decomposer)), at the 64 VIP plots for one year. To facilitate colonisation and emulate different wood beetle species, borings of different diameters are drilled into each wood piece. One of these created wood nests is placed on the ground next to a tree to simulate lying deadwood, two are attached parallel to the trunk next to the ground and another two wood nests to tree branches in the canopy of the same height. One of those on the trunk and one of the higher exposed tree branches exclude ants by using insect glue. This experimental setup allows us to link Hymenoptera diversity and interactions to decomposer interactions including the important role of predatory ants (SP6). While lying deadwood can be expected to be less attractive to bees and wasps, standing deadwood at tree branches is regularly colonised (Westerfelt et al. (2015), also observed in our ongoing studies in Germany and by the fact that forest stands with standing deadwood correlate to increased cavity-nesting bee diversity, Eckerter et al. (2021)). The five wood-nesting blocks per plot are sampled twice a year, one time in June and one time in late September at and after peak nesting seasons of cavity-nesting Hymenoptera. All

collected wood pieces, with and without ant access, are placed in mesh bags/emergence nests and the emerging insects are trapped in liquid. Bees, wasps and their parasitoids are closely linked to the food webs of decomposers in SP1.

SP5: Trophic interactions across tree regeneration stages

SP5 addresses key questions at the bridge of functional biodiversity, population and community ecology research in forests by combining information from observational and experimental approaches (see also Rehling et al. (2022), Rehling et al. (2023)). Objectives are related to mechanisms of woody recruitment of early reproducing tree species in BEF-China. Referring to findings from the BEF-China project that indicated strong multitrophic regulatory influence on tree seedling establishment already in the early stage of the experiment (Germany et al. 2019), we intend to widen the perspectives to two directions. While, first, we aim to increase the number of multitrophic interactions studied against the background of JC effects across multiple stages of the tree regeneration life cycle, we, secondly, do so along the gradient of tree diversity. Our main objectives are to quantify the contribution of tree diversity on:

1. the reproductive cycle stages of trees that are particularly affected by invertebrate interactions;
2. pre- and post-dispersal seed predation; and
3. germination and seedling herbivory as trophic interactions that affect these reproductive cycle stages as well as;
4. the contribution of generalists and specialists to these trophic interactions.

BEF-China provides the unique possibility to assess these relationships by making use of the full gradient of tree diversity established along the core plots and VIPs.

We address the major objectives organised in three work packages:

- Demography of early life stages: to assess natural tree regeneration for a selected set of tree species in the experiment (see below) along the full tree diversity gradient on the observational level;
- Key process of seed predation:
 - a) to quantify pre-dispersal seed predation along the full gradient of tree diversity established by experimental means;
 - b) to quantify dispersal and post-dispersal seed predation by means of invertebrate;
- Key process of herbivory: to assess germination and seedling herbivory experimentally by quantifying JC effects along the tree diversity experiment.

We define a pool of key tree species to work with in all work packages, ideally aiming at using identical ones when addressing different life stages and processes. Amongst the early reproducing tree species in flower at the experimental sites are phylogenetically

more closely related taxa as members of the Fagaceae by the majority having nuts as the dominant fruit type, just as some more distant taxa as members of the Betulaceae or Anacardiaceae.

(1) Natural tree regeneration

We study transition probabilities of tree life stages as incorporation, germination, establishment and survival to help identify critical stages for species recruitment. We hypothesise that the vulnerability of life-stages vary with tree species identity and change along the gradient of tree diversity.

(2) Key process of seed predation

We hypothesise that:

- pre- and post-dispersal seed predation; and
- the contribution of generalists and specialists to these processes vary along the gradient of tree diversity;
- JC effects in these processes depend on community composition of trees and seed predators.

(3) Key process of seedling herbivory

We hypothesise that, with increasing tree diversity, dilution effects (i.e. fewer species-specific interactions) next to other frequency-dependent mechanisms (involving fewer intra-specific interactions in the herb layer) lead to reduced levels of seedling herbivory and mortality and, thus, confirm JC effects to apply along the gradient of tree diversity.

Workpackage 1: Natural tree regeneration

We assess natural recruitment success in the 64 VIP plots of both Site A and Site B as a function of planted tree diversity, while taking variation due to abiotic factors into account. We make use of permanent plots in the VIPs for repeated monitoring and census. Permanent subplots (1 m² in size) within plots are located in the core area, each one next to the four corners of the core area (i.e. the central 4 x 4 tree individuals) in between the four tree individuals, summing up to a total of 256 subplots. An overall census is conducted two times each in study year 1 and study year 2 on both sites (representing each one early-season and one late-season census) to assess overall sapling density and recruitment success depending on tree diversity. For a selected set of key tree species, life stage assessment of seedlings (if possible), saplings and juveniles is done in size classes in these permanent subplots. Recruits of all size-classes in subplots are marked to quantify seedling/sapling/juvenile growth and survival. For seedlings and saplings, in addition, we visually assess leaf damage due to herbivory and fungal infection as the proportion of affected number of individuals by key tree species. These data can be linked to rates of herbivory quantified on adult trees in SP3. While in monocultures, 2- and 4-species mixtures, we sample four subplots, in high-diversity plots, we consider sampling four more subplots at halfway along the diagonal to account for

within-plot heterogeneity due to higher number of species (in particular, in cases where there is a higher proportion of overall reproducing tree species). We estimate overall herb layer cover and measure maximum height of herb layer in subplots as a proxy for herb layer productivity that is used as covariates for explaining natural tree recruitment success. For each of the subplots, light interception is measured to account for local within-plot variation due to different canopy filling. Measurements are coordinated with SP4. On the plot level, we take further co-varying influence of environmental factors (e.g. aspect, inclination, soil variables as available in the BEF-data portal and from SP2) into account for explaining natural tree regeneration success.

