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Using long-term tree diversity experiments to explore the mechanisms of temporal shifts in forest ecosystem functioning

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Plant diversity is known to influence ecosystem functioning, but the strength and direction of this relationship vary considerably among studies, most of which have a short duration. In communities with long-lived species, such as forests, traits of individual trees change from seedlings to maturity, and the environment in which trees grow also continually changes through stand development and forest succession. We argue that interactions between these individual and community-level effects over time will alter biodiversity–ecosystem functioning (BEF) relationships, likely explaining at least part of the reported variation in BEF effects among studies. We outline a series of mechanisms through which temporal changes at the tree and stand levels can alter BEF relationships and illustrate these processes using data from the long-term Satakunta forest diversity experiments in Finland. We argue that long-term forest diversity experiments are essential to robustly characterize temporal dynamics emerging from the complex interplay between plant functional traits and environmental conditions over time. These experiments can provide critical insights for predicting the consequences of biodiversity loss on ecosystem functioning and service provisioning over time.

Keywords: biodiversity, ecosystem functioning, forests, functional traits, long-term experiments, ontogeny, succession, TreeDivNet

Synthesis

Predicting long-term consequences of biodiversity loss on ecosystem functioning requires an understanding of the mechanisms underlying temporal shifts in diversity effects. In this study, we introduce a new mechanistic framework that predicts how temporal changes at both individual tree and stand level mediate tree diversity effects on ecosystem functioning. Using data from the Satakunta forest diversity experiments in Finland, we highlight the critical role of long-term experiments in testing these mechanisms by tracking changes in temporal shifts in forest diversity effects on ecosystem functioning through monitoring changes in abiotic and biotic environment and functional traits of individual trees and forest stands over time.

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Paradigm shifts in our understanding of the biodiversity-ecosystem functioning relationship: adding in the temporal perspective

Our understanding of the role of biodiversity in nature has evolved over time (van der Plas 2019). Interest in characterizing the distribution of biodiversity on Earth and concerns over human-driven biodiversity loss led to an initial focus on the effects of natural and anthropogenic environmental factors on biodiversity and ecosystem functioning (Fig. 1A). Since the early 1990s, the recognition that biodiversity loss can drive changes in ecosystem functioning has grown (Schulze and Mooney 1993) and the first experimental studies (mainly in grassland ecosystems) were established to explore the strength of biodiversity–ecosystem functioning (BEF) relationships (Tilman et al. 1996, Hector et al. 1999). These experiments manipulated plant diversity while minimizing environmental variation (Fig. 1B) and have demonstrated overall significant positive effect of biodiversity on many ecosystem processes (Balvanera et al. 2006, Cardinale et al. 2011). Positive effects of biodiversity on ecosystem functioning have also been detected in naturally assembled (i.e. non-manipulated) communities (van der Plas 2019), where environmental variation has been shown to drive both biodiversity patterns and its influence on ecosystem functioning (Fig. 1C). While the effects of plant diversity on ecosystem functioning in both experimental and naturally assembled communities are now well documented, the strength of these effects varies among studies and often increases over time (Reich et al. 2012, Guerrero-Ramírez et al. 2017, Jucker et al. 2020, Bongers et al. 2021, Wagg et al. 2022). Understanding the mechanisms underlying temporal shifts in BEF effects is important for predicting long-term consequences of biodiversity loss but remains a challenge because the majority of BEF studies are short-term, providing only snapshots of a single stand development stage. In addition, a lot of early BEF research was conducted in grasslands which largely precluded long-term assessment of responses at the individual plant level. Therefore, a knowledge gap exists in our understanding of how BEF relationships develop in ecosystems such as forests where individual organisms (trees) are

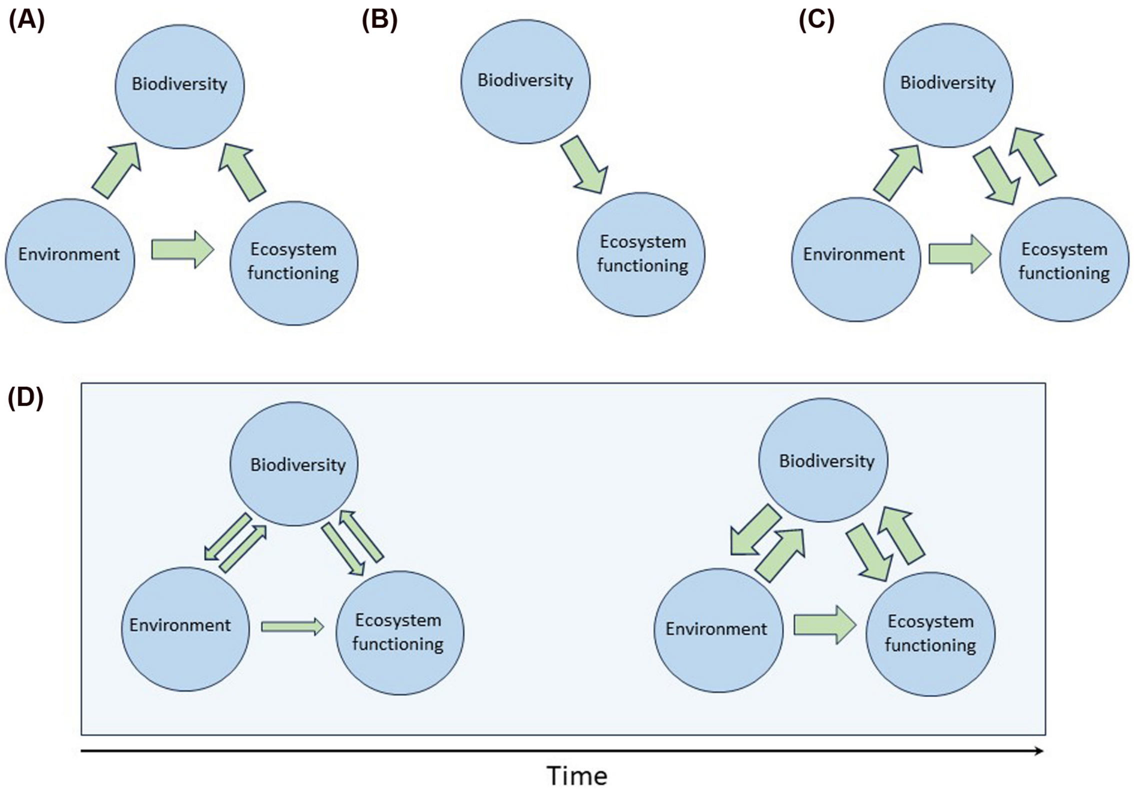

Figure 1. Paradigm shifts in our understanding of the role of biodiversity in nature. (A)–(C) from van der Plas (2019) with modifications. (A) Until the early 1990s, the dominant paradigm was that biodiversity primarily responds to environmental and anthropogenic factors, but that it has only a minor role in driving ecosystem functions. (B) Most early biodiversity – ecosystem functioning (BEF) research focused on the causal effects of random variation in biodiversity on ecosystem functioning, while minimizing environmental variation and its effects. (C) It is currently recognized that biodiversity both responds to its environment and drives ecosystem functioning, although its importance compared to the effects of other drivers (e.g. abiotic drivers and functional composition) are still under debate. (D) We propose to expand the paradigm to include effects of biodiversity on abiotic and biotic environment (e.g. changes in microclimate and herbivory) which might in turn affect ecosystem functioning. The importance of these additional effects of biodiversity on ecosystem functioning via changes in the environment is predicted to increase with time (e.g. through succession), as shown by increased thickness of arrows.

long-lived and where plant and stand development unfold over many decades.

