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Research Article

Species identity and spatial scale drive context-dependent tree diversity effects in a Finnish forest experiment

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Tree species diversity is known to affect tree growth and leaf traits, which in turn can influence various ecosystem processes. However, the reported direction of these tree diversity effects is inconsistent, indicating that their outcomes depend strongly on ecological context. Using the long-term Satakunta forest diversity experiment in Finland, we investigated how the effects of tree species diversity on growth and leaf traits vary with species identity, stand density, and spatial scale. By comparing the responses of light-demanding Scots pine *Pinus sylvestris* and shade-tolerant Norway spruce *Picea abies*, we show that the factors influencing diameter at breast height (DBH) and leaf traits differ between species with contrasting life-history strategies. Pine needle terpene concentrations were lowest in neighbourhoods dominated by conspecifics, while spruce needle terpenes were unaffected by tree species composition. Increasing canopy cover reduced spruce dry needle mass but had no effect on the dry needle mass of pines. Likewise, the factors that influenced tree growth differed between species; spruce DBH was lowest in thinned stands but was unaffected by tree species composition, whereas pine DBH did not vary significantly with plot density but was reduced in neighbourhoods containing silver birch *Betula pendula*. Our findings also indicate that diversity effects on leaf traits primarily operate at the local scale, as statistical models assessing the effect of immediate neighbours on pine terpenes yielded significant results, whereas models assessing diversity effects on a plot-level did not. In contrast, both pine and spruce DBH responded to plot and immediate-neighbour level factors, implying that tree growth is influenced by broader stand-level conditions, while leaf traits responses to diversity are more localised.

Keywords: DBH, needle traits, Norway spruce, Scots pine, species diversity, TreeDivNet

Introduction

Tree species diversity is widely recognised as a key factor in maintaining forest health and ecosystem functioning (Messier et al. 2021). Compared to trees growing in

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monocultures, trees in mixed species stands typically exhibit enhanced productivity and carbon sequestration (Liang et al. 2016, Warner et al. 2023), and are less susceptible to pests, pathogens and other natural disturbances (Jactel et al. 2017, 2021, Field et al. 2025). However, the positive effects of diversity are not universal, with several studies in the biodiversity–ecosystem functioning (BEF) literature documenting instances of neutral or even negative outcomes (Grossiord 2020, Schnabel et al. 2021, Trogisch et al. 2021). The causes of variation in the strength and direction of BEF relationships in forests need to be understood if reforestation efforts are to deliver predictable ecological outcomes (van der Plas 2019).

Several ecological and management contexts may mediate tree diversity effects. Firstly, the influence of species diversity may depend on the identities and life-history strategies of the species present, which can determine whether tree–tree interactions are predominantly facilitative (e.g. increased nutrient availability through niche partitioning) or competitive (e.g. competition for light) (Fig. 1a). For instance, neighbourhoods containing taller tree species are more likely to reduce light availability than neighbourhoods containing shorter trees, and subsequent reduction in light availability is more likely to negatively affect light-demanding species than shade-tolerant species (Valladares and Niinemets 2008, Williams et al. 2020).

Secondly, the influence of species diversity may be contingent on the density of trees within a given stand, as both positive and negative interactions between trees may be amplified in denser stands due to the closer proximity of neighbours (Fig. 1b) (Forrester et al. 2013, Tobner et al. 2014).

Finally, the influence of diversity may be more pronounced when diversity is quantified at finer spatial scales (Bellone et al. 2020, Davrinche and Haider 2021, Proß et al. 2025) (Fig. 1c). The effect of tree species diversity on tree growth and ecosystem functioning is thought to be driven by changes in abiotic conditions such as light, water and nutrient availability (Abdala-Roberts et al. 2018, Williams et al. 2020, Proß et al. 2021) which are most directly influenced by the neighbours closest to the focal trees (Richards et al. 2010). Trees may therefore respond in a more predictable manner to the species identity of nearest neighbours (e.g. those within a few metres radius of a focal tree) than tree species diversity on a wider spatial scale (e.g. on a plot level). The consideration of spatial scale may be especially important when immediate-neighbourhood diversity differs from plot-level diversity, as is the case in tree diversity experiments where the placement of individual trees within mixed species-plots is randomised to mimic natural forests (Yang et al. 2013, Tobner et al. 2014).

