

## Grant Proposal

# Aboveground-belowground interactions drive the relationship between plant diversity and ecosystem function

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## Abstract

The positive relationship between plant diversity and ecosystem functioning is likely to be co-determined by aboveground–belowground multitrophic interactions. Considering and manipulating such interactions thus is likely to significantly improve the mechanistic understanding of BEF relationships. The present proposal comprehensively investigates long-term (>4 years) plant diversity effects on soil microorganisms, nematodes, and other soil invertebrates across different ecosystems (grassland and forest ecosystems) and global change contexts (elevated [CO<sub>2</sub>], N deposition, warming, and drought) to identify general mechanisms. Complementary and well-directed laboratory experiments will be conducted to simulate soil feedback effects resulting from plant diversity-induced changes in soil food webs. This novel approach will allow investigating the balance between negative and positive plant-soil feedback effects and the consequences for ecosystem functioning. This holistic knowledge of changes in and interactions of above- and belowground processes is crucial to predict the long-term consequences of plant community simplification for ecosystem functioning. Experimental work will be complemented with the meta-analysis of previous work in order to reconcile prior inconsistent findings. The main objective of the present proposal is to disentangle the driving forces of plant diversity effects on soil biota as well as subsequent positive and

negative feedback effects on plants. In order to achieve this, the present project has four major goals:

- (1) investigate long-term plant diversity effects on soil biota and functions across multiple settings in order to derive general conclusions;
- (2) investigate the significance of plant diversity-induced positive and negative soil feedback effects on plant performance;
- (3) investigate if anthropogenic stressor effects reinforce plant diversity effects on soil biota and subsequent soil feedback effects; and
- (4) synthesize results and perform meta-analyses to understand and reconcile inconsistent findings of previous studies on plant diversity effects on soil biota, and relate subsequent changes in soil food webs to alterations in ecosystem functioning.

## **Keywords**

Biodiversity-ecosystem function, global change, long-term experiment, plant-soil feedback, soil organisms

## **List of participants**

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## **Background**

### **The consequences of biodiversity loss**

The rapid loss of species due to human activities and its important implications for ecosystem functions and services, and human well-being have prompted biodiversity research to grow into a leading field in ecological research over the last 20 years (Hooper et al. 2005, Balvanera et al. 2006, Eisenhauer 2012). Recent meta-analyses showed that the relationship between biodiversity and ecosystem functioning (BEF) is predominantly positive (Balvanera et al. 2006, Cardinale et al. 2007, Cardinale et al. 2011). While the phenomenological understanding of the relationship between diversity and ecosystem functioning is well established (but see e.g., Huston 2000), the underlying mechanisms are still intensively debated (Fornara and Tilman 2009, Jousset et al. 2011, Eisenhauer 2012, Maron et al. 2010, Schnitzer et al. 2011).

Terrestrial grasslands are one of the focal model systems for investigating the consequences of biodiversity loss (e.g., Tilman et al. 1996, Reich et al. 2001, Eisenhauer 2012). BEF studies have traditionally focused on the interactions between plant species

rather than on interactions with other trophic levels, resulting in an overly plant-centric view (Bever et al. 2010, Miki et al. 2010, Eisenhauer 2012, Eisenhauer et al. 2012a). However, plants are embedded in a multitude of above- and belowground multitrophic interactions, and the significance of these multitrophic interactions in BEF experiments is increasingly recognized. In order to understand the mechanisms linking plant diversity and ecosystem functioning, not only interactions between plants but also the consideration of plant diversity effects on consumers is needed (e.g., Thebault and Loreau 2003, Eisenhauer et al. 2008b, Eisenhauer et al. 2009b, Eisenhauer et al. 2011c). Evidence accumulates that soil organisms, such as arbuscular mycorrhizal fungi (AMF; Klironomos et al. 2000), soil pathogens (Maron et al. 2010, Schnitzer et al. 2011), herbivores (Eisenhauer et al. 2010c), plant growth promoting rhizobacteria (Latz et al. 2012) and decomposers (Eisenhauer et al. 2008b), significantly (co-)determine the positive plant diversity–productivity relationship. Integrating aboveground–belowground interactions in BEF research may thus be key to improve the mechanistic understanding of why species-rich plant communities function better than species-poor ones (Eisenhauer 2012, Eisenhauer et al. 2012a).

Plants fuel specific soil food webs (Bezemer et al. 2010, Eisenhauer et al. 2010d) by plant rhizodeposits and the accumulation of dead organic matter Eisenhauer et al. 2011d). The increasing effect of plant species richness on plant productivity over time (e.g., Cardinale et al. 2007) correlates significantly with the impact of plant diversity on the abundance and diversity of many groups of soil biota (Fig. 1a). However, only a small number of long-term (>4 years) studies has investigated plant diversity effects on soil biota (Fig. 1b; Eisenhauer et al. 2012a), and long-term soil feedback effects have virtually been neglected thus far (Eisenhauer et al. 2012a). Previous short-term studies mostly stressed the importance of key plant functional groups, such as legumes, and plant productivity in shaping soil communities and functions (Spehn et al. 2000, Zak et al. 2003, Milcu et al. 2008). This likely resulted in a biased view of the links between plant diversity and soil organisms: considering results of >30 studies, Bardgett and Wardle 2010 concluded that plant diversity exerts weak or non-existent effects on soil organism, such as decomposers. However, evidence accumulates that those short-term findings do not realistically reflect actual plant diversity effects. Recent long-term studies found significant positive effects of plant diversity on soil herbivore density and diversity (Viketoft et al. 2009, Scherber et al. 2010, Sabais et al. 2011, Eisenhauer et al. 2011d) and decomposer density and diversity (Scherber et al. 2010, Sabais et al. 2011, Eisenhauer et al. 2011d, Eisenhauer 2012). Interestingly, plant diversity has been shown to surpass plant functional groups and plant productivity as driver of soil biota six years after establishment of a field experiment (Eisenhauer et al. 2011d), supporting the notion that each plant species contributes to belowground functioning (Eisenhauer et al. 2010d). We are only beginning to understand how plant diversity may, though delayed, influence soil biota, and most data come from a single experiment (the Jena Experiment; Roscher et al. 2004), complicating general conclusions. Hooper et al. (2000) suggested a step-by-step hypothesis how plant diversity results in higher belowground diversity assuming strong bottom-up control of biodiversity in soil communities. Increased diversity of plant-derived resources increases the diversity of decomposer microorganisms, detritivores and herbivores in soil, which in turn promotes the diversity of other components of the soil food web. Indeed, Scherber et al. (2010) showed

that plant diversity effects cascade from belowground decomposers and herbivores to predators, supporting the bottom-up perspective of plant diversity effects on multitrophic interactions.

