Title

Synthesis and future research directions linking tree diversity to growth, survival, and damage in a global network of tree diversity experiments

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Abstract

Despite considerable research demonstrating that biodiversity increases productivity in forests and regulates herbivory and pathogen damage, there remain gaps in our understanding of the shape, magnitude, and generality of these biodiversity-ecosystem functioning (BEF) relationships. Here, we review findings from TreeDivNet, a global network of 25 tree diversity experiments, on relationships between levels of biodiversity and (a) tree growth and survival and (b) damage to trees from pests and pathogens. Tree diversity often improved the survival and above- and belowground growth of young trees. The mechanistic bases of the diversity effects on tree growth and survival include both selection effects (i.e., an increasing impact of particular species in more species-rich communities) and complementary effects (e.g. related to resource differentiation and facilitation). Plant traits and abiotic stressors may mediate these relationships. Studies of the responses of invertebrate and vertebrate herbivory and pathogen damage have demonstrated that trees in more diverse experimental plots may experience more, less, or similar damage compared to conspecific trees in less diverse plots. Documented mechanisms producing these patterns include changes in concentration, frequency, and apparency of hosts; herbivore and pathogen diet breadth; the spatial scale of interactions; and herbivore and pathogen regulation by natural enemies. Our review of findings from TreeDivNet indicates that tree diversity experiments are extending BEF research across systems and scales, complementing previous BEF work in grasslands by providing opportunities to use remote sensing and spectral approaches to study BEF dynamics, integrate belowground and aboveground approaches, and trace the consequences of tree physiology for ecosystem functioning. This extension of BEF research into tree-dominated systems is improving ecologists' capacity to understand the mechanistic bases behind BEF relationships. Tree diversity experiments also present opportunities for novel research. Since experimental tree diversity plantations enable measurements at tree, neighbourhood and plot level, they allow for explicit consideration of temporal and spatial scales in BEF dynamics. Presently, most TreeDivNet experiments have run for less than ten years. Given the longevity of trees, exciting results on BEF relationships are expected in the future.

Keywords (<=6)

Biodiversity experiment; Ecophysiology; Herbivory; Pathogens; Plantation forest; Research infrastructure

1. Introduction

Tree diversity in natural forests varies tremendously across the globe and ranges from aspen stands dominated by a single genotype (Mock et al., 2008) to tropical assemblages of more than 400 tree species per hectare (Liang et al., 2016). Humans have a clear effect on this diversity, through both the intentional and unintentional effects of silviculture and overexploitation (Morris, 2010). Natural forests have in many cases been replaced with less diverse secondary forests (especially in tropical regions; Newbold et al., 2015; Sloan and Sayer, 2015) or plantations (globally; Bremer and Farley, 2010; Spiecker, 2003) causing massive losses and, in some cases, some gains in forest-associated biodiversity (Betts et al., 2017; Lindenmayer et al., 2015). Historically, expectations of the consequences of reduced tree species diversity – including lower stand growth rates and increased vulnerability to damage by disease and herbivores – have been either based on observational data (Jactel and Brockerhoff, 2007; Liang et al., 2016; Paquette and Messier, 2011) or inferred from experiments in non-forested ecosystems (Cardinale et al., 2006; Hooper et al., 2012). Foundational biodiversity-ecosystem functioning (BEF) research in grasslands in particular provides a rich set of hypotheses about potential BEF relationships (Cardinale et al., 2011; Hooper et al., 2005; Tilman et al., 2014).

The notion that diverse ecosystems might be more productive (McNaughton, 1977; Trenbath, 1974; Vandermeer, 1981) or more resistant to disease or damage by herbivores (Elton, 1958; McNaughton, 1985) has periodically been proposed since Darwin (1859). Yet, the current era of BEF research dates conclusively to 1991, when discussion of the topic re-emerged at a conference in Bayreuth, Germany and in a subsequent collection of papers (Schulze and Mooney, 1994). Research from grasslands (Tilman et al., 1996; Tilman and Dowling, 1994) and mesocosms (Naeem et al., 1994) soon provided the first evidence that biodiversity can enhance primary productivity beyond what would be expected based on monoculture yield (referred to as *overyielding*). This early BEF research mainly focused on primary productivity as a key ecosystem function that integrates the effect of biodiversity on other functions, such as resistance to pests and diseases (Cardinale et al., 2012). As such, productivity emerged as the most frequently studied metric of ecosystem functioning. Yet, additional studies of other ecosystem functions in grasslands quickly proliferated, consolidating the current consensus that biodiversity supports ecosystem functioning and multifunctionality (Cardinale et al., 2006; Hector and Bagchi, 2007; Hooper et al., 2005; Tilman et al., 2012). Advances over the first 20 years of BEF research have also raised new questions about the generality of and mechanisms behind BEF relationships (Tilman et al., 2014; Weisser et al., 2017), the importance of different facets of biodiversity (e.g. species, functional and phylogenetic diversity) in shaping ecosystem functioning (Flynn et al., 2011), and the interacting effects of abiotic factors such as resource availability or drought (Craven et al., 2016).

In response to criticism (for instance Aarssen 1997, Huston 1997), BEF researchers have attempted to demonstrate that findings from controlled diversity experiments, especially the first generation of synthetic grassland and mesocosm studies, are relevant to real-world ecosystems and generalizable across ecosystem types. Over the last two decades, BEF research has expanded into a variety of ecosystems other than grasslands, including farm fields, forests, streams, lakes, and marine environments. Though BEF dynamics vary across systems, diversity repeatedly has affected ecosystem functionality (Cardinale et al., 2011; Lefcheck et al., 2015). As such, whether biodiversity positively affects ecosystem functioning is no longer widely debated, and research has largely shifted to understanding the mechanisms and context-dependency of BEF relationships.

Globally distributed tree diversity experiments hold the potential to complement past work, add generality, and address criticisms, improving our mechanistic understanding of the relationships between biodiversity and ecosystem functioning. Networks of globally distributed experiments with common experimental methodology represent the future of BEF research. Since they capture much variation in species combinations and environmental conditions, they provide more generality to the findings and permit extrapolation to a large inference population (Bauhus et al., 2017). Mirroring the development of ecology as a discipline, BEF investigations originated as a series of single-site experiments (e.g. Naeem et al. 1994, Tilman et al. 1996) and are now routinely conducted through regional networks of experiments (Hector, 1999), meta-analysis (Hooper et al., 2012; Isbell et al., 2015), and synthesis of globally collected observational data (Liang et al., 2016). Global experimental networks, including the one reported on here, represent a new and promising trend in a variety of ecological disciplines, including BEF research. In their introduction of the grassland-based Nutrient Network, Borer and colleagues (2014) note that global networks complement studies at single sites and *post hoc* synthesis of data from single-site experiments by encouraging participating researchers to use consistent methodologies, which, when applied across global ecological gradients, allow for mechanistic causal inference, providing more realistic interpretation than other experimental methods. To date, many distributed ecological networks have been only regional in scope (Fraser et al., 2013), although some, such as the Nutrient Network, have achieved global reach. Global, distributed networks will be critical if BEF researchers are to effectively counter criticisms related to realism and generality.

We review here empirical work conducted in TreeDivNet, a global network of 25 tree diversity experiments, some at multiple sites, covering 817 ha and comprising over 1.1 million trees (Verheyen et al. 2016; www.treedivnet.ugent.be). Since 1999, TreeDivNet experiments have been established in boreal, temperate, Mediterranean, subtropical, and tropical sites (Fig. 1); together they constitute the largest network of experiments in the world in which biodiversity is systematically manipulated.

All TreeDivNet experiments manipulate tree (and sometimes shrub) diversity and conduct ecological measurements to study a variety of ecosystem functions, processes, and services. The dimensions of biodiversity manipulated (e.g. genotypic richness, species richness, functional diversity, etc.), species used in experiments, and measurements taken vary within the network (Table 1). The most common approach is an experiment in which plots of trees vary in species, functional or genotypic richness and in which regular monitoring of tree growth and mortality is complemented by periodic or *ad hoc* measurements of other responses. Experimental plots are generally composed of species mixtures typical of native stands and/or plantations. Some experiments also allow the exploration of tree identity versus tree diversity effects through inclusion of multiple assemblages of equal richness (Ampoorter et al., 2015; Tobner et al., 2014). Across the network, consistency in methods has allowed for collaborative syntheses of findings across experiments (e.g. Pollastrini et al. 2014, Haase et al. 2015).

To date, researchers working in TreeDivNet have produced 143 peer-reviewed publications and 15 doctoral theses describing work at most of the network’s sites (Appendix 1). Though these reports detail the responses of a variety of ecosystem properties to tree diversity manipulations, we choose to focus on two particular ecosystem functions: tree growth and survival and herbivore and pathogen damage from (Fig. 2). These responses are measured across the network and are widely treated as critical, diversity-dependent ecological processes in the BEF literature. The consequences of plant diversity manipulations for diversity at other trophic levels, nutrient cycling, and other response variables will be systematically analyzed using formal meta-analysis in a future paper. Instead, here we review the diverse results emerging from the first generation of TreeDivNet papers and highlight both representative and striking results.

In the present work, we review BEF research in the TreeDivNet network and describe a global experimental platform for assessing BEF dynamics in forests (this section), unpack several key concepts for understanding BEF findings (section 2), review research from the network published to date on the consequences of diversity for tree growth and survival (section 3) and tree damage by pests and pathogens (section 4), and highlight opportunities for (section 5) and challenges to (section 6) novel BEF research in tree diversity experiments.

2. Key concepts underlying BEF research

Prior to reviewing findings from TreeDivNet, we briefly unpack three concepts essential to understanding recent research in the network. First, the concept of *mechanism* in BEF research provides a central gap in knowledge and motivation for this review. Second, the partitioning of biodiversity effects into *complementarity* and *selection effects* has emerged as an essential concept in BEF research, and especially in studies of plant growth or productivity. Finally, most of the reports we reviewed that address the consequences of diversity for pest or pathogen damage do so in terms of *associational effects* and their bases in bottom-up and/or top-down effects.

Since the first studies linking biodiversity to ecosystem functioning, ecologists conducting (Naeem et al., 1994; Tilman and Dowling, 1994) and criticizing (Huston, 1997; Wardle et al., 1997) BEF research have emphasized the necessity of establishing mechanistic explanations for BEF relationships. We consider mechanistic explanations of BEF findings to be reductionist descriptions of the specific biophysical patterns that give rise to the observed changes in ecosystem functioning over a gradient of increasing biodiversity. Mechanistic explanations generally refer to the traits of study organisms (both morphological and physiological), biogeochemical cycling of nutrients between organisms and their environment (often soil, litter, or water), or multitrophic dynamics observed within the experiment (Forrester and Bauhus, 2016). The most common explanation is that trait dissimilarity among associated organisms results in niche differentiation and allows the community of organisms to make better use of limiting resources (Loreau, 2000; Loreau and Hector, 2001; Tilman et al., 1997). For instance, Williams and colleagues (2017) attributed an observed increase in canopy growth at higher diversity (*the BEF relationship*) to niche differentiation among species with different strategies for light acquisition (*the mechanism*). Such mechanistic explanations of BEF are central to modern ecology (Schoener, 1986) and essential to our understanding of biodiversity (Cadotte et al., 2011; Eisenhauer et al., 2016; Mikola and Heikki, 1998).

