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Effects of enemy exclusion on biodiversity–productivity relationships in a subtropical forest experiment

Running head: Leaf pathogens modify biodiversity effects in young forest

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Abstract

1. Interspecific niche complementarity is a key mechanism posited to explain positive species richness—productivity relationships in plant communities. However, the exact nature of the niche dimensions that plant species partition remains poorly known.

2. Species may partition abiotic resources that limit their growth, but species may also be specialized with respect to their set of biotic interactions with other trophic levels, in particular with enemies including pathogens and consumers. The lower host densities present in more species-diverse plant communities may therefore result in smaller populations of specialized enemies, and in a smaller associated negative feedback these enemies exert on plant productivity.

3. To test whether such host density-dependent effects of enemies drive diversity—productivity relationships in young forest stands, we experimentally manipulated leaf fungal pathogens and insect herbivores in a large subtropical forest biodiversity–ecosystem functioning experiment in China (BEF-China).

4. We found that fungicide spraying of tree canopies removed the positive tree-species richness—productivity relationship present in untreated control plots. The tree species that contributed the most to this effect were the ones with the highest fungicide-induced growth increase in monoculture. Insecticide application did not cause comparable effects.

4. Synthesis. Our findings suggest that tree species diversity may not only promote productivity by interspecific resource-niche partitioning, but also by trophic niche partitioning. Most likely, partitioning occurred with respect to enemies such as pathogenic fungi. Alternatively, similar effects on tree growth would have occurred if fungicide had eliminated positive effects of a higher diversity of beneficial fungi (e.g. mycorrhizal symbionts) that may have occurred in mixed tree species communities.

Keywords: BEF-China, biodiversity experiment, leaf pathogens, leaf herbivores, negative density-dependence, niche complementarity, primary productivity

Introduction

The biological mechanisms that drive beneficial effects of species richness on primary productivity (e.g. Hooper et al., 2012; O'Connor et al., 2017; Tilman et al., 2001) are not well understood, despite decades of research. It is clear that species diversity effects ultimately depend on some form of functional complementarity among species, but which niche dimensions underpin this complementarity, and in which functional traits these niche differences manifest themselves, remains elusive (Flynn et al., 2011; Loreau, 2000; Paine et al., 2015; van der Plas et al., 2020). It has been proposed that complementary resource use results from spatial, temporal, or other forms of resource partitioning among species, and that this then translates into a more efficient or more complete resource use in more diverse plant communities, and therefore into a higher productivity (Loreau et al., 2001; Turnbull et al., 2016). However, surprisingly little evidence exists to date about which resources are partitioned and through which actual biological mechanisms this occurs (Barry et al., 2019; Silvertown et al., 1999; von Felten et al., 2012). An important (but also long-known) exception are ecosystems that contain species associated with symbiotic nitrogen fixers such as rhizobia. Through this symbiosis, legume species in grassland increase their own nitrogen supply, and eventually also the amount of nitrogen availability to non-legumes in the community, and productivity increases (Spehn et al., 2002). Apart from this special case, however, it is still unclear how important and general the partitioning of abiotic resources really is in promoting biodiversity—productivity relationships.

Generalized niche concepts encompass dimensions other than abiotic resources, including shared enemies (Chase & Leibold, 2003). Recent studies indeed suggest that interspecific complementarity of biotic interactions, in particular with pathogens and consumers, may underpin positive BEF-relationships (Guerrero-Ramírez & Eisenhauer, 2017; Liu et al., 2012; Maron et al., 2011; Mommer et al., 2018; Poisot et al., 2013; Schnitzer et al., 2011, 2011; Wang et al., 2019) (but also with beneficial organisms, see Yang et al., 2021). Enemies often show some degree of host-specificity, and the reduction in enemy populations at the lower host densities in more diverse plant communities may therefore reduce negative feedback from these enemies and thereby increase plant productivity. Overall, this then manifests as a negative density-dependence of host growth (Keesing et al., 2006).

Low-latitude forests exhibit a high plant species diversity and often show high herbivory rates and pathogen load (Bagchi et al., 2014; Novotny et al., 2006; Schemske et al., 2009). In these forests, enemies may therefore be important modulators of community-level productivity (Bagchi et al., 2014), and niche differentiation among species with respect to pathogen and consumer interactions may support BEF-effects (Guyot et al., 2016; Jactel & Brockerhoff, 2007;

Vehviläinen et al., 2007). However, a higher diversity of trees may also lead to a shift from specialist to generalist herbivores and pathogens, or promote populations of these enemies through dietary mixing and habitat improvement through environmental heterogeneity (Brezzi et al., 2017; Castagneyrol et al., 2012; Schuldt et al., 2010). This could weaken diversity—productivity relationships.

To test whether interactions with enemies modify diversity-productivity relationships in tree communities, we combined insecticide and fungicide application with tree species richness treatments in a large-scale forest biodiversity experiment in subtropical China (Bruelheide et al., 2014; Huang et al., 2018). The experimental plots contained 1 to 16 tree species that had been growing for 6–7 years and reached an average height of approx. 3 m when the pesticide treatments were applied to subplots for an additional two years. We monitored tree growth in pesticide-treated and control plots, and measured leaf damage in additonal control plots. We then tested whether diversity—productivity relationships were modulated by the suppression of insects and fungi by experimental pesticide application. We further investigated the species-level responses to these treatments, and their dependencies on species traits. Specifically, we predicted that the suppression of enemy-mediated impacts by pesticides would dampen BEF relationships because these were at least partially mediated by density-dependent effects of enemies.

Methods

Study site and experimental design

In 2009–2010, we established the "BEF-China" forest biodiversity experiment on two ~20 ha sites ("A" and "B"). The entire experiment comprised 566 main plots in which different species-loss scenarios were simulated (Bruelheide et al., 2014; Chen et al., 2020; Huang et al., 2018). Here, we used a subset of 62 plots in which species numbers were reduced from 16 to 1 by simulating a random, trait-independent reduction of tree species richness (Fig. 1). To create the corresponding community compositions, we started with two independent 16-species pools at each site and randomly divided these into halves, creating distinct 8-species mixtures. These mixtures were further halved and the procedure repeated until monocultures were obtained. This "broken stick" design ensured that all species were equally represented at all diversity levels. Communities with these species compositions were established by planting plots with 400 trees arranged on a quadratic 20 × 20 grid with 1.29 m inter-row distance.

In April 2014, we extended the study design by factorial split-plot treatments with insecticide and fungicide. This happened within the frame of the BEF-China project, and no additional permission was required for this field work. The new treatments (I: insecticide; F: fungicide; C: untreated control) were applied to subplots located along one side of the main plots. There also were two further subplot treatments (phosphorus fertilization and lack of weeding), but these are not part of the present analysis. Each subplot contained 4 × 4 = 16 trees. We further used the central 4 × 4 trees of the main plot for additional measurements (central control subplot).

Insecticide and fungicide solutions (4 L per subplot) were sprayed over tree crowns every 4 weeks, but only on days with no or very little wind. During the rainy season, application intervals were halved to 2 weeks to compensate for more rapid leaching. The insecticide solution contained 10 mL dimethoate (an organophosphate) and 10 mL deltamethrin (a pyrethroid). The fungicide solution contained 8 g of mancozeb (a dithiocarbamate) and 25 mL of myclobutanil (a triazole). Control subplots were sprayed with 4 L of water.