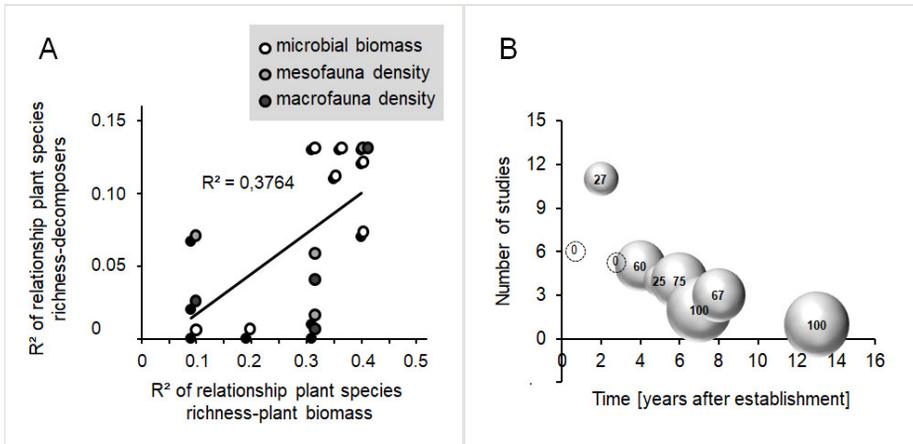


Figure 1.

Importance of the duration of the experiment for its outcome.

**a:** The effect of plant diversity on plant productivity and on the performance of decomposers increases over time. Regression between the  $R^2$  of the relationship between plant diversity and plant productivity and the  $R^2$  of the relationship between plant diversity and decomposer biomass/density. Data from the Jena Experiment from different years [plant productivity in 2003 – 2009; microbial biomass in 2003 – 2009 (white circles); meso- (gray circles) and macroinvertebrate densities (black circles) in 2004, 2006 and 2008]. [doi](#)

**b:** Long-term plant diversity studies on soil biota are rare. Relationship between sampling time since the establishment of the biodiversity experiment, number of studies investigating soil biota and percentage of significant plant diversity effects on soil biota (Eisenhauer et al. 2012a). Size of the bubbles and respective numbers indicate percentage of significant plant diversity effects (regression between number of studies and time:  $R^2=0.56$ ,  $p=0.033$ , between time and significant plant diversity effects:  $R^2=0.66$ ,  $p=0.014$ ,  $n=20$  studies). [doi](#)

## Soil feedback effects

These distinct compositional shifts in soil food webs are likely to exert significant soil feedback effects on plant performance and other ecosystem functions (Fig. 2). For instance, a study on soil nematodes in a plant diversity gradient showed that initial nematode communities generally were dominated by plant antagonists, likely exerting detrimental net effects on plant performance, whereas microbial-feeding nematodes dominated species-rich plant communities in the long term, presumably increasing nutrient cycling and being beneficial for plant performance (Eisenhauer et al. 2011b). This notion was supported by the study of Bezemer et al. (2004) reporting significantly higher numbers of total nematodes and plant-parasitic nematodes in the rhizosphere of *Cirsium arvense* in species-rich plant communities than in species-poor ones after seven years. Nevertheless, plant community biomass was marginally significantly higher in species-rich plant

communities than in species-poor ones (Bezemer et al. 2004) suggesting varying net soil feedback effects depending on plant diversity. Despite the crucial implications of these findings for basic and applied science, this assumption has not been tested comprehensively thus far.

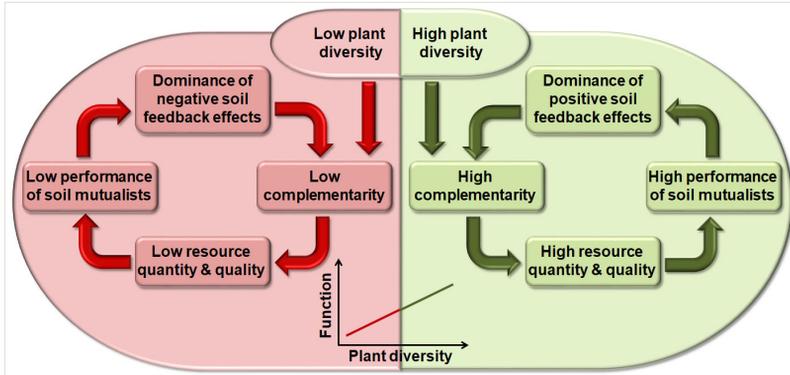


Figure 2. [doi](#)

Conceptual scheme of how aboveground–belowground interactions may influence the positive relationship between plant diversity and ecosystem functioning. The left part of the scheme illustrates how lower quantity and quality of plant inputs to the soil in species-poor plant communities (being low in resource use complementarity) may induce negative soil feedback effects. The right part of the scheme shows that higher quantity and quality of plant inputs in species-rich plant communities (being high in resource use complementarity) may cause the dominance of positive soil feedback effects. Mutualists will decrease (Wurst et al. 2008, Latz et al. 2012) and/or superimpose (Eisenhauer et al. 2012a) detrimental effects of antagonists on plants. The four proposed projects complement each other to explore the underlying mechanisms of this scheme across different experimental contexts.