We relate data on effective recruitment success with measures for seed release as they can be derived from seed trap studies conducted in WP2 for explaining natural tree regeneration along the gradient of tree diversity.

Workpackage 2: Pre- and post-dispersal seed predation

Pre-dispersal seed predation is studied experimentally on the 300 core plots of both Site A and Site B for a total of eight selected key tree species that are already reproducing. By preference, we include tree species with large- and small-sized fruits according to availability. Amongst the already reproducing trees, nuts are the predominating fruit type that may be easily studied for traces of nut-boring weevils and other specialised insect predators. For doing so, seed traps are installed beneath individuals of each of the selected tree species in every core plot containing this species (Xiao et al. 2017). Seed traps also provide information to be used in WP1 (see above). The use of two traps per plot (approx. 1/16 ha) is already in the range of seed trap densities applied in large-scale monitoring (Jones and Muller-Landau 2008) and in small-scale analysis of species-specific data to quantify seed release (Du et al. 2007). On a subset of these plots, successive bagging of a defined number of stages from premature flowers/buds to ripe seeds is carried out with pollination bags in order to enable identification of seed predators (cf. Diekötter et al. (2007)) and quantify the share of seeds attacked by insect predators by comparing open vs. enclosed seeds. At the same time, bagging excludes general vertebrate seed predators, such as squirrels and birds so that, in comparison with control branches without bagging in similar position on the same tree, the contribution also of these agents to the fate of fruits and seeds may be quantified in collaboration with our Chinese partner. Based on the identification of pre-dispersal seed predators from our bagging approach, together with information from arthropod samples collected by SP3 from the canopy (flight interception traps) in all core plots of Site A and Site B, tree-seed-predator networks are established.

Post-dispersal seed predation is studied by standardised seed offers in all 300 core plots both at Site A and Site B. Seed cards are prepared and stuffed with mixed seeds of key tree species (ideally selected amongst the overall key tree species identified for pre-dispersal seed predation). We ensure involving seeds from one of those tree species of the overlapping tree species pools from the two sites (that might serve as a seedometer); this might also involve not-yet fruiting species. Given the overall design of

the experiment, we have seed home plots, i.e. plots having matching potential seed sources as adult trees and seed away plots, i.e. plots lacking matching adult trees. This allows us to address JC effects in terms of distance-dependent seed predator pressure along the gradient of tree species diversity. Seed cards are prepared as seed mixture offer of all key species involved, while adding one separate card for the species that serves as a seedometer. In study year 2, seed cards are exposed in:

1. an open setting with full access to seed predators and seed dispersers;
2. an invertebrate enclosure; and
3. a vertebrate enclosure (as used in WP3) in collaboration with our Chinese partner.

Enclosures are made of galvanised metal hardware cloth with a mesh size of 1.5 mm for invertebrate and vertebrate exclusion and of 12.7 mm for the exclusion of vertebrates. In a subset of plots, we install control cages to be able to test for cage effects. Control cages are of the same type as vertebrate enclosures, but with three ground-level openings of 10 cm x 10 cm. Seed cards, one of which is placed in each enclosure, are made of firm, high quality sandpaper (7.7 cm x 14.0 cm, grain size 60) sprayed with repositionable glue that is fixed to the ground with nails to prevent the curling of cards (3 M Spray MountTM; Diekötter et al. (2010)). The glue ensures that seeds stay on the cards under normal weather conditions, while seed predators are still able to remove seeds. As ants play an important role as seed disperser and potential seed predators in the studied ecosystem, we cooperate with SP3 and SP6 in relating seed fate observed in our study with the abundance of known insect (and particular ant) seed predators for complementing the tree-seed predator network. To enable a clear distinction between seed predation and seed dispersal, in cooperation SP3 and SP6, we also carry out molecular gut analyses for ground-dwelling insect species with our Chinese partner.

Workpackage 3: Germination and seedling herbivory

In study year 2, we experimentally address key tree species' establishment in the 64 VIPs with a focus on germination and seedling herbivory as crucial life stages during tree reproduction. For all plots, invertebrate enclosures and open controls are used in arrangement with WP2 to study susceptibility of life stages when exposed to limited or full trophic interactions. We conduct seed addition and seedling addition for eight key tree species, respectively, each as pairs with and without enclosures. In each plot, we arrange subplots according to a split-plot design with having blocks (1.8 m x 1.2 m) in between tree individuals, comprising each three pairs (i.e. each with six subplots 0.5 m x 0.5 m in size). For eight key tree species, this yields four split-plots to be randomly positioned in the VIPs. Species are randomly allocated to subplots and species x treatment (enclosures or open control) combinations randomly assigned to split-subplots following the procedure described in Germany et al. (2019).

We perform seed addition of each species per plot at an intermediate density level. Seed density levels of woody perennial species comprise a range from 1 to 1,000 seeds m⁻², an intermediate level here would result in 50 seeds per 0.25 sq. m (following Turnbull et

al. (2000)). While seed addition is implemented and studied in the early season of the second study year, in parallel with the seed card approach in WP2 (see above), the same setting is used for transplant addition. Seedling transplants are added at an intermediate level of four individuals per subplot (following Germany et al. (2019)). We assess survival, biomass and herbivory on the plant individual level in regular monitoring intervals during the second and third study year. We distinguish leaf damage due to feeding invertebrates quantitatively and fungal infections by visual inspection and quantify the amount by means of photograph analysis. Detailed analyses of the photographs can be done by colour analysis using Winfolia software available in the Erfmeier Lab. In a joint effort with WP1, we measure light availability on the subplot level to account for local within-plot variation, as light was identified as an important determinant for seedling establishment in the given study system (Germany et al. 2019).