Tree size and growth

In September 2014, 2015, and 2016, we measured basal diameter and height of all trees in the subplots. We further measured the central 16 trees in each main plot because these are the trees that are censored as part of the regular inventories of all 566 BEF-China plots.

Tree growth was estimated as increase in basal diameter from 2014 to 2016. In small trees, increments in basal diameter can be difficult to determine, and growth may manifest predominantly in height. We therefore also used the product of basal diameter and height as a proxy for tree volume, and calculated volume growth as increment from 2014 to 2016 (see also Huang et al., 2018). To obtain species-level basal area and volume, we added the values for all tree individuals of the same species per subplot. Community-level basal diameter and volume were than obtained by summing all the species-level values per subplot.

Leaf damage

To assess the susceptibility of all tree species to herbivores and fungal pathogens, we quantified leaf damage in all monocultures in September 2016. We randomly chose five individuals per species from the central 6×6 trees of each main plot. Then, for each tree, we randomly picked three branches from different canopy layers and sampled seven young, fully expanded leaves per branch. The damage of these leaves was classified based on the fraction of leaf area affected (0, <5, <25, <50, <75, and >75%), separately for herbivory and fungal damage. Species mean leaf damage was calculated for each subplot by averaging the center of these damage classes over all leaves (e.g. 15% for the 5–25% class).

Data analysis

In our large-scale experiment, some tree individuals had been misplanted, had failed to establish, or were lost through time for a range of reasons including random mortality. Importantly, mortality was diversity-independent ($F_{1,48.4}$, P=0.6 for *log*(species richness) in a bionomial generalized mixed model with tree community composition as random term). For our analysis, we focused on the subplots in which at least 4 of the 16 trees were alive when the subplot-level treatments were established. This data set consisted of 217 of the original 4 × 62 = 248 subplots (these numbers include the central control subplot). Because the insecticide treatment was missing from the 16-tree-species diversity level, we further dropped the 16-species communities from our analysis, resulting in a data set comprising 213 subplots. However, the general effects we report here were the same when the 16-species communities were kept (data not shown), and also did not depend much on the mortality threshold applied.

All data were analyzed by general linear mixed models summarized by ANOVA. Models were fitted by restricted maximum likelihood using ASReml 4.1 (http://vsni.co.uk) in R 4.1 (http://r-project.org). Fixed effects were site (A and B), species richness (*log*-transformed), pesticide treatment (insecticide, fungicide, or control, excluding the central subplot as additional control), and the interaction of pesticide treatment with *log*-transformed species richness. The treatment that showed major effects was the fungicide treatment, with no relevant differences between control and insecticide treatments. To reflect this fact, the three-level factor 'pesticide treatment' was decomposed into two contrasts: the first captured the difference between the fungicide treatment and the two other treatments, and the second the differences between the insecticide treatment and the untreated control subplots. Community composition, which in our design is equivalent to plot, was fitted as random effect. We fitted site-specific variance components for this term ("idh" option of ASReml, allowing for different variances of the random effects at the two sites) because trees at site A had been planted one year before trees at site B and therefore were larger on average, and therefore showed a larger random between-plot variation. The dependent variable was community-level growth from 2014 to 2016, measured either as increment in tree basal area or tree volume (one value per subplot). We analyzed all data untransformed because data transformation would have introduced spurious diversity effects (see Schmid et al., 2017).

We calculated net biodiversity effects (also known as overyielding, OY) for all mixtures. OY is calculated relative to monoculture values. When monoculture plot data was missing because too few trees had survived, we used mean growth values of that species across all mixtures for the calculation of overyielding. Capitalizing on the "broken stick" design, we further determined whether each species mixture overyielded or underyielded with respect to its component halves (cf. Fig. 1). Using χ^2-statistics based on Fisher's exact test, we checked whether the fraction of overyielding communities changed with pesticide application.

To compare the responses of different species to the experimental treatments, we first multiplied the growth increments of each subplot with the number of species. This is a common procedure in the analysis of replacement experiments to make data comparable on a per individual-planted basis (Harper, 1977). For example, multiplying the value of a species in a 2-species mixture by two or multiplying the value of a species in 4-species mixture by four yields the value expect at the individual numbers in monoculture. This density-adjusted growth metric was then linearly regressed against *log*-transformed species richness. Positive (negative) slopes indicate that trees of a particular species (per planted individual) grew better (worse) in more diverse communities. Finally, we tested whether pesticide application modified these slopes, and whether these species-specific responses could be understood based on the amount of leaf damage determined in the centre of the plots with monocultures.

To explore the relation of leaf quality with leaf pathogen damage and modifications of diversity effects by the pesticide treatments, we used redundancy analysis ('rda' function in R package 'vegan'). As metrics of leaf quality, we used specific leaf area (SLA), leaf C to N ratio, leaf dry matter content (LDMC), and leaf size (measured as square-root of leaf area). These species mean leaf traits had been measured in the BEF China experiment on independent sets of trees (Kroeber et al., 2015), on average healthy leaves. SLA, C:N and LDMC are related to the position a species takes in the leaf economics spectrum (Wright et al., 2004). We included leaf size as a trait because it determines the aerodynamic coupling of leaves to the atmosphere (smaller leaves have a lower boundary layer resistance), which is one of the factors that determines leaf temperature (Leuzinger & Koerner, 2007; Raschke, 1960); further, larger leaves may be more attractive because they present a larger contiguous habitat to colonizing fungi, and a larger unit of consumable resource to insects. Leaf damage values were square-root transformed prior to the analysis to achieve a more symmetric distribution.

Finally, we tested whether the treatment-effects on overyielding could be explained by community-weighted mean (CWM) traits of the species present in a mixture (using species-mean traits and initial planting proportions to avoid mixing a-priori CWM values with CWM responses to treatments). We linearly regressed the effects of fungicide and insecticide application on overyielding against CWM values of the respective species traits used for redundancy analyses, plus wood density, the concentration of phenolics, the concentrations of tannins, and leaf toughness (Eichenberg et al., 2015; Kroeber et al., 2015).

Results

Community level

In the two control subplots (the one at the border and the one in the central part of the plot), stand-level growth from 2014 to 2016 was positively related to the logarithm of tree species richness, both for stem basal area (ΔBA; $F_{1,53.6} = 7.4$, P=0.009, Table S1a) and tree volume proxy (ΔV; $F_{1,50} = 7.0$, P=0.012, Table S1b). As expected, there was no statistical difference of these species-richness effects between control subplots at the border vs. the center of the plots [see methods; ΔBA: $F_{1,49.6} = 0.1$, P=0.77; ΔV: $F_{1,51.5}=1.7$, P=0.20; control area type × log(species richness) interaction, Table S1]. All further analyses were carried out excluding the central control subplot, i.e. we used the border control subplots only which were used for the subplot treatment randomization.

Fungicide application decreased the slope of the richness-productivity relationship (Fig. 2) [ΔBA: $F_{1,100.5} = 3.3$, P=0.074; ΔV: $F_{1,101.5}=5.4$, P=0.022; fungicide vs. control and insecticide treatment contrast × log(species richness), Table S2]. This interaction was so strong that the positive tree species richness effect vanished under fungicide application (Fig. 2). Insecticide application did not cause such effects [ΔBA: $F_{1,99.9} = 0.0$, P=0.86; ΔV: $F_{1,100.6} = 0.1$, P=0.80; control vs. insecticide contrast × log(species richness), Table S2].