Several well-known temporal processes operate in forest ecosystems, including changes in functional traits of individual trees within a stand through ontogeny and with tree age, and changes at the stand level associated with forest succession and stand development. But so far these processes have not been conceptually incorporated into the BEF framework. Recently, Staude et al. (2023) called for integration of successional thinking into BEF studies and argued that successional dynamics may strongly modify the relationship between biodiversity and ecosystem functioning and explain variability in the direction and strength of BEF relationships. While several studies have explored how and why tree diversity effects change over time, these studies have mainly focused on tree growth and productivity (Lasky et al. 2014, Huang et al. 2018, Schnabel et al. 2019, Taylor et al. 2020, Shovon et al. 2022, Urgoiti et al. 2022), while a predictive framework for temporal changes in diversity effects on other ecosystem processes is currently lacking. In addition, while effects of plant intraspecific genetic diversity on ecosystem functioning may be comparable in magnitude to species diversity effects (Bailey et al. 2009, Koricheva and Hayes 2018), no existing studies have explored temporal changes in tree genetic diversity effects on ecosystem functioning.

In this study, we propose a new framework linking temporal changes at tree and stand levels with BEF effects to provide new mechanistic insights into tree diversity effects on ecosystem function. Depauw et al. (2024) have recently conceptualized the pathways through which tree growth is related to neighborhood diversity, emphasizing the role of abiotic and biotic growing conditions, resources and functional traits. Here we go further by considering tree diversity effects at both neighborhood and community (stand) levels and including bidirectional interactions between tree diversity and abiotic and biotic environment which might in turn affect ecosystem functioning. We predict that the importance of these additional indirect effects of biodiversity on ecosystem functioning via changes in the environment will strengthen over time (Fig. 1D). Specifically, we outline how differences in tree species and genetic diversity at neighborhood and community scales can modify abiotic and biotic environmental conditions over time, which in turn affects the speed and trajectories of both individual tree and stand development resulting in differences in ecosystem functioning (Fig. 2).

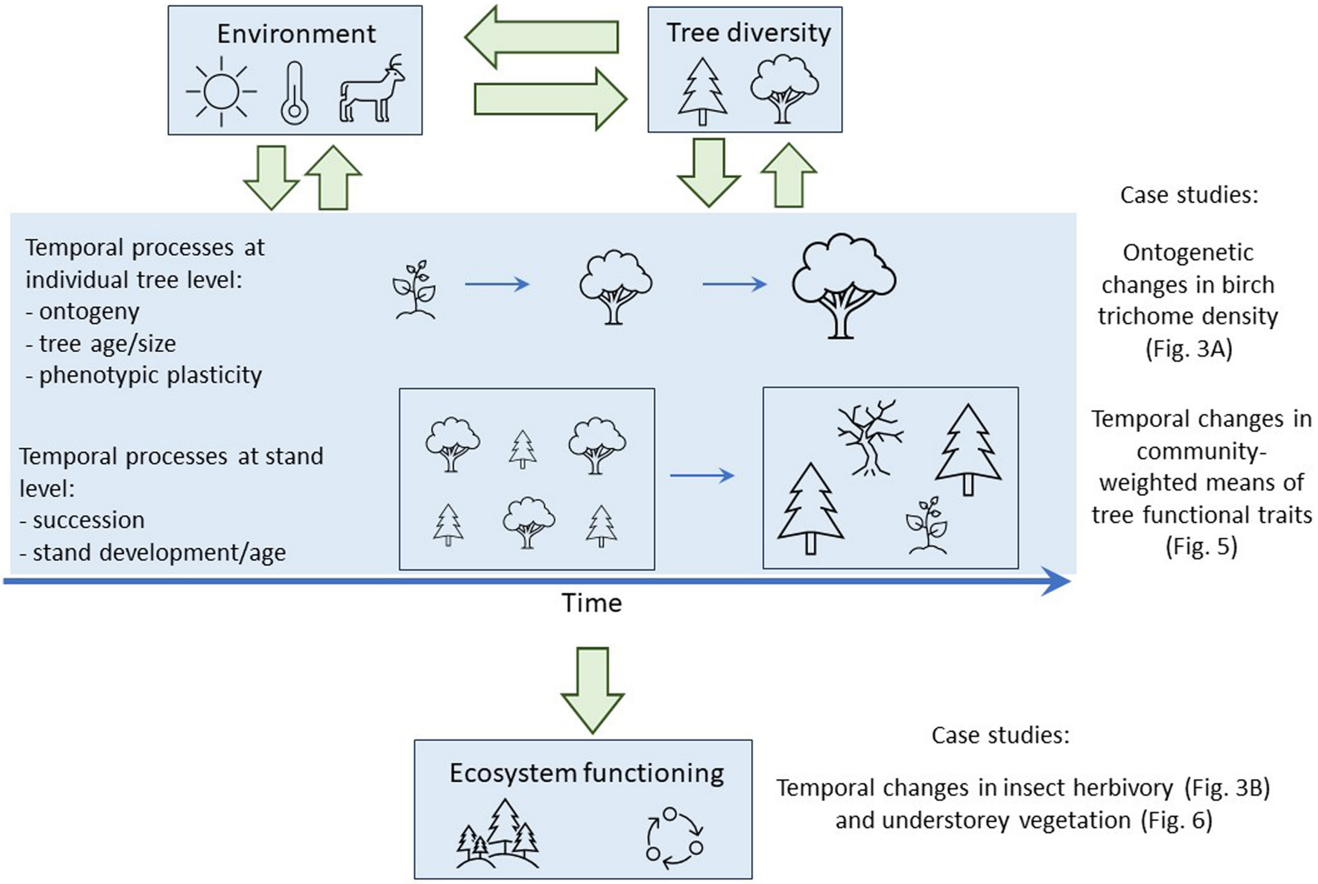

Figure 2. Proposed mechanisms of temporal shifts in tree diversity effects on ecosystem functioning. Tree diversity effects on ecosystem functioning might change over time due to either direct effect of temporal processes at individual tree or stand level (e.g. changes in tree species composition over time throughout the succession) or via indirect temporal effects through changes in biotic and abiotic environment (e.g. changes in microclimate). Case studies from the Satakunta forest diversity experiments used to illustrate the above mechanisms are also listed.

Long-term forest diversity experiments which manipulate tree species richness and tree genetic diversity enable monitoring of both individual tree and stand development over time in parallel with temporal changes in environment and ecosystem processes. Such experiments are therefore crucial for unravelling the mechanisms of temporal shifts in BEF relationships within forests. Over 30 such experiments are part of TreeDivNet, the global network of forest diversity experiments (Paquette et al. 2018). Below we discuss how temporal changes at both individual tree and stand level can affect tree diversity effects on ecosystem functioning, illustrating this with examples from the oldest experiments within TreeDivNet – the Satakunta forest diversity experiments in Finland (Box 1).

Interactions between temporal changes at individual tree level and tree diversity effects

Biodiversity effects emerge at the landscape and ecosystem scale at least in part due to processes operating at the scale of individual trees (Bongers et al. 2020, Trogisch et al. 2021). Individual interactions range from positive (i.e. facilitation) to negative (i.e. competition) and may be direct or indirect via mutualists and natural enemies. While it is clear that neighbor identity matters (Baeten et al. 2019, Di Maurizio et al. 2023, Yu et al. 2023), leading to differences between intraspecific and interspecific interactions that scale up to community level processes, a fully mechanistic understanding of biodiversity effects originating at the neighborhood scale has yet to be realized.

We propose that temporal changes at individual tree level may mediate tree diversity effects on ecosystem functioning. These changes include shifts in tree functional traits with ontogeny and age, and via phenotypic plasticity to changes in abiotic and biotic conditions. Therefore, new insights can be gained through the characterization of functional traits mediating neighbor interactions (Fortunel et al. 2016, Schnabel et al. 2024a), and by considering the dynamics of interactions through time across the lifespans of individual trees. We discuss below the role of functional trait variation via ontogeny, age and phenotypic plasticity depending on the predictability of abiotic and biotic environment, and how this trait variation might mediate tree diversity effects on ecosystem functioning over time.