Positive net biodiversity effects on a given ecosystem function are frequently described in terms of complementarity and selection effects. This practice, though influential in the BEF literature, does not pertain to mechanism in a strict sense as complementarity and selection are not lower-level processes explaining BEF effects. Hector and Loreau's (2001) canonical formulation of these concepts, which was developed in response to criticism of the interpretation of early BEF findings (e.g. Aarssen 1997, Huston 1997, Heijden et al. 1999), remains widely used. Briefly, partitioning the net effects of biodiversity into complementary and selection provides a semi-mechanistic interpretation by mathematically determining whether BEF relationships stem from additive impacts of particular species or non-additive impacts of interacting species (e.g. Potvin and Gotelli 2008, Lang'at et al. 2013, Bu et al. 2017). Complementarity effects of biodiversity occur when mixtures have a larger yield than the expectations based on the performance in monocultures. These effects can include niche partitioning and facilitation, though Loreau and Hector's method does not allow for their separation and quantification. Furthermore, to use their method, investigators must be able to quantify the contributions of individual tree species to a plot-level ecosystem response. This is relatively straightforward when summing up biomass produced by a group of plants in a plot. It can also be done by using meaningful weighting coefficients to represent species-specific contributions to ecosystem functioning (Grossiord et al., 2013). Yet emergent properties that can only be measured for the community as a whole (e.g, ecosystem resilience, structural complexity) require a different methodological approach. For instance, a random partition design, as in EFForTS-BEE (Teuscher et al., 2016), makes it possible to quantify the importance of species interactions versus identity effects even if the relative contributions of each species are unknown, and to estimate the level of change in ecosystem functioning if one particular species would be added to or lost from a composition (Bell et al., 2009). As tree diversity experiments involve measurements on individual plants, a more complex analysis that goes beyond the partitioning of complementarity and selection as in grassland studies is possible (e.g. Chamagne et al., 2016).

Associational effects describe the consequences of neighbourhood composition for the amount of damage caused by pests and pathogens to a plant (Moreira et al., 2016; Underwood et al., 2014). Associational effects range from associational resistance when a plant suffers less damage when surrounded by heterospecific neighbours (e.g. Vehviläinen et al. 2006, Cook-Patton et al. 2014, Damien et al. 2016, Jactel et al. 2017) to associational susceptibility when plants with heterospecific neighbours suffer more damage (e.g. White and Whitham 2000, Schuldt et al. 2010). Mechanistic explanations of associational effects reviewed here include the consequences of bottom-up effects (host concentration, host apparency, pest and pathogen diet breadth, and spatial scale) and one top-down effect (natural enemies) for damage to plants.

The resource concentration hypothesis (Hambäck and Englund, 2005; Root, 1973) states that herbivores are more likely to immigrate into and less likely to emigrate from patches where their resources are more concentrated. In addition to host concentration, the specific composition of tree species mixtures may influence herbivore and pathogen damage through changes in tree apparency. Plant apparency, initially defined at the species level, describes a plant’s likelihood of being found by herbivores (Feeny, 1976). The apparency concept has more recently been adapted to the case of individual trees in the BEF context and is viewed as neighbour-mediated apparency in the sense that a particular plant’s neighbours can modify its likelihood of being found (Castagneyrol et al., 2013a; Damien et al., 2016). The strength and direction of associational effects likely depends on the scale at which tree diversity influences herbivore foraging and host selection (Hambäck et al., 2014). Moreira et al. (2016) recently stressed that herbivore mobility could be a key driver of associational effects, highly mobile herbivores being more likely to disperse and choose among individual trees and patches of trees (Bommarco and Banks, 2003; Moreira et al., 2016). Tree species diversity at larger spatial scales may therefore be of greater importance for highly mobile herbivores.

In addition to the direct, bottom-up effects of plant community composition and diversity, herbivores face a wide range of natural enemies that prey upon them or alter their behaviour. These top-down effects can significantly change key ecosystem processes, such as plant biomass production and nutrient cycling (Schmitz, 2008). Ecological theory and early studies in agricultural systems indicated that plant diversity modifies top-down effects (Andow, 1991; Root, 1973), with stronger control of herbivores expected when plant diversity is high (the enemies hypothesis; Root 1973). While some BEF studies in non-forest ecosystems have shown clear support for the enemies hypothesis (e.g. Haddad et al. 2009), others have indicated that plant diversity has much weaker effects on predators than on herbivores (Scherber et al., 2010); support for the enemies hypothesis in forested ecosystems is mixed (Zhang and Adams, 2011). So far, relatively few studies have addressed the relationship between tree diversity and predators in controlled experiments and, often, only specific predator taxa or functional groups were studied, which limits our ability to draw broad generalizations. Also considering that predators are taxonomically, ecologically, and behaviourally very heterogeneous and can strongly affect each other via horizontal intraguild interactions (Finke and Denno, 2005; Grass et al., 2017), the net effect of tree diversity-mediated top-down effects on herbivores might thus depend on how tree diversity influences these intraguild interactions (see also Schuldt and Staab 2015). Predator abundance or diversity might therefore not necessarily be the best measures of predation pressure.

3. Tree growth and survival across diversity gradients

Tree mortality and growth are assessed across the TreeDivNet network (Tables 1,2). The surveyed literature included 36 publications on the relationship between diversity and tree growth and/or survival from 11 experiments. Specific responses assessed (e.g. stem growth vs. root growth) are detailed in Table 2 and vary among studies such that some experiments contributed data to multiple publications. These reports, over the first 15 years of the tree diversity experiments, generally document either no or positive effects of tree diversity on the two responses. In a single study from the BEF-China experiment (Yang et al., 2013), tree mortality was initially higher at higher species richness; the effect disappeared after replanting and, according to the authors, was due to the greater on-the-ground challenges of planting high-diversity plots. In the early stages of the Indonesian EFForTS-BEE experiment, the diversity of planted tree species had a negative effect on tree growth but a positive effect on tree survival (Gérard et al. *submitted*). Although a number of authors reported on root growth, studies of aboveground growth predominated in the reviewed works. The relationship between biodiversity and tree growth (Fig. 2) was often described in terms of complementarity and selection effects (section 3.1), niche differentiation (3.2), facilitation through mitigation of abiotic stress (3.3), and trait-dependent responses (3.4).

3.1 Complementarity and selection effects

In some cases, authors use Hector and Loreau’s (2001) formal partitioning method to quantify complementarity and selection effects (section 2). In others, complementarity and selection are invoked as conceptual explanations of diversity-growth/survival relationships and deployed to explain observed patterns (Peng et al., 2017; Sun et al., 2017; Van de Peer et al., 2016). Evidence for both complementarity and selection effects has been reported from TreeDivNet experiments (Table 2). These findings are consistent with grassland studies, in which aboveground overyielding in biomass production has been attributed to both.

Some authors presented evidence (or a lack of evidence) for complementarity- or selection-driven BEF relationships though they did not carry out formal analyses. For instance, Van de Peer and colleagues (2016) found that tree seedlings in the FORBIO experiment experienced lower variation in mortality at higher species richness. Yet this buffering effect simply stemmed from species-specific differences in mortality; more diverse plots were were less likely to contain a high share of species that tended to die easily. As such, the effect of diversity on mortality occurred through selection. Conversely, Sun et al. (2017) found that roots were more evenly distributed through the soil profile at higher species richness in the BEF-China experiment, suggesting a more complete use of soil resources, a sign of complementarity. Below, we review several concrete mechanisms that underlie these findings of complementarity- and selection-based overyielding.

3.2 Niche differentiation

In contrast to studies that measure the gross effects of tree diversity on growth and yield (through selection and/or complementarity effects), there were few published TreeDivNet investigations of the specific mechanisms underlying complementarity effects in tree monocultures and mixtures. Results from a short-term experiment, using different genotypes of willows, indicated that the expression of traits related to nitrogen use efficiency differed between mixture and monoculture (Hoeber et al., 2017). Similarly, recent work at the IDENT-Montreal site (Williams et al. 2017) has demonstrated canopy niche differentiation, resulting in a more efficient space use and light interception in mixtures than in monocultures (Pretzsch, 2014).

Differential use of available belowground resources (e.g. water and nutrients) has been shown to contribute to complementary interactions in assemblages of multiple coexisting species (Ashton et al., 2010; McKane et al., 2002; Meinzer et al., 1999). In research conducted in the BEF-China experiment, Bu et al. (2017) and Sun et al. (2017) offer examples of overyielding driven by such belowground resource use differentiation. Additionally, several ongoing studies in TreeDivNet experiments address resource use issues in order to test the mechanistic role of trait diversity in ecosystem productivity and identify the processes that explain why different community components (species or genotypes) promote resource use efficiency, productivity, and ecosystem functioning (Isbell et al., 2011). These insights will be useful in designing resource-use efficient and productive tree-based production systems (cf. Malézieux 2009 for agro-ecosystems).

3.3 Facilitation through amelioration of abiotic stress

Increasingly, tree diversity experiments have been designed to include manipulation of abiotic stressors in concert with diversity gradients. The three relevant TreeDivNet studies published to date have not provided evidence of strong interactions between abiotic stress and the diversity-growth/survival relationship. Local microclimate in BEF-China (Kröber et al., 2015) and an imposed drought gradient in FORBIO (Dillen et al., 2016) did not mediate the relationship between tree diversity and aboveground growth, nor did localized nutrient enrichment affect belowground productivity in the BIOTREE experiment (Lei et al., 2012). Several experiments in the network (Table 1; ORPHEE, IDENT, Ridgefield, Sabah, BEF-China) include further manipulations of abiotic variables thought to have an impact on BEF dynamics, but there has yet to be published work addressing the topic. As such, it remains to be seen whether findings from these experiments will corroborate work from grassland diversity experiments documenting interactions between diversity, plant performance, and abiotic stressors (Adair et al., 2009; Craine et al., 2003).

3.4 Traits and tree growth and survival

It has become commonly accepted over the last two decades that the functional traits governing how plants affect and respond to their environments do play and will continue to play a central role in the ongoing efforts to link the physiology of individuals to population dynamics and ecosystem functioning (McGill et al., 2006; Violle et al., 2007). Accordingly, some of the earlier mechanistic interpretations of biodiversity-growth/survival relationships have revolved around functional traits. For instance, communities composed of a higher diversity of functional groups (e.g. legumes, warm-season grasses, cool-season grasses, etc.) overyielded in productivity consistently in the first generation of grassland diversity experiments (Hector, 1999; Tilman et al., 1997). Extension of the trait-based BEF perspective to tree diversity experiments now allows for the assessment of how both the mean trait values and trait diversity of communities as well as individual trees' traits may affect community performance.

While early BEF research in grasslands has consistently indicated that community-level diversity of functional traits (e.g. a wide range of leaf nitrogen contents) improves community performance, several tree diversity experiments have provided evidence that mean trait values contribute more than trait diversity. For instance, in two sites in the IDENT experiment, communities dominated by species with highly branching roots (Tobner et al., 2016) and low leaf nitrogen content (Grossman et al., 2017) showed higher aboveground overyielding in productivity. Similarly, Kröber et al. (2015) found community-weighted mean trait values to explain crown growth at the community level better than functional diversity. In these cases, it appears that the prevalence of species with particular traits, rather than a diversity of traits, is responsible for positive diversity effects. Such results can indicate a selection effect, in which a given trait value promotes growth regardless of local diversity, or a complementarity effect, in which species with a particular trait value are best able to take advantage of diverse conditions. It is unclear whether the effect of the mean trait value, rather than trait diversity, is because of the early stage of stand development in these tree diversity experiments (e.g. Reich et al. 2012). The contribution of functional diversity to overyielding has been reported from the BEF-China and Gazi Bay experiments, with, for example, root trait diversity (e.g. rooting depth and specific root length) predicting greater overyielding in biomass, potentially through niche differentiation (Bu et al., 2017; Lang'at et al., 2013; Peng et al., 2017). Most TreeDivNet experiments are still in the early stages of growth, and it is expected that some traits will become more relevant with time. For instance, diversity in or a high trait mean for shade tolerance may become important as tree diversity experiments enter canopy closure and the self-thinning stages of stand development.