Relatedly, changes in soil biodiversity likely significantly feed back to plant performance. There is evidence that decomposer diversity is crucial for decomposition processes and plant N availability (Mikola et al. 2002, Heemsbergen et al. 2004, Tiunov and Scheu 2005), although effects may saturate at low levels of diversity (Bardgett and Wardle 2010). Beside species richness, ecosystem functioning may be affected by the functional differences between decomposers, and Heemsbergen et al. (2004) showed that litter decomposition was driven by the functional dissimilarity between decomposer invertebrates rather than by the number of species *per se*. Moreover, Eisenhauer et al. (2010a) found non-additive effects of microbial decomposers and invertebrate detritivores synergistically increasing plant and herbivore performance. A synthesis paper on the influence of detritivore diversity effects on carbon cycling reported significant detritivore species richness effects on decomposition in 100% (richness  $\leq 10$  species) and 64% (richness  $> 10$  species) of the studies (Nielsen et al. 2010). These distinct changes in ecosystem functioning are likely to affect N cycling and thus influence plant competition and performance (Eisenhauer 2012).

Based on a recent compilation of results (Eisenhauer et al. 2012a), negative effects of antagonists are more pronounced in species-poor plant communities, decreasing their

functioning (Maron et al. 2010, Schnitzer et al. 2011), whereas positive effects of mutualists may dominate in species-rich plant communities and increase their functioning (Fig. 2; Latz et al. 2012). Negative soil feedback effects likely are due to direct plant damage by accumulating pathogens in the rhizosphere of species-poor plant communities (Maron et al. 2010). Positive effects of soil-dwelling mutualists may be due to the enlargement of habitat space, i.e., elevated accessibility of nutrients in space, time, and chemical diversity (Eisenhauer 2012). Furthermore, decomposers and AMF may enhance the transfer of legume-fixed N to neighboring plants by recycling N fixed in legume litter and transferring N through fungal hyphae, respectively, thereby improving plant community performance in N-limited ecosystems (Eisenhauer 2012). Third, species-rich plant communities may be better protected against antagonists, e.g., due to higher densities of plant growth promoting rhizobacteria protecting plants against soil-borne pathogens (Latz et al. 2012), and predators reducing herbivore load (Haddad et al. 2009, Scherber et al. 2010). Additionally, mutualists like earthworms (Eisenhauer et al. 2008b) and AMF (der Heijden et al. 2008) may contribute to maintain plant diversity, by creating microhabitat heterogeneity and promoting sub-dominant species. Remarkably, most of the proposed mechanisms have not been studied in a comprehensive way in plant diversity experiments so far, although they are likely to considerably improve the mechanistic understanding of positive BEF relationships.

### **Plant diversity and soil feedback effects depend on other global change agents**

Notably, plant diversity effects on ecosystem functioning and soil processes may be modified by current global changes (Reich et al. 2001, Chung et al. 2007). Reich et al. (2001) showed that ecosystem responses to elevated atmospheric CO<sub>2</sub> concentrations ([CO<sub>2</sub>] hereafter) and N deposition are enhanced by plant diversity, and Chung et al. (2007) reported that these changes affect soil microbial functions. Indeed, results from the BioCON experiment (Reich et al. 2001) show that microbial biomass and respiration significantly increased with plant diversity, and even more so at elevated [CO<sub>2</sub>] in comparison to ambient levels (Fig. 3; Eisenhauer et al. 2013). More pronounced effects of plant diversity on soil biota and processes can be due to increased quantity (e.g., litter input, rhizodeposition; Eisenhauer et al. 2012b) and quality of resources (e.g., higher N content of plant residues; Milcu et al. 2008).

Plant diversity may also reduce the severity of stressor effects such as drought, i.e., plant diversity effects may be more pronounced in the presence of environmental stresses, due to the stabilizing effect on ecosystem functioning (Ives and Carpenter 2007, Eisenhauer et al. 2011c). For instance, species-rich plant communities have been shown to have significantly higher soil water content than species-poor ones (Caldeira et al. 2001), most likely because of lower evapotranspiration due to higher plant biomass and greater humidity at the soil surface. Moreover, species-rich plant communities may better access water in deeper soil layers, particularly in the presence of vertical earthworm burrows (Eisenhauer 2012; but see e.g., Mommer et al. 2010). As a consequence, higher soil water content in species-rich plant communities may reduce the detrimental effect of drought on soil processes. This evidence suggests that low resource availability, such as induced by

soil water shortage, may reinforce detrimental effects of species-poor plant communities on soil biota and related feedback effects on plants (Fig. 4).

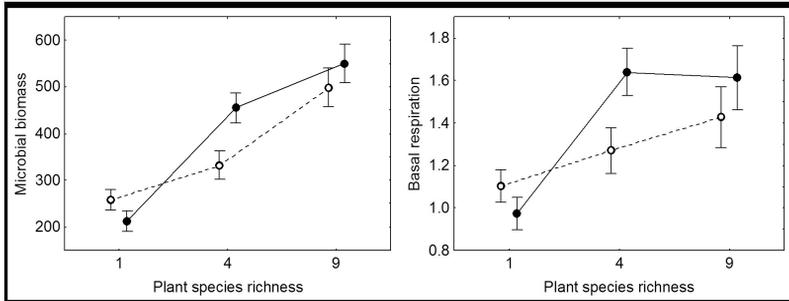


Figure 3. [doi](#)

Plant diversity effects on soil microbes more pronounced at elevated [CO<sub>2</sub>]. Microbial biomass (µg Cmic g<sup>-1</sup> soil dry mass) and basal respiration (BR; µl O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> soil dry mass) as affected by plant species richness (SR) and CO<sub>2</sub> concentrations. Dashed lines indicate ambient CO<sub>2</sub> levels, solid lines elevated CO<sub>2</sub> levels (+180 ppm). SR x CO<sub>2</sub> for Cmic:  $p=0.007$ ; SR x CO<sub>2</sub> for BR:  $p=0.03$ . Data from August 2010. Means with SE. Redrawn after Eisenhauer et al. (2013).

