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Grant Proposal

Biotic Interactions as Mediators of Context-Dependent Biodiversity-Ecosystem Functioning Relationships

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Abstract

Biodiversity drives the maintenance and stability of ecosystem functioning as well as many of nature's benefits to people, yet people cause substantial biodiversity change. Despite broad consensus about a positive relationship between biodiversity and ecosystem functioning (BEF), the underlying mechanisms and their context-dependencies are not well understood. This proposal, submitted to the European Research Council (ERC), aims at filling this knowledge gap by providing a novel conceptual framework for integrating biotic interactions across guilds of organisms, i.e. plants and mycorrhizal fungi, to explain the ecosystem consequences of biodiversity change. The overarching hypothesis is that EF increases when more tree species associate with functionally dissimilar mycorrhizal fungi. Taking a whole-ecosystem perspective, we propose to explore the role of tree-mycorrhiza interactions in driving BEF across environmental contexts and how this relates to nutrient dynamics. Given the significant role that mycorrhizae play in soil nutrient and water uptake, BEF relationships will be investigated under normal and drought conditions. Resulting ecosystem consequences will be explored by studying main energy channels and ecosystem multifunctionality using food web energy fluxes and by assessing carbon storage. Synthesising drivers of biotic interactions will allow us to understand context-dependent BEF relationships. This interdisciplinary and integrative project spans the whole gradient from local-scale process assessments to global relationships by building on unique experimental infrastructures like the MyDiv Experiment, iDiv Ecotron and the global network TreeDivNet, to link ecological mechanisms to reforestation initiatives. This innovative combination of basic scientific research with real-world interventions links trait-based community ecology, global change research and ecosystem ecology, pioneering a new generation of BEF research and represents a significant step towards implementing BEF theory for human needs.

Keywords

biodiversity-ecosystem functioning, biodiversity effects, carbon sequestration, drought, energy flux, iDiv Ecotron, mycorrhiza, MyDiv, mutualists, nutrients, TreeDivNet

State-of-the-art and objectives

Biodiversity change and its consequences for ecosystems

Earth is experiencing a multitude of environmental changes that affect the composition and functioning of ecosystems. Concern that unprecedented rates of biodiversity change will alter ecosystem functioning and the provisioning of ecosystem services has prompted roughly three decades of research evaluating the relationship between biodiversity and ecosystem functioning (BEF) (Schulze and Mooney 1994, Loreau et al. 2001). This research has provided compelling evidence for a largely positive BEF relationship in controlled experiments (e.g. Cardinale et al. 2012, Eisenhauer et al. 2019b), as well as in nature (e.g. Grace et al. 2016, Duffy et al. 2017). Despite this emerging consensus regarding the significant role of biodiversity for ecosystem functioning, variability in the strength of the relationship across environmental conditions (hereafter context dependency) and the underlying mechanisms are still not well understood (Eisenhauer et al. 2019b), which may limit the successful application of biodiversity-theory to resource management or ecological restoration. This project, submitted to the European Research Council (ERC), aims to address these critical gaps by describing how context-dependent biotic interactions provide an unappreciated mechanism underlying BEF relationships and subsequently explaining how environmental context might modify the magnitude and application of observed effects in real-world situations like ecological restorations.

Ecological theory predicts that positive biodiversity effects on ecosystem functioning should arise if intraspecific competition in communities is higher than interspecific competition (Loreau and Hector 2001) and if positive biotic interactions dominate over negative biotic interactions (Baert et al. 2018, Eisenhauer et al. 2019b). Moreover, the stress-gradient hypothesis (SGH) states that positive biotic interactions (i.e. facilitation) should be more important under stressful environmental conditions (e.g. multiple resource limitations), while negative biotic interactions (i.e. competition) may be more pronounced in benign environments (Bertness and Callaway 1994). Biotic interactions and traits related to resource use may, thus, be particularly influential drivers of gradients in competitive interactions, facilitation and biodiversity effects in ecological communities (Barry et al. 2019). If species differ in their resource-use strategies, they avoid competition for (multiple) limiting resources (hereafter resource-use complementarity). This reduction in competition should provide higher levels of ecosystem functioning compared to a community of species with more similar resource-use strategies (Eisenhauer et al. 2019b). Environments with multiple resource limitations will not only host more species with different niches (large biotope space, *sensu* Hutchinson 1978) than benign environments, but will also generate stronger biodiversity effects due to resource-use complementarity (Jousset et al. 2011, Eisenhauer et al. 2019b). Thus, resource-use complementarity amongst species may be an essential driver of BEF relationships (Tobner et al. 2014, Barry et al. 2020). Confirming this hypothesis for plants, species asynchrony (indicating complementarity over time; De Mazancourt et al. 2013, Craven et al. 2018) and spatial dissimilarity in light use in tree crowns (complementarity in space; Williams et al. 2017) have been suggested as significant biological mechanisms that underlie positive BEF relationships. Moreover, grassland studies demonstrate that more complete filling of the soil-rooting space in species mixtures (an indicator of resource partitioning) enhances ecosystem functioning (Mueller et al. 2013, Oram et al. 2017). However, apart from these few case studies and the mathematical indication of complementarity effects (Loreau and Hector 2001, Reich et al. 2012), there is poor empirical support for spatial resource-use complementarity when focusing on plant traits and resource uptake alone (Barry et al. 2020), calling for the consideration of multitrophic interactions of plants (Eisenhauer et al. 2012a, Eisenhauer et al. 2019a).

Above-Belowground Interactions in Biodiversity-Ecosystem Functioning Relationships

Aboveground-belowground interactions between plants and soil organisms may be particularly promising to explain plant BEF relationships and their context dependency (Eisenhauer 2012, Kulmatiski et al. 2012). Indeed, the link between biotic interactions and resource-use complementarity may be determined by both positive and negative biotic interactions (Schnitzer et al. 2011). While there is empirical evidence for the significant role of pathogens (Civitello et al. 2015), the role of positive interaction partners in resource-use complementarity has been underestimated by the BEF literature (Eisenhauer et al. 2012a, Eisenhauer et al. 2012b, Wright et al. 2017). Positive interactions drive a multitude of BEF mechanisms, such as increasing the number of niches of a habitat (i.e. enlarging biotope space) and increasing resistance against antagonists like pathogens (Eisenhauer 2012);

however, the relative importance of these interactions depends on environmental conditions (Guerrero-Ramírez et al. 2019). Accordingly, considering soil organisms and their interaction partners can advance our ecological understanding and help to develop improved sustainable environmental management (Eisenhauer et al. 2019a, Liu et al. 2019). In this context, the symbiosis between plants and mycorrhizal fungi represents a particularly relevant biotic interaction type (Eisenhauer 2012) to: (1) explore the context dependency of multitrophic interactions and (2) determine ecosystem processes ranging from the local (e.g. nutrient uptake) to the global scale (e.g. biogeochemical cycles).

Mycorrhizae - a Widespread Symbiosis Between Plants and Soil Fungi

Mycorrhizal fungi are a heterogeneous group of diverse fungal taxa, associated with the roots of > 90% of all plant species on Earth (Bonfante and Genre 2010). Mycorrhizae are mutualistic symbioses, where fungi acquire plant photosynthetic carbon and, in exchange, provide the host plant with soil nutrients (Smith and Read 2008). Plants have evolved partnerships with different types of mycorrhizal fungi that vary substantially in their life strategies and, thus, the mechanisms by which the fungal partners provide soil-derived resources to their plant hosts (Johnson et al. 1997, Peterson et al. 2004, Johnson et al. 2012). Up to 80% of all plant nitrogen (N) and phosphorus (P) is provided by mycorrhizal fungi and, thus, many plant species depend on these symbionts for growth and survival (van der Heijden et al. 2015). Amongst the mycorrhizal fungi described, arbuscular mycorrhizal fungi (AMF) are the oldest and most abundant monophyletic fungal phylum (Glomeromycota) that obtains carbon (C) exclusively from their host plants and form obligate associations with ~ 80% of the land plants (Brundrett 2009). The primary function of AMF for their plant host is the provisioning of soil P that would otherwise be inaccessible to the plant (Smith and Read 2008). A second type, the ectomycorrhizal fungi (EMF), has evolved repeatedly within diverse fungal saprotroph phyla in the Asco- and Basidiomycota (Read and Perez-Moreno 2003, Bruns and Shefferson 2004). In contrast to AMF, EMF provide N in exchange for assimilates and can mobilise both organic and mineral plant resources from diverse substrates. Some EMF are not obligate mycorrhizal fungi, but are at least in part saprotrophic (Peterson et al. 2004, Plett and Martin 2011). Thus, AMF and EMF may have substantially different life-history traits causing them to play different roles in ecosystems (Bonfante and Genre 2010, van der Heijden et al. 2015). Although beneficial effects of mycorrhizal fungi dominate the literature, their influence on plant growth and fitness may depend on environmental conditions, for example, soil fertility and moisture, varying from negative to positive (Hoeksema et al. 2010, van der Heijden et al. 2015). This context dependency is reflected by a continuum of mycorrhizal functioning that is often referred to as a positive–negative response continuum or a mutualism-parasitism continuum (Johnson and Graham 2013).