4. Herbivore and pathogen damage across diversity gradients

Of the reviewed TreeDivNet literature, 36 publications presented research from 12 experiments assessing herbivore and/or pathogen damage (hereafter "damage"; Tables 1,3). As was the case for measurements of tree growth and survival, some experiments were included in multiple reports as different responses (Table 3) were measured. The studies were distributed relatively evenly across tropical, boreal, and temperate sites and focused on a wide variety of invertebrate leaf herbivory, including broadleaf chewing and skeletonizing, hole feeding, galling, mining, rolling, and sucking as well as needle herbivory. Relatively few reports addressed pathogen damage (five papers) or vertebrate herbivory (four), and none addressed woody stem herbivory. No study to date has addressed tree diversity effects on belowground herbivores or pathogens. Investigators documented associational resistance, associational susceptibility or neutral effects of tree diversity on herbivores and pathogens, which calls for a better understanding of the mechanisms at play. Proposed mechanisms for the relationship between biodiversity and damage (Fig. 2) generally pertained to either pest and pathogen access to hosts (section 4.1) or to top-down effects from natural enemies (section 4.2). Several studies assessed integrated assessments of the relationships between tree diversity and tree growth and survival as well as between tree diversity and damage (section 4.3).

4.1 Bottom-up effects change host accessibility to herbivores and pathogens

To date most research on biodiversity-damage relationships has emphasized a suite of likely interacting bottom-up effects that influence tree vulnerability to damage from pathogens and heribvores, including: host concentration and frequency, plant apparency, the degree of specialization (diet breadth) of herbivores and pathogens, and the spatial arrangement of trees within and among mixed forest patches.

The resource concentration hypothesis (section 2) has received mixed support from TreeDivNet studies. For instance, in tree neighbourhoods with a low diversity where host trees are more concentrated, herbivory was more intense for oaks and pines in the ORPHEE experiment (Castagneyrol et al., 2014, 2013b; Damien et al., 2016), but less intense in the BEF-China experiment (Schuldt et al. 2015) and the IDENT-Freiburg site (Wein et al. 2016). For pathogen infestation, which is also expected to increase with host concentration (Civitello et al., 2015), the few available studies from TreeDivNet yielded inconsistent results as well (Hantsch et al., 2013, 2014b; Schuldt et al., 2017). In the following sections, we will discuss how deviations from the original resource concentration hypothesis can be partially accounted for by taking into account the degree of specialization of herbivores and pathogens and the scale at which tree diversity effects occur.

Before herbivores or pathogens can damage a focal tree, they need to find or reach it. Working on the ORPHEE experiment, Castagneyrol et al. (2013) showed that oak colonization by specialist herbivores increased with the relative size of oaks with respect to their neighbours: oaks that were relatively taller than their immediate heterospecific neighbours were more heavily attacked. Similarly, in the BEF-China experiment, Schuldt et al. (2015) showed that herbivory became more pronounced as trees grew larger. As such, the effect of tree diversity on herbivore damage viz a viz host apparency ultimately depends on the relative growth rate of associated species in a mixture. These apparency-mediated effects of tree diversity on herbivory have since been reported for other tree and herbivore species (Damien et al., 2016; Guyot et al., 2015).

In the BEF-China experiment, tree species richness promoted generalist herbivore abundance (Zhang et al., 2017), which resulted in associational susceptibility (Schuldt et al., 2015). Interestingly, analyses by Brezzi et al. (2017) in natural forests located near the experiment found that herbivory interactively depended on tree species richness and phylogenetic diversity. Herbivory increased with tree species richness only when phylogenetic diversity was low. On the contrary, when phylogenetic diversity was high, tree species richness had no effect on herbivory. Brezzi et al. (2017) proposed that this was because in high diversity conditions, even generalist herbivores were not able to exploit all tree species (e.g. from species with vastly different leaf chemistry and structure) and benefit from dietary mixing - the consumption of multiple foods by generalists (Bernays et al., 1994). Therefore, phylogenetically diverse plant communities have the potential to bolster local generalist herbivore density and activity by providing nutritional diversity and diluting the negative effects of chemical defences in herbivore diets. Although dietary mixing is often given as a potential mechanism behind diversity-herbivory relationships, it has not been empirically demonstrated in the TreeDivNet literature.

It is likely that tree diversity effects on herbivores and pathogens are mediated by spatial scale, and specifically by the distribution of different tree species within mixtures. For instance, the regular planting design of the ORPHEE experiment is such that each individual tree has a similar neighbourhood in a given mixture (Castagneyrol et al., 2013a). In contrast, random distribution of trees within plots may create monospecific patches of trees and immediate neighbours embedded within mixed plots. In the TreeDivNet experiments where it was possible to test the effect of tree diversity on herbivores and pathogens across scales, tree diversity effects were found to be stronger in the immediate tree neighbourhood scale than at the plot scale (Satakunta: Muiruri et al. 2016, FORBIO: Setiawan et al. 2014, BIOTREE: Hantsch et al. 2013, Kreinitz: Hantsch et al. 2014a). In one well-documented example of the consequences of scale for pest damage, Damien and colleagues (2016) found that pine processionary moth, a specialist herbivore, increased in abundance with pine concentration and thus caused more damage in monocultures than in mixtures. This finding agrees with the prediction of the resource concentration hypothesis for specialists (section 2). However, at the individual pine level, the probability of a pine being attacked by the pine processionary moth displayed the opposite general pattern, being lower in monocultures than in mixtures. This finding matches the resource dilution hypothesis (Otway et al., 2005), which predicts that herbivore abundance can be diluted among many hosts at high host frequency, and may be explained by the aggregation of attacks on the fewer and more apparent pines in mixed stands (Bañuelos and Kollmann, 2011; Plath et al., 2012; Régolini et al., 2014). As such, tracking the origins of colonizing herbivores and pathogens is a major challenge of future studies on associational effects in TreeDivNet. In particular, investigators will need to know the proportion of herbivores and pathogens that reproduce and stay within plots, and the proportion of herbivores and pathogens that newly colonise plots every year.

4.2 Top-down control by enemies

As TreeDivNet experiments currently represent relatively young forest stands, relationships and interactions across trophic levels might differ from more mature forest ecosystems with established predator and herbivore population cycles. Correspondingly, most of these studies, which were conducted across a range of environmental conditions from boreal to tropical, did not find evidence for an increase in predator abundance or diversity with increasing tree diversity (Riihimäki et al. 2005, Vehviläinen et al. 2008, Schuldt and Scherer-Lorenzen 2014, Campos-Navarrete et al. 2015, Moreira et al. 2016, Yeeles et al. 2017, Zhang et al. 2017, but see Setiawan et al. 2016 and Esquivel-Gomez et al. 2017). Although effects of tree diversity can be more difficult to detect with observational approaches (Kambach et al., 2016; Nadrowski et al., 2010), studies conducted along tree diversity gradients in mature forests have often revealed no or even negative effects of tree diversity on predator abundances or species richness (e.g. Schuldt et al. 2008, 2011, 2014, Oxbrough et al. 2012, Zou et al. 2013). Nevertheless, some groups of predators and parasitoids can be promoted by tree diversity (e.g. Sobek et al. 2009, Staab et al. 2014, 2016), although the exact mechanisms are still unclear.

Direct or indirect measurements of predation rates may provide better insight into whether and how predator top-down effects change with tree diversity (Roslin et al., 2017), as indicated by several recent studies quantifying predation pressure exerted by insectivorous birds or predatory arthropods. Bird predation was unrelated to tree diversity at the plot level in the ORPHEE and Satakunta experiments (Castagneyrol et al., 2017; Muiruri et al., 2016) and along a tree diversity gradient in a mature tropical forest (Leles et al., 2017). In the BEF-China experiment, predation rates were influenced by tree species richness on only one of the three tree species studied (Yang et al., 2017b). However, at a finer spatial scale, Muiruri et al. (2016) found that bird predation rates on focal trees increased with neighbour tree diversity, indicating that diversity effects can be scale-dependent (see also Bommarco and Banks 2003, which might explain some of the deviating results from agricultural and grassland systems). Assessments of predation and parasitism rates by arthropods again showed mixed results, with positive (Leles et al., 2017; Staab et al., 2016), inconsistent (Riihimäki et al., 2005), or no detectable effects (Abdala-Roberts et al., 2016) of tree diversity on predation and parasitism rates.

Overall, tree diversity does not unambiguously promote predators and the top-down control of herbivores, and the predictions of the enemies hypothesis (section 2) may not be generally applicable to forest ecosystems. This is underscored by the finding that insect herbivory increased with tree diversity in several systems, including forests and several TreeDivNet expeirments (e.g. Schuldt et al. 2010, 2015, Haase et al. 2015, Wein et al. 2016) and that higher predation rates do not necessarily result in reduced herbivory (Castagneyrol et al. 2017; see also Grass et al. 2017).

4.3 Connections between tree growth and damage

Tree growth is intimately and reciprocally related to damage by herbivores and pathogens. When viewed from the bottom-up, plant vigor (Cornelissen et al., 2008) can either increase damage by providing more resources for herbivores and pathogens (Price, 1991) or reduce damage through robust defenses and lower concentrations of available nutrients (White, 1984). Alternatively, from the top-down, damage can reduce growth by forcing plants to devote resources to defenses (Coley et al., 1985) or increase it by favoring compensatory growth (McNaughton, 1983). As such, expectations for the direction and strength of the relationship between growth and damage are not clear. To date, most published TreeDivNet publications address either tree growth and mortality or damage by pests and pathogens, but not both; only five papers present integrated findings on both growth and damage. In two of these studies (Dillen et al., 2016; Plath et al., 2011), diversity did not have a consistent effect on either growth or damage, whereas the authors of the other three publications (Haase et al., 2015; Muiruri et al., 2015; Riedel et al., 2013) documented complex and interacting relationships between diversity, growth, and damage.

In their systematic review of data from three TreeDivNet experiments, Haase and colleagues (2015) found that trees growing in mixtures experienced both higher height growth and higher rates of invertebrate herbivory than expected based on observations from monocultures. They concluded that higher diversity may have led to increased growth in spite of reductions in plant health caused by herbivory. Riedel et al. (2013) assessed this possibility through an additional experimental manipulation: the application of insecticide to polycultures in the Sardinilla experiment. Their finding that tree growth was highest in insecticide-treated polycultures, intermediate in monocultures, and lowest in untreated mixtures suggests that insect herbivory can indeed reduce growth, and sometimes can do so enough to cancel out positive diversity-growth effects. The relationship between tree diversity and herbivore damage at one trophic level can also interact with herbivory at a different trophic level. Muiruri and colleagues (2015) found that the consequences of tree diversity for both tree growth and insect herbivory depended on the intensity of moose browsing experienced by trees in the Satakunta experiment. Progressively more intense moose browsing ultimately canceled out any signal of a positive diversity-growth relationship and converted a negative diversity-insect herbivory relationship to a positive one. Under light moose browsing, trees in diverse stands grew more and experienced less insect herbivory than in monoculture; under high moose browsing, on the other hand, trees in diverse stands grew equivalently and experienced more herbivory than in monoculture.