Shifts in tree functional traits with ontogeny and age

Plant functional traits are important predictors of species interactions, community assembly, and ecosystem function (Funk et al. 2017). While most trait-based approaches characterize variability at the species and community scales, traits are also highly variable within species, including considerable intra-individual variation via ontogeny and phenotypic

Box 1. Description of the Satakunta forest diversity experiments

Satakunta forest diversity experiments (https://www.sataforestdiversity.org/) have been established in SW Finland in 1999–2000. One of the experiments manipulates tree species diversity whereas another manipulates within-species genetic diversity. Taken together, these long-term experiments provide a unique opportunity to compare effects of trees species and intraspecific genetic diversity on boreal forest ecosystem functioning and services.

The Satakunta tree species diversity experiment (61°N, 22°E) consists of three areas, each containing 38 plots planted with monocultures, 2-, 3- and 5-species mixtures of Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, Siberian larch *Larix sibirica* (*Larix archangelica*), silver birch *Betula pendula* and black alder *Alnus glutinosa*. There are two replicates of each treatment per area (six replicates altogether). Species mixtures were composed to create a gradient from purely coniferous stands through mixed broadleaf and coniferous stand to purely broadleaf ones.

Plots are 20 × 20 m and contain 13 rows with 13 seedlings in each row (i.e. 169 seedlings per plot) planted at 1.5 m intervals. In mixed stands, different tree species were planted in equal proportions (50 : 50, 33 : 33 : 33 or 20 : 20 : 20 : 20 : 20), but tree positions within a plot are randomized to mimic natural stands. Tree material used in this experiment originated from a local tree nursery, is genetically diverse and of local southern Finnish provenances.

The Satakunta birch genetic diversity experiment (61°48′N, 21°39′E) consists of a single area with 48 20 × 20 m plots, each of which was planted with 100 silver birch *Betula pendula* trees with 2 m spacing and position of each genotype randomized. Genotypic diversity was originally established by planting various combinations of 1, 2, 4 and 8-genotype mixtures of eight genotypes known to vary in resistance to fungal pathogens and herbivores, as well as growth characteristics: K5834, JR$^1/_4$, V5818, K2674, 36, V5952, O154, K1659 (Poteri et al. 2001, Viherä-Aarnio and Velling 2001, Barton et al. 2015). All silver birch genotypes used in the experiment have southern Finnish origin (61–63°N) and have been obtained by micropropagation of vegetative buds of mature trees. Subsequent molecular analyses revealed mis-identification of one of the eight genotypes (K1659), and differential mortality led to unbalanced representation of genotypes within the polycultures (Barantal et al. 2019). Therefore Shannon–Weiner diversity index rather than number of planted genotypes per plot is used in statistical analyses.

Both experiments were thinned in 2013 to reduce tree density by half while keeping proportions of the different species/genotypes equal. In the species diversity experiment, one replicate of each treatment per area was left unthinned to offer the opportunity to compare tree species diversity effects at two different tree stand densities. Both experiments are currently at the stem exclusion stage of boreal forest stand dynamics.

plasticity, driven by genetic and environmental heterogeneity (Herrera 2017, Westerband et al. 2021). A major source of functional trait variation within species occurs within individual plants as they grow and develop through ontogenetic stages (Barton and Koricheva 2010, Barton 2024). However, the contribution of such developmental trait variation to stand-level biodiversity effects is largely unknown and represents an important knowledge gap in biodiversity research.

Plants undergo dramatic shifts in form and function as they develop and grow. There are multiple dimensions of developmental change, which are not necessarily synchronous, leading to complex variability in how plants interact with the abiotic and biotic environments over time. Specifically, plants not only get larger over time (Meinzer et al. 2011), but also increase in structural complexity due to shifts in architecture (Laurans et al. 2024). They also pass through genetically regulated phase change, leading to a series of ontogenetic stages, e.g. seedling, juvenile, adult, senescent (Jones 1999, Poethig 2013). Plant functional traits also change considerably during these developmental processes (Barton 2024), shifting resource utilization and driving variation in growth rates and interactions with neighboring plants (Barton and Koricheva 2010, Espinosa et al. 2016, Bongers et al. 2020).

For monocultures – particularly those in which seedlings are planted synchronously like plantations, experimental forests, and forests recovering from disturbance or being restored following land use change – species ontogenetic patterns will closely align with stand-level dynamics. However, in diverse stands, species variability in ontogenetic patterns, the simultaneous presence of plants of all ontogenetic stages (Cope et al. 2020), and emerging properties of diverse communities will lead to more complex patterns of variation in functional traits. The generalizability of the contribution of developmental trait variation to BEF effects depends on whether traits follow consistent developmental trajectories among species and across habitat types. In other words, the extent to which developmental trait variation is fixed versus plastic will determine its predictive potential in the context of biodiversity effects.

Trait responses to predictable changes in abiotic and biotic environment

Fixed ontogenetic trait variation evolves in plants that experience predictable shifts in environments as they grow and develop (Barton 2024). Such anticipatory plant strategies are expected to maximize life-time fitness through phenotypic adjustment that maximizes function across predictable sequences in environmental conditions (Mertens et al. 2021). For example, in forests most tree seedlings recruit into shady environments under intense competition for light and space, later transitioning to sunnier conditions as they emerge into the canopy. This ontogenetic niche shift is predicted to drive the evolution of distinct functional strategies in seedling/juvenile versus adult stages (Poorter 2007). Evidence generally supports this prediction, with decreases in leaf area and increases in leaf mass per area and photosynthetic rates having been reported for many species of tropical and temperate trees as they transition from seedlings to adults (Thomas and Winner 2002, Fortunel et al. 2020). Ontogenetic increases in leaf-level photosynthesis in combination with shifts in architecture to enhance individual-level light capture are certainly the primary drivers of early increases in stand-level productivity. These increases are then followed by declines in productivity as plants saturate the canopy and begin to senesce (Hinckley et al. 2011, Guo and Ren 2014), illustrating how intra-individual variability scales up to affect ecosystem dynamics. However, in even-aged forest plantations which are established on clearcuts and in forest stands naturally recovering from major disturbances (e.g. fire or windthrow), seedlings may conversely experience sunny conditions which become shadier when canopy closure is reached. In this case, opposite changes might be expected in terms of functional traits, i.e. increase in leaf area and decrease in leaf mass per area and photosynthetic rates as plants develop from the seedling/juvenile to adult stage.

In addition to changes in abiotic environments, plants often experience predictable shifts in herbivory as they grow, underlying the evolution of fixed ontogenetic trajectories of defence traits (Boege and Marquis 2005, Barton and Koricheva 2010). For example ontogenetic declines in defence traits coincide with escape from ground-dwelling vertebrate herbivores in boreal trees (Swihart and Bryant 2001) and in heteroblastic tree species in New Zealand (Burns 2010, 2016). Ontogenetic patterns in resource-use and defence traits are thus common, occurring in species undergoing predictable environmental shifts as plants grow and develop.

Role of trait phenotypic plasticity in mediating forest diversity effects

Biodiversity varies spatially at micro- and macro-scales, and the immediately surrounding neighborhood diversity is not likely to be a predictable source of environmental heterogeneity for plants. In addition, as trees grow and get larger, they expand their interaction radii thus getting access to new resources and interactions with more neighbors which in turn modifies the abiotic and biotic environment for the trees. Plants have evolved phenotypic plasticity as an alternative to fixed phenotypic expression, enabling them to adjust phenotypes to improve performance under unpredictable environmental heterogeneity (Sultan 2000, Alpert and Simms 2002). Phenotypic plasticity contributes to ontogenetic trait variation in complex ways. Plasticity can vary across ontogenetic stages as a consequence of expression lags, developmental constraints, and epigenetic effects from earlier stages or generations (Pigliucci 1998, Fischer et al. 2014, Avramov et al. 2017, Lawrence-Paul et al. 2023), leading to variability in the direction and magnitude of ontogenetic trait trajectories within species (Barton 2014, Ochoa-López et al. 2015). Plasticity can even alter the timing of ontogeny, for example by delaying or accelerating vegetative phase change (Rose et al. 2019). Phenotypic plasticity in response to neighborhood diversity is likely to correlate with the well documented decreases in resource competition, herbivory, and disease associated with high plant diversity (Jactel et al. 2021, Feng et al. 2022, Yu et al. 2023).