The Global Role of Mycorrhizal Fungi for Ecosystem Functioning

The global extent, distribution and functional composition of forests is central to our understanding of the functioning of the terrestrial biosphere (Crowther et al. 2015, Steidinger et al. 2019). Forests harbour a large proportion of global biodiversity, contribute substantially to biogeochemical cycles and provide a plethora of ecosystem services, including water quality control, timber stocks and C sequestration (Pan et al. 2011, Crowther et al. 2015). Notably, many of these critical services depend on the traits of trees like mycorrhizal association (Averill et al. 2019) and several recent studies highlight the significant role of mycorrhizal fungi in driving soil C sequestration (Steidinger et al. 2019). Based on a database of > 1.1 million forest inventory plots, climatic variables were shown to drive the global distribution of mycorrhizal associations. While only ~ 2% of all plant species associate with EMF, they represent ~ 60% of all tree stems on Earth (Steidinger et al. 2019). EMF trees dominate forests of seasonally cold and dry climates (e.g. high latitudes and elevation). By contrast, AMF trees were shown to dominate warm tropical forests and co-occur with EMF trees in temperate biomes (Steidinger et al. 2019), suggesting that co-existing AMF and EMF plants in many ecosystems may co-determine ecosystem functioning (Chen et al. 2019).

Across these different biomes, AMF and EMF vegetation were shown to store substantial amounts of C in aboveground biomass (241 and 100 gigatons (GT), respectively; non-mycorrhizal vegetation: 29 ± 5.5 GT C only; Soudzilovskaia et al. 2019). Moreover, soil C stocks are positively related to the community-level biomass fraction of ectomycorrhizal plants globally (Averill et al. 2014), indicating that anthropogenic changes in vegetation cover related to mycorrhizal type is likely to have significant consequences for C dynamics. Such knowledge is particularly relevant, as soil contains more C than the atmosphere and vegetation combined (Tarnocai et al. 2009). EMF-dominated ecosystems were found to store ~ 1.7 times more C per unit of soil N than AMF ecosystems (Averill et al. 2014), causing differences in the ratio between different elements (hereafter ecosystem stoichiometry). Soil C storage thus depends on tree-mycorrhizal interactions that may represent essential traits in whole-plant nutrient economics (Averill et al. 2019) and are key for the competition between plants and decomposers (Cheeke et al. 2017, Luo et al. 2018). Accordingly, AMF and EMF have dissimilar priming effects on soil microorganisms that subsequently drive soil enzyme activities, decomposition (Brzostek et al. 2015), the relationship between belowground C allocation and N uptake (Keller and Phillips 2019) and C and N sequestration (Wilson et al. 2009). These significant effects on nutrient dynamics point towards the importance of mycorrhizal fungi for ecosystem stoichiometry and multiple ecosystem functions (Finlay 2004, van der Heijden et al. 2015).

Most studies on the effects of AMF and EMF trees have been done in laboratory or nursery conditions (Courty et al. 2010) or are based on regional or global correlations (Steidinger et al. 2019). However, by focusing on sites where AMF and EMF plants co-occur, researchers can control for climatic factors that often co-vary with mycorrhizal dominance across large spatial scales, for example, mean annual temperature and precipitation (Craig et al. 2018). In such a forest setting, it may be possible to develop a more nuanced view of mycorrhizal effects on multiple ecosystem functions. For instance, a recent study showed that EMF stands contain more soil organic matter in the topsoil, while AMF stands contained more soil organic matter when subsoil to 1 m depth was included (Craig et al. 2018). This study revealed that observed patterns were driven by an accumulation of microbial residues in AMF-dominated soils. These findings highlight the role of soil microbial activity and turnover in the storage of C in the soil (Schmidt et al. 2011, Lange et al. 2015). Further, these results indicate that shifts in the mycorrhiza community composition of forests may alter the stabilisation of soil C and provide exciting perspectives for future large-scale studies on mycorrhiza effects on multiple ecosystem functions. Importantly, AMF and EMF forests show systematic differences in nutrient dynamics, such as is exemplified by mineral vs. organic N cycling (Lin et al. 2017). Thus, if AMF and EMF trees complement each other in their ecosystem effects, they may exert strong biodiversity effects on ecosystem functioning. Changing dominance of different mycorrhizal types may help explaining variations in multitrophic interactions and context-dependent BEF relationships (Eisenhauer et al. 2019b).

Context-Dependent Biodiversity Effects on Ecosystem Functioning

Unlike most controlled BEF experiments, real landscapes are heterogeneous and exhibit strong gradients in abiotic conditions, such as precipitation regime or nutrient availability. To apply results from BEF experiments to natural landscapes and to develop biodiversity-based management applications, we need to understand the environmental and biotic context dependency of BEF relationships (Isbell et al. 2017b, Eisenhauer et al. 2019b). By combining distributed networks of experiments with detailed studies of BEF mechanisms in targeted experiments, we are gaining novel insights into which environmental contexts strengthen BEF relationships. First meta-analyses of experimental results on primary productivity revealed that tree BEF relationships are sensitive to soil conditions and increase over time (Huang et al. 2018). BEF relationships have been shown to be positive and strongest in complex environments and to become non-significant in simple environments, while gradients in resource availability can induce BEF relationships ranging from positive to negative (reviewed in Eisenhauer et al. 2019b). Large-scale studies showed that the positive effect of functional diversity on productivity (Ratcliffe et al. 2015) and multifunctionality (Ratcliffe et al. 2017) increases towards drier climates across European forests. However, BEF relationships may not scale linearly with increasing abiotic stress (Baert et al. 2018) and, despite some first insights, we still have scant knowledge about how and why ecosystem effects of the diversity and functional composition of communities vary. Moreover, biodiversity effects can differ across spatial and temporal scales (Cardinale et al. 2011, Gonzalez et al. 2020), ecosystem compartments (e.g. soil depths; Fischer et al. 2019) and processes (Meyer et al. 2018). Exploring abiotic and biotic context dependency of BEF relationships are key research lines to understand the mechanisms behind the relationships amongst biodiversity, ecosystem functioning and service supply. These insights will bridge remaining gaps amongst ecological theory, experimental results, management-relevant scales and societal needs.

The Role of Mycorrhizal Fungi in BEF Relationships with Focus on Proposed Work

This section summarises important knowledge gaps and main promising research directions to link to the proposed work packages (WPs) that are expected to advance BEF research.

Similar to their plant partners, different mycorrhizal types and taxa have evolved ways to lower competition in space and time and possess various traits (Koide 2000, Smith et al. 2000, Jansa et al. 2005, van der Heijden and Scheublin 2007, Ma et al. 2018) that may play a critical role in BEF relationships (Klironomos et al. 2000, Schnitzer et al. 2011, Eisenhauer 2012, Luo et al. 2018, Eisenhauer et al. 2019a; -> WP I). The functional characteristics of AMF are thought to be phylogenetically conserved (Powell et al. 2009) and microcosm studies showed that more phylogenetically dispersed AMF communities (Maherali and Klironomos 2007) and AMF species diversity (e.g. Vogelsang et al. 2006, Reinhart and Anacker 2014) can enhance ecosystem functioning (mostly related to plant performance). Thus, trait differences reducing plant competition in high-diversity communities should increase complementarity effects (Eisenhauer 2012).

Resource acquisition by mycorrhizal fungi often targets plant-unavailable or limiting resources, such as N, P and water (Jeffries et al. 2003) and different mycorrhizal types considerably vary in their morphological and physiological traits that facilitate dissimilar soil-nutrient uptake processes and influence on ecosystem stoichiometry (Lindahl et al. 2007, Bever et al. 2010, Dumbrell et al. 2011, Wagg et al. 2015, Chen et al. 2019, Chen et al. 2016; -> WP II). However, mycorrhizal associations are not always beneficial, thus forming a continuum from positive to negative that depends on environmental conditions and the developmental state of the associations (Johnson et al. 1997, Hoeksema et al. 2010, Argüello et al. 2016; -> WP II, WP III). AMF and EMF co-exist in soil and are able to build extensive hyphal networks that may interconnect various plant species (Leake et al. 2004, Simard and Durall 2004, Horton 2015). The mycorrhizal-mediated transfer of limiting resources to plant hosts may be partly based on the translocation of resources amongst plants via the hyphal networks interconnecting them (Selosse et al. 2006, van der Heijden and Horton 2009, Johnson et al. 2012, Klein et al. 2016). In fact, ~ 60% of the world's trees are expected to be connected to neighbouring trees via EMF networks (Steidinger et al. 2019), forming so-called “wood-wide-webs” (Simard et al. 1997). These resource transfer mechanisms have potential relevance for nutrient dynamics, complementarity effects and, thus, BEF relationships (Ferlian et al. 2018b; -> WP I, WP II).