The study design allows us to address seedling mortality, growth performance, herbivory and pathogenic infestation as a function of plot identity (home vs. away - depending on whether an adult tree of the same species identity is present or not) and to study this kind of JC effect along the gradient of tree diversity.

SP6: Trophic interactions and ecological functions of ants under changing tree diversity

The overall objectives of SP6 are to test if experimentally manipulated tree diversity influences the diversity, trait distribution, trophic interactions and ecosystem functions of ants. We identify three interdependent main aims that are the leading themes of the work packages (WP) and jointly allow to address the objectives:

1. Quantify the diversity and functional trait distribution of ants in all 300 core plots; this not only allows us to functionally characterise all collected ant species and to test if ant diversity and traits change with tree diversity, but also provide important baseline data for our other objectives and deliver a generic diversity variable available to other SPs and synthesis. This objective also incorporates ant specimens collected by SP1 and SP3;
2. Identify the trophic position and assess trophic interactions of ants by performing resource-choice experiments in the 300 core plots and by measuring $\delta^{15}\text{N}$ from specimens in the 64 VIP plots; with these data, we can calculate trophic redundancy, trophic niche breadth on species and community level and infer whether the trophic interactions of single species and the entire ant community are related to tree diversity. We also test which traits relate to trophic niche breadth and relative trophic positions. Data on preferences for macronutrients (from resource-choice experiments) feed back to the stoichiometry projects (SP2, SP3) and allow for a more complete quantification of nutrient limitations and element flows;
3. Measure the ecosystem function 'scavenging' in the VIP plots and test how the interplay between tree diversity, ant diversity, trait distribution and trophic interactions influences ecosystem functionality. This third objective builds upon

the other two objectives and integrates across components of biological organisation to link diversity and interactions to a function.

(i) Diversity and functional traits: We hypothesise that, in line with preliminary results (Skarbek et al. 2020), species diversity of ants increases with tree diversity. Mechanistically, this is mediated by increased heterogeneity of microhabitats and resources (following the habitat-heterogeneity hypothesis, MacArthur (1972)), for example, due to a more diverse leaf litter providing more shelter and more diverse food objects. We expect that, in plots with high tree diversity, morphological traits of ants have a relatively broader distribution compared to low diversity-plots, which reflects the broader range of niche opportunities with increasing tree diversity. The underlying mechanisms are trait-specific, for example, in accordance with the size-grain hypothesis for locomotory traits, such as leg length (Kaspari and Weiser 1999, Grevé et al. 2019). Our comprehensive trait measurements facilitate a functional classification of all ant species, which allows inference on the proportion of predators and other trophic groups (Sosiak and Barden 2021). Here, we hypothesise that, following the enemies' hypothesis (Root 1973, Staab and Schuldt 2020), functional morphospace shifts towards relatively more predacious ant communities from monocultures to mixtures with high tree diversity. At the trait level, this becomes manifest in shifts in traits related to prey capture, such as relatively longer mandibles.

(ii) Trophic interactions and trophic positions: As we expect that degree of predatory life style of ants increases with tree diversity, we expect associated changes in trophic interaction networks. We hypothesise that the amount of resource use and, in particular, generality and redundancy in the choice experiments, increases with ant diversity and trait distribution (e.g. Houadria et al. (2016)) and, thus, with tree diversity. While at first sight this may appear contradictory, a higher level of prey in the diet increases a colony's demand for nutrients lacking in prey and facilitates foraging for additional nutrients, which then leads to higher overall trophic complexity. We disentangle the potential mechanisms behind the relationship between tree diversity and trophic interactions of ants (Loreau and Hector 2001) into 'complementarity', i.e. when tree diversity influences resource partitioning and resource use amongst ant species or 'selection', i.e. when single ant species with, for example, wide trophic niche breadth contribute disproportionately to interactions. The first mechanism occurs when the relative contribution of species to interactions scales with tree diversity. The latter mechanism is expected when species with certain traits or trait combinations (objective i) are performing well, independent of context and tree diversity or when the influence of few behaviourally or otherwise dominant species increases with tree diversity (compare Schuldt et al. (2017a)). As, following objective (i), we expect more predacious ants in more diverse plots, this community shift is reflected in resource preferences and stable isotopes. The entire ant community and particularly omnivorous species with broad trophic niches adjust their nutrient demands accordingly (Dussutour and Simpson 2009, Staudacher et al. 2018) and, for example, forage relatively more for carbohydrates (as these are otherwise limited in prey) and relatively less for nitrogen (as this nutrient is abundant in prey). Degree of predatory foraging is validated from stable isotopes, with an expected positive

relationship between tree diversity and community mean of $\delta^{15}\text{N}$ values indicating the relative increase of prey in the diet from monocultures to high diversity mixtures. Total isotopic niche breadth (i.e. ant community level niche breadth measured as range of $\delta^{15}\text{N}$) could also increase with tree diversity, as ants may utilise additional different resources when heterogeneity is high (Walsh and Tucker 2020).

(ii) Ecosystem functions: We hypothesise that the function 'scavenging', measured as the retrieval rate of standard carrion baits (Fayle et al. 2011, Gray et al. 2015) increases with tree diversity. Mechanistically, this is mediated by tree diversity and depends on ant diversity and trait distribution (objective i), as well as trophic interactions and positions, again mediated by tree diversity (objective ii). For example, under high tree diversity, the prevalence of ants with a more carnivorous diet and the corresponding set of traits accelerates scavenging (generalist predator ants often also scavenge), as the per-species contribution to the function is increased. A similar relationship is expected if single ant species have higher $\delta^{15}\text{N}$ and, thus, a higher trophic position, suggesting that they are more sustained by animal-derived food in more diverse plots. Likewise, we expect that scavenging rates are positively related to the redundancy of the ant-resource network, as increased trophic generality increases the retrieval of complementary food objects (in this case, protein from carrion). In the same framework (Loreau and Hector 2001) that is applied to trophic interactions, we separate 'complementary' from 'selection' effects. This allows us to test whether mechanisms related to relationships between tree diversity and trophic interactions are similar to mechanisms behind the relationship for ecosystem functions. As carrion is a highly attractive food simultaneously providing several resources (as opposed to the resource-choice experiments targeting single nutrients), selection effects could be prevalent when single competitively dominant ant species have a tendency for monopolising baits. Ultimately, our data allow us to predict how ant diversity decreases in simplified ecosystems and how ant-mediated ecosystem functions depend on diversity and interactions across trophic levels.