Trait-based approaches offer a useful way of investigating BEF relationships and the mechanisms underlying the

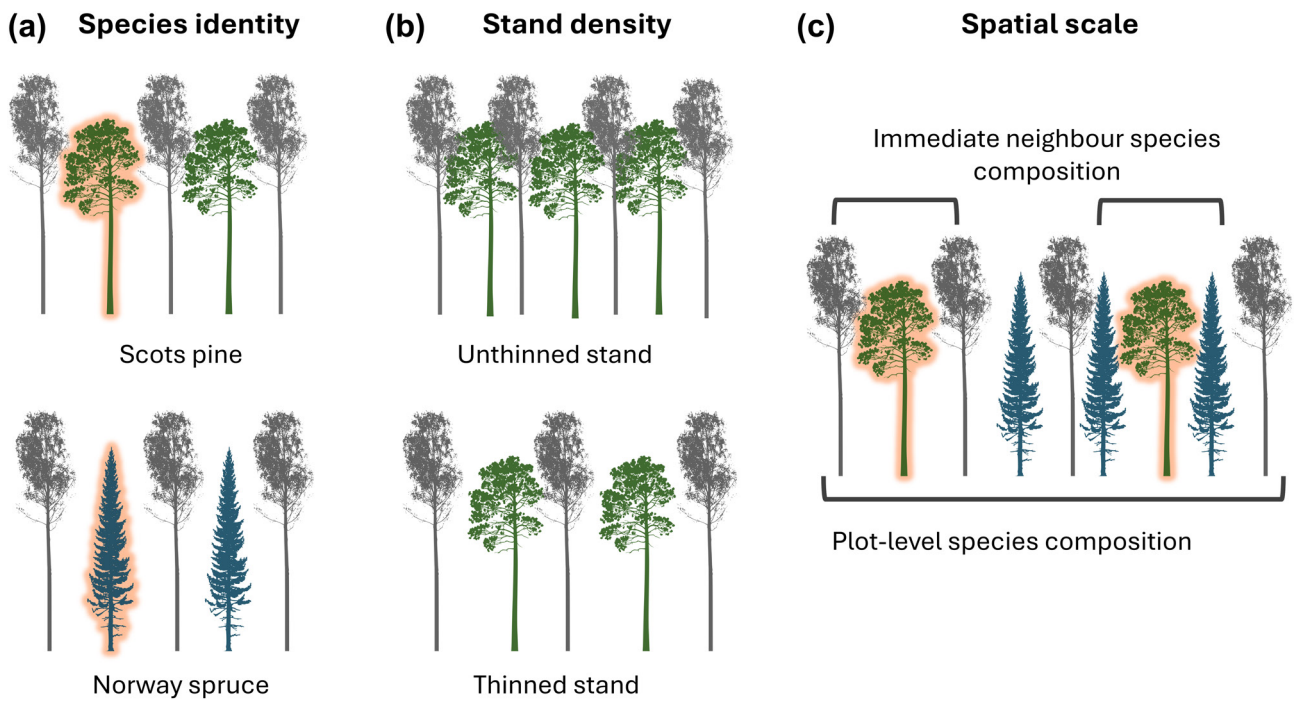

Figure 1. Conceptual diagram summarising factors examined to explain inconsistent effects of tree diversity on ecosystem functioning. (a) Species identity: tall silver birch reduces light availability, which is expected to cause a greater response in light-demanding Scots pine (top) than shade-tolerant Norway spruce (bottom). Plots containing shorter neighbouring species would not reduce light availability in the same way. (b) Stand density: competitive and facilitative effects are predicted to be stronger in denser stands. (c) Spatial scale: both highlighted pine trees are considered to be growing in pine–spruce–birch mixtures when species composition is measured on a plot level, but when only immediate neighbours are considered, the pine on the left is growing among tall light-blocking birches and the pine on the right is growing among shorter spruce trees that block less light.

variable outcomes of tree diversity (Callaway et al. 2003). Plant functional traits capture differences in growth strategies, responses to stress, as well as investment into physical and chemical defences (Rozendaal et al. 2006, Reich 2014), and are linked to ecosystem processes such as nutrient cycling, herbivory, and carbon storage (Díaz and Cabido 2001, de Bello et al. 2011, Lavorel 2013, Yuan et al. 2018). Tree growth, for instance, is often measured through diameter at breast height (DBH), which can then be used in species-specific allometric equations to estimate tree biomass and carbon storage (Wang 2006). Likewise, chemical and morphological leaf traits influence herbivory (Awmack and Leather 2002) and light capture for photosynthesis (Givnish 1988), and are used to distinguish fast-growing trees with low levels of defences from slow growing trees that invest more into defence (Reich 2014).