The diversity and type of mycorrhizal networks have been recognised as significant drivers of water uptake during extended droughts (Augé 2001). This could suggest that a more diverse composition of mycorrhizal fungi may buffer their functioning throughout short-term (pulse) environmental disturbances, such as drought (Augé 2001), which may contribute to enhanced plant community resistance at high plant diversity (Isbell et al. 2015, Craven et al. 2018). Forest decline due to drought has already been observed in various regions of the world (Allen et al. 2010) and has gained additional topicality due to increasing frequencies. In fact, there is some indication that tree diversity may lend resistance and resilience to forests under drought conditions (Grossiord et al. 2014). However, whether such beneficial effects are mediated by mycorrhizal fungi is largely unknown (-> WP III).

Biodiversity is a significant driver of ecosystem multiple ecosystem functions (Eisenhauer et al. 2018b, Meyer et al. 2018), mainly mediated by multitrophic interactions (Hines et al. 2015, Lefcheck et al. 2015, Soliveres et al. 2016) including plant-mycorrhizal interactions (van der Heijden et al. 2015). There are several ways to determine ecosystem multifunctionality and some debate around it, but one particularly promising and novel approach represents the assessment of multitrophic energy fluxes that can serve to relate food web structure to the quantification of critical functions like detritivory, herbivory and predation (Barnes et al. 2018, Barnes et al. 2020; -> WP IV). For instance, the energy flux to decomposers may not only indicate decomposition (Schwarz et al. 2017), but also soil biological activity (Thakur et al. 2018) related to soil C storage (Lange et al. 2015; -> WP V). Given the critical role of interactions between plants and mycorrhizal fungi, as well as their strong dependence on environmental conditions (Hoeksema et al. 2010), this symbiosis may represent a key biotic interaction type to better understand context-dependent BEF relationships (-> WP VI). To study this hypothesis, an integrative approach is needed for synthesising respective information across environmental conditions (e.g. soil fertility and water availability), ecosystem compartments (e.g. above- vs. belowground, topsoil vs. subsoil), multiple ecosystem functions and different spatial and temporal scales. Such information is critical to land managers for real-world applications.

The Importance of Tree BEF Studies and Promising Links to Real-World Applications

To advance BEF theory, study mycorrhiza-mediated BEF mechanisms and to disentangle the effects of mycorrhizal types from that of plant species identity and other abiotic and biotic interactions, it is crucial to manipulate mycorrhizal types along a plant diversity gradient in experimental studies (Wagg et al. 2015). In this context, tree diversity experiments provide the advantage of a more balanced ratio and realistic combinations of AMF- and EMF-associated species compared with grasslands (Smith and Read 2008). Furthermore, they allow for studying performance and biotic interactions within plant communities on the individual, neighbourhood and plot scale (van der Plas et al. 2016, Grossman et al. 2018), facilitating the spatial scaling of BEF and underlying mechanisms (Isbell et al. 2017b, Eisenhauer et al. 2019b). In addition to the fate and functioning of natural forests, results of tree diversity experiments will have direct implications for managed ecosystems, for example, tree plantations and reforestation initiatives, that are in the current focus to restore ecosystems, manage multiple ecosystem services and mitigate increasing climate-change effects (Crowther et al. 2015). Indeed, recent studies have pinpointed many potential benefits of increased biodiversity in production forests (e.g. Isbell et al. 2017a). There are multiple important examples for major current reforestation/afforestation initiatives, such as in the framework of the UN Decade on Ecosystem Restoration (2021-2030), the Bonn Challenge and the European Green Deal. Such reforestation activities are particularly relevant for testing and harnessing the real-world implications of BEF research and the ecosystem consequences of different management decisions (Verheyen et al. 2016, Gellie et al. 2018). Thus, BEF theory should be applied to guide these activities to “incentivise forest managers to preserve, grow, and manage forests sustainably” (European Commission 2019) to establish multifunctional forests under future environmental conditions.

Main Objectives and Overarching Hypothesis

The functioning and service supply of ecosystems in the face of anthropogenic environmental and biodiversity change represents a cornerstone of ecological research and a pressing societal issue. Despite broad consensus about a positive BEF relationship, the underlying ecological mechanisms and their context-dependencies are not well understood. This proposal aims at filling this knowledge gap by providing a novel conceptual framework for integrating biotic interactions across guilds of organisms, more specifically between plants and mycorrhizal types, to explain resource-use complementarity in plants and its consequences for plant performance and community multifunctionality. Using a combination of field and mesocosm experiments, as well as meta-level analyses (Fig. 1a), the proposed work will test the overarching hypothesis that ecosystem functioning increases when more tree species associate with functionally dissimilar mycorrhizal fungi. This is because – in addition to other trait differences between tree species – different mycorrhizal types will increase coverage of biotope space for and reduce competition amongst plants, subsequently increasing resource-use complementarity. Taking a whole-ecosystem perspective (Fig. 1b), we propose to explore the role of interactions between trees and mycorrhizal fungi in driving biodiversity effects on ecosystem functioning (I) and how these interactions influence as well as depend on nutrient dynamics and ecosystem stoichiometry (II). Given the increasing environmental pressures that forests face, the need for land managers to adapt to climate change and the significant role that mycorrhizal fungi play in soil nutrient and water uptake, tree diversity–ecosystem function relationships will be investigated under ambient climatic and drought conditions (III). Resulting ecosystem consequences will be explored by studying main energy channels and ecosystem multifunctionality using food web energy fluxes (IV) and by assessing soil carbon storage (V). Finally, integration of such knowledge on the drivers of mycorrhiza-mediated BEF mechanisms will allow us to understand context-dependent BEF relationships (VI). This interdisciplinary and integrative project spans the whole gradient from local-scale process assessments to global ecological relationships by building on unique experimental infrastructures like the MyDiv Experiment and the iDiv Ecotron and the global tree diversity experimental network TreeDivNet, to link the main ecological mechanisms to reforestation initiatives in order to provide management recommendations (Fig. 1a). The proposed work thus represents a novel combination of multiple experimental platforms to advance BEF research and to provide a predictive framework for context-dependent BEF relationships. This innovative combination of basic research with real-world applications links trait-based community ecology, global change research and ecosystem ecology, pioneering a new generation of BEF research and represents a significant step towards implementing multitrophic BEF theory for human needs.

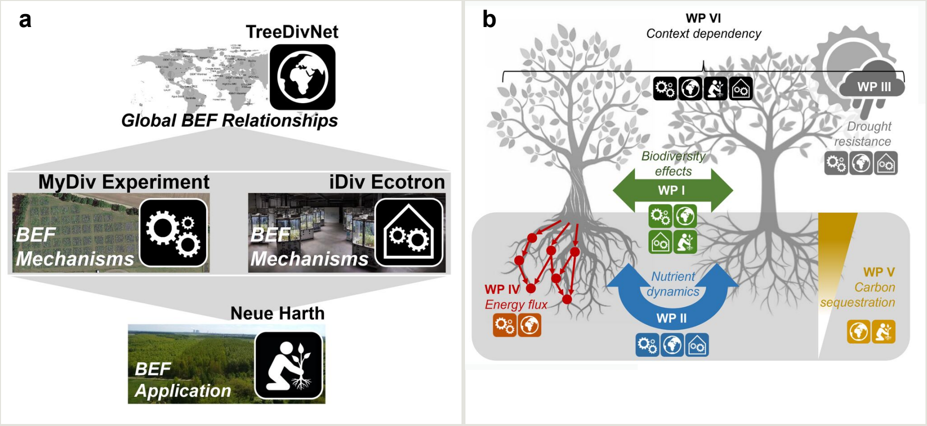

Figure 1.

Structure, research platforms and work packages (WPs) of the proposed project. (A) WPs will work and collaborate in four main research platforms. Hypothesised mechanisms between biodiversity and ecosystem function (BEF) will be studied in the MyDiv Experiment and the iDiv Ecotron. While the MyDiv Experiment allows exploring BEF relationships under natural environmental conditions, the iDiv Ecotron enables studies under more controlled conditions and the test of additional drivers (e.g. nutrients, drought). The global experimental network TreeDivNet will allow us to generalise our findings and/or to study context-dependent BEF relationships. The local reforestation site Neue Harth will allow us to directly test the real-world, management-relevant implications of BEF relationships. Platforms are represented with different icons that are used in (B) to indicate which WP builds on these platforms. The six different WPs take complementary approaches to study important ecosystem components and facilitate synthesis.