5. Opportunities: moving forward in BEF experiments

Grassland diversity experiments, and especially a few located in the American Midwest and northern Europe (e.g. Hooper et al. 2005, Hautier et al. 2015, Weisser et al. 2017), have advanced BEF research since its inception. Tree diversity experiments share and extend some key elements with the field’s grassland-dominated past, while also complementing past work with novel elements. Specifically, we propose that experiments in TreeDivNet build on and extend to tree-dominated ecosystems several ongoing themes in grassland diversity research: the use of remote sensing to scale from individual trees to plots and stands in the construction of stand models and estimation of water use and plant traits (section 5.1), the exploration of above- and belowground compartments of ecosystems (5.2), the mechanisms connecting plant physiology with ecosystem functioning (5.3), and the broadening of BEF research to include dimensions of biodiversity beyond species richness (5.4). Furthermore, tree diversity experiments also make possible new avenues of research. These experiments provide unique insights compared to grassland experiments because forests develop over longer time scales and are structurally more complex than grasslands. Changes in community structure over these developmental times scales is expected to precipitate changes in BEF dynamics in ways that may not be analogous to grassland dynamics (5.5). Pertaining to each of these research trajectories is the observation that, unlike grasslands, tree diversity experiments allow growth/survival and damage to be assessed for individuals as well as at the community level. The location of individuals in grassland experiments is unknown, very difficult to track, or transient; in tree diversity experiments, the exact location of each individual is known, allowing for spatial analysis across scales and analysis of patterns in mortality and growth. Such analysis contributes novelty to the extension of BEF research into tree diversity experiments. We review these potential areas of innovation below with specific examples from TreeDivNet sites.

5.1 Remote sensing of tree function, diversity and performance

Recent methodological advancements in remote sensing allow detailed spatial analysis relating individual tree growth, survival, or physiological function to tree neighbourhood and local environment, which facilitates the detailed investigation of biotic interactions. They also allow for monitoring and analysis of broad areas of forest encompassing both tree diversity experiments and entire forest ecosystems. Tree diversity experiments also have the advantage of controlling plant density, which is critical for separating biomass and diversity and can be confounded in statistical methods for detecting diversity using remote sensing methods (Wang et al., 2016). Spectral diversity using hyperspectral data are increasingly used to detect plant functional types (Ustin and Gamon 2010), and spectral diversity appears to correlate strongly with functional and phylogenetic diversity in grassland systems (Gholizadeh et al in review; Schweiger et al in review). In controlled tree experiments, spectral profiles have been shown to accurately differentiate species and even genotypes within species (Cavender-Bares et al., 2016) and to predict critical functional traits, such as plant water potential (Cotrozzi et al., 2017), demonstrating promise for remote detection of functional identity, diversity, and productivity. Such detection capacity will likely prove useful in forest systems (Foody and Cutler, 2003; Somers and Asner, 2014). In natural forest systems, recently developed methodological approaches for harnessing hyperspectral data to detect taxonomic identity (Féret and Asner, 2014) and functional diversity (Schneider et al., 2017) have been quite successful and can also be applied to forest experiments.

5.1.1 Tree and canopy models from laser scanning

Local neighbourhood analysis has been revolutionized using terrestrial laser scanning allowing a three-dimensional analysis of individual crown shapes (Metz et al., 2013; Olivier et al., 2016; Seidel et al., 2015, 2011a) and canopy space filling (Seidel et al., 2013). Compared to traditional methods, neighbourhood analyses using terrestrial laser scanning account for detailed crown characteristics of individuals that typically vary depending on the species, environmental conditions and plasticity (Metz et al., 2013; Olivier et al., 2016). Such a precise tool is promising for spatially explicit analyses of competition and interactions on the single-tree level in heterogeneous and mixed systems, such as tree diversity experiments. Terrestrial laser scanning can also be used for estimation of above-ground biomass (Seidel et al. 2011b, Kankare et al. 2013, Nölke et al. 2015). Because younger trees typically show greater crown plasticity (Muth and Bazzaz, 2002), canopy interactions can be analysed using a terrestrial laser scanner in the early phase of a tree diversity experiment (e.g. ongoing research in EFForTS-BEE). Furthermore, detailed analysis of canopy expansion using terrestrial laser scanning has been used to disentangle competition for light and abrasion (Hajek et al., 2015), improving our understanding of the mechanisms of canopy interactions that are needed to generalize findings from tree diversity experiments. Compared to traditional measurements, data acquisition using terrestrial laser scanning is more accurate and less time-consuming, even if multiple scans of the forest scene are recommended for detailed neighbourhood analysis (Seidel et al., 2015; Van der Zande et al., 2011). Using airborne laser scanning allows for quantification of individual tree growth, allometry, and competition over a spatially extensive area (Ma et al., 2017; Pedersen et al., 2012), but the high survey cost is a major limitation for the use of this technology in tree diversity experiments. Low-cost unmanned aerial vehicles equipped with laser scanners (Wallace et al., 2012) or digital cameras (Mikita et al., 2016; Wallace et al., 2016) allow for the derivation of three-dimensional models of the canopy. Such models can be used to assess the relationship between crown interaction, ground-based measures of tree growth, and local neighbourhood density. Airborne laser scans are still limited in detecting canopy characteristics below the canopy surface, so that their use would be limited to mixtures with co-dominant species. However, recent improvements (Ayrey et al., 2017) promise to facilitate for the use of airborne LIDAR to perform neighbour analysis in TDN sites

5.1.2 Assessing tree water use through thermal imaging

Recent advances in thermal imaging from remote sensing allow researchers to assess tree water stress (Bellvert et al., 2016, 2014; Zarco-Tejada et al., 2012) and evapotranspiration (Brenner et al., 2017; Hoffmann et al., 2016). Evapotranspiration is a key ecosystem function that is often estimated using surface heat models since the spatially distributed measurements of evaporated water are cumbersome. The TreeDivNet experiments offer a unique opportunity to build and validate land surface heat models accounting for vegetation and soil properties. Indeed, such experiments allow for measurements of the effect of canopy structure on surface temperature in identical meteorological conditions and often provide additional supporting information such as soil water content and standard meteorological variables. First attempts at the estimation evapotranspiration and water stress at plot- or tree- level with a combination of thermal, visible and/or infrared cameras mounted on unmanned aerial vehicles have been performed in some TreeDivNet sites (IDENT-Montreal; IDENT-Macomer; FORBIO; EFForTS-BEE) and more are planned in the near future. Cross-site measurements at TreeDivNet experiments would allow for testing the hypothesis that more diverse communities more efficiently use water resources. Additionally, some of the TreeDivNet experiments include an irrigation treatment so that they can be used to assess whether more diverse communities are more resistant to drought and to test the stress gradient hypothesis.

5.1.3 Hyperspectral methods in tree diversity experiments

The development of methods to efficiently quantify leaf functional traits affecting key canopy processes, such as photosynthesis, is a key priority for ecologists. Variation in functional traits at a range of scales - within individuals, within species, across species—contributes to ecosystem function. However, in practice there are large trade-offs in collecting information at these different levels (e.g. Baraloto et al. 2010, Violle et al. 2012, Asner et al. 2015). For instance, measurement of leaf nitrogen by elemental analysis is common because of the strong relationship between leaf nitrogen and photosynthesis, but is destructive, challenging and time intensive in tall vegetation, making it difficult to cover large areas at a range of sampling scales. Non-destructive spectroscopic methods offer a solution to this problem. As many leaf properties such as foliar carbon, nitrogen, phenolics, or leaf dry matter content show specific near infrared reflectance spectra, target leaf traits can be easily assessed at different scales, from ground leaf powder to fresh leaves, entire tree canopies or forest ecosystems, once compound-specific calibrations have been established (Couture et al., 2016; Eichenberg et al., 2015; Foley et al., 1998).

Methods relating the reflectance of canopies to their biochemical and biophysical properties, either through empirical or physical modelling approaches, are at the forefront of a rapidly evolving field of research creating novel opportunities for the quantification of key canopy traits (Asner et al., 2017; Cavender-Bares et al., 2017; Homolová et al., 2013). Hyperspectral imaging from unmanned aerial vehicles holds much promise for the study of interactions between individual trees and their neighbourhoods. Furthermore, in comparison to field spectrometry, there is great potential for efficient replication within and across individuals—achieving similar replication with a field spectrometer from branch samples would be challenging and destructive, while capturing spectra from a mobile crane would be slow. Data collection at this scale can allow development of models for functional traits and the detection of species (Somers and Asner, 2014), facilitating descriptions of community taxonomic and functional composition at the ecosystem scale (Rocchini, 2007). There is also strong potential to map forest disease and pathogen outbreaks (Hanavan et al., 2015; Pontius et al., 2005; Pontius and Hallett, 2014). Combining different remote sensing technologies (laser scanning, hyperspectral, thermal) provides great potential to study interactions at the tree- and community-level between tree diversity, tree growth and survival, and pathogen and herbivore damage (Broadbent et al., 2014).

5.2 Aboveground and belowground approaches to BEF

BEF studies in both grassland and forest ecosystems have more often tended to focus on measuring aboveground functions, such as plant aboveground productivity and leaf herbivory rather than belowground functions (but see Eisenhauer et al. 2012, Domisch et al. 2015, Seabloom et al. 2017). Yet a considerable part of the total plant biomass is located below ground and soil processes such as decomposition and nutrient mineralisation play a key role in biogeochemical cycles, soil biodiversity, and functioning (Eisenhauer, 2012; Nico Eisenhauer et al., 2012b). A recent synthesis study in the framework of a large long-term grassland BEF experiment analysed the effects of plant diversity on the performance of 50 ecosystem variables, including a considerable number of belowground functions (Meyer et al., 2016). Notably, belowground variables mostly comprised environmental variables and only one plant-related variable, whereas among the aboveground variables, plant variables predominated. This may reflect the negligence but also the difficulty of measuring biotic functions in opaque and cryptic belowground systems. Other investigators have also made first efforts toward balancing above- and belowground variables in BEF studies (Allan et al., 2013; Eisenhauer, 2012; Isbell et al., 2011).

The above- and belowground compartments of ecosystems inherently rely on each other, with the aboveground compartment serving as supplier of carbon resources to the belowground food web in the form of plant litter, whereas the belowground compartment and its biotic communities release nutrients to plants and the aboveground food web (Wardle et al., 2004). This contributes to correlations of above- and belowground diversity that have been found in several studies (Hooper et al., 2000; Wardle and van der Putten, 2002). However, most studies lack mechanistic interpretations of these observations.

Despite the strong relationships among the aboveground and belowground compartments and, thus, potential coupling of ecosystem functions, there is evidence that their functional characteristics substantially differ. For instance, the two compartments are influenced by different environmental variables. Aboveground, one of the most crucial variables is light availability, an important driver for niche differentiation in plants (Morin et al., 2011; Yachi and Loreau, 2007), with minor direct effects on the belowground system. In a grassland experiment, it was found that effects of plant diversity on soil animal abundance and diversity are weaker compared to those aboveground (Scherber et al., 2010; Weisser et al., 2017). Accordingly, in the BIOTREE and Satakunta experiments, tree species diversity did not affect belowground plant biomass and production (Domisch et al., 2015), though other studies found effects of tree species diversity on aboveground growth (section 3). Diversity effects may also change with soil depth as densities of roots and, thus, nutrient uptake and plant resource input into soil decrease gradually (Allan et al., 2013). Moreover, aboveground-belowground interrelationships need time to establish in BEF experiments (e.g. (Strecker et al., 2016; Weisser et al., 2017)). We therefore stress the need to perform long-term experiments that move beyond transient dynamics to capture more equilibrium-based results over the course of stand development (N. Eisenhauer et al., 2012).