Plant functional traits often respond to diversity-mediated differences in growing conditions, making them a powerful lens through which to study BEF relationships. For example, variation in defensive traits has been investigated as a cause of different levels of herbivory between trees growing in monocultures and species mixtures (Castagneyrol et al. 2017, Muiruri et al. 2019, Wang et al. 2022). While some studies suggest that trees express higher levels of defences in species mixtures, other studies report the opposite (Felix et al. 2023), potentially explaining why trees in more diverse forests do not always experience reduced herbivory (Jactel et al. 2021). Traits related to resource acquisition, growth, and stress tolerance have also shown context-dependent responses to diversity (Kambach et al. 2019, Williams et al. 2020, Davrinche and Haider 2021).

In this study we use data from the Satakunta Tree Diversity Experiment in SW Finland to assess how BEF relationships are influenced by species identity, stand density, and the spatial scale at which diversity is measured. We focus on Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, two commercially important conifer species that differ in their life-history strategies and which are commonly planted in monocultures to maximise timber production (Huuskonen et al. 2021). We analysed traits previously shown to respond to stand diversity and variation in growing conditions including DBH, dry needle mass, and needle terpene content (Iason et al. 2011, Gebauer et al. 2011, Riikonen et al. 2016, Aldea et al. 2021, Kamaitytė-Bukelskienė et al. 2021, Ruiz-Peinado et al. 2021). Using these traits, our study aims to answer the following questions:

- Do trait responses to tree species diversity differ between light-demanding Scots pine and shade-tolerant Norway spruce?
- How does the identity and life history-strategy of neighbouring species affect focal tree traits?
- Do trait responses to diversity differ between thinned and unthinned stands?
- Does the effect of tree species diversity on trait expression differ when measured at plot-level and local neighbourhood scales?

Material and methods

Experimental site

Fieldwork was conducted at the Satakunta tree species diversity experiment in SW Finland in July 2022. Established in 1999, the experiment consists of three areas spaced 20–30 km apart, each containing 20 × 20 m plots planted either as monocultures or as species mixtures containing 2, 3 or 5 species (https://www.sataforestdiversity.org/ and Muiruri et al. (2019) for additional details). The five tree species in the experiment are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and silver birch *Betula pendula* (hereafter referred to as pine, spruce and birch, respectively) alongside black alder *Alnus glutinosa* and Siberian larch *Larix sibirica* (Supporting information). Trees were originally planted at 1.5 m intervals so that a total of 169 seedlings were present in each plot. The proportion of each species planted in mixed plots was kept constant, but the positioning of trees within plots was randomised. Plots were periodically cleared of naturally regenerating tree seedlings to maintain original species compositions. A thinning treatment was applied to half of all plots in 2013 to reduce the initial planting density by 50% while keeping species proportions equal, leaving one thinned and one unthinned replicate of each plot species composition within each area of the experiment.

Sampling plan

Pine and spruce trees were sampled in Area 1 and 3 of the experiment. Area 2 was not used due to extensive moose browsing in the first years following experiment establishment which left some plots unsuitable for sampling. Within each area, samples and measurements were taken from pine and spruce trees growing in plots with the following compositions: pine monocultures, spruce monocultures, two-species mixtures containing pine and spruce, pine and birch, or spruce and birch, and three-species mixtures containing pine, spruce and birch (Supporting information).

Five focal trees per species were randomly selected in each plot, avoiding plot edges and trees next to each other. In total, 76 Scots pines and 79 Norway spruces were sampled, with lower numbers in some plots due to natural mortality. Trunk circumference was measured at 1.3 m to calculate DBH. Four branches were cut from each tree at a consistent mid-crown height (4–6 m) using a telescopic pruner, sampling different sides of the crown to capture within-tree variation while maintaining comparable canopy position across trees.

Undamaged needles from the previous year's growth were sampled from cut branches. The current year's needles had not yet matured at the time of fieldwork so were avoided to minimise phenological effects on terpene content (Kamaitytė-Bukelskienė et al. 2021). Due to differences in needle size and morphology, the sampling procedure was species-specific. Between 15 and 20 needle pairs still attached to their sheaths were collected from pines, whereas 4–6 entire shoots were taken from spruces as separating individual needles was impractical (Supporting information). Samples were immediately placed in cool bags to prevent spoilage,

and then dried using silica gel owing to logistical constraints that prevented the use of liquid nitrogen in the field (Chase and Hills 1991).

Canopy cover and immediate neighbour species composition

Total canopy cover and the species composition of immediate neighbours around each focal tree was assessed by walking around the trunk of each focal tree at a 2 m radius. Using a GRS densitometer (Geographic Resource Solutions, USA) observations were taken at 10 evenly spaced positions (Fig. 2a) (Muiruri and Koricheva 2017). At each position the crosshair view was recorded as either 'sky', 'pine', 'spruce' or 'birch' (Fig. 2b). The proportion of observations for each tree species (out of 10) was then converted into a percentage to give 'pine cover', 'spruce cover' and 'birch cover' scores (ranging from 0% to 100%), representing the relative contribution of each species to local canopy cover. Total canopy cover (regardless of species) was calculated as the sum of each individual species' canopy cover.