Overyielding of basal area and volume growth (Fig. 3) was significantly positive for control (ΔBA: $t_{23}=2.00$, P=0.028; ΔV: $t_{23}=2.19$, P=0.019) and insecticide application (ΔBA: $t_{25}=2.47$, P=0.010; ΔV: $t_{25}=2.30$, P=0.015), but not for fungicide application (ΔBA: $t_{24}=0.26$, P=0.4; ΔV: $t_{24}=0.3$, P=0.4). The difference between fungicide application from the two other treatments was confirmed by mixed-model ANOVA (ΔBA: $F_{1,48.1}=4.6$, P=0.036; ΔV: $F_{1,48.4}$, P=0.047). Overyielding in the insecticide treatment did not differ from control conditions (ΔBA: $F_{1,47.3}=0.15$, P=0.7; ΔV: $F_{1,47.6}$, P=0.9; Table S3).

In the control treatment, 12 out of 17 communities had a higher ΔBA and 13 out of 17 a higher ΔV than expected based on their component halves (Fig. 4; cf. Fig. 1). The insecticide treatment was very similar to the control treatment (13 of 22 and 14 of 22 communities that overyielded in ΔBA and ΔV, respectively). Under fungicide application, these numbers dropped to 9 out of 21 and 8 out of 21 for ΔBA and ΔV, respectively. This reduction in the fraction of overyielding communities was significant for ΔV (P = 0.028; Fisher's exact test).

Species level

Productivity responses of species within a community (here referred to as 'population') were assessed after correcting for relative density differences, as explained in Methods. Specifically, we examined how diversity effects on the productivity of individual species were modified under pesticide application. In general, the species that showed the strongest reduction in biodiversity effects under pesticide application also were the ones that benefited most from pesticide application when grown in monoculture (Fig. 5). This relationship was statistically significant for fungicide application ($P < 0.001$) and marginally significant for insecticide application ($P = 0.064$). The reduction in biodiversity effect under pesticide application was statistically weakly related ($P=0.09$, Fig. 6) to the fraction of leaf area damaged by fungi in untreated monoculture, and unrelated to the fraction of leaf area damage by insects ($P=0.26$, Fig. 6).

Redundancy analysis revealed a significant association of the four leaf traits with the leaf fraction damaged by insects and fungi ($P < 0.001$; Fig. 7). In particular, species mean fungal damage significantly correlated with leaf size and SLA ($r = 0.51$ for both traits, $t_{27} = 3.23$, $P = 0.005$, Pearson's product moment correlation), whereas insect herbivory correlated with leaf dry matter content (LDMC: $r = 0.44$, $t_{27} = 2.36$, $P = 0.025$).

Community-weighted means (CWM) of traits

CWM of leaf traits did not explain statistically significant amounts of variation in the modulating effects of pesticides on biodiversity effects, including the overyielding of basal area and volume growth (Table S4).

Discussion

Here we explored how experimental insecticide and fungicide application changed the effects of tree species richness on species- and stand-level basal area and volume growth as proxies of productivity. The objective of these treatments was to suppress enemies, specifically insect herbivores and fungal pathogens, but we cannot rule out that beneficial organisms also were affected. We found positive tree species richness effects on stand productivity under control conditions (no pesticide application), but these were greatly reduced or even vanished when fungicide was applied, but not when insecticide was applied. These findings indicate that mechanisms related to interactions with fungi, most likely foliar fungal pathogens, resulted in a negative density-dependent growth of tree populations, and that this promoted community-level BEF relationships in subtropical forest, in-line with findings in grassland BEF experiments (Klironomos, 2002; Maron et al., 2011; Schnitzer et al., 2011). In the following, we first discuss the results for stand-level metrics and then those for the species level.

Tree foliar fungal pathogens often are highly species-specific. They also disperse passively so that their spread strongly depends on the density of suitable hosts in their immediate surrounding (for example on the number of conspecific neighbor trees). A high tree-species richness can therefore suppress such specialized enemies. An independent analysis of fungal diversity and abundance in a larger set of BEF-China plots confirmed this notion (Rutten et al., 2021). One possibility therefore is that fungicide reductioapplication eliminated the community-level benefits of complementary foliar pathogen-related niches (see Chase & Leibold, 2003; Turnbull et al., 2016). Another possibility is that fungicide application suppressed beneficial organisms, either in the canopy or in the soil (e.g. mycorrhizae – fungicide was applied to canopies but a fraction may have leached into soils). Overall, this suggests that tree species diversity not only promotes productivity by interspecific resource niche partitioning (resulting in a competition reduction), but also by trophic niche partitioning resulting in a reduction of apparent competition (Chase & Leibold, 2003; Holt, 1977), i.e. competition-like interactions mediated by other organisms.

If a reduction in apparent competition due to enemy suppression was the sole effect of fungicide application, one would expect an increase in productivity both at low and high tree species richness, although to different extents. In our study, the growth of highly-diverse tree communities averaged lower under fungicide application than in control plots. This might indicate general detrimental effects of fungicide application on tree community productivity, for example direct toxic effects or indirect effects through the suppression of beneficial leaf micro-organisms. These would then have lowered community-level productivity in this treatment without altering the beneficial effect of tree species richness. Another possibility is that diversity effects were mediated by beneficial organisms that mediated complementarity among tree species but were suppressed by fungicide application, for example mycorrhizal fungi (Yang et al., 2021). Finally, fungicide application may have promoted herbivory, and thereby reduced tree community productivity. Indeed, a parallel study in untreated BEF-China plots indicated that herbivory increases more strongly with tree species richness when leaf pathogen damage is low (Schuldt et al., 2017). This indicates that fungal pathogen and insect herbivore manipulations are not fully independent, since the respective other group of enemies may be affected indirectly. In our study, the elimination of a biodiversity effect on tree stand growth by fungicide is evident, but identifying the specific mechanisms that underpin this phenomenon would require additional experiments.

Fungicide and insecticide application exerted different effects in our study. This suggests that different mechanisms were at play for fungi and insects. The absence of insecticide effects can potentially be explained by the absence of tree-growth suppression by herbivores. Schuldt et al. (2017), in a large set of untreated plots of BEF-China, found a positive association of herbivore damage and tree growth, which may either be interpreted as increased susceptibility of fast-growing trees to herbivores, or as growth over-compensation of these trees when attacked by herbivores. Another possibility is that the host density reductions realized in 16-tree species plots did not sufficiently hinder herbivores – unlike sessile leaf fungi – in moving from one host tree to the next or among experimental plots, or that the mobility of insects is higher and a larger stand area would have to be treated for such density-dependent effects to manifest. Finally, the absence of insecticide effect might also be explained by insect herbivore populations that were not host-density-dependent, and these even may have benefited from better nutrition due to dietary mixing. Similar positive effects of tree species richness on herbivores and herbivory were observed in the additional plots of the BEF-China experiment referred to above (Schuldt et al., 2017), in plots with a higher genetic diversity within species (Hahn et al., 2017), and in nearby natural forest stands (Brezzi et al., 2017). In contrast, foliar fungal infestation in the experiment was suppressed by tree diversity (Saadani et al., 2021). Taken together, these observations suggest that leaf fungi benefited from higher host densities in monoculture, and their suppression therefore led to increased productivity at low diversity and a weakened species-richness effect at the community-level. In contrast, insect herbivores did not cause such an effect, or even benefited from more diverse communities, resulting in no weakening of the tree species—richness effect on community-level productivity when insects were excluded.