Diverse forests are associated with dominance of positive over negative tree–tree interactions as facilitation is stronger and competition weaker between interspecific than intraspecific neighbors (Yu et al. 2023). In young forest stands, neighbor interactions tend to be weak, but as plants grow, there is evidence of plasticity in resource use traits that directly contribute to tree growth, such as leaf chlorophyll and phosphorus concentration and branching architecture, in response to neighborhood diversity (Bongers et al. 2020). This suggests a role of plasticity in response to diversity underlying ontogenetic patterns in functional traits. Although the cues eliciting the plasticity were not identified, it is likely that shifting light availability within diverse neighborhoods is involved. Diversity may also intersect with ontogeny through a transition from facilitative to competitive interactions across ontogenetic stages, although the underlying mechanistic traits are often not identified (Espinosa et al. 2016).

Biodiversity effects involving shifts in herbivory via associational resistance and susceptibility (Barbosa et al. 2009) similarly reflect plasticity in trait expression (Felix et al. 2023), indicating that plants can detect and respond to signals associated with neighborhood diversity. Whether such plasticity in defence traits reflects shifting resource allocation associated with biodiversity effects on resource use (e.g. increased resource availability via complementarity and relaxed competition), or whether associational effects on herbivore and predator dynamics alter biotic induction in diverse neighborhoods remains unclear and deserving of future research.

Using long-term forest diversity experiments to explore ontogenetic patterns in plant functional traits and herbivory

A major challenge with investigating the role of ontogeny in BEF relationships is that it is not possible to disentangle fixed and plastic trait variation over time or among ontogenetic stages because these patterns are typically not tracked for individual genotypes. As with phenotypic plasticity, ontogenetic trait variation is a feature of individual genotypes, and so inferring it from comparisons made across individuals can be misleading (Barton 2024). Genotypic diversity experiments offer a compelling opportunity to characterize trait variation across ontogeny at the scale of genotypes, while simultaneously testing the effect of neighborhood diversity on these ontogenetic trait trajectories via phenotypic plasticity. Replicated plants within genotypes are a unique characteristic of genotypic diversity experiments, providing the necessary replication to analyze these patterns with statistical models. Although it is generally assumed that interspecific diversity drives ecosystem effects more than intraspecific diversity, there is clear evidence that genotypic diversity within species can play a significant role in species interactions and ecosystem dynamics (Bailey et al. 2009), that these effects vary among biomes (Wan et al. 2022), and can shift over time (Crutsinger et al. 2008). However, most genotypic diversity experiments are relatively short-lived (Castagneyrol et al. 2012), characterizing only part of the full ontogenetic trait trajectories.

The Satakunta birch genetic diversity experiment (Box 1), established in 2000, is the longest running genotypic diversity forest experiment in the world. Because of this experiment's longevity, we can characterize trait variation at the genotype-scale throughout ontogeny. Furthermore, defence traits are of particular interest given that previous studies of this experiment have documented significant variation among these silver birch genotypes in rates of herbivory by various guilds, including leaf-chewing, mining, rolling, tying, and galling insects, and moreover, that genotypic diversity effects vary among genotypes (Barton et al. 2015, Barantal et al. 2019). Here, we present new results for leaf trichomes, sampled from silver birch during early juvenile stages (2003, 2004), at the sapling stage (2009), and at the mature adult stage (2016). Silver birch leaf surfaces are characterized by the presence of glandular trichomes with flavonoid aglycones, which have previously been shown to provide resistance to insect herbivores and pathogenic fungi (Valkama et al. 2005a, b). Further details on measurement and statistical analysis of trichome density are available in the Supporting information.

Trichome density varied by an order of magnitude among the seven silver birch clones throughout their ontogeny (Fig. 3A). Significant variation was detected among the genotypes ($F_{6,\,218} = 14.72$, $p < 0.0001$) and through ontogeny ($F_{3,1259} = 95.80$, $p < 0.0001$). Moreover, we detected genetic variation in the ontogenetic trajectories, as evidenced by a significant genotype × year interaction ($F_{18,1218} = 5.40$, $p < 0.0001$). There was a tendency for trichome density to decrease as plants developed from the juvenile to adult stages, although these patterns varied among the genotypes (Fig. 3A). Genetic variation in ontogenetic patterns is a requirement for these anticipatory strategies to evolve (Mertens et al. 2021), and most previous evidence of genetic variation and heritability of ontogenetic trait trajectories comes from short-lived and herbaceous species that are more tractable (Barton 2007, Ochoa-López et al. 2018). Longitudinal studies that track replicated genotypes across their lifespans, as in this experiment, are the only robust way to detect genetic variation in ontogenetic trajectories, and this result adds to the limited but important evidence that woody plants express genetic variation in ontogenetic trajectories even in the context of field conditions (Cope et al. 2019, Cole et al. 2020).

Biodiversity effects were tested as plasticity in trichome density of the genotypes in response to genotypic diversity (Shannon diversity index calculated at the plot level). Using linear mixed models to compare trichome density among trees grown in stands of different genotypic diversity, we found that genotypic diversity did not explain significant variation in trichome density overall ($F_{1,340} = 0.05$, $p = 0.8205$), or conditionally among the genotypes (genetic diversity × genotype interaction: $F_{8,237} = 1.13$, $p = 0.3444$). There were also no significant changes in effects of genetic diversity on

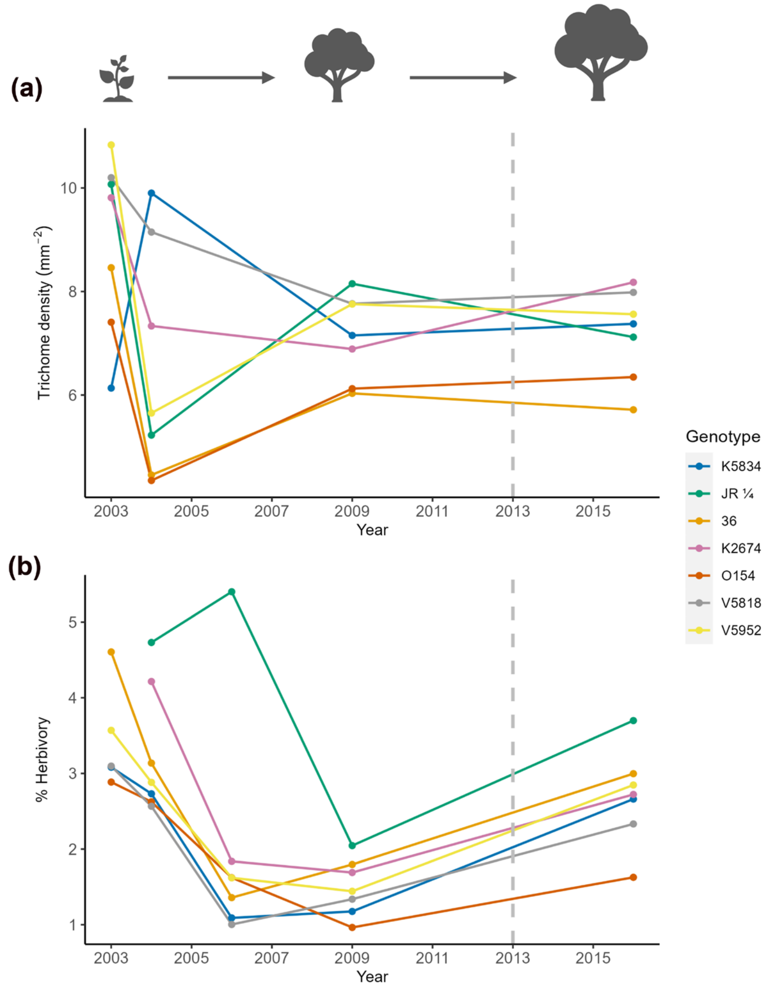

Figure 3. Temporal changes in leaf trichome density (a) and chewing insect damage (b) among the seven silver birch *Betula pendula* genotypes at the Satakunta birch genetic diversity experiment. Vertical dashed line indicates the year of the thinning treatment.

trichome density over time (genetic diversity × year interaction: $F_{2,\ 1215} = 1.86$, $p = 0.1564$). Although evidence is growing that plants express trait phenotypic plasticity in response to neighborhood diversity (Felix et al. 2023), previous studies have focused largely on interspecific diversity effects. Trait plasticity in response to intraspecific/genotypic diversity is predicted to occur via similar pathways (responses to abiotic and biotic shifts due to presence of particular neighbors), but there are as yet few tests of this (Bailey et al. 2009). In our experiment, trichome density did vary significantly among plots even after controlling for diversity and genotype effects ($\chi^2_1 = 34.76$, $p < 0.0001$, from χ^2 likelihood ratio tests for random factors), indicating the presence of phenotypic plasticity in response to some unidentified environmental heterogeneity. That ontogeny accounts for more trait variability in silver birch than neighborhood diversity confirms similar findings from other forests (Moreira et al. 2017) and underscores the importance of developmental variation in plant form and function.