Trait measurements

Sampled needles were kept in silica gel until completely dry. This process allowed spruce needles to detach from twigs while keeping pine needle pairs intact. Ten randomly selected needles (ten individual needles for spruce, ten intact needle pairs for pine) were then weighed for each tree from which average dry needle mass values were calculated.

The terpene profiles of dried needles were analysed using thermal desorption gas chromatography–mass spectrometry (TD-GCMS) using a method adapted from previous studies (Helin et al. 2020, Večeřová et al. 2021, Bakó et al. 2024). For each tree, a 30–60 mg sub-sample of collected material (2–3 pairs of dried needles for pines, ~20 individual dried needles for spruces) was weighed and transferred to thermal desorption tubes. Each prepared tube was then analysed using a TD100-xr thermal desorption unit (Markes) coupled with a 5977C GC/MSD instrument (Agilent) fitted with a HP-5MS column (0.25 mm diameter, 0.25 µm film, Agilent).

Tubes were desorbed at a temperature of 300°C for 10 min under a nitrogen flow of 50 ml min^{-1}, then purged for 0.5 min to the desorption trap set at 4°C. The trap was then desorbed for 4 min at 300°C and samples were injected into the column with a split ratio of 1:20. The column was set to start at a temperature of 40°C rising to 220°C at a rate of 6°C per min over 30 min, followed by 10 min at 300°C. The electron impact (EI) ion source was held at 230°C and the MS quad at 150°C, and the scan range was set from m/z 50 to 650.

Monoterpenes were identified by comparing fragmentation patterns to the National Institute of Standards and Technology (NIST) library and by calculating retention indexes and comparing them to literature sources (Adams

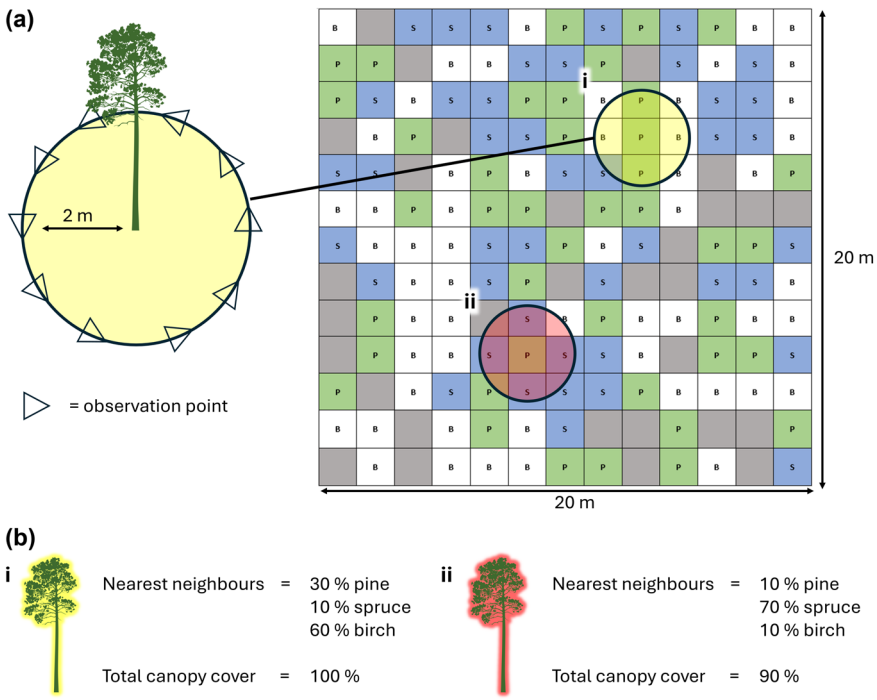

Figure 2. Conceptual diagram showing how canopy cover and nearest neighbour measurements were taken in the Satakunta tree diversity experiment. (a) 20 × 20 m plots with different species compositions were selected. In this example a pine–spruce–birch mixture plot is shown which had not undergone a thinning treatment, where green squares labelled 'P' represent pines, blue squares labelled 'S' represent spruces, white squares labelled 'B' represent birches, and blank grey squares indicate trees that were dead or missing. Canopy cover observations were then made at ten points around each focal tree. (b) Nearest neighbour identities and total canopy cover varied within each plot due to the randomised planting, thinning, and natural mortality, as shown by pines (i) and (ii).