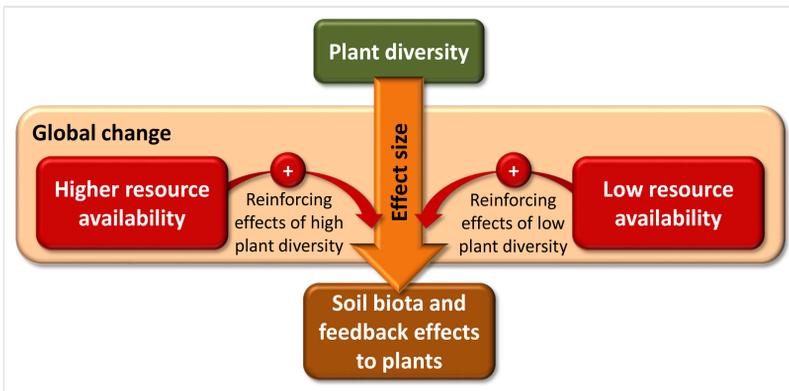


Figure 4. [doi](#)

Conceptual figure showing how global change drivers like temperature increase and drought may increase plant diversity–ecosystem function relationships.

Thus, resource-based, global change-induced deterioration of species-poor plant communities and amelioration of species-rich ones may increase the ‘functional gap’ between low and high diversity assemblages. Although single factor experiments may only poorly reflect actual changes induced by co-occurring global changes, interactions between plant diversity and global change effects have hardly been investigated (Chung et al. 2007). However, this knowledge is essential to realistically predict future changes and may help to identify the mechanisms how plant diversity shapes belowground food webs and processes as well as subsequent soil feedback effects.

## Current gaps in knowledge and the present proposal

Soil feedback effects may significantly impact the complementarity of plants (Eisenhauer 2012). The balance between the feedback effects of soil mutualists and antagonists is therefore an overlooked aspect of ecosystem functioning. The mostly unnoticed loss of soil biodiversity and/or key belowground species may have even stronger impacts on ecosystem functioning and plant complementarity than the loss of single plant species (Eisenhauer et al. 2012a, Eisenhauer et al. 2012b). Identifying key soil biotic groups and shedding more light into the soil ‘black box’ is therefore crucial to realistically predict the consequences of biodiversity loss for the ‘functional fate’ of natural systems (Duffy 2009). The proposed project addresses this critical gap in knowledge by investigating the role of soil antagonists (herbivores and pathogens) and mutualists (in the broadest sense, including decomposers, AMF, plant growth promoting rhizobacteria) in shaping the relationship between plant diversity and productivity (and related ecosystem functions). In order to improve the mechanistic understanding of the BEF relationship subprojects (SPs) I-III base on a field work package (WP), in which long-term plant diversity effects on soil biota and the underlying effect paths will be studied in unique and complementary experiments. Studies in grassland and forest ecosystems in Germany and the USA and in varying global change contexts will allow identifying generalities. In a second WP complementary, well-directed laboratory experiments will be performed to test the significance of positive and negative soil feedback effects as well as the respective soil biotic drivers. The novelties of the proposed project encompass the standardized investigation of plant diversity effects on soil biota across different abiotic and biotic contexts, and – most importantly – the implementation of realistic and comprehensive soil feedback experiments to identify main drivers and consequences of soil feedback effects. Moreover, the different field experiments have been carefully selected since they represent the longest running and extensively sampled trials in the world, allowing the investigation of realistic plant diversity effects and the usage of a plethora of explanatory variables measured by affiliated researchers. The overarching meta-analysis work in SP IV will synthesize the existing information on plant diversity effects on soil biota, soil biodiversity effects on plant performance as well as on soil feedback/soil biota effects on plant performance in plant diversity gradients. This work will exceed previous attempts (Fig. 1; Bardgett and Wardle 2010) by using and completing one of the most exhausting datasets available (Cardinale et al. 2007, Cardinale et al. 2011). Overall, the holistic approach and the integrative nature of the proposal represent a crucial next step in BEF research (Cardinale et al. 2011).

## Objectives and work programme

### Objectives

The relationship between plant diversity and ecosystem functioning is likely to be co-determined by aboveground–belowground multitrophic interactions. Considering and

manipulating such interactions thus is likely to significantly improve the mechanistic understanding of BEF relationships. The present proposal investigates long-term (>4 years) plant diversity effects on soil microorganisms, nematodes, and other soil invertebrates across different ecosystems (grassland and forest ecosystems) and global change contexts (elevated [CO<sub>2</sub>], warming, and drought) in order to extract general mechanisms. Complementary and well-directed laboratory experiments will be conducted to simulate soil feedback effects resulting from plant diversity-induced changes in soil food webs. This approach will allow investigating the balance between negative and positive soil feedback effects and the consequences for ecosystem functioning. Experimental work will be complemented with the meta-analysis of previous work in order to reconcile prior inconsistent findings. The main task of the present proposal is to disentangle the driving forces of plant diversity effects on soil biota as well as subsequent positive and negative feedback effects on plants. The present project has four major goals:

1. Investigate long-term plant diversity effects on soil biota and functions in multiple settings in order to derive general conclusions
2. Investigate the significance of plant diversity-induced positive and negative soil feedback effects on plant performance
3. Investigate if anthropogenic stressor effects reinforce plant diversity effects on soil biota and subsequent soil feedback effects
4. Synthesize results and perform meta-analyses in order to understand inconsistent findings of previous studies on plant diversity effects on soil biota, and relate subsequent changes in soil food webs to alterations in ecosystem functioning.

## Work programme and proposed research methods

### Subproject I: Good polycultures or bad monocultures? The role of positive and negative soil feedback effects in grassland plant diversity experiments

Aims: Two complementary experiments will be conducted to study soil feedback effects in species-poor and species-rich plant communities in two long-term grassland biodiversity experiments (WP I.1), and to investigate how soil biota (antagonists and mutualists) (interactively) shape the relationship between plant diversity and productivity (WP I.2). The aim of this subproject is to investigate the role of antagonists (herbivores and pathogens) and mutualists (including decomposers, AMF, plant growth promoting rhizobacteria, rhizobia) in shaping the relationship between plant diversity and productivity (Fig. 2, Eisenhauer 2012).