We have also conducted new analyses of changes in insect herbivory over time (2003, 2004, 2006, 2009 and 2016) assessed on the same silver birch trees where glandular trichomes were measured. This allowed us to test whether the genotypic differences and ontogenetic changes in trichome densities are also reflected in herbivory and whether genotype and ontogenetic stage interact with genetic diversity effects on herbivory. Linear mixed models revealed significant variation in insect herbivory between birch genotypes ($F_{6,101} = 6.84$, $p < 0.0001$) and over time ($F_{4,2821} = 46.56$, $p < 0.0001$) (Barton et al. 2015, Barantal et al. 2019). Genotype × year interaction was also significant for insect herbivory ($F_{23,2818} = 4.13$, $p < 0.0001$), suggesting that clone susceptibility to herbivores changes through ontogeny (Fig. 3B). Genotypic diversity did not explain significant variation in insect herbivory overall ($F_{1,73} = 0.05$, $p = 0.829$), but genetic diversity effects differed among ontogenetic stages, as indicated by the significant genotypic diversity × year interaction ($F_{4,2769} = 3.54$, $p = 0.0069$). However, there was no significant relationship between trichome density and herbivory among clones ($F_{1,151} = 0.34$, $p = 0.552$) suggesting that ontogenetic changes in trichome density did not contribute to temporal changes in effects of genetic diversity on insect herbivory on birch clones. Other unmeasured defence or nutritive traits may be more important than glandular trichome density underlying chewing herbivory on silver birch in this experiment.

Interactions between temporal changes at stand level and tree diversity effects

Two parallel processes occur over time in forest stands: succession, which involves changes in species composition over time, and stand development, which is associated with changes in stand density and structure (Kimmins 2004, Fig. 2). Both processes may influence tree diversity effects on their own, but it is often difficult to separate their individual effects and therefore we will consider them together. In addition, forest management affects both forest succession and stand development. For instance, in commercial production forests succession and stand development may be affected by controlling species composition through planting and removal of unwanted species through thinning, which affects stand density and structure. As a result, successional effects may be less pronounced in managed forest stands and stand development enhanced as compared to naturally established stands. Despite an increased focus on nature conservation measures in modern forestry, most of the productive forested area in Fennoscandia is managed as production forests (Eggers et al. 2022). Long-term forest diversity experiments such as the Satakunta experiment in Finland, where tree age is uniform, tree species composition is controlled through planting, and natural regeneration is suppressed, are therefore similar to commercial production forests.

We propose that temporal changes at the stand level may interact with tree diversity effects on ecosystem functioning through at least three interconnected mechanisms:

1) changes in relative abundance of dominant tree species in forest stands over time;
2) changes in abiotic (e.g. microclimate) environment in forest stands over time;
3) changes in biotic (e.g. herbivory) environment in forest stands over time.

These three mechanisms might result in divergent temporal trajectories of stand development and succession as well as variation in the rates of succession and stand development in monocultures versus mixed species stands that in turn affect the magnitude of forest diversity effects on ecosystem functioning (Fig. 2).

Changes in relative abundance of dominant tree species in forest stands over time

We predict that the relationship between tree species diversity and ecosystem functioning will change over time as early successional species, which are dominant initially, are displaced by late successional species. In boreal, temperate, and tropical wet forests where decreasing light availability through succession is the main limiting factor, early successional tree species are likely to have fast growth and leaf traits suited for fast or 'acquisitive' resource capture [high specific leaf area (SLA), mass-based leaf nitrogen concentration and net photosynthetic rate], whereas late-successional species are characterized by slow growth and 'conservative' resource capture traits (low SLA, leaf nitrogen concentration and net photosynthetic rate) (Wright et al. 2004). In contrast, in tropical dry forests where water rather than light availability is the limiting resource, species with conservative functional traits are likely to dominate in dry and hot conditions in early successional stages whereas species with acquisitive traits are likely to become more dominant in later successional stages as the environment becomes wetter and cooler (Lohbeck et al. 2013).

Therefore, increased dominance of late successional species over time will change tree functional traits in mixed species stands which will in turn affect ecosystem functioning. This is consistent with the 'mass ratio hypothesis' (Grime 1998) which suggests that the most abundant autotrophic species, and their functional traits, have the greatest influence on ecosystem functioning because of their large contribution to primary productivity and energy fluxes. As no changes in relative abundance of tree species over time will occur in monocultures, functional differences between monocultures of early successional species and mixtures of early and late-successional species are likely to increase whereas differences between monocultures of late-successional species are likely to decrease throughout succession (Fig. 4).

Changes in the relative abundance of dominant tree species over time may also affect the relative importance of different mechanisms underlying tree diversity effects on forest ecosystem functioning. For instance, the relative importance of selection effects is likely to decrease during succession (Staude et al. 2023) as fast-growing, highly productive tree species tend to be early-successional species. In contrast, the importance of complementarity effects in mixed stands may instead increase over time, particularly in mixtures of early and late-successional species which are likely to differ more in their functional traits and hence be more efficient in resource partitioning. For instance, substantial overyielding and increase in species diversity effects over time have been reported in the Sardinilla tropical tree diversity experiment (Schnabel et al. 2019), likely due to species mixtures always including both early- and late-successional species.

Changes in abiotic environment throughout succession and stand development

Microclimate is one of the key regulators of ecosystem functioning in forests and is known to strongly influence litter decomposition, primary productivity and understorey plant communities (De Frenne et al. 2021). Forest microclimate is known to change through stand development and succession. For instance, older stands with tall, dense and closed canopies let less light through than more open younger and/or early successional stands which results in lower temperatures in older forest stands (Frey et al. 2016). Lower temperatures