To better understand the role of the belowground system in BEF relationships and its interrelationships with the aboveground system, it is further essential to not only measure belowground ecosystem functions, but also to manipulate belowground traits in designs of diversity experiments. In the MyDiv, B-Tree, and BiodiversiTREE experiments within TreeDivNet, first steps have been made into this direction by crossing tree species diversity gradients with treatments of tree mycorrhizal type. Mycorrhizae play a critical role in plant nutrient and water uptake from soil and, consequently, in the plants' competitive capabilities as well as in their overall performance.

5.3 Linking tree physiology to ecosystem functioning

Tree diversity studies offer opportunities to address fundamental questions in plant physiology and plant-plant interactions. These fundamental questions include elucidating responses to drought and other environmental changes, effects of above- and belowground resources and conditions on biomass allocation and morphological adjustment, and properties of mycorrhizal networks. Although some tree diversity studies have considered these topics (e.g. water relations; Lübbe et al. 2016), it is rare for the literature to consider them through the lens of diversity. Common to these three issues is a need to consider how the neighbourhood of target individuals influences their physiological responses, a challenge that can be partially addressed through the use of tree diversity experiments in the field. Utilising a network of experiments, across gradients of environmental change, potentially offers a chance to disentangle the relative importance of different drivers, as has been suggested for observational approaches with varying degrees of control (Baeten et al., 2013; Verheyen et al., 2017). Synthesizing results from such efforts may lead to greater understanding of physiological responses and ultimately ecosystem level effects. Identifying the "how" is only part of the challenge; understanding "why" plants adapt in particular ways will help to design the next generation of process-based models. Here we briefly describe trending questions in plant physiology and suggest how individual tree diversity studies, and networks, could add insight to these important challenges.

5.3.1 Drought responses and water relations

Research on the causes and consequences of drought-induced mortality and water relations within plants (e.g. Allen, Breshears et al. 2015, Corlett 2016, Landsberg, Waring et al. 2017) is often carried out through pot experiments with or without other environmental changes (e.g. Kelly et al. 2016, Rodríguez-Calcerrada et al. 2017) and on one or a few species across time or environmental gradients (e.g. Diaconu et al. 2016, Schuldt et al. 2016). There are instances of forest ecosystems being subjected to experimentally induced drought treatments (Binks et al., 2016; Lempereur et al., 2015) and other environmental changes (Norby et al., 2016) but generally without consideration of the effects of diversity. Drought experiments have, however, demonstrated differential sensitivity of species in their ability to adjust to drought. There is, thus, a real opportunity to use tree diversity experiments with experimental drought treatments to investigate acclimated and ontogenetic response mechanisms.

Water relations have been the interest of some in tree diversity experiments (Kröber et al., 2015; Kröber and Bruelheide, 2014; Kunert et al., 2012; Lübbe et al., 2016a). Indeed, Lübbe et al. (2016b) have recently shown, using seedlings of five naturally co-occurring temperate broadleaved tree species grown in monocultures and mixtures, that neighbouring species diversity can significantly influence a tree's hydraulic architecture and leaf water status regulation. For instance, common hornbeam and, to a lesser extent, sycamore developed a more efficient stem hydraulic system in heterospecific neighbourhoods when under drought, while common beech was generally more efficient in conspecific neighbourhoods. It might be expected that neighbourhood interactions given different species mixtures will scale in a complex manner to ecosystem level outcomes, due to intraspecific and interspecific variability in hydraulic traits and the potential for hydraulic redistribution (Anderegg, 2015; Blackman et al., 2017). Further work is required across experiments, with different species, and at the individual plant level to assess how hydraulic traits respond to neighbourhoods and environmental conditions and thence scale up to the whole ecosystem.

5.3.2 Biomass allocation and morphological adjustment

Allocation of biomass/carbon within plants is an important area in plant physiological research, given the need for vegetation to co-ordinate nutrient, water, and carbon uptake, and the dependence of these processes on the biotic as well as the abiotic environment. Allocation is not the only way plants can respond to resources and conditions; they can also adjust morphologically and anatomically in their organs and alter the physiological characteristics of the cells that form them (Freschet et al., 2015; Poorter and Ryser, 2015). It is especially important to understand these adjustments in relation to parameterising vegetation models that aim to predict future responses to global change. Allocation also has economic implications where tree plantations are used for timber production e.g. determining how much net primary production is allocated towards stem wood production versus leaf and root growth and how changes in allocation may affect timber quality, for example through increased or reduced branch dimensions (Campoe et al., 2012; Forrester et al., 2017).

How allocation changes and how morphology adjusts within tree plantations of differing diversity therefore remain important research topics, which tree diversity experiments can help to elucidate. This has been done for a limited number of species mixtures and sites (e.g. Nouvellon et al. 2012, Van de Peer et al. 2017, Williams et al. 2017) but clearly could be examined more widely. Understanding of environmental and physiological constraints on carbon allocation could be improved with *in situ* whole labelling experiments (Epron et al., 2012) or crown modeling from terrestrial laser scanning (Metz et al. 2013), but this remains a challenge. Massey et al. (2006) showed that one dipterocarp species grew taller in conspecific neighbourhoods, but that biomass was not different in the different treatments because of greater branching and leaf area in heterospecific stands. The propensity for greater branching in mixed stands has also be observed in older plantations (Potvin and Dutilleul, 2009), while recent evidence suggests that richness-productivity relationships are promoted by interspecific niche differentiation at early stages of stand development, enhanced by architectural plasticity of species (Williams et al. 2017).

5.3.3 Mycorrhizal interactions

Mycorrhizae are known to play a central role in facilitating nutrient uptake for plants in exchange for carbon subsidies (Jiang et al., 2017; Smith and Read, 2008; Treseder, 2013). Indeed, because of the reciprocal transfer of nutrients and carbon in particular, and potential differences among symbioses, plant-fungal interactions can mediate forest productivity, condition, and patterns of regeneration. Thus, mycorrhizae can influence forest vulnerability to herbivore, pathogen and drought damage (Smith and Read, 2008), and may lie behind the different effects of particular plant species' combinations on carbon and nutrient dynamics (e.g. Wurzburger and Hendrick 2009).

Both the environment and neighbouring hosts affect the formation of mycorrhizae on plant roots (Molina and Horton, 2015). Some studies have shown a strong influence of host identity on mycorrhizal communities (Aponte et al., 2010; Ishida et al., 2007; Morris et al., 2008; Smith et al., 2009; Tedersoo et al., 2008)that seems to increase with phylogenetic divergence of the hosts. Other studies have shown that generalist fungi can be expected to be present in greater numbers in mixed forests because of their ability to associate with multiple hosts (Cavard et al., 2011). The mediation of carbon dynamics is particularly evident through common mycorrhizal networks i.e., connectivity between plant individuals through a common mycorrhiza (Teste et al., 2009). Researchers in grasslands have suggested that particular fungal partners preferentially supply nutrients to those individuals best placed to provide carbon in return, i.e., those in the highest light environments (Weremijewicz et al., 2016; Zheng et al., 2015).

There is clearly opportunity for tree diversity experiments to explore these ideas, particularly given the different light environments engendered by different diversity neighbourhoods (Sapijanskas et al., 2014). Tree diversity experiments could also offer insight into molecular mechanisms, given recent debates as to whether effector proteins are conserved across host species, or whether there are host specific pathways (Sedzielewska-Toro and Delaux, 2016). Tree diversity experiments can deliberately manipulate mycorrhizal status, and other nutrient acquiring mechanisms (e.g. cluster roots), to investigate their effects on plant growth and other ecosystem processes (e.g. Perring et al. 2012, Grossman et al. 2017). Whether plant-fungal relationships and trait expression depend on the neighbourhood of target individuals, as well as the composition at the plot scale, remains largely unknown, although in one TreeDivNet experiment, mycorrhizal diversity was linked to tree phylogenetic diversity (Nguyen et al., 2016). The recently established MyDiv, B-Tree, and BiodiversiTREE experiments will elucidate the interactive effects of tree diversity and mycorrhizal type (ecto- and endomycorrhizae) on ecosystem functioning. The positive BEF relationship is often attributed to niche differentiation among functional traits of different species, thereby e.g. increasing nutrient uptake. In these experiments, the significance of above-belowground interactions in BEF relationships will be studied. The rationale of this experiment is that tree communities associated with different mycorrhizal types perform better than those with only one, and that the type and diversity of association(s) with mycorrhizae will influence BEF relationships.

5.3.4 Capacity of diversity to ameliorate abiotic stress

Biodiversity loss has been demonstrated to contribute to changes in ecosystem functioning to the same or to a greater extent when compared with other global change factors (Hooper et al., 2012; Tilman et al., 2012). Yet, factors such as climate change and nutrient enrichment are expected to alter species interactions, changing the ecological consequences of biodiversity for ecosystem functioning(Paquette et al., 2017; Tylianakis et al., 2008). Contemporary ecological theory and principles of plant ecophysiology suggest that abiotic stress should mediate biodiversity-ecosystem functioning effects. The stress gradient hypothesis (Bertness and Callaway, 1994) predicts that plant-plant facilitation will be more pronounced under abiotic stress - drought, frost (or cold temperatures), wind, or heat - and that competition will dominate under low-stress conditions (Wright et al., 2017). Under stressful conditions, the role of diversity in regulating plant performance may become stronger or weaker, or even switch directions (e.g. reducing productivity instead of increasing it). In grassland experiments in which biodiversity gradients have been crossed with manipulations of free-air CO_2, water availability, or induced warming, these global change factors have interacted with diversity to affect ecosystem functioning (Cowles et al., 2016; Reich et al., 2001a). And in European forests, the relationship between diversity and growth has been shown to vary with environmental conditions. Across six regions, forest diversity was more strongly associated with a suite of 26 functions in drier sites with longer growing seasons than in moister and shorter-season sites (Ratcliffe et al., 2016). Diversity also reduced the negative consequences of climate and warming trends on saplings (Ruiz-Benito et al., 2017) and had a more pronounced positive effect on tree growth in less productive sites (Jucker et al., 2016; Toïgo et al., 2015). Though these findings generally conform to expectations from the stress-gradient hypothesis, this is not always the case in forested ecosystems (Forrester, 2014). And recent meta-analysis has also indicated that drought and nutrient availability, though they affected plant productivity, did not substantially interact with the positive diversity-productivity relationships documented in experimental grasslands (Craven et al., 2016) These findings may not be generalizable, however, across other ecosystem types, global change factors, and response variables.

5.4 Dimensions of diversity – beyond species richness

Species richness remains the default metric of biodiversity in most BEF experiments, despite ecologists' growing awareness that other dimensions of biodiversity affect ecosystem functionality (Naeem et al., 2012). For some time, BEF investigators have explored the consequences for ecosystem functioning of diversity of functional traits (functional diversity; Tilman 1997, Reich et al. 2001) and diversity in the evolutionary relationships among sympatric individuals, from the intraspecific (genetic diversity; Crutsinger et al. 2006) to the lineage (phylogenetic diversity; Maherali and Klironomos 2007) level. In some cases, data from experiments designed around gradients in richness have been re-analysed, allowing for retrospective analysis of the contributions of, for instance, functional or phylogenetic diversity to productivity (Cadotte et al. 2009; some of the experiments in Flynn et al. 2011).