Brief background: Plant diversity effects on ecosystem functioning increase over time (Cardinale et al. 2007, Fargione et al. 2007, Reich et al. 2012). In contrast to the phenomenon itself, the underlying mechanisms are not well understood (but see e.g., Fornara and Tilman 2009). Given the significance of soil antagonists (Petermann et al. 2008, Schnitzer et al. 2011, Maron et al. 2010) and soil mutualists (Klironomos et al. 2000, Eisenhauer et al. 2008b, Eisenhauer et al. 2011c, Latz et al. 2012) in shaping the relationship between plant diversity and ecosystem functioning, the question arises if and

to what extent positive and negative soil feedback effects (co-)determine this relationship. Furthermore, it is unclear if increasing plant diversity effects over time are due to deteriorating species-poor, ameliorating species-rich mixtures, or both.

#### Hypotheses:

1. Soil biota strengthen the relationship between plant diversity and productivity (Maron et al. 2010, Schnitzer et al. 2011)
2. Negative soil feedback effects reduce the performance of species-poor plant communities, whereas positive soil feedback effects contribute to increased productivity of species-rich plant communities (Fig. 2; Eisenhauer 2012, Maron et al. 2010, Schnitzer et al. 2011)
3. Soil feedback effects increase the significance of complementarity effects of plant diversity (Fig. 2; Eisenhauer 2012)
4. Positive soil feedback effects are due to (i) a better exploitation of the soil profile, elevated nutrient cycling, and higher resource diversity, whereas negative soil feedbacks are due to direct plant damage (Eisenhauer 2012).

Work Package (WP) I.1: Soil samples will be taken in two long-term grassland plant diversity experiments, (a) the *Jena Experiment* (<http://www.the-jena-experiment.de>) in Germany and (b) the *BioCON experiment* in Minnesota, USA (<http://www.biocon.umn.edu>). Both experiments have a similar experimental design with plant monocultures and 16-species polycultures of the plant functional groups grasses, forbs, and legumes. However, they differ considerably in the composition of soil food webs (Eisenhauer et al. 2011d, Eisenhauer et al. 2012b) due to pronounced differences in soil texture (Reich et al. 2001, Roscher et al. 2004). The investigation of these two experiments allows comparing the major drivers of soil feedback effects in varying environmental contexts.

Soil cores will be taken from 12 monocultures (4 replicates per plant functional group) and 12 16-species polycultures (24 soil samples per experiment). The 24 soil samples will be divided into three subsamples; every third will be planted with one dominant representative of the three plant functional groups, grasses (Jena: *Phleum pratense*, BioCON: *Bromus inermis*), forbs (Jena: *Plantago lanceolata*, BioCON: *Solidago rigida*), and legumes (Jena: *Trifolium pratense*, BioCON: *Lupinus perennis*) (3 plant individuals per Magenta box; 72 boxes per experiment, 144 boxes in total). After 6 weeks, plants will be harvested and the soil will be sampled for identifying soil nematodes (modified Baermann method; Eisenhauer et al. 2011b), plant growth promoting bacteria (quantitative PCR; Latz et al. 2012), and soil mesofauna (heat extraction; Eisenhauer et al. 2011d). Roots will be washed and the colonization by AMF will be determined (Eisenhauer et al. 2009a). Structural equation modeling (SEM; Eisenhauer et al. 2012b) will be used to investigate the relative importance of positive (plant growth promoting bacteria, microbial feeding nematodes, AMF, decomposer mesofauna) and negative soil feedbacks (plant feeding nematodes, herbivore mesofauna) for plant performance in former monoculture and polyculture soils in both grassland biodiversity experiments. Therefore, the density and/or diversity of the varying groups of soil biota will serve as explanatory variables.

WP I.2: The second WP aims at experimentally testing the mechanisms derived from WP I by manipulating important functional groups of soil biota in a plant diversity gradient. A plant diversity gradient (1, 3, 6 species) will be established in microcosms following the design proposed by Bell et al. (2009). The design will be replicated twice with two different plant species pools; ending up with 36 microcosms (Bell et al. 2009). Soil will be sampled at the field site of the Jena Experiment and sterilized. The soil will be washed to reduce nutrient effects due to the sterilization procedure and inoculated with a bacterial suspension from the field site of the Jena Experiment (Eisenhauer et al. 2009a). The plant diversity treatment will be crossed with the following soil biota treatments: 1. presence of mycorrhizal fungi (*Glomus intraradices* and *G. mosseae*; Eisenhauer et al. 2009a), 2. presence of plant feeding nematodes (Wurst et al. 2008), 3. presence of earthworms < (*Aporrectodea caliginosa* and *Lumbricus terrestris*; Eisenhauer et al. 2009a), control (without addition of soil biota), and the combination of all three groups of soil biota (5 soil biota treatments x 36 plant composition treatments = 180 microcosms). The relationship between plant diversity and primary productivity will be determined as affected by soil biota treatments. All three groups of soil biota likely shape the relationship between plant diversity and productivity (Eisenhauer 2012). The two groups of soil mutualists may independently increase the functioning of species-rich plant communities as earthworms likely increase soil N availability, whereas AMF increase P availability for plants (Eisenhauer et al. 2009a). Effects of plant feeding nematodes may be most pronounced in species-poor plant communities (Eisenhauer et al. 2011b). Thus, the steepest relationship between plant diversity and productivity should be found in the combined treatment of all three groups of soil biota. In addition to the differential effect of mutualists and antagonists on species-rich and species-poor plant communities, earthworms likely decrease the detrimental effect of nematodes (Wurst 2010), in particular in species-rich assemblages (Fig. 2; Eisenhauer 2012). In order to explore potential mechanisms how soil biota affect the plant diversity–productivity relationship, <sup>15</sup>N labeled litter will be used to investigate changes in nutrient cycling based on <sup>15</sup>N signatures in plant shoot tissue at the end of the experiment (Eisenhauer et al. 2009a). Root depth distribution will be investigated in three different soil depths (0-5, 6-10, and 11-15 cm) to investigate the effects of soil biota on the exploitation of habitat space (Eisenhauer et al. 2011b). Moreover, analyses of organic compounds in soil solution will be performed using liquid chromatography-mass spectroscopy (Wurst et al. 2009) in order to investigate if plant diversity and soil biota affect the diversity and composition of organic compounds, rhizodeposits, and resource species. Compounds such as phenolics, flavonoids, and organic acids will be identified (Wurst et al. 2009). Additionally, soil ammonium and nitrate concentrations will be measured to investigate soil N availability for plants. The additive partitioning approach will be used to investigate the relevance of complementarity and sampling effects (Loreau and Hector 2001). In addition to general linear models (GLMs) investigating treatment effects on the BEF relationship, SEM will be used to identify direct and indirect effect paths for each group of soil biota in influencing plant productivity.