2007). Individual sesquiterpenes were also distinguished but could not be identified due to a lack of reference compounds.

The software Analyzer Pro XD (SpectralWorks) was used to quantify the relative concentrations of terpenoids in each sample from their GCMS chromatograms. Monoterpenes were quantified using the quantifier ion m/z 93, except for camphor and borneol, which were quantified using m/z 95 (Räisänen et al. 2009). Sesquiterpenes were quantified using the main quantifier ion m/z 161 (Szmigielski et al. 2012). The relative abundance of each terpenoid was quantified using peak areas, which have a linear relationship with compound concentrations (Malhotra 2023). Peak area values were then divided by the mass of the dried needles previously weighed for each sample to give a relative peak area/µg dried needle measurement for each compound identified.

Statistical analysis

All statistical analyses were conducted in R ver. 4.3.1 using the packages 'lme4', 'lmerTest', 'emmeans' and 'performance' (Bates et al. 2015, Kuznetsova et al. 2017, Lüdecke et al. 2021, Lenth et al. 2024, www.r-project.org). The influence of plot-level tree species composition and stand density (i.e. whether a plot was thinned or unthinned) on DBH, average dried needle mass and total concentrations of monoterpenes and sesquiterpenes were first assessed using separate linear mixed models (LMMs) with plot species composition, thinning, and their interaction as fixed factors and plot nested within area as a random effect (Table 1). Post hoc comparisons between specific different plot types were made using emmeans package using Tukey adjustment (Lenth et al. 2024).

The effect of immediate neighbours (measured as respective species contributions to canopy cover) and total canopy cover on the DBH and leaf traits of the focal trees was then assessed using four separate LMMs accounting for the influence of pine cover, spruce cover, birch cover, and overall canopy cover, respectively (Table 1b). Models testing the relationship of spruce cover and birch cover on pines traits, and the relationship of pine cover and birch cover on spruce traits were run using reduced datasets, restricted to data only from plots in which the specific neighbouring species occurred (e.g. influence of birch cover on pine traits was only assessed using data from pine–birch and pine–spruce–birch plots). These models also included plot nested within area as a random effect.

Separate models were fitted for data collected from Scots pine and Norway spruce so that differences between each species' traits response could be examined. Needle mass, monoterpene and sesquiterpene data were log-transformed prior to analysis to meet assumptions of normality, and model fit was assessed using the *check_model* function from the R package 'performance' (Lüdecke et al. 2021).

Results

Terpenoid profiles of Scots pine and Norway spruce

Spruce needles contained a greater diversity of monoterpenes than pine needles, with 21 and 14 monoterpenes identified in each species, respectively (Supporting information). Conversely, sesquiterpene richness was greater in pine needles, with 23 sesquiterpenes identified in pine and 14 in spruce needles (Supporting information). Both monoterpenes and sesquiterpenes were found at significantly higher concentrations in pine needles than in spruce needles (Fig. 3c, d, g, h).

Terpene concentrations were variable in both tree species, but the concentrations of individual monoterpenes and sesquiterpenes were highly correlated with each other and with their summed values (mean R^2 between individual compounds and summed totals: pine monoterpenes = 0.76, pine sesquiterpenes = 0.85, spruce monoterpenes = 0.72, spruce sesquiterpenes = 0.88). The major monoterpenes of pine needles were α-pinene, β-pinene, Δ-carene, camphene and bornyl acetate, whilst spruce needles contained α-pinene, camphene, limonene and β-myrcene at the highest concentrations.

Effects of plot-level species composition and thinning on growth and leaf traits

Pine DBH was significantly influenced by plot-level diversity and was lowest in pine–birch mixtures (Fig. 3a, Table 2a). The DBH of spruce was not influenced by plot species composition but was significantly lower in unthinned plots compared to thinned plots (Fig. 3e, Table 2a)

Spruce dry needle mass was influenced by plot-level species composition with marginal significance and was lowest in spruce monocultures, and highest in spruce–birch and spruce–birch–pine mixtures, however, post hoc pairwise comparisons were not significant (Fig. 3f, Table 2a).

There was no significant effect of plot species composition on terpene concentrations for either species, and likewise no significant interactions between effects of plot level species composition and thinning (Table 2a).

Table 1. Models used to (a) assess influence of plot tree species composition and stand density on focal tree DBH and leaf traits and (b) to assess the influence of immediate neighbours' canopy cover on focal tree DBH and leaf traits.