More recent experiments have been designed to include a richness gradient, while also incorporating orthogonal gradients in functional group, functional and/or phylogenetic diversity (e.g. Reich et al. 2004, Gravel et al. 2012, Perring et al. 2012, Cadotte 2013, Ebeling et al. 2014, Tobner et al. 2014, 2016, Grossman et al. 2017) or nesting a manipulation of genetic diversity within the richness gradient (e.g. Bruelheide et al. 2014, Moreira et al. 2014, Barsoum 2015). Much less common are designs in which richness is held constant while another dimension, such as genetic (Barton et al., 2015; Fernandez-Conradi et al., 2017) or functional (Hantsch et al., 2014b; Scherer-Lorenzen et al., 2007; Tobner et al., 2014) diversity, is manipulated. It is now quite common for BEF experiments – whether with herbaceous species or trees – to be designed to assess the consequences for ecosystem functioning of multiple dimensions of diversity, including trophic diversity (Cook-Patton et al., 2014; Parker et al., 2010; Verheyen et al., 2016). Because trees (and shrubs in the case of some experiments, including BEF-China) are often easier to monitor and manage at the level of the individual, such manipulations may, in some cases, be more tractable in tree diversity experiments. Experiments where genetic, phylogenetic, functional, and trophic diversity is manipulated rather than or in addition to species richness, will refine the developing consensus that biodiversity generally supports ecosystem functioning in many systems.

5.5 Consequences of stand succession for BEF

It has been documented in grassland diversity experiments, but not yet in tree diversity experiments, that BEF relationships change over time (Reich et al., 2012; Thakur et al., 2015). This is unsurprising given the critical role that succession plays in natural communities. Yet it is reasonable to expect that forest succession, and thus the temporal development of BEF relationships in forests, may take place over longer time scales than those relevant to grassland succession, and that differences in the structural complexity of forests and grasslands might also translate to differences in BEF relationships.

Ecosystem development, or succession, takes place over different time scales in grasslands and forests. As temperate grasslands mature following disturbance or planting, secondary succession takes place through species turnover and both biotic and abiotic modification of the soil over the course of decades (25-75 years; Reynolds et al. 2003, Kahmen and Poschlod 2004, McLauchlan et al. 2006). If there is a lack of disturbance (i.e., an absence of fire or only moderate grazing), this trajectory can terminate with a transition from grassland to forest. Secondary forest development in this context varies depending on location, but again, absent landscape-scale disturbance, may not stabilize as old-growth for hundreds of years (Franklin and Spies, 1991; Tyrrell and Crow, 1994). Biodiversity supported productivity in both long-running grassland BEF experiments at the Cedar Creek, Minnesota site after just one or two years after planting (Reich et al., 2001a; Tilman et al., 1997a) and this relationship was still becoming stronger 13 years after this (Reich et al., 2012). We speculate that BEF relationships observed in the first generation of tree diversity experiments (e.g. Vehviläinen and Koricheva 2006) will also change in intensity, and perhaps direction, over time, and that the timescales of these changes will be longer than those relevant to grassland experiments. For instance, Damien et al. (2016) found that the early beneficial effects of pine-birch association on pine attack by a specialist herbivore (Castagneyrol et al., 2014) decreased with time as trees grew taller. In contrast, because the density of plants and relative abundances of species are fixed at establishment (though they may change over time) in tree diversity experiments, BEF dynamics may be more stable in mature experiments than in mature grassland experiments, in which density and composition can change. An exception in this regard is the Climate Match experiment that includes as part of its design different ratios of selected provenances to explore the long-term consequences of differing proportions of trees of distinct origin.

Because forests differ from grasslands in various aspects, the mechanistic bases and dynamics of BEF relationships may be different than those documented for grasslands. Differences in structural complexity between the two biomes stem from differences in diversity of their dominant plant growth forms. Grasslands are dominated by herbaceous species, primarily grasses and forbs with maximum vegetation height rarely exceeding 2 m. Forests, in contrast, may consist of numerous vegetation strata ranging from canopy trees (potentially exceeding 100 m in height) to subordinate tree and woody shrub layers and herbaceous understory vegetation at ground level. In reality, then, producer biodiversity in forests is defined not only by tree diversity, but also the diversity of shrubs and herbaceous plants. These components of producer biodiversity interact with each other (Barbier et al., 2008; Both et al., 2011) and are expected to interact to affect forest ecosystem functioning. In addition, in forests stand thinning and gap formation are typical features of stand development in both natural and managed forests. In some forests, thinning and gap formation result in significant alterations to the compositional and structural features of stands and consequently, BEF relationships. To date, most tree diversity experiments have focused on manipulating tree diversity, addressing understory diversity as a response variable. Notable exceptions include the BEF-China (Bruelheide et al., 2014; Yang et al., 2017a) and IDENT-Macomer experiments, which consist of both tree and shrub diversity gradients, providing further opportunity for exploration of these dynamics.

Additionally, as the basis of forest productivity, trees not only dominate primary production in forests, but also play the role of ecosystem engineer (Jones et al., 1994; Seitz et al., 2016). Trees alter forest functioning through the extent to which they shade understory woody and non-woody species (Messier et al., 1998), alter the soil surface and sub-surface via litter deposition (Hobbie et al., 2006; Reich et al., 2005) and root exudates (Grayston et al., 1997) and exert afterlife effects through decomposition of necromass by fungal symbionts (Langley et al., 2006; Read et al., 2004). Finally, tree diversity experiments present an opportunity to explore the relationship between diversity and the temporal stability of key ecosystem processes at various organizational levels, and to elucidate the drivers behind them. For instance, a recent investigation documented greater stability in biomass production at the community level in mixed forests than in monocultures, but a negative or neutral effect of diversity on biomass stability at the species level (del Río et al., 2017).

The maturation of tree experiments over time will also provide opportunities to address topics of applied and basic ecological interest. Continued stand development will provide opportunities for research linking diversity treatment to implications for management of mixed-species plantations and forests, a key goal of TreeDivNet (Nock et al., 2017; Verheyen et al., 2016). Forest managers will have the option of assessing the effectiveness of, for instance, pruning or harvesting techniques across stands of varying diversity. And, as discussed above, tree-tree interactions will continue to grow stronger as canopies close and self-thinning becomes more common. In addition, though understory plant (Ampoorter et al., 2015; Germany et al., 2017), microbial (Nguyen et al., 2016), herbivore (Vehvilainen et al., 2007), bird (Teuscher et al., 2016) and predator (Esquivel-Gomez et al., 2017) communities have already responded, in some cases, to tree diversity treatments, we expect that these associated communities will continue to change, and perhaps stabilize, over time. The development of these communities will certainly affect tree vulnerability to herbivore and pathogen damage as well as tree growth and survival.

6. Challenges in future TreeDivNet research

Experiments in TreeDivNet have already contributed to our understanding of the relationships between tree diversity and tree growth and survival and between tree diversity and herbivore and pathogen damage to trees. Further research from the network will grapple with several challenges, including tree mortality, design limitations, and appropriate integration of modeling.

Tree mortality will present managers of tree diversity experiments with consequential choices about how to maintain their experiments over the coming decades. In establishing TreeDivNet sites, most investigators chose to replace transplants that died shortly after being planted. This was essential as the identity and density of experimental trees are, in all cases, a key independent variable for diversity experiments. Yet experimental managers will not be able to respond to future mortality with replanting: new trees would be dramatically smaller and younger than neighbours and, besides, mortality of adult trees in later years of the experiment will likely result from important interspecific interactions rather than merely from seedling transplant shock. Faced with this mortality, managers will need to decide whether to simply allow the composition and density of plots to change or whether to systematically thin to retain the original or near-original design of their experiments. These choices will affect the way experimental results are interpreted. For instance, as trees die, the plot level of analysis may become either less useful because of compromising the initial design or more useful because community assembly mechanisms are then similar to natural forest ecosystems. In any case, neighbourhood approaches to quantifying diversity will remain appropriate.

A common feature of TreeDivNet experiments is that they follow a replacement design: total tree density (i.e., number of trees per plot of the same area) is held constant along diversity gradients such that the concentration (i.e., number of tree individuals) and frequency (i.e., relative abundance) of each species decreases with tree species richness. Most species mixtures in the TreeDivNet experiments are thus equiproportional such that species concentration and frequency covary with tree species richness (but see BIOTREE-Simplex: Scherer-Lorenzen et al. 2007). Yet, recent studies on non-tree systems and modelling approaches stressed the importance of disentangling the relative effects of host concentration and frequency to explain associational effects (Hahn and Orrock, 2016; Hambäck et al., 2014; Kim and Underwood, 2015; Underwood et al., 2014). Allowing the relative share of tree species in mixtures to vary, as in the SIDE experiment, will allow for a better understanding of the mechanisms underlying host concentration effects. Another limitation of most, if not all, TreeDivNet experiments is that trees are regularly spaced within each plot, which does not then consider the possible effect of more heterogenous spacing, as is found in natural forests, on many ecosystem processes.

Tree plantation experiments obviously have limitations, which have often been discussed in depth in reviews and reports of original results, but these findings could be greatly complemented with simulation studies (e.g. Bunker 2005, Morin et al. 2014). Simulation models could be used to extend the findings of experiments over both larger and longer scales. BEF research has been developed mostly for systems at equilibrium and where demography is responsible for dynamics. Tree plantations are restricted to a particular segment of tree life cycle and therefore do not integrate all aspects of population dynamics. Models could partly solve this issue, and we expect they will perform best when combined with such data-intensive experiments. On the other hand, building a model forces an experimentalist to rigorously identify relevant processes, along with appropriate measurements of some critical quantities such as growth rates, biomass allocation, and competition mechanisms (Grimm et al., 2017). We envision that the co-development of TreeDivNet experiments with models should be part of the future and will benefit both fundamental and applied research.

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Author Contributions

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Figures

Figure 1. The 25 experiments of TreeDivNet in the boreal (bo), temperate (te), Mediterranean (me), subtropical (st) and tropical (tr) regions of the world; see Table 1 for the characteristics of the experiments. Experiments in grey consist of sites in different countries. Experiments in bold are the experiments from which early results on tree growth and survival and damage are discussed in this paper.