## Subproject II: Tree diversity effects on soil biota and soil feedback effects

Aims: Complementing the work proposed in SP I in temperate grasslands, this subproject will investigate the composition and functioning of soil biota in two functional tree diversity experiments (WP II.1), and it will use this information to perform a soil feedback experiment manipulating the diversity of soil invertebrate decomposers (WP II.2). This subproject is unique since, in contrast to SP I, both tree diversity experiments span a continuous gradient in the functional diversity of tree assemblages, a biodiversity index that has been shown to have high explanatory power for ecosystem functioning and exceeds the significance of the number of plant functional groups (e.g., Cadotte et al. 2009). However, the role of plant functional diversity (despite the number of functional groups) for soil biota performance has largely been neglected so far.

Brief background: The positive relationship between plant diversity and ecosystem functioning is well-established (Cardinale et al. 2011; but see e.g., Huston 2000). Almost all manipulative biodiversity experiments carried out thus far have used fast-growing and small model systems, in most cases semi-natural grassland communities (Scherer-Lorenzen et al. 2007) and manipulated the number of species. However, forest ecosystems cover a huge proportion of the terrestrial surface and harbour essential ecosystem processes (Grams et al. 2007, Scherer-Lorenzen et al. 2007), such as the storage of carbon. There is some evidence that tree mixtures perform better than average monocultures due to facilitative processes and reduction of intraspecific competition (Pritsch et al. 2009, Morin et al. 2011). In particular, there is very limited information on the effects of tree diversity on soil biota and processes (but see e.g., Cesarz et al. 2007 for tree diversity effects on earthworms). In turn, elevated performance of decomposers in diverse tree assemblages may also positively feed back to tree performance and competition *via* the mechanisms listed above. For instance, soil invertebrates have recently been shown to determine tree litter diversity effects on decomposition (Vos et al. 2010) and thus nutrient cycling. Consequently, decomposer diversity effects are likely to influence essential ecosystem processes (Fig. 2).

### Hypotheses:

1. Functional tree diversity significantly increases the activity, abundance, diversity and functioning of soil microorganisms and invertebrates (Hättenschwiler 2005, Cesarz et al. 2007)
2. Functional tree diversity increases the aboveground (tree biomass productivity resulting in higher litter biomass) and belowground (elevated rhizodeposition) C input into the soil (Pritsch et al. 2009, Morin et al. 2011)
3. Changes in decomposer communities due to alterations in tree diversity (Cesarz et al. 2007) have significant feedback effects on the performance and competition of/ between tree species, e.g. due to changes in N cycling (Eisenhauer 2012).

WP II.1: Two tree diversity experiments will be sampled for soil microbial functions and invertebrates manipulating functional tree diversity at two different spatial scales and in two varying biomes. Similar to the approach in SP I, two long-term experiments with a similar

design but different environmental contexts will be studied. (a) One block (=48 plots) of the Functional Tree Diversity experiment in Cloquet, MN, USA (<http://cfc.cfans.umn.edu/Research/index.htm>) will be sampled for soil microbial functions and community composition. In August 2012 and 2013, five soil samples (diameter 2 cm, depth 10 cm) will be taken per plot (plot size 14.4 m<sup>2</sup>) and microbial respiration, biomass, and C use efficiency (Eisenhauer et al. 2010d), PLFAs (to analyze biomarkers for bacteria, fungi, protozoa, fauna, and plants; Pritsch et al. 2009), and ectomycorrhizal diversity (as important component for plant nutrient uptake; Pritsch et al. 2009) will be analyzed. In addition, real-time PCR will be used to determine the abundance of key functional genes in the nitrogen cycle (nitrogen fixation, ammonia oxidation, and denitrification; Hai et al. 2009). This information is of crucial importance since N is one of the most limiting elements in terrestrial ecosystems (LeBauer and Treseder 2008), and N availability plays an essential role in the relationship between plant diversity and function (Fornara and Tilman 2009). The combination of respiration, PLFA, ectomycorrhiza diversity, and functional gene measurements will allow attributing changes in soil microbial functioning in response to tree diversity to changes in community composition. (b) All 24 plots of the BIOTREE experiment in Bechstedt (<http://www.biotree.bgc-jena.mpg.de/deutsch/mission/index.html>) will be sampled for soil microbes (microbial respiration, biomass, and C use efficiency; Eisenhauer et al. 2010d), soil microarthropods (soil corer with 5 cm diameter, heat extraction; Eisenhauer et al. 2011d), and earthworms (mustard extraction of two 0.5 x 0.5 m subplots per plot; Eisenhauer et al. 2008a) in spring and autumn 2013 and 2014. For both microbes and microarthropods, 16 soil samples will be taken per plot to cover some spatial heterogeneity (plot size 1700 m<sup>2</sup>) and pooled. I performed these soil microbial measurements already in fall 2009 and 2011 (using the same sampling regime), and the respective data will serve to analyze response changes over time. While gross soil microbial measurements will be done in both experiments and allow comparisons, other analyses will account for the different spatial scales of the experiments and thus complement each other.