How do our findings compare to findings from other biodiversity experiments? In the Cedar Creek grassland biodiversity experiment, experimental removal of arthropods and soil and leaf fungi promoted biodiversity effects on plant growth (Seabloom et al., 2017). Similar effects were also found in the European multi-site BIODEPTH grassland biodiversity study (Mulder et al., 1999). This finding is in line with the idea that more species-diverse plant communities support a larger or more active community of enemies (Bernays et al., 1994; Brezzi et al., 2017; Castagneyrol et al., 2012 [genotype diversity]; Hahn et al., 2017; Siemann, 1998). Therefore, to date there is some evidence that biodiversity—productivity relationships are mediated by enemies including consumers and pathogens, but virtually nothing is known about the importance of particular processes that underlie this effect (Staab & Schuldt, 2020). First, more species-rich plant communities may support a larger consumer community because of a higher resource availability or a more complex canopy that provides more physical and micro-climatic niche space. Second, a high plant diversity may allow consumers to stoichiometrically optimize their diet through mixing (e.g. lipids and proteins; Goverde et al., 2002). Third, specialized pests may suffer from a lower host density in more diverse plant communities. Fourth, consumers often are under strong top-down control (Hairston et al., 1960; Schmitz et al., 2000), and it appears possible that the strength of such trophic cascades is plant-diversity-dependent. Whether consumers will intensify or weaken plant diversity—productivity relationships will therefore depend on the relative balance of these processes, and such differences may well explain the different overall effects that have been reported in the different experiments.

Going some way towards investigating mechanisms underpinning the above-discussed stand-level responses, we also analyzed species-level responses of basal-area and volume growth to treatments. Indeed, leaf damage by fungi and insects significantly differed among tree species, and both were correlated with particular species mean leaf traits. For example, we found that species with larger leaves were more prone to fungal leaf damage. Large leaves may generally be thinner, i.e. have a higher specific leaf area (SLA) and possess traits that make them more prone to consumption, for example higher protein concentrations (Wright et al., 2004). Furthermore, in analogy to island biogeographic theory (MacArthur & Wilson, 1967), large leaves present larger contiguous colonizable habitats, and may result in a higher ratio of colonization to extinction events and a higher leaf damage. We reason that this effect should be more important for sessile pests such as leaf fungi than for mobile insects. Finally, large leaves are thermodynamically more decoupled from the atmosphere (Wright et al., 2017), which is relevant for leaf temperature when sunlit, although other factors such as canopy architecture often are as important (Leuzinger & Koerner, 2007). However, while trait differences were related to leaf damage values at the species level, we were unable to relate trait values to pesticide effects on community level productivity.

In conclusion, our study suggests that in subtropical forest complementarity for niches related to biotic interactions, in particular with fungi, promotes community-level diversity effects. Although the underlying responses differed among tree species, establishing a link to the species' traits proved difficult. However, establishing links between diversity effects and species' traits is notoriously difficult, most likely because the species' relevant niche dimensions are not sufficiently captured by the traits commonly considered, and our study probably is no exception.

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Conflict of Interest

The authors declare no conflict of interest.

Author contributions

All authors contributed to design and implementation of this experiment; YH collected the original field data presented here, in part with support from field helper teams; YH, BS and PAN analysed the data; YH and PAN wrote the manuscript with input and final approval from all authors.

Data Availability

All data are available on Dryad: https://doi.org/10.5061/dryad.3r2280gjp (Niklaus 2022).

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Tables

Table 1 List of the tree species used to create the species richness gradient. Code refers to the labels used in the figures. Species nomenclature follows the Flora of China (http://www.efloras.org and http://frps.eflora.cn).

Species	Code	Type
Ailanthus altissima (Miller) Swingle	AiAl	Deciduous
Alniphyllum fortunei (Hemsley) Makino	AlFo	Deciduous
Betula luminifera H. Winkler in Engler	BeLu	Deciduous
Castanea henryi (Skan) Rehd. et Wils.	CaHe	Deciduous
Castanopsis eyrei (Champion ex Bentham) Tutcher	CaEy	Evergreen
Castanopsis fargesii Franchet	CaFa	Evergreen
Castanopsis sclerophylla (Lindley & Paxton) Schottky	CaSc	Evergreen
Celtis biondii Pampanini	CeBi	Deciduous
Choerospondias axillaris (Roxb.) Burtt et Hill	ChAx	Deciduous
Cyclobalanopsis glauca (Thunberg) Oersted	CyGl	Evergreen
Cyclobalanopsis myrsinifolia (Blume) Oersted	CyMy	Evergreen
Elaeocarpus chinensis (Gardner & Champion) J. D. Hooker ex Bentham	ElCh	Evergreen
Elaeocarpus glabripetalus Merrill	ElGl	Evergreen
Elaeocarpus japonicus Siebold & Zuccarini	ElJa	Evergreen
Idesia polycarpa Maximowicz	IdPo	Deciduous
Koelreuteria bipinnata Franch.	KoBi	Deciduous
Liquidambar formosana Hance	LiFo	Deciduous
Lithocarpus glaber (Thunb.) Nakai	LiGl	Evergreen
Machilus grijsii Hance	MaGr	Evergreen
Machilus leptophylla Handel-Mazzetti	MaLe	Evergreen
Machilus thunbergii Siebold & Zuccarini	MaTh	Evergreen
Manglietia fordiana Oliv. in Hook (Old name: *Manglietia yuyuanensis*)	MaYu	Evergreen
Meliosma flexuosa Pampanini	MeFl	Deciduous

Nyssa sinensis Oliver	NySi	Deciduous
Phoebe bournei (Hemsley) Yen C. Yang	PhBo	Evergreen
Quercus fabri Hance	QuFa	Deciduous
Quercus phillyreoides A. Gray	QuPh	Evergreen
Quercus serrata Murray	QuSe	Deciduous
Rhus chinensis Mill.	RhCh	Deciduous
Sapindus abruptus Loureiro (*Sapindus mukorossi* Gaertner, *Sapindus saponaria* L.)	SaMu	Deciduous
Schima superba Gardn. et Champ.	ScSu	Evergreen
Triadica sebifera (Linnaeus) Small (old name: *Sapium sebiferum*)	SaSe	Deciduous

Figure legends

Figure 1 Experimental design. At two sites, 31 tree communities of distinct species composition were established. The 4-letter abbreviations indicate tree species (see Table 1). The numbers of the different communities correspond to the numbers in Figure 4.

Figure 2 Effects of insecticide and fungicide on the relationship between biodiversity and stand-level basal area growth. Squares show raw means for each diversity level, error bars are standard errors. Lines and shaded areas show model-predicted means and standard errors.