Workpackage 1: Diversity and functional traits

The fieldwork for all WPs is conducted in Site A in the first year and in Site B in the second year in order to minimise possible influence due to annual variation in ant populations. To comprehensively sample leaf-litter ants in all 300 core plots, we use Winkler extraction, which is a standardised and representative collection method for ants (Agosti et al. 2000). Per plot, four independent replicates are taken, summing to a total of 1200 samples. At the four corners of the central 6 x 6 tree planting positions, 1 m² of leaf litter (including the first few mm top soil) is collected during dry weather and sifted through a mesh (7 mm) to remove coarse debris, such as leaves and twigs. The sifted coarse material is returned to the position where the sample was taken to minimise plot disturbance. The remaining fine organic material is placed in Winkler extractor bags for 48 h. During the extraction time, ant specimens fall into collection jars with ethanol as preservation liquid. All ant specimens are identified to species or morphospecies with primary taxonomic literature and by comparison to reference material (e.g. Staab et al. (2018b), Skarbek et al. (2020)). Combined with the ant data from WP2 and the ant specimens from SP3 (pitfall traps,

canopy beating) and SP1 (deadwood and soil) that we likewise process, these data allow us to quantify ant diversity per plot. In return, saproxylic taxa from the Winkler samples, such as termites, are given to SP1 for further analysis.

For all collected ant species (from WP1 and WP2), a suite of morphological traits is measured under a digital high-resolution microscope (Keyence VHX-5000). This substantially expands already available trait data that are restricted to a limited set of traits and species (Skarbek *et al.* 2020). To include possible intraspecific trait variation (Wong and Carmona 2021), we measure ten worker ants per species. For polymorphic ants (e.g. *Pheidole* or *Camponotus*), only minor workers are considered. Trait measurements follow established protocols (Parr *et al.* 2017) and comprise Weber's length (as proxy of body size), head length, head width, mandible length, mandible width, eye length, eye position, scape length, clypeus length and metafemur length. These traits relate to the trophic ecology of ants (Gibb and Cunningham 2013, Parr *et al.* 2017). Our comprehensive trait data facilitate a functional classification (Sosiak and Barden 2021) of all ant species in the BEF-China experiment and, amongst other information, provide inference on the proportion of predators. Ultimately, these data allow us to quantify trait distribution per plot in response to tree diversity. To test whether intraspecific traits and variability therein are related to tree diversity, we specifically measure additional specimens for selected ant species. Possible candidates for plot-specific trait measurements are *Ectomomyrmex astutus*, *Pheidole nodus* or *Tetramorium wroughtonii* that are common in the BEF-China experiment (Skarbek *et al.* 2020). Traits are measured on five individuals per plot.

For analysis of trait distribution, community-weighted mean trait values are calculated (Laliberté and Legendre 2010). As morphological traits inevitably scale with body size, we not only analyse all raw trait measurements, but also trait values corrected for body size by regressing the respective values (per specimen) with Weber's length. As for ants, a comprehensive backbone phylogeny at genus level is freely available (Economo *et al.* 2018) and it is straight-forward to calculate measures of phylogenetic diversity as surrogate for unmeasured traits (Staab *et al.* 2021). Likewise, the trait data permit the calculation of functional diversity to quantify trait variability, which can also be tested for their relationship to tree diversity.

Workpackage 2: Trophic interactions and trophic positions

To test if tree diversity influences trophic interactions, we perform resource-choice experiments in all 300 core plots (Site A in the first year, Site B in the second year). By assessing the attendance of ants at different nutrients (i.e. baits), such experiments allow us to quantify nutrient demands as a surrogate for trophic interactions in a standardised and replicable way (Kaspari *et al.* 2008, Peters *et al.* 2014). Baits are in liquid form in 15 ml plastic centrifuge tubes each filled with 8 ml of six surrogate solutions: carbohydrate (200 g sucrose per 1 l H₂O), nitrogen (200 g glycine per 1 l H₂O), phosphorous (40 g monosodium phosphate per 1 l H₂O), lipid (cooking oil), salt (40 g sodium chloride per 1 l H₂O) and H₂O (as control). Tubes are closed with inserted cotton balls that prevent

leaking and act as wicks making solutions available to foraging ants. Per plot, all six nutrients are exposed in four replicates, summing to a total 1,200 individual choice experiments with 7,200 baits. Experiments are conducted at the centre of the outer edges of the square defined by the central 6 x 6 tree planting positions, which ensures a distance of over 3 m to the nearest Winkler sampling location. To further minimise interference with leaf-litter ant collection in a plot, Winkler extraction and resource-choice experiments are separated by at least one week. Tubes are placed on the ground in a row in randomised order with 5 cm distance between individual tubes. After 2 h, all ants foraging at the solutions are collected by quickly closing screw caps. Ants are identified as described in WP1. Experiments take place during dry weather, sparing the hottest part of the day (12:00-15:00 h) when ant activity is comparatively lower. Relative ant attendance at baits allows us to quantify resource preferences in relation to local availability (data from SP2 and SP3). By relating data from monocultures to mixtures, we distinguish whether relationships between tree diversity and trophic interactions are due to complementarity or selection effects (*Loreau and Hector 2001*). Interactions between individual resources (lower level) and ant species (higher level) are quantified as bipartite networks to calculate redundancy, amongst further network properties (*Dormann et al. 2009*).