	Question	Model
(a)	What is the influence of plot-level diversity and thinning on DBH and leaf traits?	'trait' ~ Plot species composition × Thinning + (1 | Area/Plot number)
(b)	What is the influence of overall canopy cover on DBH and leaf traits?	'trait' ~ % Canopy cover + (1 | Area/Plot number)
	What is the influence of pine cover on DBH and leaf traits?	'trait' ~ % Pine cover + (1 | Area/Plot number)
	What is the influence of spruce cover on DBH and leaf traits?	'trait' ~ % Spruce cover + (1 | Area/Plot number)
	What is the influence of birch cover on DBH and leaf traits?	'trait' ~ % Birch cover + (1 | Area/Plot number)

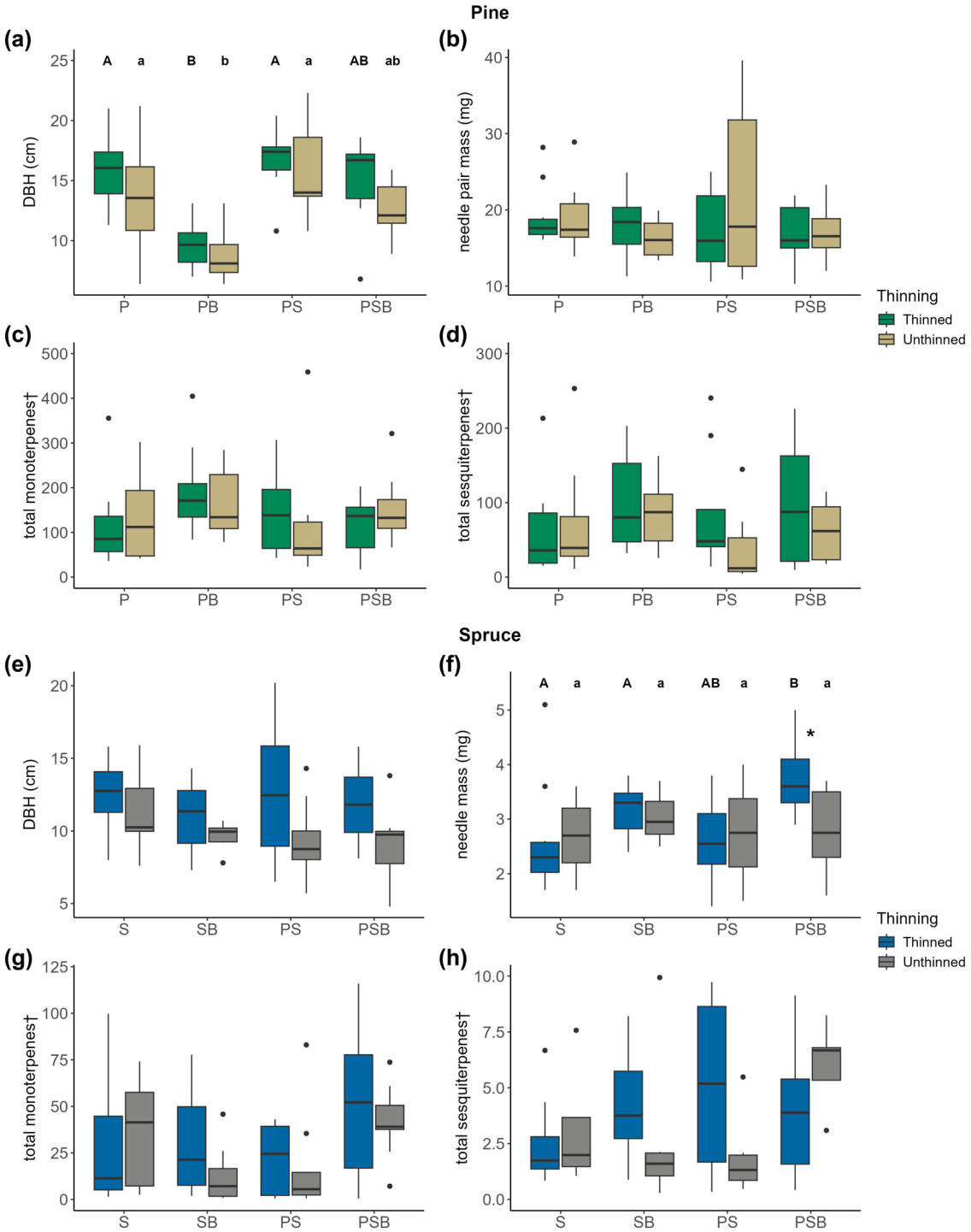

Figure 3. Boxplots of DBH, needle mass, monoterpenes and sesquiterpenes in Scots pine (a–d) and Norway spruce (e–h) growing in thinned and unthinned plots with different species compositions. Letters on x-axis refer to species present in each plot (S = spruce, P = pine and B = birch). Post hoc results are shown as follows: different lowercase letters = significant differences among species compositions within unthinned stands, different uppercase letters = significant differences among species compositions within thinned stands. Note that y-axis scales differ between pine and spruce panels to reflect large species-level differences in trait values. †Monoterpenes and sesquiterpene data given as average GCMS peak area μg^{-1} dried needles.