WP II.2: Results derived from WP II.1 (invertebrate decomposer data in BIOTREE) will be used to perform a soil feedback experiment in microcosms. Differences in the composition in the decomposer community in high and low tree diversity treatments (Cesarz et al. 2007, Eisenhauer et al. 2011a) will be used to set up a decomposer richness gradient (1, 3, 6 species; according to the design proposed by Bell et al. 2009), investigating the soil feedback effects on tree sapling performance, competition and co-existence of three common tree species in Central Europe. Eighteen decomposer replicates will be crossed with three tree monocultures (*Pinus sylvestris*, *Fagus sylvatica*, and *Betula pendula*; species from the pool of the BIOTREE experiment differing in important functional traits, such as litter type, root architecture, and leaf N concentration; Scherer-Lorenzen et al. 2007) as well as the mixture of the three tree species, ending up with 72 microcosms. Following the signature of <sup>15</sup>N labelled litter material into tree leaf/needle tissue and measurement of root depth distribution will be used to investigate if decomposer treatment effects on tree performance (e.g. biomass and height) are due to changes in nutrient cycling and/or rooting depth (Eisenhauer 2012). Additionally, soil ammonium and nitrate concentrations will be measured to investigate soil N availability for plants in the varying

treatments. The additive partitioning approach will be used to investigate the relevance of complementarity and sampling effects (Loreau and Hector 2001) in trees in the varying soil biota treatments (Wagg et al. 2011). The experiment will be performed in controlled chamber conditions (phytotrons) applying a specific  $^{13}\text{C}$  signal ( $^{13}\text{C}$  labeling experiment; Grams et al. 2010). After the experiment (4 months), the  $^{13}\text{C}$  and  $^{18}\text{O}$  signals in tree tissue will be measured to investigate tree competition for soil water (Grams et al. 2007) as one potential mechanism how decomposers may affect plant complementarity (Eisenhauer 2012). Complementary to the investigation of rhizodeposits in SP I, belowground carbon translocation and uptake by decomposers will be studied by measuring the  $^{13}\text{C}$  signal in decomposer tissue (Pollierer et al. 2007).

### **Subproject III: Does global change intensify plant diversity effects on soil biota and subsequent feedback effects?**

Aims: Global change agents affecting resource availability for plants may increase plant diversity effects on soil biota and processes. Two complementary WPs will be implemented studying plant diversity impacts on soil microorganisms as affected by varying resource availability due to global changes (WP III.1), as well as subsequent soil feedback effects in a laboratory experiment identifying the driving groups of soil biota by using soil of a field experiment orthogonally manipulating plant diversity and warming (WP III.2).

Brief background: The world's ecosystems are losing biodiversity at unprecedented rates due to global change agents, such as nitrogen (N) deposition, warming climate, and changes in precipitation regimes (Sala 2000, IPCC 2007). Despite an increasing appreciation that the consequences of global change can be better understood if these varying agents of change are studied in concert (Reich et al. 2001, Eisenhauer et al. 2012b), there is a paucity of multifactor long-term studies, particularly of belowground processes (Blankinship et al. 2011). Changes in plant diversity are driven by global change agents (Reich 2009); however, plant diversity may also modify the magnitude of global change effects (Reich et al. 2001). As outlined above, resource shortage, such as induced by drought and warming (reduced water and N availability), may particularly deteriorate the functioning of species-poor plant communities, whereas higher resource availability, such as induced by elevated  $[\text{CO}_2]$  and N deposition, likely ameliorates the functioning of species-rich communities (Reich et al. 2001). This global change-induced 'functional gap' between low and high diversity plant communities likely cascades into soil food webs and changes belowground processes (Fig. 4) and feedback effects.

The proposed project explores these interrelationships in three world-leading long-term plant diversity experiments in which global change agents are also manipulated. The project will identify general patterns of the interaction between plant diversity and resource availability (soil C, N, and water) by measuring the interaction effect on soil microbial biomass and functions at several sites, using standardized methodology. The present SP will focus on soil microbial functions since soil microorganisms are the backbone of nutrient cycling and a multitude of other ecosystem functions in terrestrial ecosystems (der Heijden et al. 2008). The three experiments will complement each other by focusing on three of the

most influential global change drivers, namely changes in  $[\text{CO}_2]$ , N deposition, and climate (Sala 2000). As powerful alternative to re-sampling the same experiment, the present subproject will replicate samplings across experiments; i.e., significant effects across sites are extremely unlikely to be transient. Moreover and in line with SP I and II, a soil feedback experiment and the detailed investigation of soil microbes and nematodes will allow attributing changes in soil feedback effects to specific groups of soil biota.

#### Hypotheses:

1. Plant diversity maintains soil processes subjected to drought/warming (resource shortage) due to higher soil water content in species-rich plant communities (Caldeira et al. 2001)
2. Plant diversity reinforces the effects of increased resource availability on soil processes due to enhanced ecosystem responses (e.g., biomass production and rhizodeposition) (Figs 3, 4; Reich et al. 2001)
3. Global change agents will increase the 'functional gap' between low and high diverse plant communities, i.e., differences in function between high and low diversity communities will be greater in ecosystems subjected to global change perturbations
4. Reinforced plant diversity effects on soil biota due to resource shortage result in significant soil feedback effects on plants. I expect positive soil feedback effects to dominate in species-rich plant communities and negative soil feedback effects to dominate in species-poor plant communities experiencing resource shortage.

WP III.1: (a) In the Jena Experiment in Germany, summer drought (-35% to -58% precipitation) has been simulated since 2008 on all large plots of the main experiment. A subset of plots (1, 4, and 16 species plots;  $n = 43$ , 86 subplots) will be sampled in October 2012 for soil microbial functions (biomass, respiration, C use efficiency, and microbial nutrient limitation; Eisenhauer et al. 2010d). The measurement of soil microbial nutrient limitations will allow investigating if global change effects are due to changes in nutrient availability. On each plot, five soil samples (2 cm diameter, 10 cm depth) will be taken, pooled, sieved (2 mm mesh), and analysed using an  $\text{O}_2$ -microcompensation apparatus (Scheu 1992). (b) In the BioCON experiment in Minnesota, USA,  $[\text{CO}_2]$  (ambient, +180 ppm) and N deposition (ambient, +4 g  $\text{N}/\text{m}^2 \times \text{yr}$ ) have been manipulated in a plant diversity gradient since 1997. A subset of plots with 1, 4, and 16 plant species will be sampled in July 2013 for soil microbial functions as explained above (90 plots). (c) In the BAC experiment in Minnesota, USA (Fig. 4e; [http://www.cedarcreek.umn.edu/research/researchsummaries/bac\\_experiment.shtml](http://www.cedarcreek.umn.edu/research/researchsummaries/bac_experiment.shtml); collaboration with Prof. David Tilman and Prof. Peter Reich), a plant diversity gradient (1, 4, 16 species) has been subjected to ambient and increased (+3°C) temperature since 2007. In August 2013, the 32 plots (= 64 subplots) will be sampled for analyzing soil microbes as detailed above. Warming is likely to affect soil biota mainly by significantly decreasing the soil water content (7.2% in ambient, 5.8% in warmed plots,  $p=0.003$ ; own preliminary results; measured in September 2011). The collaborators in all three experiments will provide data on plant community performance and resource availability (soil C, N, and  $\text{H}_2\text{O}$ ).