Baits are particularly suitable to sample abundant ants that recruit nestmates. Those species regularly monopolise baits and are expected to establish many and strong multitrophic interactions. Thus, the resource choice experiments reveal candidate species for plot-specific trait measurements (WP1). The same species (e.g. *E. astutus*, *P. nodus*, *T. wroughtonii*) are used for analysing potential shifts in species-level trophic niche and relative trophic position using stable isotopes ($\delta^{15}\text{N}$; it is not possible to reliably measure $\delta^{13}\text{C}$ with the available material preserved in ethanol, *Tillberg et al. (2006)*) from specimens collected in the 64 VIP plots. To assess community-level niche breadth per plot, we include all other species found on the VIP plots. Before drying and milling specimens, the gaster is removed to rule out contamination by recently consumed food (*Feldhaar et al. 2010*). Data from SP2 that analyses CNP from the soil and litter provide a plot-specific baseline for natural $\delta^{15}\text{N}$ before enrichment in the food web. $\delta^{15}\text{N}$ data allow us to assess the trophic position of the focal ant species (*Blüthgen et al. 2003*, *Roeder and Kaspari 2017*) and whether trophic position is related to tree diversity. Specimens for $\delta^{15}\text{N}$ are taken from the same samples from which traits are measured (thus likely belonging to the same colony) to allow testing whether, mediated by tree diversity, individual trait values are reflected in trophic position and, thus, foraging ecology (*Gibb and Cunningham 2013*).

Workpackage 3: Ecosystem functions

To quantify the ecosystem function 'scavenging', we perform carrion retrieval experiments in a rapid ecosystem functioning assessment framework (*Meyer et al. 2015*) in the 64 VIP plots. Accounting for the different strategies in scavenging for invertebrate and vertebrate carrion, with invertebrate carrion often being taken whole by scavengers and vertebrate carrion usually fragmented in place, we distinguish between both types. As a

standardised surrogate for dead invertebrates, we use fish food pellets made from dried soldier fly larvae (Fluval Bug Bites). Fish food pellets have been successfully used in scavenging experiments with ants (e.g. *Gray et al. (2015)*). Compared to dead arthropods, pellets have the advantage of a standardised size and nutrient content. We use pellets of three sizes (> 1.4 mm, 1.4-2 mm, 5-7 mm) to ensure that carrion is attractive to a broad range of ant species. Ten pellets of each size are placed on custom-made plastic trays with 30 dents. As a surrogate for vertebrate carrion (*Cornaby 1974, Eubanks et al. 2019*), we use chicken wings (individual wet weight noted) placed on plastic trays to prevent ants from sheeting carrion with soil. Per plot, four replicates consisting of one tray with pellets and one tray with a chicken wing is performed, totalling in 512 measurements of scavenging (256 for invertebrate and vertebrate carrion, respectively). Scavenging experiments are conducted at the corners of the central 6 x 6 tree planting positions next to the Winkler sampling locations of WP1, but at least one week after sampling for both other WPs in the plot.

After exposing the carrion in the morning (during dry weather), trays are checked after 0.5, 1, 2 and 4 h. For invertebrate carrion, we, at each time step, score missing pellets (separated by size class). For vertebrate carrion, the number of ant individuals visible at the chicken wing are estimated per time step and voucher specimens for each species collected, in case the species cannot be identified in the field. Considering multiple time steps allows distinguishing between total function rates (at the end of the experiment) and recruitment rates, which can independently contribute to scavenging (*Gray et al. 2015*). The functional rate for invertebrate carrion can directly be obtained from the proportion of missing pellets, while for vertebrate carrion, unconsumed leftovers are collected at the end of the experiment, weighed and oven-dried at 60°C to constant weight. To calculate the amount of removal, we first convert the wet weight before field exposure to dry weight with a calibration curve established with additional weighed and subsequently dried chicken wings. Scavenging is calculated from the difference in dry weight of the carrion piece before and after field exposure.

Scavenging data are related to tree diversity and to ant variables obtained in WP1 (diversity, trait distribution) and WP2 (trophic interactions, $\delta^{15}\text{N}$). We test whether potential effects of complementarity and selection on the ecosystem function (*Loreau and Hector 2001*) are directly driven by tree diversity or whether they are mediated by properties within the higher trophic level. For disentangling these possible direct and indirect pathways amongst the different interdependent variables, path models are particularly suitable (*Shipley 2009*).

Z2: Data management and synthesis

The overall objectives of Z2 are to:

- ensure efficient data management and promote synergies in the processing of data amongst *MultiTroph*'s SPs through extensive services provided by training courses and the maintenance and ongoing development of the BEF-China data portal, as well as supporting data and code open access publication strategy;

- develop early synthesis connecting *MultiTroph*'s SPs, based on available and newly-generated data that link up network structure, multidiversity and multifunctionality. Multidiversity assembly and trophic interactions need time to establish (Reich et al. 2012). For this reason, including previous data from BEF-China is essential.

The main aims and guiding hypotheses are:

(i) Continuing and updating the data portal. In preparation for *MultiTroph*, we have updated and migrated the BEFdata portal from Leipzig to Halle University (<https://data.botanik.uni-halle.de/bef-china/>). Halle University has provided the required server capacity and technical surroundings to run the portal. Amongst other features, the BEF portal now has a flexible design and can work with screens of all sizes (e.g. tablet, mobile phone). In addition, we have implemented an improved data search. On Github, about 30,000 lines of code have been added and large parts of the old code have been rewritten (<https://github.com/befdata/befdata>). While the data of the BEF-China projects (the former Research Unit FOR 891 "BEF-China", the TreeDi graduate school and numerous Chinese projects) are curated together, their access and re-use are organised in different subprojects, allowing separate access rules and proposals.