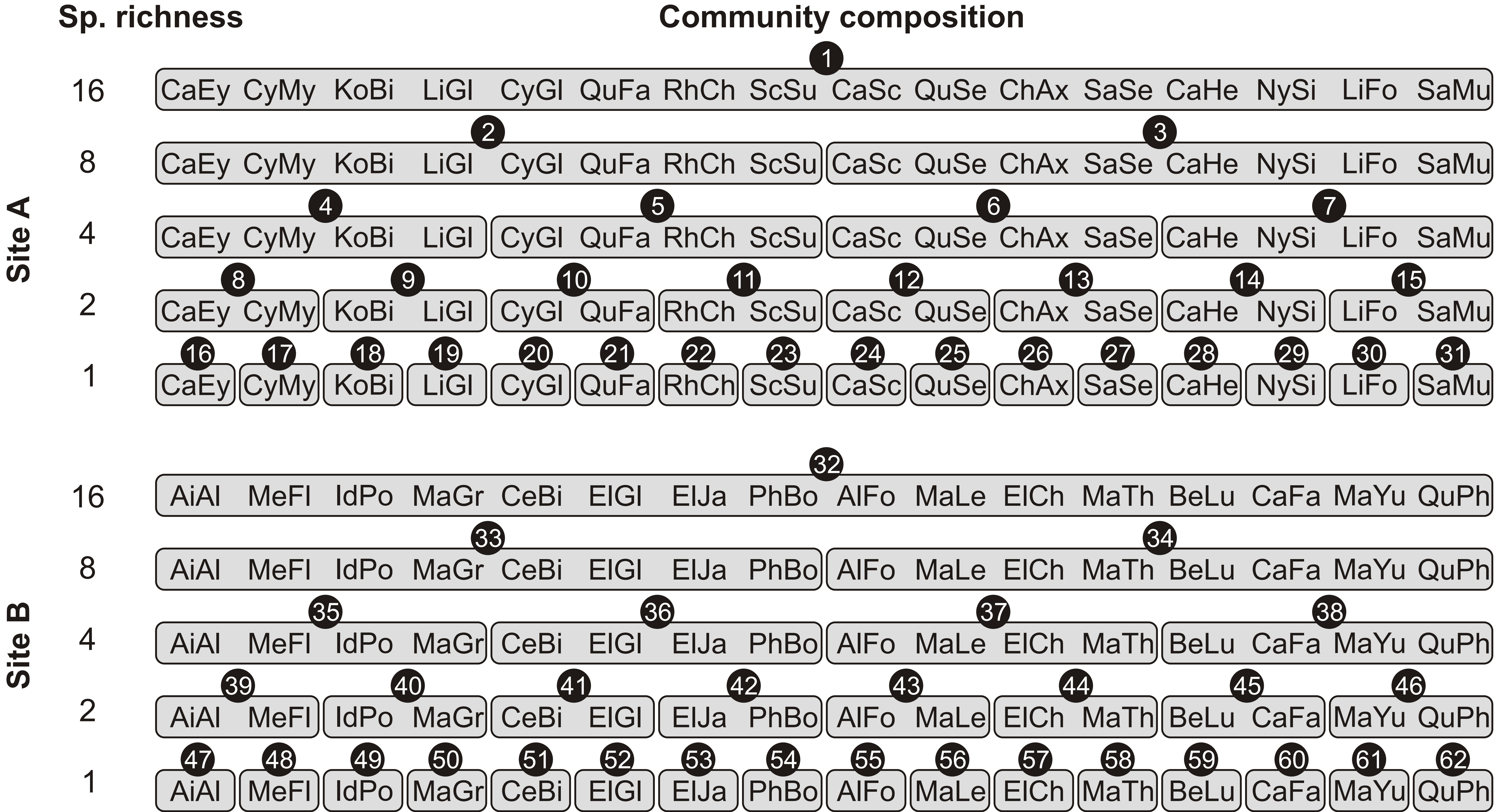
Figure 3 Net biodiveristy effects (overyielding) of basal area and volume growth rates in tree species mixtures to which fungicides and insecticides were applied, or which served as untreated controls. Bars indicate means ± se.

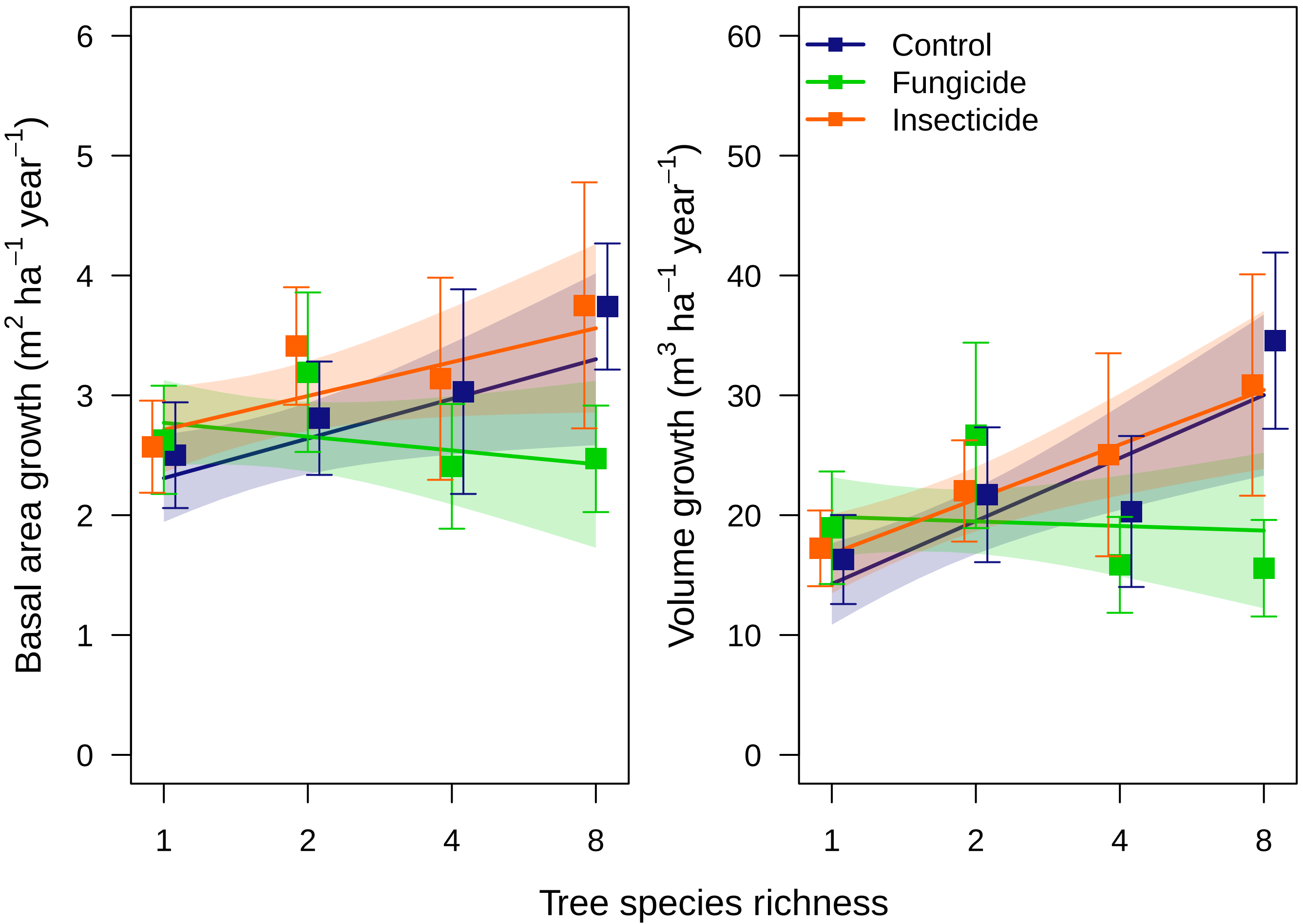
Figure 4 Stand-level basal area growth in dependence of tree species richness and pesticide treatment. Black and white symbols indicate communities that overyield and underyield relative to their component halves, respectively. Grey symbols indicate communities for which no data is available for at least one half and the overyielding response therefore cannot be determined. Numbers refer to the community compositions in Figure 1.