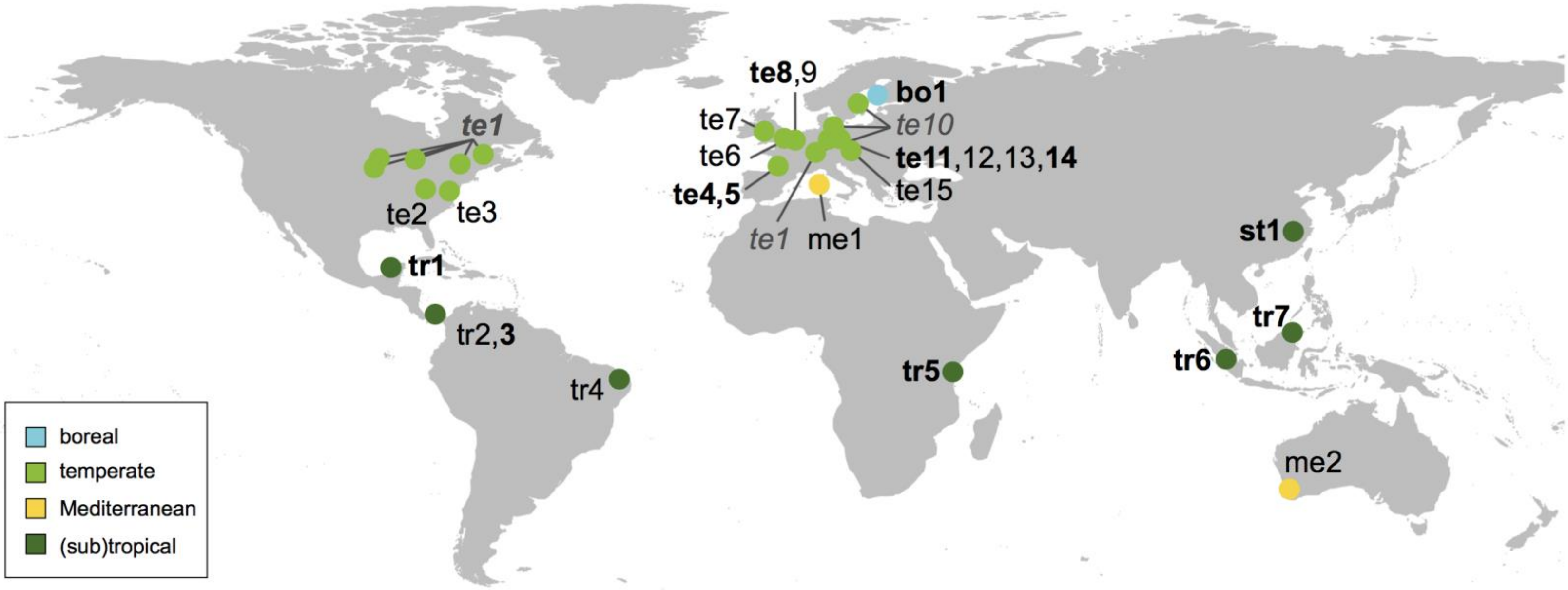
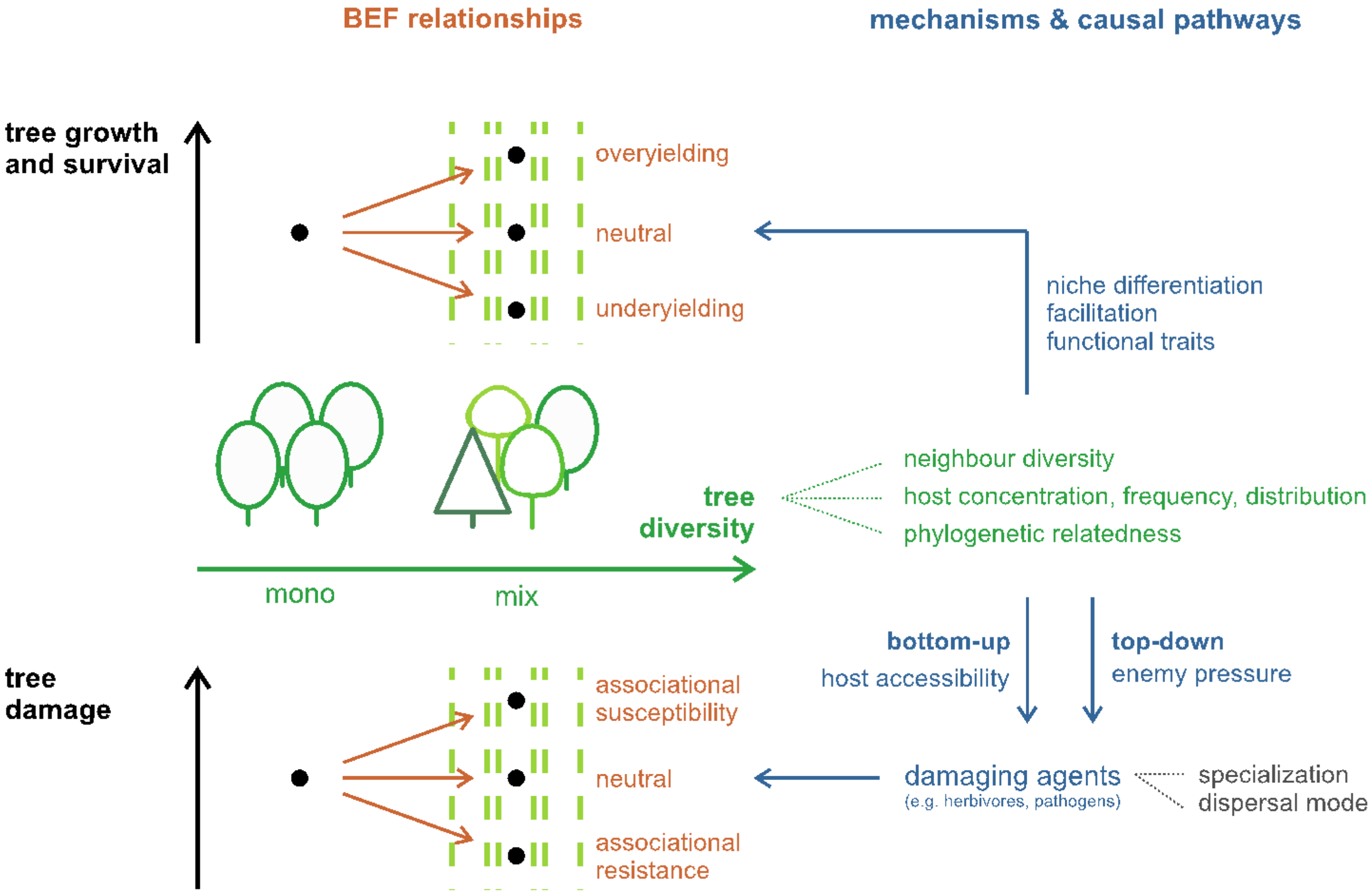


Figure 2. Consequences of biodiversity (green) for tree mortality and growth and damage (from herbivores and pathogens). Relationships between biodiversity and each response (orange) can vary from underyielding/associational resistance to overyielding/associational susceptibility. Research reviewed here both documents the direction and strength of these responses and the underlying mechanisms (blue) that give rise to them.



Tables

Table 1. The 25 experiments of TreeDivNet are established in different ecoregions around the globe (Code, see Fig. 1) to investigate the relations between forest ecosystem functioning and tree diversity: species richness (SR), functional diversity (FD), genetic diversity (GD), phylogenetic diversity (PD), and evenness (EV). Different aspects of tree growth, survival, and damage are monitored. See www.treedivnet.ugent.be for more information on the experiments.

Code	Experiment[a]	Plant Year	no Sites	no Plots	Diversity Manipulation[b]	Species Pool	Tree Growth & Survival[c]	Tree Damage[d]
bo1	Satakunta	1999	4	163	SR, GD, PD	5	Growth (AG) Mortality	Herbivory (Insects, Vertebrates) Pathogen Damage Natural Enemies
te1	IDENT[a]	2009, 2010, 2012, 2013	5	1192	SR, FD, PD	20	Growth (AG, BG) Mortality Form Phenology Stress Tolerance Yield Stability	Herbivory (Insects) Pathogen Damage
te2	SIDE	2012	1	182	SR, EV	14	Growth (AG)	Branch & Shoot Damage
te3	BiodiversiTREE	2013, 2014	2	139	SR, FD	16	Growth (AG)	Herbivory (Insects,

							Mortality Phenology Resource use	Vertebrates) Pathogen Damage
te4	ORPHEE	2008	1	256	SR, FD	5	Growth (AG) Mortality Form Stress Tolerance Phenology Yield Stability	Herbivory (Insects) Pathogen Damage Natural Enemies Pest Resistance
te5	Communitree	2009	1	90	GD	1	Growth (AG, BG[e])	Herbivory (Insects)
te3	Climate Match[a]	2011	2	177	SR, GD	4	Growth (AG) Mortality Phenology	Herbivory (Insects) Pathogen Damage
te7	BangorDIVERSE	2004	1	92	SR, FD	7	Growth (AG, BG) Mortality Form Resource Use	-
te8	FORBIO[a]	2010, 2012	3	127	SR, GD	10	Growth (AG) Mortality Form	Herbivory (Insects) Crown Discolouration Branch & Shoot Damage

te9	TWIG	2017	1	22	SR, FD	4	Growth (AG)[e] Mortality Form[e]	-
te10	ECOLINK-Salix	2014	3	99	GD	1	Growth (AG) Resource Use Yield Stability Wood Quality	Herbivory (Insects) Pathogen Damage
te11	BIOTREE[a]	2003, 2004	4	117	SR, FD, EV	19	Growth (AG, BG) Mortality	Herbivory (Insects) Pathogen Damage
te12	HighDiv-SRC	2015	1	45	SR	4	Growth (AG) Yield Stability Wood Quality	Herbivory (Insects) Pathogen Damage
te13	MyDiv	2015	1	80	SR, FD	10	Growth (AG) Mortality	-
te14	Kreinitz	2005	1	98	SR, FD	6	Growth (AG) Mortality	Herbivory (Insects) Pathogen Damage
te15	B-Tree	2013	1	44	SR, FD	4	Growth (AG, BG) Mortality Resource Use	-
me1	IDENT[a]	2014	1	308	SR, FD, PD	12	Growth (AG)	Defoliation

							Stress Tolerance	Discolouration
me2	Ridgefield[a]	2010	1	124	SR, FD	8	Growth (AG) Mortality	-
st1	BEF-China[a]	2009/2010	2	566	SR, GD, FD, PD	60	Growth (AG, BG) Form Mortality Resource Use Yield Stability	Herbivory (Insects) Pathogen Damage Natural Enemies
tr1	UADY	2011	1	74	SR, GD	6	Growth (AG)	Herbivory (Insects) Natural Enemies
tr2	Agua Salud	2008	1	267	SR	10	Growth (AG) Mortality Form Resource Use	Shoot Damage
tr3	Sardinilla	2001/2003	2	32	SR, FD	26	Growth (AG) Mortality Resource Use	Herbivory (Insects)
tr4	BrazilDry	2016	1	155	SR	16	Growth (AG) Mortality	Herbivory (Insects)
tr5	Gazi Bay	2004	1	32	SR	3	Growth (AG)	-

							Mortality	
tr6	EFForTS-BEE[a]	2013	1	56	SR	6	Growth (AG) Mortality Form Stress Tolerance	Herbivory (Insects) Pathogen Damage[e]
tr7	Sabah[a]	2010	1	124	SR, FD, GD	16	Growth (AG) Mortality	-

[a] Extensive information on the design of the experiments can be found for BEF-China (Yang et al. 2013; Bruelheide et al. 2014; Schmid et al. 2017), BIOTREE (Scherer-Lorenzen et al. 2007), Climate Match (Barsoum 2015), EFForTS-BEE (Teuschner et al. 2016), FORBIO (Verheyen et al. 2013, 2016), IDENT (Tobner et al. 2014; Grossman et al. 2017), Ridgefield (Perring et al. 2012), and Sabah (Hector et al. 2011).