The main aim:

1. *MultiTroph*'s data management is to provide data management along the entire data lifecycle. However, as the structure of the database has been updated, we focus on improving functionality, such as developing tools for extracting and merging data for synthesis datasets, thus leveraging reproducible scientific analyses. We work closely with the National Research Data Infrastructure (NFDI) initiative, particularly with NFDI4Biodiversity (<https://www.nfdi4biodiversity.org/>) focusing on biodiversity data, to which we are connected through iDiv;
2. We provide reproducible workflows into which the particular data analyses are integrated;
3. We offer regular training activities on using the data portal to support all activities of the data life cycle (e.g. data generation, documentation, building pipelines, archiving and publishing); Finally,
4. We work to combine paper proposals, which are a key element in BEF data, with applications that are required for working on the BEF-China platform and which are administered by the BEF-China steering committee. Paper proposals offer a safe environment to share data to propagate data ownership through scientific workflows.

(ii) Analysing multitrophic network structure and multidiversity. We anticipate that tree diversity effects on multidiversity of higher trophic levels are, to a large part, indirect and mediated by the structure of interaction networks linking producer and higher trophic levels. We hypothesise that increasing tree species richness increases trophic complementarity and affects further network characteristics through specialisation of network partners. We expect increasing specialisation with increasing producer richness

as a general mechanism of trophic networks, which, in turn, promotes higher trophic level multidiversity. However, differences may be expected for antagonistic versus mutualistic networks (Thébault and Fontaine 2010) and more mobile groups (with their ability to utilise resources across larger spatial scales; see also Ebeling et al. (2018)) and higher trophic levels (often less affected by changes in plant diversity; for example, Scherber et al. (2010) and Schuldt et al. (2019)) are hypothesised to show less pronounced relationships with the manipulated tree communities.

(iii) Link network characteristics and multidiversity to ecosystem (multi)functionality. In general, we expect individual ecosystem functions and ecosystem multifunctionality to be promoted by higher diversity across trophic levels (Barnes et al. 2018, Buzhdygan et al. 2020). We hypothesise that cascading effects of tree diversity via interaction network structure and multidiversity also play important roles in modifying process rates and the stability of ecosystem functions. The degree of generalisation and specialisation in the interaction webs strongly determine the outcome of such cascading effects: specialisation of network partners increases the importance of trophic complementarity in explaining ecosystem functioning (Poisot et al. 2013). Trophic complementarity may increase with increasing multitrophic diversity (Gravel et al. 2016). In contrast, a strong dominance of generalist (highly connected) species might lead to less pronounced effects of diversity, as generalists might maintain high functionality by occupying a broader niche space already at lower diversity (Maureaud et al. 2020). Finally, we expect network structure to also influence the variability of ecosystem functions, with particularly functional redundancy within the networks (e.g. high average number of consumers per host, i.e. community-level vulnerability; Peralta et al. (2014)) reducing variability in functions across space and/or time.

Our work is organised in three work packages, according to the main objectives outlined above. The applicants have extensive expertise on these issues, from data management of large-scale BEF data (Nadrowski et al. 2013, Peters et al. 2018, Löffler et al. 2021) to biodiversity-ecosystem functioning research (Huang et al. 2018, Schuldt et al. 2018) and the analysis of ecological interactions (Schuldt et al. 2010, Schuldt et al. 2017a) and networks (e.g. Schuldt et al. (2017c), Weißbecker et al. (2019), Wang et al. (2020)) across trophic levels, with long-lasting experience in the assessment, organisation, handling and synthesis of data from the BEF-China platform (Bruehlheide et al. 2011, Bruehlheide et al. 2014, Schuldt et al. 2019).

Workpackage 1: Data portal

1. We integrate existing datasets from BEFdata and prepare them for network analysis, for example network data on plant-herbivore (<https://data.botanik.uni-halle.de/bef-china/datasets/627>), ant-aphid (<https://data.botanik.uni-halle.de/befchina/datasets/566>) or host-parasitoid (e.g. trap-nesting bees, wasps and their parasitoids (<https://data.botanik.uni-halle.de/bef-china/datasets/564>)) interactions.
2. We develop the computational workflow in the Galaxy workflow management system (<https://galaxyproject.org/>). Galaxy is an open, web-based platform for

accessible, reproducible and transparent computational research. In particular, R code can be easily integrated (<https://galaxyproject.org/toolshed/set-up-r-environment/>). We provide the blueprints of this workflow to all projects in *MultiTroph* and provide assistance in implementing them. The idea is to assist scientists in *MultiTroph* publishing their data together with all underlying programming code (mostly done in R) and software in a single container (e.g. Merkel (2014)).

3. We provide regular training workshops and networking activities on data and code pipelines (applied for in Z1). In addition, we provide a helpdesk for students and PIs.
4. We implement the combination of paper proposals and work permits in BEFdata.

Workpackage 2: Multitrophic network analysis and multidiversity

We integrate across networks of the BEF-China experiment using existing taxon data in the data portal (e.g. tree species composition, herb layer composition, herbivores, fungal pathogens, predators, soil bacteria and fungi), as well as data from new projects in *MultiTroph* as these data become available. While *MultiTroph* has the advantage that most interactions are directly observed (e.g. cavity-nesting wasps preying on herbivorous aphid species), we also use co-occurrence networks (e.g. soil microbiota sequenced from deadwood of a particular plot), which allows including non-trophic interactions observed at the plot scale. Co-occurrence networks have been used previously in BEF-China, for example for quantifying mycorrhiza networks (Weißbecker et al. 2019).