Methodology

From Experiments to Real World: the Platforms Used across the Proposal

The MyDiv Experiment - a Field Experiment on the Role of Mycorrhizae in BEF

In 2015, the MyDiv Experiment (Fig. 2a; https://www.idiv.de/en/mydiv) was set up to address critical knowledge gaps related to biotic interactions as underlying mechanisms of BEF relationships and the role of mycorrhizal types in resource-use complementarity in plant communities in particular (Ferlian et al. 2018a, Ferlian et al. 2018b). The experiment was established to test the main hypothesis that tree communities with diverse mycorrhizal types will show increased soil resource-use complementarity compared to tree communities with a single mycorrhizal type. Therefore, treatments combining high tree species richness with the presence of both mycorrhizal types are expected to increase resource uptake and, consequently, resource-use complementarity – in addition to other complementarities, for example, crown heights and shapes – resulting in the highest levels of ecosystem functioning (Fig. 2b). The MyDiv Experiment manipulates the two main mycorrhizal types (via tree species selection) along a deciduous tree species richness gradient comprising monocultures, two-species and four-species mixtures. The mycorrhizal treatment is comprised of tree communities that, according to literature, predominantly associate with AMF (five tree species; *Acer pseudoplatanus*, *Aesculus hippocastanum*, *Fraxinus excelsior*, *Prunus avium* and *Sorbus aucuparia*), EMF (five tree species; *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Quercus petraea* and *Tilia platyphyllos*) or mixtures of these ten tree species. The site, design, basal measurements and evidence for the successful establishment of the MyDiv Experiment are provided in Ferlian et al. (2018b). In preparation of this proposal, we analysed the roots of all tree species in all plots in autumn 2019 to verify the successful establishment of the experimental treatments. Next-generation sequencing (NGS) and traditional staining of root material confirmed that AMF trees are primarily colonised by AMF and EMF trees are primarily colonised by EMF (analysed in 2017; [Heklau et al. 2021]). The MyDiv Experiment includes specimens of an oak clone phytometer (PhytOakMeter; Herrmann et al. 2016) and is part of the global network of tree diversity experiments 'TreeDivNet' (Paquette et al. 2018). Phytometers enable highly standardised physiological process measurements in response to the abiotic and biotic environment (Eisenhauer et al. 2018a).

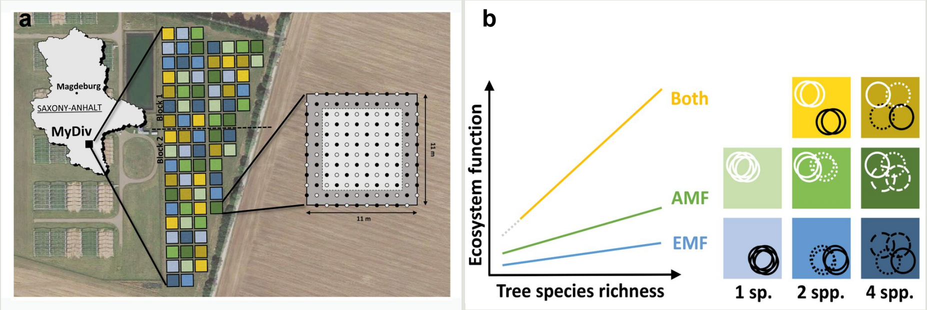

Figure 2.

(A) Location of the MyDiv Experiment, experimental design with colour coding and within-plot experimental design with the core area (light grey) and planting pattern (Ferlian et al. 2018b). (B) Conceptual figure illustrating the main hypothesis (BEF plot) and the underlying resource-use scenarios in tree species that co-exist in a community and are limited by a set of resources (biotope-space quadrats; n = 10 for treatment/coloured quadrat). AMF: arbuscular mycorrhizal fungi, EMF: ectomycorrhizal fungi, Both: both mycorrhizal types. The positive relationship between tree species richness (1, 2 and 4 species) and ecosystem functioning is expected to differ amongst tree communities. Communities of only AMF tree species will have higher ecosystem functioning and show stronger tree diversity effects compared with only EMF tree species, as indicated by different intercepts and slopes of the relationships, respectively. The soil at the experimental site is N-rich and presumably P-limited, favouring AMF-tree species performance. Accordingly, the biotope space occupied by the tree species (represented by circles with different line types; black circles: EMF species, white circles: AMF species) in each community differs as indicated by different positions of the circles within the boxes. We expect that ecosystem functioning will be highest at the highest tree diversity level in tree communities associated with both mycorrhizal types. Here, soil resource-use complementarity should be maximised as indicated by the lowest level of overlap amongst circles and the highest exploitation of the available biotope space. Figures were modified after Ferlian et al. (2018b).

Notably, given the significant establishment effects of ecological experiments, including disturbances (Eisenhauer et al. 2012b), the proposed research is the first focusing on the MyDiv Experiment. This means that the proposed research is not the continuation of any funded project, but a novel, concerted programme to advance ecosystem research. This research programme is well prepared. From the start of the experiment, we established a series of continuous measurements that will serve as important baseline information for all work packages (WPs). The respective data are stored in a standardised way in the iDiv database. In yearly tree inventories, we have been measuring tree height, diameter at breast and at 5 cm height, vitality and damage in all trees forming the core area of each plot (n = 64 trees; Fig. 2a). Moreover, we are performing yearly measurements of wood decomposition rates, soil microbial biomass and respiration, while microbial community structure via NGS and PLFAs/NLFAs (see below) is assessed every second year. Key chemical and physical soil variables (soil pH and C, N and P) are also measured every second year. Soil texture was assessed in 2015. Additionally, a soil core of 1 m depth was taken from each plot in 2015 and 2020, subdivided into eight layers (0-5, 5-10, 10-20, 20-30, 30-40, 40-50, 50-60 and 60-100 cm depth) and archived. This sampling will be repeated every 5 years to study soil C sequestration (Lange et al. 2015).

The iDiv Ecotron - an Experimental Facility to Study Multitrophic BEF

Recently, the iDiv Ecotron was set up to address the perpetual claim that BEF research in terrestrial ecosystems needs to move beyond the manipulation of diversity at single trophic levels to embrace the multitrophic complexity of ecological communities (Naeem et al. 1994, Eisenhauer and Türke 2018, Eisenhauer et al. 2019b, Schmidt et al. 2021). This facility symbolises a paradigm shift in biodiversity research: while multitrophic biodiversity has long been studied as one important response variable in changing ecosystems, for example, by the use of climate chambers, these novel 'biodiversity chambers' now allow international and interdisciplinary teams of researchers to explore the consequences of different scenarios of multitrophic biodiversity change and alterations of biotic interactions for multiple ecosystem functions (Soliveres et al. 2016) in above- and belowground networks (Wardle et al. 2004, Schmidt et al. 2021). The iDiv Ecotron is composed of 24 highly flexible EcoUnits (Fig. 3a, b). The size of the EcoUnits enables the maintenance and study of complex food webs of specialist and generalist invertebrates across several months, as well as interactions amongst tree saplings of different species (Fig. 3c). Moreover, the lysimeter configuration allows us to incubate intact soil monoliths (diameter: 0.5 m; depth: 0.8 m; Fig. 3b) with the complex soil communities therein. The possible compartmentalisation of each EcoUnit into four independent subunits (i.e. 96 subunits in total) enables experiments with high replication. Moreover, all EcoUnits are equipped with a video-camera system, freely-programmable multi-colour (wavelength) LED lamps, irrigation system and temperature gradient along the soil profile to enable the spatial and temporal control of environmental factors, as well as the simulation and study of environmental gradients within and across EcoUnits.

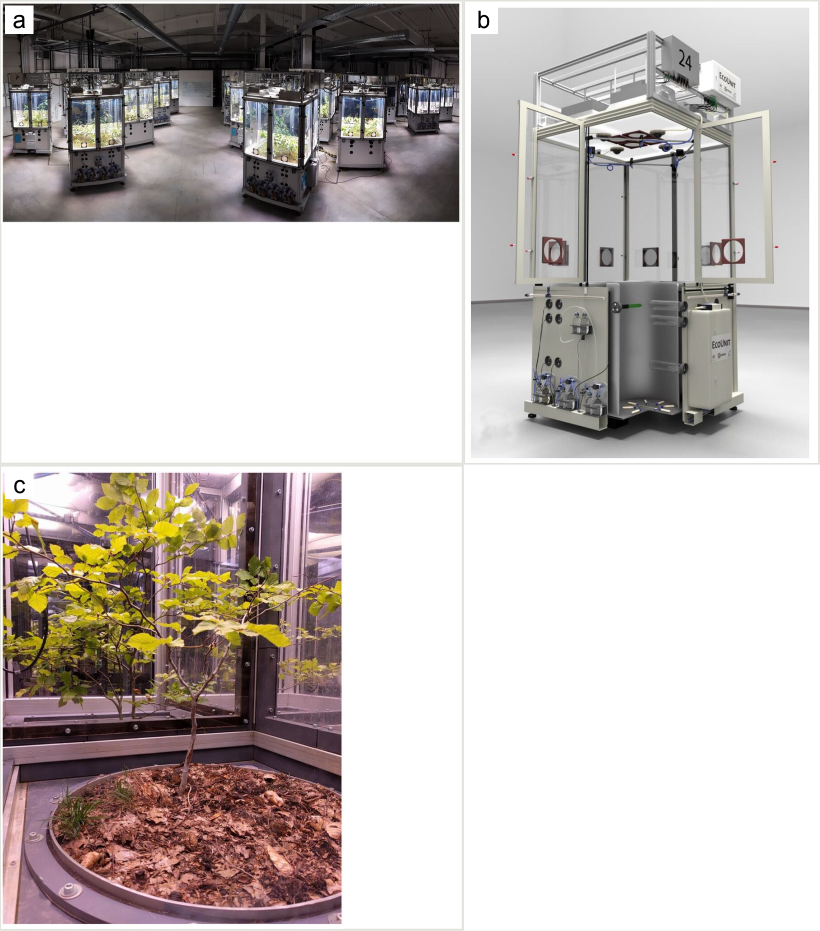

Figure 3.