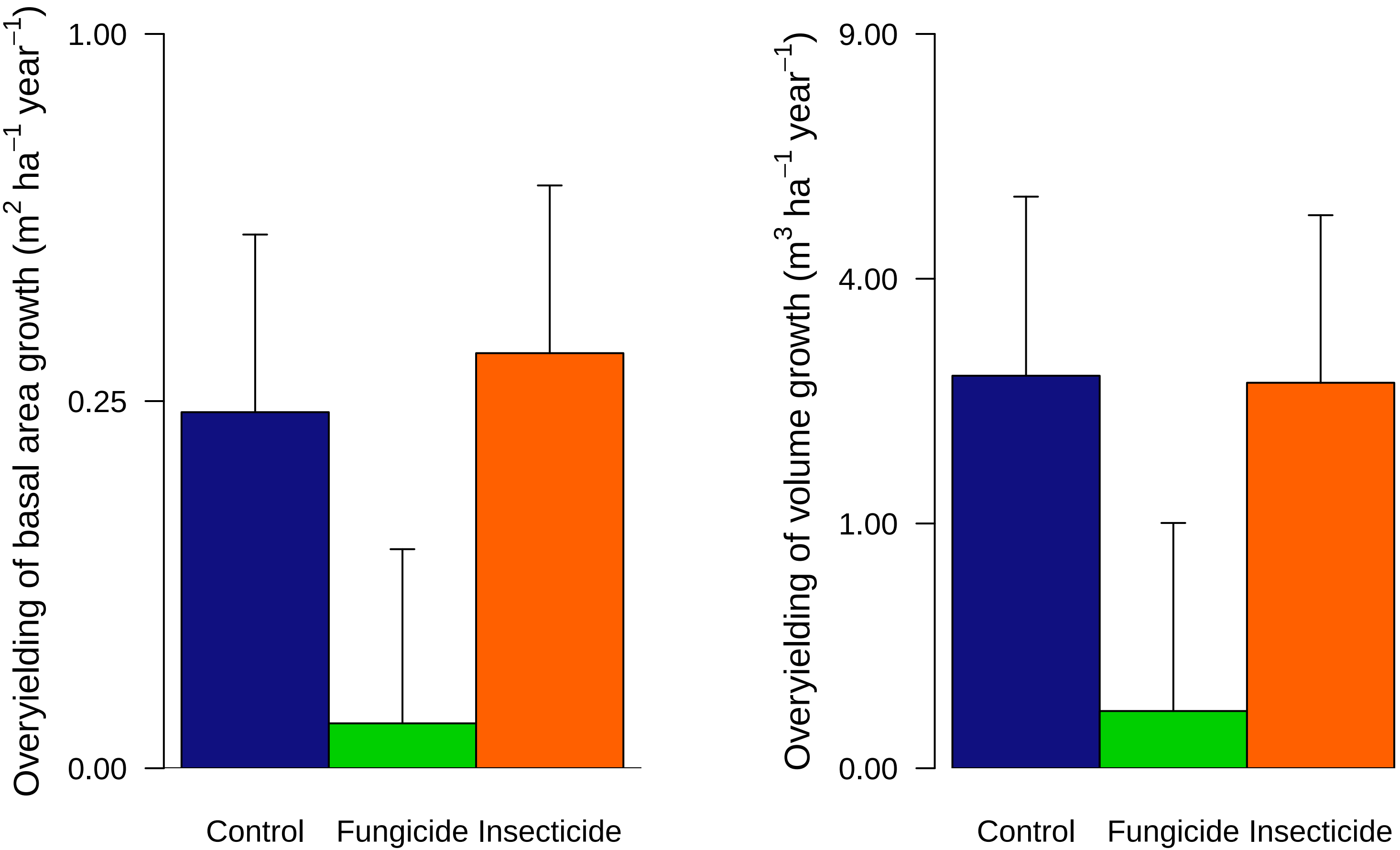
Figure 5 Changes of species-level tree-species-richness effects under fungicide (left) and insecticide (right) application, in dependence of pesticide effects in monoculture. Species that grew better in monoculture when pesticides were applied (higher values on X axis) benefitted relatively more from growing in species-rich tree communities under control conditions (lower values on Y axis, indicating a reduction of biodiversity effect when pesticides were applied). For species abbreviations see Table 1. Y axis: first, basal area increments of all species was regressed against log(tree species richness), correcting for the lower per-species planting density in more species-diverse plots (see Methods). Then, the pesticide-induced change in slope was calculated. X axis: growth modifications in monocultures treated with the respective pesticide. Solid regression lines indicate statistically significant relationships.

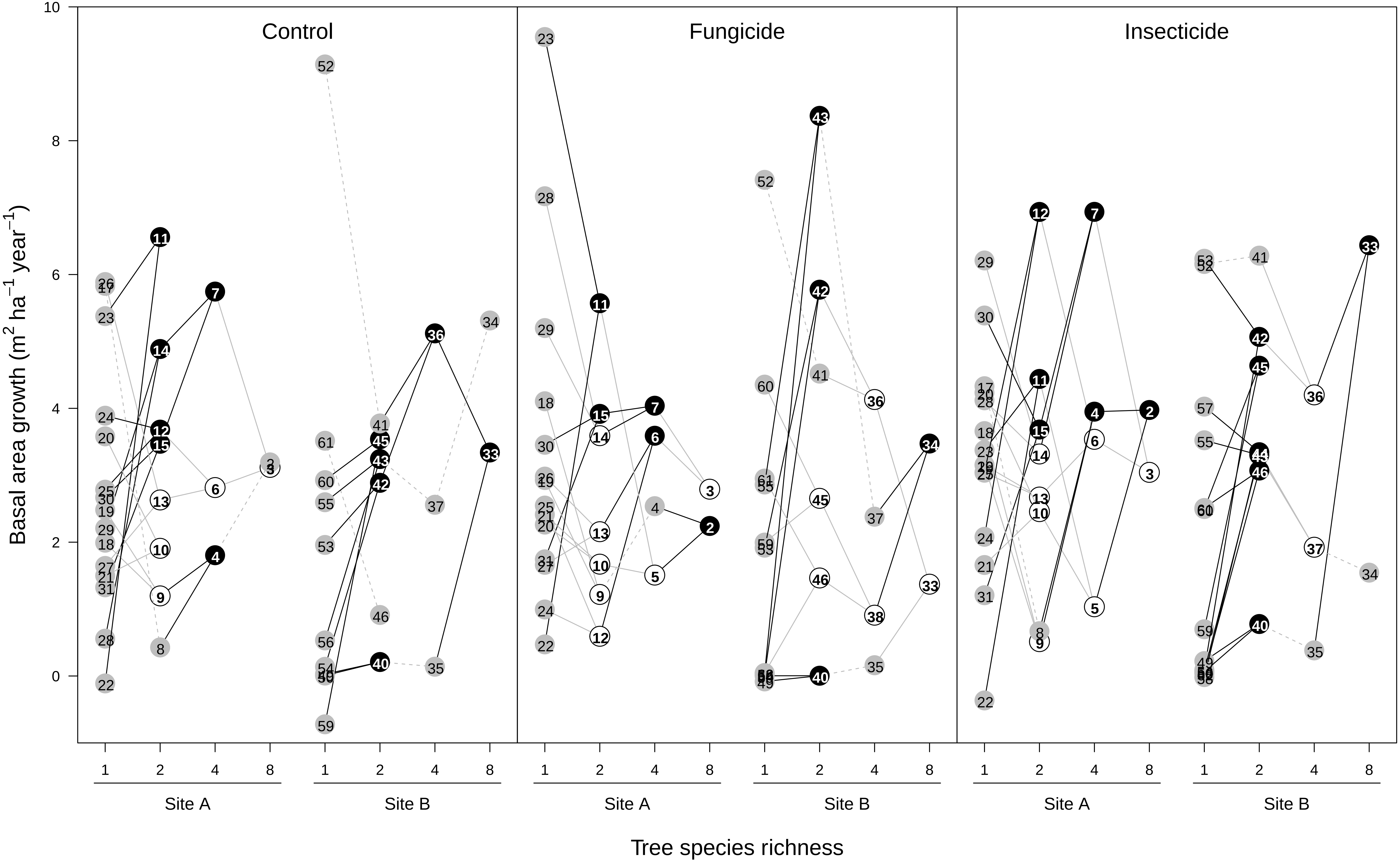
Figure 6 Fungicide-mediated (left) and insecticide-mediated (right) modifications of tree species richness effects on the growth of tree species, in dependence of the leaf area fraction that was damaged in monoculture by leaf fungi and insect herbivores. Dashed regression lines indicate relationships for which P>0.05. For species abbreviations see Table 1.