To integrate data across individual networks, we use linear mixed models and structural equation modelling (SEM) and analyse the relative effects of direct and indirect pathways between tree diversity (measured as taxonomic, functional and phylogenetic diversity, as well as tree species composition), network structure (mean correlation of key metrics among networks; see also Pocock et al. (2012)) of mutualistic and antagonistic networks and the associated multitrophic diversity of higher trophic levels. SEMs have been successfully used before on our set of study plots to address initial questions of multitrophic diversity and ecological networks (e.g. Fornoff et al. (2019), Schuldts et al. (2019), Wang et al. (2019)).

For each network, we use metrics quantifying key network characteristics at the level of the whole web (as well as at the species-level, see below), such as the degree of specialisation of the overall network or of specific species (e.g. Blüthgen et al. (2006)) and (weighted) connectance (realised proportion of possible links, which might increase if biodiversity loss particularly affects specialist species, although patterns can be more complex if generalists benefit from high host diversity; Spiesman and Inouye (2013)), modularity (degree of compartmentalisation, where, for example, less modular network compartments driven by specialised interactions might be observed with decreasing multitrophic diversity; for example, Welti and Joern (2015)) and nestedness (degree of shared interaction partners amongst species, which might decline, for example, with a decrease in tree diversity due to a disruption of interactions; see Neff et al. (2021)). At

high nestedness, specialist species of one trophic level tend to interact with a subset of the species of the other trophic level that generalist species interact with (*Bascompte 2009*), calculated, for example, as NODF (nestedness metric based on overlap and decreasing fill, *Almeida-Neto et al. (2008)*). Following *Poisot et al. (2013)*, we then define trophic complementarity as the reciprocal of NODF (and quantitative indices when data on interaction strengths amongst species are available, *Peralta et al. (2014)*).

Network metrics are quantified using common software in R (e.g. bipartite, igraph, network, tidygraph). Our initial focus is on networks that connect two trophic levels, for example, plant-pollinator or plant-herbivore webs (e.g. *Wang et al. (2020)*), which is subsequently expanded to establish multitrophic linkages by connecting highly resolved networks (plant-decomposer (SP1, 2), plant-herbivore (SP5), plant-omnivore (SP6) plant-herbivore-predator (SP3) and plant-herbivore-predator-parasitoid (SP4) networks) that become available in *MultiTroph*'s SPs (also allowing for a comparison of patterns at an earlier (available data of BEF-China) and later (*MultiTroph* data) stage of ecosystem development). In addition to analysing community network characteristics, we quantify the role of trophic groups, e.g. by assessing interaction strength and specialisation asymmetry (*Dormann et al. 2009*) and of individual nodes, for example, by identifying key species on a certain trophic level (*Timóteo et al. 2022*) and relating their impact to niche breadth and functional traits for an understanding of underlying mechanisms (*Tylianakis and Morris 2017*). As theory predicts that network metrics can be related to network dimensions and diversity (*Thébault and Fontaine 2010*), we construct null models to compare the different measures with the mean expected nestedness and modularity of a given species richness and to assess whether realised interaction patterns are different from chance. As mentioned above, the derived metrics are connected across networks and trophic levels by calculating their average correlation strength (see *Pocock et al. (2012)*, *Felipe-Lucia et al. (2020)*) and integrating these correlations into linear mixed models and SEMs linking up tree diversity, multitrophic diversity and network structure.

Multitrophic diversity is quantified by using multidiversity measures, such as the average of standardised diversity indices (e.g. *Allan et al. (2015)*, *Schuldt et al. (2018)*, *Peters et al. (2019)*). To test for effects of the spatial neighbourhood of surrounding study plots, the overall diversity (total number of tree species and of higher trophic levels) or the dissimilarity in diversity (local α across plots and/or β amongst plots) of the neighbouring plots can be integrated as additional predictors into the models (*Barnes et al. 2016*; the same applies for general environmental effects: see WP3). Likewise, interactions with the mobility of the taxa considered in the analyses (based on taxon-specific dispersal abilities) can be added to the modelling framework.

Workpackage 3: Multidiversity and ecosystem (multi)functionality

We relate diversity and network data of WP2 to individual ecosystem functions and to multifunctionality. Ecosystem functions not only include primary productivity (*Huang et al. 2018*), but also, for example, erosion control (available data as well as SP2), microbial activity (available data and SP1, 2), nitrogen cycling (available data and SP1, 2), leaf

decomposition (available data), wood decomposition (available data and SP1), herbivory resistance (available data and SP3, 5), predation (available data and SP3, 4, 6) and parasitism (available data and SP4) (for a full list of measurements on these functions from nearby natural forests; see *Schuldt et al. (2018)*).

Several functions (e.g. primary productivity, herbivory (see SP3) and parasitism (see SP4)) can be followed over time from the establishment of the experiment to the current state of closed-canopy stands. This allows analysing how key functions and related trophic interactions develop over time (see also *Yeeles et al. (2017)*) and to what extent they shift from abiotic control during initial forest stages to increasing biotic control at advanced stages. Abiotic data (temperature and moisture) are available for 35 plots at each site on an hourly basis since 2015 and can be interpolated from digital elevation models (*Schnabel et al. 2025*). Moreover, the temporal development of soil conditions can be modelled from available data of previous work in BEF-China by SP2. In addition, terrestrial laser scanning data have been collected repeatedly over time (*Kunz et al. 2019*) and canopy cover is measured by SP4, which can be used to infer microclimatic conditions and light availability across a wider range of study plots through allometric regressions. Structural equation modelling, based on distance matrices (*Barnes et al. 2016*), is used to assess the relative strength of space and the abiotic environment versus tree species diversity and biomass on productivity, herbivory and parasitism.