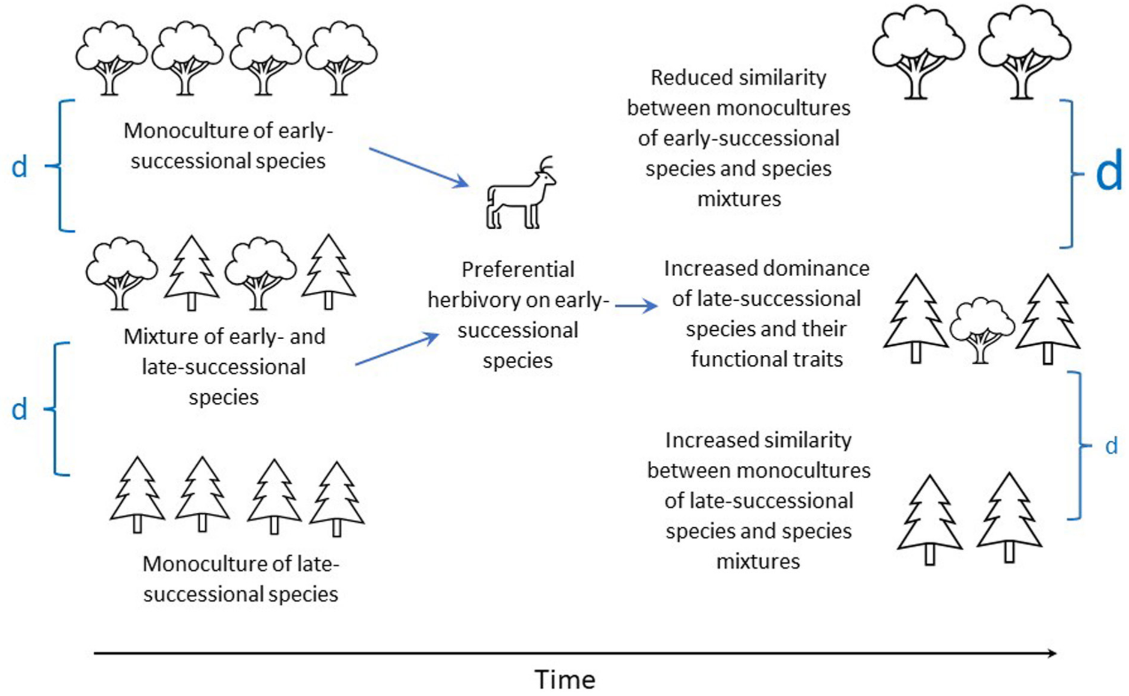

Figure 4. Conceptual diagram showing changes in the magnitude of differences between tree monocultures and species mixtures (d) in ecosystem functioning throughout the forest succession and stand development. The size of d reflects the magnitude of the effect.

in turn result in less evaporation thus maintaining higher levels of soil moisture under more mature forest canopies (Jucker et al. 2018).

Two recent studies conducted as part of long-term forest diversity experiments have shown that tree diversity can increase forest temperature buffering (Zhang et al. 2022, Schnabel et al. 2024b) due to increased canopy cover, canopy density and structural diversity in the mixed species stands (Pretzsch 2014, Jucker et al. 2015). Both studies were conducted in young forest stands, but we predict that buffering effects of trees on soil and air temperature and humidity are likely to strengthen over time as tree canopies become larger and their structural complexity increases in mixed stands. This enhanced microclimate buffering in mixed stands could also become more important over time in the face of an increasingly variable global climate. Canopy density (or permeability) can have cascading effects on soil microclimate, with soil temperature decreasing and soil moisture increasing as less light reaches the ground surface resulting in reduced surface evaporation (von Arx et al. 2013). These altered soil conditions have been observed to enhance decomposition rates in mixed species stands as compared to monocultures (Joly et al. 2017).

In addition to microclimate amelioration, abiotic facilitation in mixed species stands may occur via nutrient enrichment (Wright et al. 2017, Barry et al. 2019), for instance through presence of nitrogen-fixing plant species. Rates of nitrogen fixation can change throughout succession due to effects of disturbances such as fire on N-fixing species (Zackrisson et al. 2004); this in turn results in changes in N availability over time which may affect tree diversity effects on ecosystem functioning. Similarly, the forest floor in young boreal forest stands establishing after disturbances such as fire or clearcutting have minimal depth and low organic matter which gradually increase over time with stand development (Shrestha and Chen 2010). This might be one of the contributing factors explaining stronger effects of tree species diversity on fine root productivity in older stands (Ma and Chen 2017).

Changes in biotic environment throughout the succession and stand development

In boreal and temperate forests, large mammalian herbivores such as deer and moose play an important role at early stand development stages, but their influence is reduced over time as tree canopies outgrow the browsing line. Successional trajectories of forest stands can be modified by large herbivores such as moose through selective browsing of more palatable early-successional species at the sapling stage (Milligan and Koricheva 2013, Kolstad et al. 2018). As early successional tree species are likely to be preferred by large mammalian herbivores, we predict that intensive herbivory is likely to speed up succession in mixed species stands and hence increase functional differences between monocultures of early successional species and mixed stands of early and late-successional species over time. On the other hand, differences between monocultures of late-successional species and mixtures of early- and late-successional species over time are likely to decrease if mixed stands experience intensive herbivory (Fig. 4).

In young boreal and temperate forest stands where mammalian browsers are widespread, interactions between forest diversity effects and mammalian herbivory on ecosystem functioning have been observed. For instance, in the Satakunta experiments, browsing by moose has been shown to modify effects of tree species diversity on birch tree growth and insect herbivory (Muiruri et al. 2015). The observed interactions between moose browsing and tree species richness effects could be explained by lower canopy cover of more diverse stands compared with birch monocultures, leading to increased re-growth capacity and more high-quality foliage of browsed birch trees in more open diverse stands. Significant interactions between deer herbivory and tree species diversity effects have also been observed by Cook-Patton et al. (2014). In the absence of deer, tree seedlings survived better in monocultures, whereas in the presence of deer, both seedling survival and growth were higher in species mixtures. This was due to selective browsing on competitive dominants and associational protection of susceptible species by less palatable species.

Browsing preferences by mammalian herbivores may also affect the relative abundance of different tree species in the forest stands. This will lead to changes in dominant tree functional traits which will in turn affect ecosystem functioning in accordance with the 'mass ratio hypothesis' (Grime 1998), as discussed above. For instance, in the Satakunta tree species experiment, silver birch and Scots pine were preferred by moose at early stages of stand development (Vehiläinen and Koricheva 2006, Milligan and Koricheva 2013). Furthermore, pine was more preferred by moose than birch (Milligan and Koricheva 2013) and is known to be particularly susceptible to moose browsing when overtopped by birch (Bergqvist et al. 2014), as happens in young even-aged pine–birch stands. This resulted in a decrease in the proportion of pine in pine–birch mixtures over time. To illustrate how temporal changes in relative abundance of pine affect functional trait means at community level, we conducted new analyses exploring temporal changes in community-weighted means of functional traits in pine–birch mixtures (Fig. 5). Scots pine and silver birch are both light demanding pioneer species but have very different functional traits as pine is an evergreen conifer and birch is a deciduous broadleaf species. Compared to Scots pine, silver birch has higher specific leaf area (SLA), leaf nitrogen content, wood density and specific root length (Fig. 5). Over time, as proportion of pine in pine–birch mixtures decreased, community-weighted means of the functional traits in the mixed stands exhibited significant changes in both pre- and post-thinning periods (2002–2011: $F_{1,16}=4.65$, $p=0.0465$, 2014–2023: $F_{1,17}=5.88$, $p=0.0267$) and became more similar to birch monocultures (Fig. 5), which is likely to reduce the difference in ecosystem functioning between birch monocultures and pine–birch mixtures and increase the difference between pine monocultures and pine–birch mixtures. Note that the above example does not take into account ontogenetic changes and phenotypic plasticity of tree functional traits in response to neighbourhood diversity (Felix et al. 2023) as well as differences in leaf trait variation within individuals between monocultures and mixtures (Proß et al. 2024) which might further mediate the relationship between tree diversity and ecosystem functioning.

To explore how temporal changes in relative abundance of pine and birch and their associated functional traits might affect ecosystem functioning, we have examined temporal changes in % cover of different functional groups of understorey vegetation in the Satakunta tree species diversity experiment in pine monocultures, birch monocultures, and pine–birch mixtures (Fig. 6). Understorey species composition and cover was assessed in the Satakunta tree species diversity experiment in 2003, 2011 and 2019 following methodology described in Ampoorter et al. (2014) and the Supporting information. In pine monocultures, the percentage cover of dwarf shrubs increased over time, as would be expected in coniferous stand, while percentage cover of grasses and forbs decreased. In birch monocultures, the percentage cover of dwarf shrubs and grasses remained fairly stable over time while the percentage cover of forbs decreased similarly to pine monocultures. Temporal changes in percentage cover of dwarf shrubs and grasses in birch–pine mixtures were intermediate to those in component monocultures, i.e. slight increase in % of dwarf shrub cover and slight decrease in % of grass cover. However, % cover of forbs remained higher and more stable in pine–birch mixtures as compared to either pine or birch monocultures. Although at the time of data collection the effects of decreased proportion of pine in pine–birch mixtures on understorey have manifested only for one of the three understorey functional groups, temporal patterns of % cover by forbs in pine/birch stands at the Satakunta experiments provide an example of divergent temporal trajectories in monocultures and the species mixture.