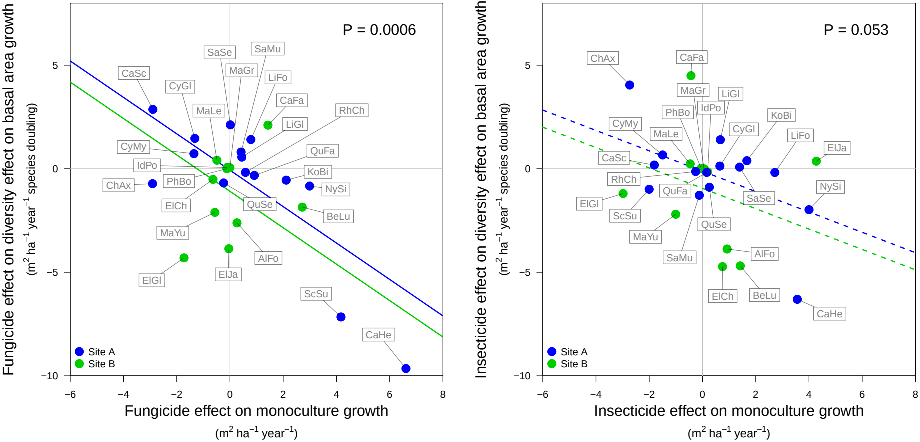
Figure 7 Redundancy analysis relating leaf traits (blue) to leaf damage observed in monocultures (red). CN: leaf C to N ratio; SLA: specific leaf area; LDMC: leaf dry matter content; SIZE: leaf size (square-root of leaf area). Leaf herbivory and leaf fungal damage are average fractions of leaf area affected; see Methods for details. For species abbreviations see Table 1.

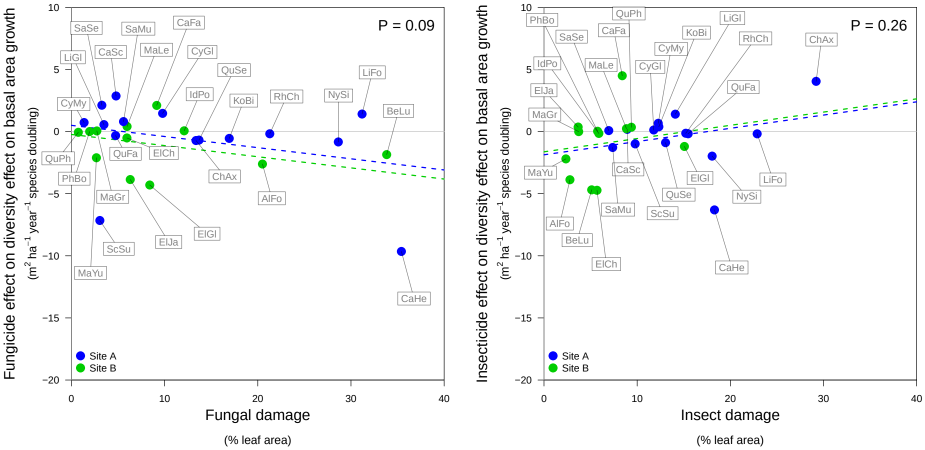

Sp. richness
Community composition
Site A
16
1
CaEy CyMy KoBi LiGl CyGl QuFa RhCh ScSu CaSc QuSe ChAx SaSe CaHe NySi LiFo SaMu
8
2
CaEy CyMy KoBi LiGl CyGl QuFa RhCh ScSu
3
CaSc QuSe ChAx SaSe CaHe NySi LiFo SaMu
4
4
CaEy CyMy KoBi LiGl
5
CyGl QuFa RhCh ScSu
6
CaSc QuSe ChAx SaSe
7
CaHe NySi LiFo SaMu
2
8
CaEy CyMy
9
KoBi LiGl
10
CyGl QuFa
11
RhCh ScSu
12
CaSc QuSe
13
ChAx SaSe
14
CaHe NySi
15
LiFo SaMu
1
16
CaEy
17
CyMy
18
KoBi
19
LiGl
20
CyGl
21
QuFa
22
RhCh
23
ScSu
24
CaSc
25
QuSe
26
ChAx
27
SaSe
28
CaHe
29
NySi
30
LiFo
31
SaMu
Site B
16
32
AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo AlFo MaLe ElCh MaTh BeLu CaFa MaYu QuPh
8
33
AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo
34
AlFo MaLe ElCh MaTh BeLu CaFa MaYu QuPh
4
35
AiAl MeFl IdPo MaGr
36
CeBi ElGl ElJa PhBo
37
AlFo MaLe ElCh MaTh
38
BeLu CaFa MaYu QuPh
2
39
AiAl MeFl
40
IdPo MaGr
41
CeBi ElGl
42
ElJa PhBo
43
AlFo MaLe
44
ElCh MaTh
45
BeLu CaFa
46
MaYu QuPh
1
47
AiAl
48
MeFl
49
IdPo
50
MaGr
51
CeBi
52
ElGl
53
ElJa
54
PhBo
55
AlFo
56
MaLe
57
ElCh
58
MaTh
59
BeLu
60
CaFa
61
MaYu
62
QuPh