We make use of the network characteristics of WP2 (e.g. trophic complementarity; *Poisot et al. (2013)*) and multidiversity metrics (see WP2) to analyse their contribution to network-specific ecosystem functions (e.g. plant-herbivore network characteristics predicting herbivory; see also *Wei et al. (2015)*) and to overall ecosystem functioning, i.e. multifunctionality. Multifunctionality is calculated using common approaches, such as average and threshold multifunctionality (*Byrnes et al. 2014, Schuldt et al. 2018*). Using generalised multilevel path analysis (a form of SEM, implemented as 'piecewise SEM' in R), we compare models with direct effects of species richness on multifunctionality to those with cascading effects through network characteristics and multidiversity (for a similar approach focusing on land use instead of richness, see *Barnes et al. (2017)*).

In addition, multifunctionality and its dependence on network structure is modelled by quantifying total energy flow and storage across trophic levels (*Buzhdygan et al. 2020*; see WP1), using suitable R packages (e.g. fluxweb; *Gauzens et al. (2019)*). Network models of energy dynamics can be parameterised with existing data on key ecosystem functions or by calculating metabolic rates (*Jochum et al. 2021*). While Z2 initially focused on energy flux networks of the early stages of the BEF-China experiment (available data from BEF-China RU and TreeDi), temporal shifts can be studied by updating these networks with data generated in *MultiTroph* (i.e. at a more advanced stage of ecosystem development).

Finally, we also relate network structure to the spatial and temporal variability of multiple ecosystem functions and multifunctionality, by quantifying variability within and across study plots and time periods (using the inverse of the coefficient of variation of these functions) and relating this to functional redundancy within the ecological networks (using

community-level vulnerability, i.e. the average number of consumers per host species, as a measure of redundancy; *Peralta et al. (2014)*).

Project updates

This section summarises updates on the project implementation since its inception, highlighting new activities and career milestones of project members.

Additional work package funded by the University of Freiburg: Carrion decomposition and decomposer interactions

In future work, we will examine the role of ants in BEF-relationships and trophic networks. Related to this, we implemented a new work package, not included in the original proposal, to study a function that seems to be strongly connected to the occurrence of ants. Carrion decomposition on the forest floor is a new functional aspect in this context and BEF-China more broadly. Carrion is a concentrated, ephemeral and spatially unpredictable source of energy and nutrients (*Carter et al. 2006*). Despite making up only a small fraction of the detritus pool in forest ecosystems (*Barton et al. 2019*), carrion is a hotspot for diverse arthropod communities and decomposer activity. These localised pulses have a disproportionately large impact on nutrient cycling and decomposer diversity (*Carter et al. 2006, Johnson-Bice et al. 2023*), thereby contributing substantially to forest ecosystem functioning.

Tree species richness is known to enhance the diversity of higher trophic levels (*Fornoff et al. 2019, Schuldt et al. 2019, Chen et al. 2023*) and promote ecosystem functioning (*Fornoff et al. 2019, Schnabel et al. 2025*). It may also influence insect decomposer communities and, in turn, accelerate the decomposition of animal carrion. However, because carrion decomposition is not directly linked to trees, it has not been studied in BEF experiments (*Grossman et al. 2018*). Moreover, the influence of tree diversity on carrion decomposition may be modulated, or even masked, by other factors such as forest structure, topography and competition between decomposer groups.

With its experimental manipulations of topography and tree species richness, the BEF-China platform (*Bruehlheide et al. 2014*) offers an ideal setting to study how forest environments affect carrion decomposition. In this additional work package, implemented within the research framework of *MultiTroph*, we investigate how decomposer communities and carrion decomposition respond to tree diversity. We compare the effects of tree species richness to other factors, including canopy cover, slope steepness and key decomposers and examine whether environmental effects on decomposition are mediated by changes in the decomposer community.

We deployed 1,719 mouse carcasses across 96 forest plots in May 2023 and July 2024. In each plot, three pieces of carrion are placed around each of three randomly selected trees (9 pieces of carrion per plot). Carrion decomposition is monitored over a period of up to seven days. Each piece of carrion is photographed twice: once approximately two

days after deployment (± 1 day) and again after 4.5 days (± 1 day). Decomposition is assessed using a seven-point scoring system (1 = fresh up to 7 = only remains), based on established decomposition stages (Payne 1965, *Farwig et al. 2014*).

In the week following the decomposition experiment, we deploy one carrion-baited trap per plot to sample arthropod communities. Traps are designed to capture both flying and crawling insects and operate for two days before arthropods are collected, cleaned and preserved for identification. Specimens are sorted by morphotype, identified using morphological keys or DNA barcoding (via COI sequencing) and matched to species using the NCBI database.

We test the following specific hypotheses:

1. tree species richness enhances carrion decomposer diversity by providing greater resource and habitat heterogeneity or by modifying forest structure and microclimate and thereby accelerates carrion decomposition;
2. canopy cover influences decomposer diversity and decomposition rates, with the direction of effects varying across seasons, arthropod communities or their interactions;
3. slope steepness affects decomposer activity indirectly or directly promotes decomposition through increased carrion fragmentation and aeration; and
4. carrion decomposition is strongly driven by dominant decomposers, particularly ants, whose effects may be negative (via competition) or positive (via direct consumption), depending on local conditions, season and year.

Career milestones of project members

During the project, all of our junior principal investigators funded by the DFG achieved remarkable career milestones, each securing a professorship or permanent position. Manuela Sann became the head of the Invertebrates Department at the Museum of Natural History Bern. Michael Staab became Professor of Animal Ecology and Trophic Interaction at the University of Lüneburg. Simon Thorn became Professor of Specialised Animal Ecology at the University of Marburg. Felix Fornoff received a position as Assistant Professor at the University of Freiburg. Steffen Seitz received an offer for a professorship at the University of Oldenburg.

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Declaration

We have used artificial intelligence, ChatGPT-5, on 12 August 2025 to shorten and summarise parts of the text. All AI-produced material was reviewed for accuracy.

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Conflicts of interest

The authors have declared that no competing interests exist.

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