In addition to aboveground biotic environment, changes in belowground biotic environment could also lead to temporal shifts in plant diversity effects on ecosystem functioning. Eisenhauer et al. (2012) highlighted the role of soil biota in increasing plant diversity effects on productivity over time. They suggested that over time accumulation of plant pathogens in soil may decrease the productivity of monocultures while the beneficial effects of plant mutualists such as mycorrhizae may increase productivity of diverse plant communities. Long-term tree diversity experiments can be used to understand the role of soil biota in development of BEF relationships in forests (Ferlian et al. 2018). For instance, a recent study in the MyDiv forest diversity experiment that uses tree species that associate with either arbuscular (AM) or ectomycorrhizal (EM) fungi to create gradients in tree species richness and mycorrhizal associations (Dietrich et al. 2023) found that AM and EM tree communities differed in their productivity in terms of temporal development and tree diversity effects. Positive diversity–productivity relationship was found in EM tree communities but not in AM tree communities. In addition, annual increment of basal area of EM tree species increased over time whereas increment of AM tree species decreased. Although communities containing both AM and EM species did not benefit in terms of productivity, Dietrich et al. predicted that dissimilar mechanisms underlying BEF relationships in AM and EM trees may increase

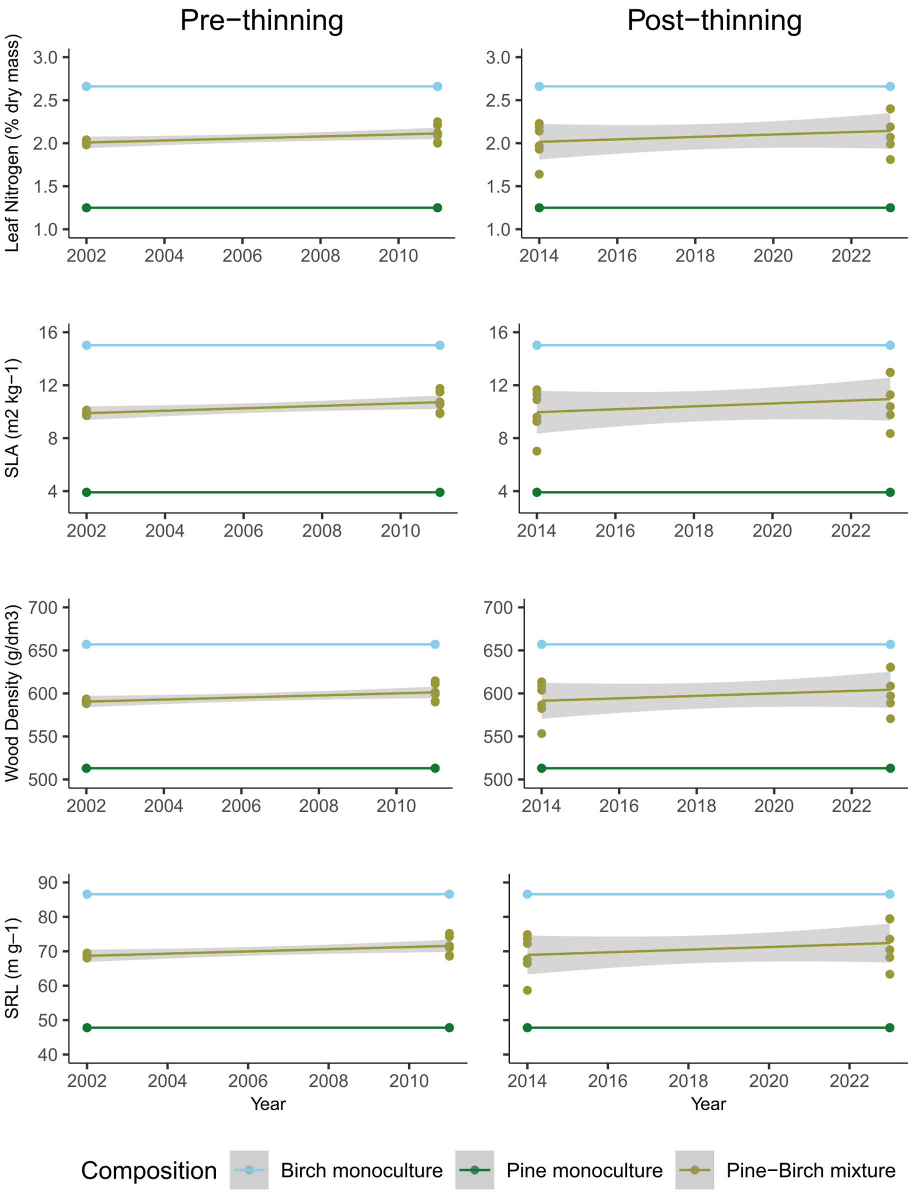

Figure 5. Temporal patterns in community-weighted means (CWM) of four tree functional traits (leaf nitrogen content, specific leaf area (SLA), wood density and specific root length (SRL) in Scots pine–silver birch species mixtures (PB) relative to monocultures of silver birch *Betula pendula* (B) and Scots pine *Pinus sylvestris* (P) in the Satakunta tree species diversity experiment. Grey shading indicates 95% confidence intervals. As the plots have been thinned in 2013, temporal changes are shown separately for period before thinning (2002–2011) and period after thinning (2014–2023). To calculate CWM, functional traits of pine and birch were obtained from TRY database (Kattge et al. 2011) and weighted by relative abundance of pine and birch in plots based on tree survival surveys conducted in 2002, 2011, 2014 and 2023. Due to decline in pine abundance in pine–birch mixtures over time as a result of preferential pine browning by moose, CWM for all four traits in pine–birch mixtures increased significantly in both pre- and post-thinning period, suggesting that in terms of functional traits mixed stands became more similar to birch monocultures and less similar to pine monocultures. Such temporal changes in CWM of mixed stands can affect the magnitude of tree species diversity effects on ecosystem functioning. Note that for simplicity only changes in CWM dues to relative abundance of tree species in a stand are illustrated but additional changes in tree functional traits over time due to ontogenetic changes and phenotypic plasticity are also expected.

ecosystem functioning in stands containing higher tree species diversity and combination of both mycorrhizae types in the long run. This prediction was supported by the latest results from the MyDiv experiment (Sachsenmaier et al. 2024) which showed that only mixtures containing both AM and EM species outperformed their respective monocultures in terms of productivity during and after drought. Long-term observations are thus clearly essential to fully understand the role of soil biota in strengthening of BEF relationships over time in forest ecosystems.