[b] Extra treatments investigated: water availability (ORPHEE, IDENT – sites Macomer and Sault-Sainte-Marie); fertilization with nitrogen and phosphorus (IDENT – site Freiburg); nitrogen deposition and non-native weed cover (Ridgefield); liana removal (Sabah); no management vs. thinning (BIOTREE); addition of high-value tree species (BIOTREE); shrub species richness (2, 4, 8), herbivore exclusion, leaf foliar pathogen exclusion, phosphorus addition, and weeding (BEF-China)

[c] Tree Performance is measured for the following categories: Tree Growth Aboveground (‘AG’), e.g., height, diameter, biomass, leaf area index, crown cover, full terrestrial laser scan; Tree Growth Belowground (‘BG’), e.g., fine-root biomass, fine-root length; Mortality; Tree Form, e.g., space occupation, branchiness, crown width; Phenology, e.g., timing bud burst; Resource Use, e.g., water

use, nutrient use, plant-water relationships; Wood Quality; Yield Stability; Stress Tolerance, e.g., water stress, resistance and resilience to drought.

[d] Tree Damage is investigated for the following topics: Insect Herbivory - may be studied separately for, e.g., leaf chewers, gallers, hole feeders, miners, rollers, suckers, tiers; Vertebrate Herbivory by, e.g., moose; Pathogen Damage, e.g., fungi; Crown Discolouration; Branch & Shoot Damage by, e.g., herbivores, management; Natural Enemies of herbivores that limit tree damage through biotic regulation, e.g., parasites or predators of insect herbivores.

[e] Monitoring of the variable has not started yet in this recently planted experiment, but is planned for the near future.

Table 3. Summary of literature assessing tree growth and survival in TreeDivNet experiments through early 2017.

Code[a]	**Experiment**[a]	**Diversity Manipulation**[b]	**Effect of Diversity**[c]		**Aboveground/ Belowground**	**Mechanistic Explanations**[d]	**Source**
			Survival	**Growth**			
st1	BEF-China	SR	NA	0	Aboveground	Abiotic Variables	Li et al. (2014)
			NA	+	Aboveground	Trait Identity & Diversity Climate	Krober et al. (2015)
			NA	+	Aboveground	Niche Partitioning Facilitation Trait Identity	Fichtner et al. (2017)
			NA	+	Aboveground	Species Identity **Selection**	Peng et al. (2017)
			NA	+	Belowround	Trait Identity & Diversity Niche Partitioning ~~**Complementarity**~~	Sun et al. (2017)
			NA	+	Both	Niche Partitioning **Complementarity**	Bu et al. (2017)
			NA	+	Aboveground	Trait Diversity Niche Partitioning Complementarity	Niklaus et al. (2017)
			-	NA	NA	Methodological Issues	Yang et al. (2013)
			0	NA	NA	Trait Identity Species Identity	Yang et al. (2017)
			NA	+	Aboveground	Trait Diversity Niche Partitioning Temporal Scale	Hahn et al. (2017)
		GD	NA	-	Aboveground		
te11	BIOTREE	SR	NA	0	Belowground	Species Identity Competition Nutrients	Lei et al. (2012a)
			NA	0 / +	Belowground	Higher Turnover Faster Exploration	Lei et al. (2012b)
			NA	+	Belowground	~~Traits~~	Haase et al. (2015)
			NA	0	Belowground	Trait Identity	Domisch et al. (2015)

tr6	EFForTS-BEE	SR	NA	+	Aboveground	Plant Density	Gerard et al. (2017)
te8	FORBIO	SR	0	NA	NA	~~**Complementarity**~~	Van der Peer et al. (2016)
			NA	0	Aboveground	Species Identity Precipitation	Dillen et al. (2016)
			NA	0 / +	Aboveground	Species Identity Phylogenetic Diversity	Setiawan et al. (2017)
			NA	0	Aboveground	Competition	Van der Peer et al. (2017)
tr5	Gazi Bay	SR	NA	0	Aboveground	Trait Identity	Kirui et al. (2008)
			NA	+	Aboveground	Species Identity **Selection**	Kirui et al. (2012)
			0	+	Aboveground	Trait Identity	SigiLan'at et al. (2013)
te1	IDENT	SR, FD, PD	NA	0	Belowground	Trait Identity Species Identity	Khlifa et al. (2016)
			NA	+	Aboveground	Trait Identity Trait Diversity **Selection**	Tobner et al. (2016)
			NA	+	Aboveground	Niche Partitioning **Complementarity**	Williams et al. (2017)
			NA	+	Aboveground	Trait Identity Trait Diversity **Complementarity**	Grossman et al. (2017)
te14	Kreinitz	SR	NA	+	Belowground	Density Effects	Haase et al. (2009)
			NA	0	Aboveground		
tr7	Sabah	SR	0	0	Aboveground	Portfolio Effect Growth-Mortality Tradeoffs	Tuck et al. (2016)
tr3	Sardinilla	SR, Composition	NA	0	Belowground	Portfolio Effect	Salisbury and Potvin (2015)
			0	+	Aboveground	**Selection**	Potvin and Gotelli (2008)
			NA	+	Aboveground	Competition Neighbor Size & Architecture ~~**Complementarity**~~	Potvin and Dutilleul (2009)
			0	0	Aboveground		Plath et al. (2011)
			0	+	Aboveground	Release from Herbivory	Riedel et al. (2013)
			NA	+	Aboveground	Competition Plant-Soil Feedbacks	Sapijanskas et al. (2013)
bo1	Satakunta	SR	NA	0	Aboveground	Exposure to Herbivory	Muiruri et al. (2015)

[a]As in Table 1; [b]SR = Species Richness, FD = functional diversity, PD = phylogenetic diversity; [c]positive (+), negative (-), and/or null (0); [d]as either measured or proposed by authors with strikethrough indicating a mechanism that was ruled out. Complementarity or selection effects (Hector and Loreau 2001) are bolded when authors invoked as a potential class of mechanisms.

Table 3. Summary of literature assessing herbivore and pathogen damage in TreeDivNet experiments through mid-summer 2017.

Code[a]	Experiment[a]	Diversity Manipulation[b]	Agent	Effect of Diversity[c]	Specialization	Mechanistic Explanations[d]	Source
st1	BEF-China	SR	Leaf Herbivores	+	Generalist	Diet Mixing Host Size	Schuldt et al. (2015)
			Leaf Suckers	+	Specialist	Host Vigor	Staab et al. (2015)
			Leaf Herbivores	+	Generalist	Herbivore-Pathogen Facilitation Traits Species Distribution	Schuldt et al. (2017)
			Leaf Pathogens	-	Specialist		
			Leaf Removers	0	Generalist	Dietary Mixing Resource Concentration Traits	Hahn et al. (2017)
		GD	Leaf Removers	+			
te11	BIOTREE	SR	Leaf Pathogens	-	Generalist	Host Dilution	Hantsch et al. (2013)
		FD	Leaf Pathogens	0	NA	Host Identity	Hantsch et al. (2014)
			Leaf Tiers	+	Generalist	Resource Concentration Traits	Morath (2013)
			Leaf Suckers	-	Specialist		
			Leaf Removers	0	Generalist		
			Leaf Gallers	0	Specialist		
			Leaf Miners	0	Specialist		
te5	Communitree	SR	Leaf Herbivores	+	Generalist	Apparency Diet Mixing Spillover	Castagneyrol et al. (2012)
			Leaf Miners	0	Specialist		
		GD	Leaf Removers	-	Generalist	Diet Mixing Patch Dynamics	Fenandez-Conradi et al. (2017)
tr6	EFForTS-BEE	SR	Leaf Herbivores	0	Generalist	Traits	Arns (2016)
te8	FORBIO	SR	Leaf Pathogens	0	Generalist	Host Dilution	Dillen et al. (2016)
				-	Generalist	Natural Enemies Abiotic Factors	Dillen et al. (2017)
te1	IDENT	SR	Leaf Removers	+	Generalist	Diet Mixing	Wein et al. (2016)
te14	Kreinitz	SR	Leaf Removers	-	Specialist		Alaouni et al. (2014)
			Leaf Hole Feeders	-	Specialist		
			Leaf Pathogens	-	Specialist	~~Resource Concentration~~	Hantsch et al. (2014)
			Soil Pathogens	-	Specialist	Traits Natural Enemies	Wurst et al. (2015)
te4	ORPHEE	SR	Leaf Miners	-	Specialist	Resource Concentration Apparency	Castagneyrol et al. (2013)
			Leaf Removers	-	Genearlist		
			Needle Parasites	0	Specialist	Apparency	Castagneyrol et al. (2014)
				+	Specialist	Resource Concentration Apparency	Damien et al. (2016)
tr3	Sardinilla	SR	Leaf Removers	+	Specialist	Resource Concentration	Plath et al. (2012)
				-	Specialist	Diet Mixing Patch Dynamics	
				-	Generalist	Resource Concentration Diet Mixing Natural Enemies	Plath et al. (2011)

bo1	Satakunta	GD	Leaf Rollers	+	Specialist		Barton et al. (2015)
			Leaf Miners	0	Specialist		
			Leaf Gallers	-	Specialist		
			Leaf Tiers	0	Specialist		
			Leaf Chewers	-	Generalist		
			Leaf Miners	-	Specialist	Host Identity	Morath (2013)
		SR	Needle Parasites	-	Specialist	Natural Enemies	Kaitaniemi et al. (2007)
			Vertebrate Herbivores	+	Generalist	Resource Concentration	Milligan and Koricheva (2013)
			Leaf Removers	- / +	Specialist	Resource Concentration	Morath (2013)
			Leaf Suckers	-	Specialist	Resource Concentration	
			Leaf Gallers	-	Specialist	Resource Concentration	
			Leaf Rollers	+	Specialist	Resource Concentration	
			Leaf Miners	0 / +	Specialist	~~Apparency~~	
			Leaf Herbivores	- / +	Generalist	Other Biotic Factors	Muiruri et al. (2015)
			Vertebrate Herbivores	0	Generalist	Host Vigor Abiotic Factors	
			Leaf Gallers	-	Specialist	Host Vigor Host Size Abiotic Factors	Muiruri and Koricheva (2016)
			Leaf Miners	-	Specialist		Vehvilainen et al. (2007)
			Leaf Herbivores	-	NA		
			Leaf Herbivores	+	NA		
			Leaf Herbivores	+	NA		
			Vertebrate Herbivores	-	Specialist	Host Concentration	Vehvilainen and Koricheva (2006)
			Vertebrate Herbivores	+	Generalist		
tr1	UADY	SR, GD	Leaf Removers	- / +	Specialist	Diet Mixing ~~Natural Enemies~~	Abdala-Roberts et al. (2015)
			Leaf Removers	0	Generalist		
			Leaf Miners	0	Specialist	Natural Enemies	Abdala-Roberts et al. (2016)
			Leaf Herbivores	0	NA	Traits	Moreira et al. (2014)
bo1, te11, te14	Multiple Site	GD	Leaf Pathogens	-	NA	~~Resource Concentration~~	Hantsch et al. (2013)
bo1, te4, te11, te14, tr3	Multiple Site	SR	Leaf Herbivores	0	NA	Abiotic Factors	Kambach et al. (2016)
bo1, te4, te11	Multiple Site	SR	Leaf Removers	+	Generalist	Resource Concentration ~~Traits~~	Haase et al. (2015)

[a]As in Table 1; [b]SR = Species Richness, GD = genetic diversity, FD = functional diversity; [c]positive (+), negative (-), and/or null (0); [d]as either measured or proposed by authors with strikethrough indicating a mechanism that was ruled out.

Appendices

Appendix 1. Compilation of all empirical papers published and graduate theses completed using data from TreeDivNet experiments as of mid-summer 2017. Papers presenting particular experiments or detailing theoretical concerns are not listed here. Updates to this list are available at www.treedivnet.ugent.be.

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