The iDiv Ecotron. (A) Photo showing the iDiv Ecotron facility with EcoUnits. (B) Technical drawing of an EcoUnit illustrating the lysimeter function with soil sensors and root scanners. (C) Photo of a preliminary experiment in preparation of this proposal with beech saplings. In the proposed experiments, we will use the same lysimeter set-up to be able to incubate up to 96 independent mesocosms. Figures were modified after Schmidt et al. (2021).

TreeDivNet - a Global Network of Tree Diversity Experiments

The global nature of environmental problems, such as climate change, desertification and biodiversity loss, requires the establishment of research approaches that, in most cases, exceed the capacity of single countries or research groups (Eisenhauer et al. 2019b) and that cover a wide range of environmental and geographical conditions (Maestre and Eisenhauer 2019). As a consequence, interdisciplinary and international collaboration in ecology (and beyond) has expanded significantly in the last decade (Craven et al. 2019) and there is growing interest in developing global networks of ecological experiments and surveys (Maestre and Eisenhauer 2019). Collaborative research networks, such as the Nutrient Network (Borer et al. 2014) and TreeDivNet (Verheyen et al. 2016; https://treedivnet.ugent.be), have provided key scientific insights into how natural and semi-natural ecosystems function and respond to multiple global environmental change drivers (Maestre and Eisenhauer 2019). Here, we propose to work in the global network of tree diversity experiments TreeDivNet that encompasses > 1.1 million trees in 28 experiments (Fig. 4; Paquette et al. 2018) to study context-dependent biotic interactions and BEF relationships. First syntheses across participating experiments exemplify the collaborative nature and scientific power of this network (e.g. Grossman et al. 2018, Cesarz et al. 2022 We have been involved in TreeDivNet since 2015 through our own add-on studies (Cesarz et al. 2022) and the participation of the MyDiv Experiment (Ferlian et al. 2018b). Preliminary analyses in preparation of this proposal indicate that mycorrhizal type can be used as a tree trait in syntheses given the representation of AMF and EMF species across experiments (Fig. 4). Using data from the experiments and the TRY database (Kattge et al. 2011), we compiled a novel database of mycorrhizal association types for 454 unique tree species-experiment combinations. This information will be verified using NGS in selected experiments and used as an explanatory variable in meta-level analyses. In 2013, we led a study on soil microbial biomass and activity in eleven TreeDivNet experiments (Cesarz et al. 2022), setting an important baseline regarding: (1) experience leading projects within this network, (2) establishing collaborations with many TreeDivNet members and (3) starting a database on soil abiotic and biotic properties.

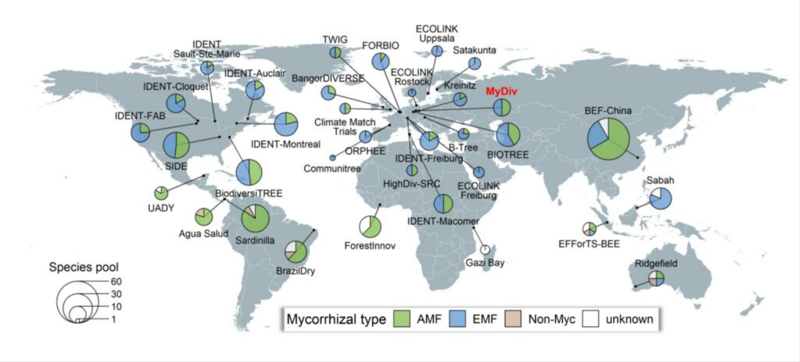

Figure 4. doi

The global network of tree diversity experiments “TreeDivNet”. Each experimental site is represented by one pie chart (some experiments have multiple sites). The sizes of the pie charts correspond to the respective tree species pool of the experiment. Based on information from TRY (retrieved in December 2019; Kattge et al. 2011), the representation of different mycorrhizal types in tree species is indicated by different colours. This dataset will be made available to all TreeDivNet members.

Neue Harth - a Reforestation Initiative after Open Coal Mining

There are many human activities that threaten the biodiversity and functioning of ecosystems, but habitat destruction is one of the most pervasive ones (Díaz et al. 2019).

Many natural ecosystems have been destroyed in the course of land-use change. One of the most devastating examples is open-coal mining, which basically results in purely mineral soils, often with low water-holding capacity, being brought to the surface and then requiring restoration. In Germany, coal production mainly serves the purpose of electrical power generation. According to the occurrence of brown coal, major formerly-forested areas have been destroyed in Central Germany ("Mitteldeutsches Braunkohlerevier"; Fig. 5 a). After coal production, ecosystems are restored and are supposed to serve multiple purposes, such as recreation, biodiversity maintenance and agricultural production. Land managers also aim at restoring multifunctional forests, such as the case in the area of the "Neue Harth" in the south of Leipzig, Germany (Fig. 5b).

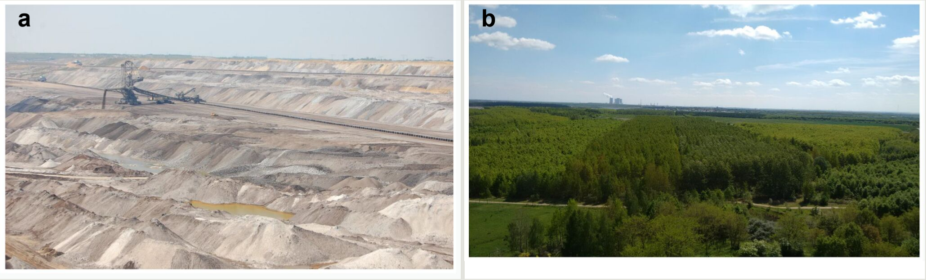

Figure 5.

Reforestation of destroyed ecosystems. (A) Consequences of open coal mining in the south of Leipzig, Germany (2009; photo: Ronny Schmidt, GeoWerkstatt Leipzig e.V.). Roughly 800 ha of mixed forest were destroyed between 1921 and 1999. (B) Reforested area close to Leipzig, Germany (2015; photo: N. Eisenhauer). Forest patches were planted as monocultures and mixed forests of different diversity levels and now allow the study of the ecosystem consequences of different management decisions.

We have been in contact with the forest managers of the Neue Harth, who strongly support scientific work in these reforested areas. Together, we were able to assess the extent, tree species identity and diversity of restored forest patches. In this area, we defined 18 independent ~ 20-year old forest stands (> 2 ha each), containing 10 different tree species associating with different mycorrhizal types (*Acer campestre* [AMF], *Acer platanoides* [AMF], *Betula pendula* [EMF], *Fagus sylvatica* [EMF], *Robinia pseudoacacia* [AMF; association with N-fixing rhizobacteria], *Tilia cordata* [EMF], *Pinus sylvestris* [EMF], *Populus balsamifera* [EMF], *Quercus rubra* [EMF] and *Quercus robur* [EMF]), ranging from monocultures to 6-species mixtures. This setting represents a real-world reforestation scenario with tree species of high local relevance. The two oak species (with *Q. robur* being the phytometer species in the MyDiv Experiment) occur in replicated monocultures (n = 2 for both species), 2-species mixtures (n = 3) and 5-species mixtures (n = 3), enabling studies on the ecosystem consequences of diversifying oak plantations both in terms of tree species richness and mycorrhizal type. Further, recently developed analytical methods will allow us to explore complementarity and selection effects with these data (Clark et al. 2019). Similar starting conditions (e.g. disturbed soil) and planting procedures (e.g. tree species, planting density) facilitate direct comparison between reforestation sites and tree diversity experiments, which is often challenging in other systems/set-ups (Eisenhauer et al. 2016).

Work Packages

The proposed work is divided into six highly complementary work packages (WPs; addressing the six main objectives outlined above) that are further subdivided into 18 tasks (TAs) in total. Four WPs will be carried out by more experienced scientists (Prof. Dr. Nico Eisenhauer and three postdocs) and the other two WPs will be conducted by PhD students. Each scientific TA is supposed to deliver at least one publication in an international, peer-reviewed journal. Team members will have complementary expertise and work together in joint experiments, sampling campaigns and synthesis projects. WPs I and VI will provide the conceptual backbone of the project, integrate the information from all other WPs and facilitate collaboration through multiple workshops. This interdisciplinary and integrative project ranges from local-scale process studies to global syntheses, to link the main ecological mechanisms to reforestation initiatives. The interdisciplinary nature of the project will build bridges between microbial, plant and ecosystem ecology and between basic research and applied aspects related to the restoration of multifunctional forests.