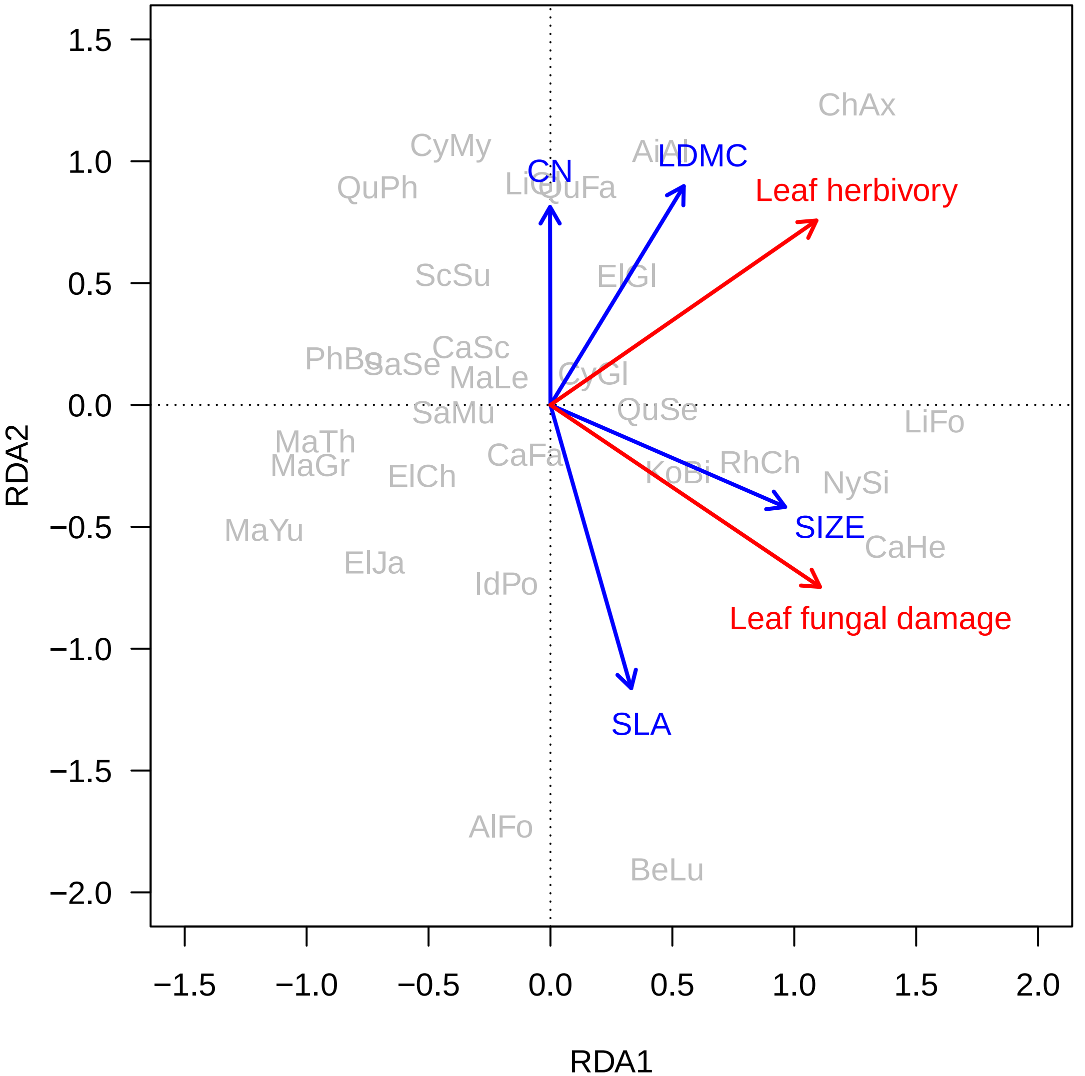

Basal area growth (m^2 ha^{-1} $year^{-1}$)
0
1
2
3
4
5
6
Volume growth (m^3 ha^{-1} $year^{-1}$)
0
10
20
30
40
50
60
Control
Fungicide
Insecticide
1
2
4
8
1
2
4
8
Tree species richness


Overyielding of basal area growth (m^2 ha^{-1} $year^{-1}$)
1.00
0.25
0.00
Control
Fungicide
Insecticide
Overyielding of volume growth (m^3 ha^{-1} $year^{-1}$)
9.00
4.00
1.00
0.00
Control
Fungicide
Insecticide


Control
Fungicide
Insecticide
Basal area growth (m² ha⁻¹ year⁻¹)
0
2
4
6
8
10
1
2
4
8
Site A
Site B
Tree species richness


P = 0.0006
Fungicide effect on diversity effect on basal area growth
(m^2 ha^{-1} year^{-1} species doubling)
Fungicide effect on monoculture growth
(m^2 ha^{-1} year^{-1})
5
0
−5
−10
−6
−4
−2
0
2
4
6
8
SaSe
SaMu
CaSc
MaGr
LiFo
CyGl
CaFa
MaLe
RhCh
LiGl
CyMy
QuFa
IdPo
KoBi
PhBo
ChAx
NySi
ElCh
QuSe
BeLu
MaYu
AlFo
ElGl
ElJa
ScSu
CaHe
● Site A
● Site B
P = 0.053
Insecticide effect on diversity effect on basal area growth
(m^2 ha^{-1} year^{-1} species doubling)
Insecticide effect on monoculture growth
(m^2 ha^{-1} year^{-1})
5
0
−5
−10
−6
−4
−2
0
2
4
6
8
ChAx
CaFa
MaGr
LiGl
IdPo
PhBo
CyMy
CyGl
KoBi
MaLe
LiFo
ElJa
CaSc
RhCh
NySi
SaSe
QuFa
ElGl
ScSu
QuSe
MaYu
AlFo
SaMu
ElCh
BeLu
CaHe
● Site A
● Site B


Fungicide effect on diversity effect on basal area growth
(m^2 ha^{-1} $year^{-1}$ species doubling)
P = 0.09
10
5
0
−5
−10
−15
−20
0
10
20
30
40
Fungal damage
(% leaf area)
SaSe
SaMu
CaFa
LiGl
CaSc
MaLe
CyGl
QuSe
LiFo
CyMy
IdPo
KoBi
RhCh
NySi
BeLu
QuPh
QuFa
ElCh
ChAx
PhBo
MaGr
AlFo
ElGl
ScSu
ElJa
MaYu
CaHe
Site A
Site B
Insecticide effect on diversity effect on basal area growth
(m^2 ha^{-1} $year^{-1}$ species doubling)
P = 0.26
10
5
0
−5
−10
−15
−20
0
10
20
30
40
Insect damage
(% leaf area)
QuPh
PhBo
LiGl
CaFa
KoBi
SaSe
RhCh
ChAx
CyMy
IdPo
MaLe
CyGl
ElJa
QuFa
MaGr
MaYu
CaSc
ElGl
LiFo
QuSe
NySi
SaMu
ScSu
AlFo
BeLu
ElCh
CaHe
Site A
Site B


ChAx
CyMy
AiAl
LDMC
CN
QuPh
LiGl
QuFa
Leaf herbivory
ScSu
ElGl
CaSc
PhBo
SaSe
MaLe
CyGl
SaMu
QuSe
LiFo
MaTh
CaFa
MaGr
RhCh
KoBi
ElCh
NySi
SIZE
MaYu
CaHe
ElJa
IdPo
Leaf fungal damage
SLA
AlFo
BeLu
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
RDA2
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
RDA1