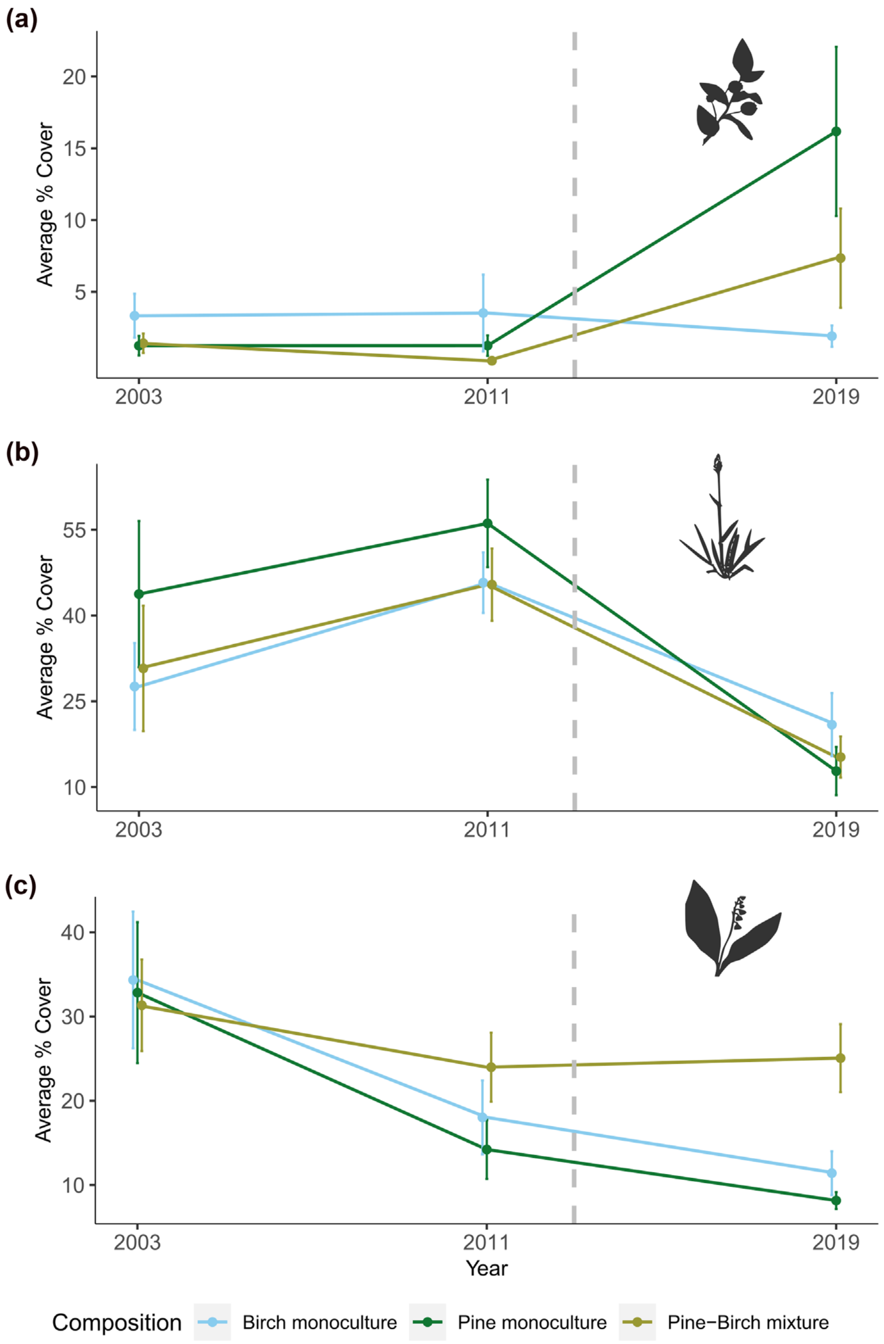

Figure 6. Temporal changes in percentage cover (mean ± SE) of dwarf shrubs (a), grasses (b) and forbs (c) in the understorey of silver birch *Betula pendula* monocultures, Scots pine *Pinus sylvestris* monocultures and bine–birch mixtures in the Satakunta tree species diversity experiments (areas 1 and 3). Vertical dashed line indicates the year of the thinning treatment.

The importance of long-term studies for exploring the mechanisms of temporal shifts in forest ecosystem functioning

Understanding underlying mechanisms of temporal shifts in tree diversity effects on ecosystem functioning is crucial for predicting the long-term consequences of biodiversity loss on ecosystem functioning and service provisioning. By drawing examples from the Satakunta forest diversity experiments and other long-term forest diversity experiments within TreeDivNet, we have demonstrated that accounting for changes in abiotic and biotic environment and functional traits of individual trees and forest stands over time helps to explain temporal shifts in forest diversity effects on ecosystem functioning. Long-term experimental studies such as the Satakunta forest diversity experiments enable the continual tracking of changes in forest ecosystem functioning in tree stands of different genetic and species composition and richness over time while controlling for differences in other environmental factors. Importantly, both ontogenetic trajectories of individual trees and forest stand development and successional stages can be followed in such experiments. While other approaches such as use of chronosequences could be used to detect temporal changes in forest ecosystem functioning (Taylor et al. 2020), they do not allow monitoring of the same individual trees and stands over time and hence have limited power to establish the underlying mechanisms of temporal shifts in tree diversity effects on ecosystem functioning. Furthermore, long-term studies are vital for exploring the effects of tree diversity on belowground processes as changes in root growth, soil microbial community structure and nutrient cycling dynamics can take a long time to manifest.

While the Satakunta experiments are the oldest experiments within the global network of forest diversity experiments (TreeDivNet), they are ca 25 years old currently and hence represent relatively early stages of forest succession and stand development. Therefore, to expand our understanding of changes in abiotic and biotic environment and tree functional traits at later stages of tree growth, stand development and succession studies in relatively young forest diversity experiments could be combined with analysis of data from national forest inventories where permanent plots are regularly revisited. While tree diversity is not experimentally manipulated in these stands, it is possible to select the plots which represent different levels of tree diversity (Gamfeldt et al. 2013). The power of combining young forest diversity experiments with observational studies in mature stands to analyze the effects of tree diversity on ecosystem functioning across all successional stages has been demonstrated by Baeten et al. (2013) and this approach could be harnessed to assess temporal changes in tree functional traits and stand abiotic and biotic environment.

While the discussed mechanisms underlying temporal shifts in tree diversity effects are likely to apply to all forest biomes, the rates of temporal changes at individual tree and stand level will differ between tropical, temperate and boreal forests as stand development is much faster in the tropics. The global network of forest diversity experiments TreeDivNet (Paquette et al. 2018) thus provides a unique opportunity to compare the progression of temporal changes at tree and stand level and the resulting changes in tree diversity effects on ecosystem functioning across different forest biomes.

We emphasize here the importance of changes in abiotic and biotic conditions in forest stands over time in affecting the magnitude and direction of forest diversity effects on ecosystem functioning. This can inform the design of the future forest diversity experiments. For instance, while herbivore exclosures are commonly used to study long-term effects of herbivory on forest ecosystems (Kolstad et al. 2018), the majority of existing forest diversity experiments exclude large herbivores altogether through fencing and hence preclude studies of interactive effects of herbivory and tree diversity on ecosystem functioning (Muiruri et al. 2015). Given the importance of mammalian browsing on stand development in boreal and temperate stands and possible interactions between browsing and tree diversity effects, we propose that mammalian herbivore exclosures are incorporated into the design of forest diversity experiments. Each diversity treatment can then be replicated inside and outside of the mammalian exclosure (Cook-Patton et al. 2014). In addition, most forest diversity experiments consist of even-aged forest stands where all plots are planted simultaneously, similarly to forest plantations and managed stands established through planting after a major forest disturbance such as clearcut or forest fire. Canopy structure and understorey of such single-aged stands may be very different from those in stands established through natural colonization and containing trees of different ages, resulting in potentially very different abiotic conditions. Uneven-aged stands can be achieved by planting tree seedlings at staggered time intervals (Schwarz et al. 2021) and we need more tree diversity experiments implementing this type of planting to explore the temporal dynamics of abiotic environment and forest diversity effects in uneven-aged stands.

Finally, we would like to emphasize the importance of availability of research funding specifically aimed at long-term studies such as the forest diversity experiments. Regular measurements of the same processes in the same stands are required to assess temporal shifts in forest diversity effects on ecosystem functioning and to decipher the underlying mechanisms. Current research funding landscape generally discourages such long-term research through emphasizing the importance of novelty of grant proposals. Some funding schemes supporting long-term research do exist (e.g. through the Ecological Continuity Trust in the UK and the new long-term research grants by the British Ecological Society or funding for Research Units within the German Research Foundation which allows the maintenance of the Jena experiment, one of the oldest grassland biodiversity experiments in the world). However, these schemes either provide very limited funding which is insufficient to cover the costs of field work and experiment maintenance or are focused on particular countries. This prevents the establishment and maintenance of long-term experimental and observational studies across the globe representing different biomes. Until adequate funding and support for long-term studies is provided, we will continue to have only snapshots of effects at individual stand ages and successional stages thus precluding critical insights for predicting the consequences of biodiversity loss on ecosystem functioning and service provisioning over time.

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Data availability statement

Data and code are available from Zenodo: https://doi.org/10.5281/zenodo.10792480 (Koricheva et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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