WP I: Biodiversity effects

This WP will focus on the strength of BEF relationships and how net biodiversity effects (NBEs), complementarity effects (CEs) and selection effects (SEs) (based on the additive partitioning method; Loreau and Hector 2001) are modulated by mycorrhizal fungi. The overarching hypotheses are that NBEs and CEs will be strongest when high-diversity tree communities associate with a high diversity of functionally dissimilar mycorrhizal types (H-I-1; Eisenhauer 2012); and that biodiversity effects change over time, with a dominance of SEs in young experiments/early years and increasing NBEs and CEs over time (H-I-2; Eisenhauer et al. 2012b, Reich et al. 2012, Huang et al. 2018).

This WP will support all other WPs by coordinating the planned work, providing baseline data for internal and external collaborators, as well as supervising and mentoring postdocs and PhD students (TA-1-1). To provide baseline data on root mycorrhization for all other WPs, we will analyse the diversity and colonisation rate of AMF and EMF in roots using microscopy and NGS (amplicon and shotgun sequencing) in collaboration with iDiv's Metagenomics Support Unit (Prof. Dr. Francois Buscot and Dr. Anna Heintz-Buschart). We will analyse the mycorrhiza diversity in tree roots in the MyDiv Experiment and in four selected experiments in TreeDivNet. These additional experiments (IDENT-Montreal, IDENT-FAB, IDENT-Macomer, BEF China) were chosen based on the criteria that they: (i) have at least three AMF and three EMF tree species in their species pool, (ii) were set up > 5 years ago and (iii) have the same diversity levels as the MyDiv Experiment (1, 2 and 4 species).

Similar to what was done in 2017 (Heklau et al. 2021) and 2019 in the MyDiv Experiment, we will sample roots of three AMF and EMF tree species, respectively, with five replicates per diversity level (4 experiments x 6 tree species x 3 diversity levels x 5 replicates = 360 samples in total). In the MyDiv Experiment, we will analyse roots of all tree species for all plots (200 samples). The collected root material will be split into two subsamples. One will be immediately frozen and stored for DNA extraction and NGS (mycorrhiza diversity); the second subsample will be fixed in formaldehyde-acetic acid (AMF; Eisenhauer et al. 2009) and 10% glycerine solution (-20°C; EMF), respectively, to determine root colonisation rates by mycorrhizal fungi. While analysing data from all five experiments will allow us to study general patterns of mycorrhiza diversity across tree diversity gradients, the repeated sampling in the MyDiv Experiment will allow us to explore potential changes over time. In this WP, we will focus on tree growth as a key measure of ecosystem functioning related to biomass production and C sequestration. In TA-I-2, we will analyse NBEs, CE and SEs (Reich et al. 2012) as affected by tree diversity, mycorrhizal type and experiment year (2015-2022) in the MyDiv Experiment, based on yearly forest inventory data on all tree individuals in the core area. In TA-I-3, we will perform a meta-level analysis of tree diversity effects (NBEs, CE and SEs) on tree biomass production as affected by mycorrhizal fungi (Fig. 4) across TreeDivNet experiments (extending the dataset and analyses of Guerrero-Ramírez et al. 2017). This WP will be led by Prof. Dr. Nico Eisenhauer. In WP I, we will collaborate with all members of the Scientific Advisory Board (SAB; see below) and organise the kick-off workshop (Fig. 6).

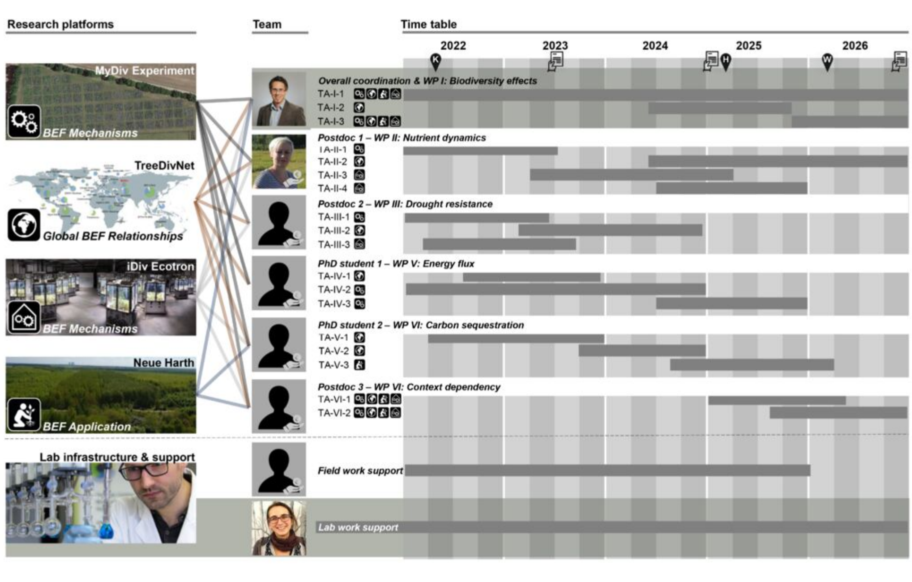

Figure 6. doi

Timetable of the proposed project. Given are the main research platforms and the duration of each task (TA) within work packages (WPs). Pin icon: workshops; sheet icon: regular ERC reporting; K: Kick-off workshop, H: Hands-on workshop; W: Wrap-up workshop; hand icon: requested personnel. Icons on TAs indicate the research platform where the research will be conducted to illustrate the potential for collaboration.

Work package II: Nutrient dynamics

This WP will investigate the potential nutrient-related mechanisms underlying mycorrhiza-mediated tree diversity effects. Taxonomically and functionally diverse mycorrhizal communities may increase ecosystem functioning by enhancing the access and use of the available resource pool to plants resulting in relaxed plant-plant competition for soil resources (van der Heijden et al. 1998, Klironomos et al. 2000). Thus, we expect that the presence of two distinct mycorrhizal types with different lifestyles and foraging strategies (AMF and EMF) may have important implications for resource partitioning amongst their associated plant hosts and for plant and soil stoichiometry (H-II-1; Ferlian et al. 2018b). Moreover, more fertile soils and/or the addition of limiting N and P as mineral fertilisers should reduce the beneficial mycorrhiza effect on tree communities (H-II-2; Suz et al. 2014).

In this WP, we will focus on soil nutrient dynamics as well as plant and soil stoichiometry as affected by tree diversity and mycorrhizal types. In TA-II-1, we will study C, N and P concentrations of leaves, soil and soil microbial biomass in the MyDiv Experiment. Briefly, as done in Ferlian et al. (2017), 10 vital, intact and mature sun leaves will be collected from different branches of five tree individuals per species and plot. In addition, ~ 200 g of soil will be taken from the root zone of each tree at a depth of 0–10 cm for soil and soil microbial analyses. Part of the collected leaf and soil material will be dried, ground and transferred into tin capsules for C and N analyses using an elemental analyser (Vario EL II, Elementar Analysensysteme GmbH, Hanau, Germany). Plant and soil P concentrations will be determined by measuring digested material via inductively coupled plasma optical emission spectroscopy as done in Guiz et al. (2018). Microbial biomass C and N will be determined by a chloroform fumigation-extraction method (Brookes et al. 1985). Similarly, microbial biomass P will be measured using a combination of methods proposed by McLaughlin et al. (1986) and Kouno et al. (1995) that is also based on comparisons between fumigated and non-fumigated soils. In TA-II-2, we will analyse leaves and soil from 10 selected long-term TreeDivNet sites that differ in soil fertility and water availability (Cesarz et al. 2022), but have approx. equal representation of AMF and EMF tree species (Fig. 4). Following the same methods as in TA-II-1, we will determine leaf and soil CNP. In TA-II-3, we will perform a mesocosm experiment in the iDiv Ecotron (Schmidt et al. 2021). We will use the lysimeter set up of the iDiv Ecotron to establish 22 different tree communities. We will set up monocultures of all ten tree species of the MyDiv Experiment species pool (n = 10), as well as twelve different four-species mixtures: four containing only AMF tree species, four containing only EMF species and four containing both AMF and EMF species (two species per mycorrhizal type). These 22 communities will be incubated under four different nutrient treatments: ambient nutrient conditions, addition of N, addition of P and addition of both N and P (n = 88 in total). Mineral fertiliser amounts will be added according to the protocol of the IDENT site in Freiburg. We will plant four tree saplings per lysimeter. The soil will be steam-sterilised prior to filling the lysimeters, thoroughly washed and re-inoculated with 2 kg of fresh soil from the respective plot of the MyDiv Experiment (taken outside of the core area). The experiment will run for 8 months. As described in TA-II-1, we will analyse CNP concentrations of leaves, soil and soil microbial biomass to explore potential shifts in ecosystem stoichiometry in response to the nutrient addition, tree diversity and mycorrhiza treatments. For TA-II-4, we will use the Ecotron experiment of TA-II-3 to perform a tracer study to explore tree nutrient uptake as affected by the tree and mycorrhiza treatments. To this end, we will use ^{15}N-labelled tree litter material (Eisenhauer et al. 2012a), as well as rare elements (Li^+, Rb^+, Sr^{2+}) applied to the soil (Gockele et al. 2014) and nutrient tracer concentrations will be measured according to Gockele et al. (2014). This work will be supported by Dr. Annette Jesch (nee Gockele), who is the lead author of the cited tracer study and in my lab for the next three years. A postdoc with experience in plant and soil ecology, experimental ecology and meta-analysis will lead this WP and collaborate with Prof. Kris Verheyen (SAB, forest BEF) and Prof. Matthias Rillig (SAB; mycorrhizal ecology).