Effects of immediate neighbours and total canopy cover on leaf traits and growth

Pine DBH was influenced by the species composition of immediate neighbours (Table 2b) and showed a marginally positive relationship with spruce cover ($p = 0.052$, Fig. 4c) and a strong negative relationship with birch cover ($p < 0.001$, Fig. 4d). Spruce DBH was not significantly influenced by the species composition of immediate neighbours.

Table 2. Results from LMMs assessing the effects of (a) plot level species composition and stand density and (b) immediate neighbour % canopy cover on DBH, needle mass, monoterpenes and sesquiterpenes of focal Scots pine and Norway spruce trees. Significant p-values ($p < 0.05$) are shown in bold, marginally significant p-value ($p = 0.05–0.1$) are shown in bold italics.

	Species	Predictor	DBH			Needle mass			Monoterpenes			Sesquiterpenes		
			df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value
(a)	Pine	Composition	3, 8.29	14.729	**0.001**	3, 7.690	0.635	0.614	3, 8.068	1.327	0.331	3, 6.899	1.158	0.392
		Thinning	1, 8.33	3.245	0.113	1, 7.742	0.059	0.815	1, 8.083	0.030	0.867	1, 6.926	0.000	0.990
		Composition × Thinning	3, 8.29	0.263	0.851	3, 7.690	0.692	0.583	3, 8.068	0.376	0.773	3, 6.909	0.387	0.766
	Spruce	Composition	3, 6.956	0.648	0.609	3, 8.144	3.034	***0.092***	3, 70.01	2.152	0.101	3, 8.052	0.646	0.607
		Thinning	1, 6.958	6.208	**0.042**	1, 8.150	1.311	0.285	1, 70.01	0.147	0.703	1, 8.056	1.183	0.308
		Composition × Thinning	3, 6.956	0.404	0.755	3, 8.144	1.741	0.235	3, 70.01	0.649	0.586	3, 8.052	0.649	0.605
(b)	Pine	% Canopy	1, 65.61	0.002	0.963	1, 74.00	0.575	0.451	1, 69.96	1.593	0.211	1, 72.39	3.601	***0.062***
		% Pine	1, 37.27	1.230	0.275	1, 74.00	1.536	0.219	1, 25.90	5.497	**0.027**	1, 18.88	6.466	**0.019**
		% Spruce	1, 34.00	4.039	***0.052***	1, 34.00	0.564	0.458	1, 32.29	0.265	0.610	1, 31.29	0.026	0.872
		% Birch	1, 35.00	18.782	**<0.001**	1, 17.02	0.331	0.573	1, 35.00	3.450	***0.072***	1, 35.00	0.899	0.349
	Spruce	% Canopy cover	1, 75.48	3.698	***0.058***	1, 76.05	9.841	**0.002**	1, 68.70	0.339	0.562	1, 75.87	0.715	0.401
		% Pine cover	1, 24.06	0.507	0.483	1, 24.23	0.000	0.986	1, 36.14	0.617	0.437	1, 36.12	1.029	0.317
		% Spruce cover	1, 53.03	0.102	0.751	1, 35.19	10.29	**0.003**	1, 30.14	0.633	0.432	1, 39.74	0.004	0.949
		% Birch cover	1, 35.13	0.111	0.741	1, 35.95	0.874	0.356	1, 35.99	0.319	0.576	1, 36.53	0.074	0.787

In contrast, pine DBH was not affected by total canopy cover (Table 2b, Fig. 4a) whereas spruce DBH displayed a marginally negative relationship with total canopy cover (Table 2a, Fig. 5a).

Pine dry needle mass was unaffected by the species composition of immediate neighbours (Table 2b), but higher pine cover was associated with significantly lower concentrations of monoterpenes ($p = 0.027$, Fig. 4j) and sesquiterpenes ($p = 0.019$, Fig. 4n). In addition, pine monoterpenes displayed a marginally significant relationship with increasing birch cover ($p = 0.072$, Fig. 4j). The species composition of neighbouring trees had no effect on spruce needle monoterpenes (Fig. 5j–l) or sesquiterpenes (Fig. 5n–p), however spruce cover had a significant negative relationship with dry needle mass (Table 2b, $p = 0.003$, Fig. 5g).

Total canopy cover was associated with a marginally significant decrease of pine sesquiterpenes ($p = 0.062$, Fig. 4m) and a significant decrease of spruce dry needle mass ($p = 0.002$, Fig. 5e).