**WP III.2:** The soil feedback experiment will be performed in the frame of the BAC experiment since plots are large enough to sample sufficient amounts of soil and since other research groups will provide unique complementary data on soil biota: we will determine the abundance and pathogen suppressive activity of soil streptomycetes (Bakker et al. 2010), and the abundance of protozoans, representing important microbial grazers, using a modified most-probable number method (e.g., Scherber et al. 2010, Eisenhauer et al. 2012b). In addition, soil nematodes will be extracted and identified (Eisenhauer et al. 2011b). Nematodes, the most abundant and diverse soil Metazoa, represent the complexity of soil food webs as they comprise all major trophic groups and allow calculation of a number of functional indices, such as predictors of soil feedback effects (Ferris et al. 2001, Eisenhauer et al. 2011b). Approximately 150 g of soil (fresh weight) will be taken on each of the 64 subplots of the BAC experiment (10 soil cores, 2 cm diameter, 10 cm depth). The soil from each plot will be divided into three subsamples and placed in three Magenta boxes (7.7 x 7.7 x 9.7 cm) to investigate the soil feedback effects on three pre-grown model plant species belonging to three different plant functional groups (grass, forb, legume; ending up with 192 experimental units). The model plant species will be selected based on their dominance in the plots of the BAC experiment, and three individuals will be planted into each Magenta box. After 4 weeks, plants will be destructively harvested and shoot, root, and total biomass will be assessed. Soil ammonium and nitrate concentrations will be measured to investigate soil N availability for plants. In addition to GLMs of treatment effects on plant performance, SEM will be used to identify driving functional groups of soil biota by considering the data on soil microbes, protozoans, and nematodes determined in the present WPs and by collaborating groups.

#### **Subproject IV: Plant diversity effects on soil biota and subsequent feedback effects: synthesis and meta-analysis**

**Aims:** Based on the conclusions and implications of two recent review papers (Jiang and Pu 2009, Eisenhauer 2012), this work aims at gaining a better understanding of the relevance of multitrophic interactions in biodiversity experiments. Meta-analyses will be performed investigating (a) plant diversity effects on different groups of soil biota, (b) effects of soil biodiversity on plant productivity, and (c) the effects of soil antagonists and mutualists on the relationship between producer diversity and ecosystem functioning.

**Brief background:** (a) As outlined above, the significance of plant diversity effects on soil biota is controversial, and a meta-analysis may enable the establishment of a general theory. (b) Similarly, evidence is equivocal regarding how soil biodiversity affects plant performance (Bardgett and Wardle 2010). Distinguishing varying experimental approaches and functional groups of soil biota may help answer the question how important soil biodiversity is for ecosystem functioning and plant productivity. Interestingly, Wolters 2001 highlighted the relevance of belowground biodiversity for ecosystem functioning by proposing that the number of soil biota species needed to maintain ecosystem functioning may depend on the number of functions investigated. This is in accordance with findings on the relevance of plant diversity for ecosystem multifunctionality (Hector and Bagchi 2007,

Isbell et al. 2011). Indeed, the latter studies found that the more ecosystem processes were considered, the more plant species were found to affect overall functioning. To my knowledge, however, no study has so far investigated the effect of soil biodiversity on ecosystem multifunctionality. (c) Moreover, evidence is accumulating that pathogens (Petermann et al. 2008, Maron et al. 2010, Schnitzer et al. 2011, Latz et al. 2012.), herbivores (Mulder et al. 1999, Eisenhauer et al. 2010c), mycorrhizal fungi (Klironomos et al. 2000, Wagg et al. 2011), and decomposers (Eisenhauer et al. 2008b, Eisenhauer et al. 2009b, Eisenhauer et al. 2010b) affect the BEF relationship. However, this assumption has not been tested in a meta-analysis approach considering and comparing the findings of different experiments in varying ecosystems (Jiang and Pu 2009).

**Methods:** A database will be set up considering studies in which (a) soil biota have been studied in plant diversity gradients, (b) soil biodiversity effects on plant performance have been investigated, and (c) plant diversity and, simultaneously, presence/density/diversity of above- and belowground consumers have been manipulated. Available datasets of BEF studies (e.g., Cardinale et al. 2007, Cardinale et al. 2011) will form the basis of the present database. In addition, a literature research will be performed to update and extend this database. Then, the database will be divided into three sub-databases in order to address tasks (a) – (c). The databases will specify experimental conditions and responses of appropriate BEF studies, such as experimental duration, study system (field vs. laboratory, ecosystem type, climate etc.), plant/soil biota diversity gradient, method of manipulation of plant/soil biota diversity, method of manipulation of above- and belowground consumers, efficiency of manipulation method, trophic group studied/manipulated, organisms studied/manipulated, ecosystem functions investigated, significance and shape of main and interactive effects, difference in the slope of BEF relationships in the varying treatments, and mechanisms proposed to affect soil biota, plant performance, or the BEF relationship. Effect sizes will be calculated using Fisher's z transformation of correlation coefficients (Jiang and Pu 2009). The objectives are to investigate if:

1. plant diversity effects on soil biota increase over time and become significant (Fig. 1a),
2. plant diversity effects on soil biota differ between varying trophic groups (Scherber et al. 2010),
3. soil biodiversity effects on plant performance saturate at low diversity levels (Bardgett and Wardle 2010),
4. soil biodiversity affects ecosystem multifunctionality (Wolters 2001),
5. antagonists influence the BEF relationship by decreasing the performance of species-poor communities (Maron et al. 2010), and
6. mutualists influence the BEF relationship by increasing the performance of species-rich communities (Latz et al. 2012).

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