Work package III: Drought resistance

This WP will investigate if mycorrhizal fungi can mitigate drought effects on trees. The increasing frequency and intensity of droughts is threatening the biodiversity and functioning of forest ecosystems (Anderegg et al. 2013). Management strategies aimed at buffering climate change effects include planting tree mixtures rather than tree monocultures, as the latter might have a higher susceptibility to detrimental drought effects (Hutchison et al. 2018). Mycorrhizal fungi do not only play a major role in soil N and P uptake, but the extensive hyphal network is also involved in water uptake and may mitigate detrimental drought effects on plants (Augé 2001). The overarching hypotheses are that tree stands with a higher tree diversity and mycorrhiza diversity will be more resistant to drought stress (H-III-1; Isbell et al. 2015, Craven et al. 2018, Eisenhauer 2018a); and that tree individuals in stands with low intraspecific competition and neighbours with dissimilar mycorrhizal types will experience less drought stress across environmental fluctuations (H-III-2; Salmon et al. 2018).

In this WP, we will focus on tree growth, survival and physiology as important indicators of tree performance under drought conditions. In TA-III-1, we will analyse detailed tree inventory data from the MyDiv Experiment including the exceptionally dry summers in 2018 and 2019. We will analyse tree growth and mortality as well as $\delta^{13}C$ in leaves as a proxy of stomatal conductance (as done in Eisenhauer and Scheu 2008; leaf material was collected in 2018 and 2019 and will be compared with leaf $\delta^{13}C$ during normal years). Moreover, we will perform drought-event-based drone flights (~ 2 per year; one during the drought and during a normal reference period), equipped with a hyperspectral and thermal camera for leaf water content (Fang et al. 2017) and stomatal conductance proxies (Sagan et al. 2019), respectively. For calibration, leaf water content and stomatal measurements will be conducted in parallel at the species level. Together, these measurements allow us explore tree physiology as affected by tree diversity and mycorrhiza type and current environmental conditions and natural fluctuations. In TA-III-2, we will perform a meta-level analysis of tree diversity effects on the detrended temporal stability (Isbell et al. 2015) of tree biomass production (annual increment) as affected by mycorrhizal fungi across experiments of TreeDivNet (Guerrero-Ramírez et al. 2017). In TA-III-3, we will perform a mesocosm experiment in the iDiv Ecotron (Schmidt et al. 2021) to study the effects of tree diversity, mycorrhizal type and drought under standardised conditions that will allow us to investigate tree-mycorrhiza interactions, as well as tree physiological responses (leaf thickness, N content, specific leaf area, leaf conductance) in more detail (Sendek et al. 2019). In short, using the lysimeter function of the iDiv Ecotron, we will set up replicated monocultures of all 10 tree species of the MyDiv Experiment species pool (n = 20; Ferlian et al. 2018b) and 20 different four-species mixtures: all five possible combinations of only AMF tree species, all five possible combinations of only EMF species and 10 selected combinations of AMF and EMF species (representing all replicates of the monocultures and four-species mixtures of the MyDiv Experiment). These 40 communities will be incubated under ambient rainfall (precipitation events every other day) and under reduced rainfall (-50%, every fourth day; Sendek et al. 2019; n = 80 in total). We will plant four tree saplings per lysimeter. The soil will be steam-sterilised prior to filling the lysimeters, thoroughly washed and re-inoculated with 2 kg of fresh soil from the respective plot of the MyDiv Experiment (taken outside of the core area). The experiment will run for 8 months. We will perform repeated assessments of tree growth and physiology (see above), for example, related to water stress ($\delta^{13}C$), as well as soil biological activity using soil microbial respiration and detritivore feeding activity (Eisenhauer et al. 2018a, Thakur et al. 2018). This WP will be led by a postdoc with experience in plant physiology, experimental ecology and meta-level analysis. In WP-III, we will collaborate with Prof. Kris Verheyen (SAB; forest BEF), Prof. Dr. Bernhard Schmid (SAB; BEF theory) and Prof. Dr. Christian Wirth (plant ecology & physiology, proximal and remote sensing).

Work package IV: Energy flux

This WP will investigate tree diversity and mycorrhiza effects on energy flux and ecosystem multifunctionality. Biodiversity is known to determine multitrophic energy use efficiency, flow and storage in grasslands (Buzhdygan et al. 2020). In high-diversity plant communities, a higher quantity and diversity of plant inputs was shown to favour a more fungi-dominated soil microbial community (Eisenhauer et al. 2017) that may play a critical role in soil carbon storage (Lange et al. 2015). Thus, the ratio between bacterial and fungal biomass may provide important insights into soil microbial functioning and efficiency (Eisenhauer et al. 2010). Such shifts in microbial community composition are likely to have cascading effects on higher trophic levels (Scherber et al. 2010, Eisenhauer et al. 2013) and thereby influence ecosystem multifunctionality (Eisenhauer et al. 2018b, Meyer et al. 2018). Multitrophic ecosystem multifunctionality can be inferred from the energy flux through soil food webs (Schwarz et al. 2017, Barnes et al. 2018, Barnes et al. 2020). The overarching hypotheses of this WP are that tree diversity increases the relative importance of the fungal energy channel in the soil, particularly so in the presence of functionally dissimilar mycorrhizal fungi (H-V-1; Eisenhauer et al. 2017), ultimately increasing soil energy flux and multitrophic ecosystem multifunctionality (H-V-2; Barnes et al. 2018).

In this WP, we will explore the structure and functioning of soil food webs. In TA-IV-1, we will collect soil from 12 selected long-term tree diversity experiments in TreeDivNet (Fig. 4; including the MyDiv Experiment; as done before, but increasing the number of experiments in comparison to Cesarz et al. 2022) and analyse the biomass of major soil microbial groups using phospholipid and neutral fatty acid analysis (PLFAs and NLFAs; Wagner et al. 2015). In TA-IV-2, we will establish two subplots of 4 x 4 m in the MyDiv Experiment to manipulate tree resource inputs into the soil. Both subplots will receive a water-permeable weed tarp that will allow us to manipulate aboveground litter input. On one subplot per plot, we will remove the collected leaf material (belowground plant inputs only), while we will put collected leaf litter under the tarp of the other subplot (aboveground and belowground plant inputs). We will analyse the soil food web structure by studying soil microbial communities (P/NLFAs), nematodes and soil meso- and macrofauna to determine the main energy channels (Eisenhauer et al. 2013, Eisenhauer et al. 2017). We expect to see stronger EMF effects in the treatment with aboveground plant inputs due to their role as saprotrophs (van der Heijden et al. 2015), providing an experimental test for the hypothesis that the different mycorrhiza types provide nutrients from complementary sources (Ferlian et al. 2018b). In TA-IV-3, we will explore multitrophic ecosystem multifunctionality by modelling energy fluxes in soil food webs in the MyDiv Experiment. The calculations of energy flux will be based on a well-established quantitative food-web method (Barnes et al. 2018, Gauzens et al. 2019). Using data of TA-IV-2, the topology of the network, group metabolic demand, energy loss to predation, assimilation efficiencies and feeding preferences, we will calculate energy fluxes through each of these communities using the ‘fluxweb’ package in R (Gauzens et al. 2019). This approach has been used successfully to determine belowground herbivory, detritivory and predation (Schwarz et al. 2017, Barnes et al. 2020), as well as ecosystem multifunctionality (Barnes et al. 2018). This WP will be led by a PhD student with a strong background in soil animal ecology and statistical modelling. We will collaborate with Prof. Dr. Ulrich Brose (food web modelling); the student will be co-supervised by Dr. Olga Ferlian (soil energy channels).

Work package V: Carbon sequestration

This WP will investigate tree diversity and mycorrhiza effects on soil C storage. Plant diversity has been shown to increase grassland soil C storage (Fornara and Tilman 2008, Lange et al. 2015) by favouring a more fungi-dominated soil microbial community (Lange et al. 2015, Liu et al. 2018). Although mycorrhiza are known to play a critical role in soil C storage (Averill et al. 2014), interaction effects of AMF and EMF have not been studied so far in a tree diversity context. Our main hypotheses are that high-diversity forests with functionally dissimilar mycorrhizal types have higher soil C storage than low-diversity forests (H-V-1; Ferlian et al. 2018b); and that this effect is mediated by a more active soil microbial community (H-V-II; Lange et al. 2015).

In this WP, we will investigate the drivers of soil C storage. In TA-V-1, we will collect soil from all 28 tree diversity experiments in TreeDivNet (Fig. 4; as done before, Cesarz et al. 2022) and analyse total soil organic C concentration (Lange et al. 2015) and active soil microbial biomass (Eisenhauer et al. 2010). In 2021, a total of ten soil subsamples (soil depths 0-10 cm and 10-50 cm) will be taken per plot to create a bulk sample. Part of this sample will be used for soil C analysis (a, dry), while another part will be used for microbial analyses (b, fresh): (a) The soil will be sieved (2 mm mesh), dried and milled. Total C of ground samples will be determined by an elemental analyser after combustion at 1,150°C

(Elementaranalysator vario Max CN, Elementar Analysensysteme GmbH, Hanau, Germany). Inorganic C concentration will be measured by elemental analysis after removing organic C for 16 h at 450°C in a muffle furnace by oxidation. Organic C concentration will be calculated from the difference between total and inorganic C concentrations (Lange et al. 2015). C stocks will be calculated as the product of bulk soil density and its concentration of C (Schrumpf et al. 2011); (b) The fresh soil will be sieved at 2 mm and active soil microbial biomass will be determined via substrate-induced respiration using an O_2-microcompensation apparatus (Eisenhauer et al. 2018b). Data on soil P/NLFAs from TA-IV-1 from a subset of the TreeDivNet experiments will allow more detailed analyses of relationships amongst microbial community structure, activity and soil C storage. Moreover, in TA-V-2, we can build on the database of a previous project in TreeDivNet (Cesarz et al. 2022) that can be used to explore the change of tree diversity effects on soil microbial properties over time (Thakur et al. 2015) and how this is affected by mycorrhizal type. In TA-V-3, we will test the real-world implications of the findings from BEF experiments by assessing soil C storage in the reforestation plantations of the Neue Harth (Fig. 5b). As done in TA-V-1, we will determine soil organic C concentrations, soil microbial community structure (P/NLFAs) and soil microbial activity to test if diversifying oak plantations has any beneficial effects on soil microbial functions and C storage. This WP will be led by a PhD student with a strong background in soil ecology, who will be co-supervised by Dr. Simone Cesarz (soil microbial communities and functions) and supported by Prof. Dr. Kris Verheyen (SAB, forest BEF), Prof. Dr. Bernhard Schmid (SAB, forest BEF) and Prof. Dr. Christian Wirth (forest carbon dynamics).

Work package VI: Context dependency

This WP will investigate the context dependency of BEF relationships (Eisenhauer et al. 2019b) and the underlying role of tree-mycorrhiza interactions in different environmental conditions (Hoeksema et al. 2010). Empirical evidence is mounting that the consequences of biodiversity change may not be predictable from a single, universal BEF relationship (Baert et al. 2018). Although, the different shapes of BEF relationships have been synthesised before (Eisenhauer et al. 2019b), a mechanistic understanding of such variable biodiversity effects is elusive. Considering the changes in key biotic interactions is highly promising not only to better understand and predict BEF relationships, but also to develop sustainable management strategies under different environmental conditions. Our main hypotheses are that changes in tree-mycorrhiza interactions across environmental contexts are a powerful predictor of tree diversity-ecosystem functioning relationships (H-VI-1); and that tree diversity effects on ecosystem functioning will increase: (a) under nutrient- and water-limited conditions and (b) with an increasing number of environmental contexts and ecosystem functions (H-VI-II; Isbell et al. 2011).

In this WP, we will integrate work across all other WPs by investigating the context dependency of BEF relationships and the role of tree-mycorrhiza interactions explaining these differences. In TA-VI-1, we will build on an extensive literature review of empirical and theoretical work on this topic, as well as discussions in workshops (Fig. 6) to produce a review paper outlining how different environmental conditions should influence plant-mycorrhiza interactions and how these altered biotic interactions may shape BEF relationships. In TA-VI-2, we will perform a meta-analysis of published data and data produced in WPs I – V on the role of mycorrhizal fungi in tree diversity effects on ecosystem functioning as affected by different environmental conditions (e.g. soil fertility and water availability; Baert et al. 2018), the number and identity of ecosystem functions (Isbell et al. 2011, Meyer et al. 2018), different ecosystem compartments and soil layers (Xu et al. 2020, Xu et al. 2021) and different temporal and spatial scales (Eisenhauer et al. 2012b, Eisenhauer et al. 2019b). This WP will be led by a postdoc with a strong background in ecological theory, synthesis and meta-level analyses. In WP VI, we will collaborate with all members of the Scientific Advisory Board (SAB; see below) and organise two workshops ("Hands-on" and "Wrap-up"; Fig. 6).

Risks and Solutions

Large projects like the one proposed here are always associated with multiple potential risks that threaten the success of subprojects. However, we have ample experience with running and coordinating large experimental platforms like the iDiv Ecotron, as well as large research consortia with ~ 100 members like the Jena Experiment (Weisser et al. 2017). The key to avoiding major failures is careful and joint planning, clear communication and continuous exchange amongst group members (Eisenhauer et al. 2019a); all of this will be fostered by monthly meetings, in addition to weekly lab group meetings. Moreover, potential issues could arise related to data use and authorship. To avoid any conflicts, we follow the approach of the Jena Experiment by providing full transparency (using internal [MyDiv Experiment] and external [TreeDivNet] project and paper proposals) and agreeing on clear data use and publication policies (Eisenhauer et al. 2019a). Inspired by successful ERC projects (BIODESERT, PASTFORWARD), we have established a very experienced Scientific Advisory Board of top scientists (Prof. Paola Bonfante, Prof. Matthias Rillig, Prof. Bernhard Schmid and Prof. Kris Verheyen) who will provide complementary scientific input.

Ecological experiments can fail due to many logistic reasons. Here, we will avoid major risks by proposing cutting-edge research in well-established experiments. TreeDivNet is a well-functioning collaborative network; the MyDiv Experiment (since 2015; Ferlian et al. 2018b) and the iDiv Ecotron (since 2017; Schmidt et al. 2021) are running smoothly (several experiments including trees); we are well equipped to support the planned work; we have had very successful collaborations building on mutual trust with all listed collaboration partners. In case an Ecotron experiment fails, the ≥ 4-year contracts should allow us to repeat the experiment or complementary local infrastructures like the new iDiv greenhouse could be used. Thus, we are convinced that the postdocs and PhD students will have ideal working conditions and a strong network of collaboration partners. These assets are further complemented by the worldwide unique research environment of the home institution: iDiv is a global hub for biodiversity research with regular workshops in the synthesis centre sDiv (https://www.idiv.de/en/sdiv.html), weekly seminars with world-leading scientists, a world-class graduate school (yDiv; https://www.idiv.de/en/ydiv.html), a highly integrative and collaborative research culture and the home of other world-leading biodiversity researchers and experiments.

The comparably young age of included experiments (< 20 y) could be criticised. While this is a common phenomenon in ecological experiments, including BEF (Eisenhauer et al. 2012b), young plantations may represent particularly important study systems, as the developments in these young forests are key to determine the structure and composition of future forests. The establishment success of young plantations is particularly relevant for reforestation initiatives, representing a promising case for implementing BEF theory (Eisenhauer et al. 2019b). Research in the Neue Harth will allow us to study real-world BEF relationships.

Scientific and Broader Impact

Scientific impact. Each task is expected to deliver at least one scientific publication in leading multidisciplinary and disciplinary journals with major advances in ecosystem ecology and BEF. Moreover, we will make our data (e.g. mycorrhizal type, soil microbial and abiotic data) available to TreeDivNet (and beyond), which will facilitate the contribution to further syntheses. In addition, we will publish summaries of our main results in journals for foresters and land managers, such as that which has been done recently (Eisenhauer 2018b, Eisenhauer and Vogel 2018).

Outreach and societal impact. Since 2014, we have been very active in public outreach with 18 TV shows/interviews, 21 radio interviews, 189 print articles, 334 online articles and 55 other outreach activities, including public talks and demonstrations for politicians. In the framework of this proposal, it is planned to produce an educational video on ‘Human benefits of the tree-fungi friendship’ that provides information on the main outcomes of our research in collaboration with the YouTube Channel MinuteEarth. The applied aspects of this proposal related to reforestation are at the heart of current scientific debate and political agendas (e.g. European Commission 2019) and, thus, represent a significant step towards implementing BEF theory for human needs.

Open science. We are committed to open science and we will publish our findings in open-access journals, including underlying datasets and code, if applicable. This approach is supposed to fight the publication bias of under-represented, less well-funded areas of the globe and non-significant results. We strongly believe that our approach to fair open access publishing will serve as a role model, not only for soil ecology, but for scientific publishing in general.

Schedule and Intermediate Goals

The present project encompasses several independent sub-projects (Fig. 6), which will allow all team members to publish papers early on and to synthesise their data in high-impact papers towards the end of the funding phase. Postdoc 1 will be employed for five years due to the more laborious studies and co-supervision of PhD students, while postdocs 2 and 3 will be employed for three and two years, respectively. The two PhD students will each be employed for four years. Technical support will be provided by two technicians; one lab technician is iDiv-funded staff of Prof. Dr. Nico Eisenhauer’s lab group and one technician will be funded through this project for 4 years to support the planned fieldwork. Workshops will represent important means for scientific exchange and synthesis with SAB members, selected invitees and local forest managers.

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Proposal title

Biotic Interactions as Mediators of Context-Dependent Biodiversity-Ecosystem Functioning Relationships – BIOCODE

Funding program

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