Discussion

Understanding how tree species diversity influences forest ecosystem functioning remains an important question in ecology. Although many studies demonstrate positive biodiversity–ecosystem functioning (BEF) relationships, mounting evidence suggests that the strength and even direction of these relationships vary widely among forest types and environmental conditions (Ratcliffe et al. 2017, van der Plas 2019). Our findings contribute to this debate by showing that trait responses to tree species diversity, which in turn can influence ecosystem functioning, depend strongly on contextual factors including tree species identity and stand density, and that this context dependence is particularly evident when diversity is analysed at smaller spatial scales.

Context matters: tree species identity, plot composition and plot density

Needle traits and tree growth responses to tree species diversity differed strongly between the two focal species, reflecting their contrasting life-history strategies. Scots pine, a light-demanding species, showed substantial variation in DBH and needle terpene content depending on the identity of neighbouring species (Fig. 6a), while these traits were largely unaffected by stand composition for shade-tolerant Norway spruce. In contrast, dry needle mass showed no variation in pine, but was influenced by plot composition in spruce, and was lowest in spruce monocultures (Fig. 6b).

These findings partially align with the expectation that light demanding species exhibit greater trait plasticity under variable growing conditions (Valladares and Niinemets 2008, Riikonen et al. 2016), however the higher plasticity of spruce dry needle mass suggests that shade-tolerance alone cannot fully explain differences in species responses to diversity. A similar conclusion was reached by Williams et al. (2020) who measured the responses of leaf size, leaf nitrogen and specific

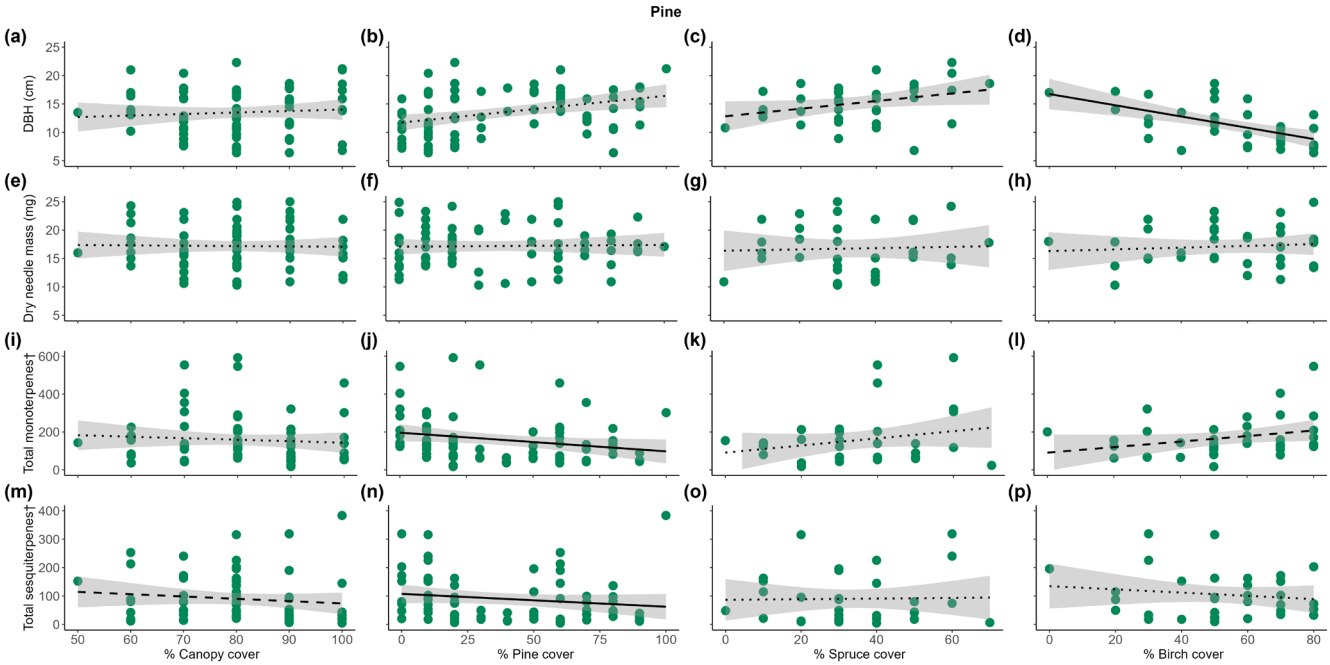

Figure 4. Relationships between Scots pine traits (DBH, needle mass, and terpene concentration), overall neighbouring tree canopy cover and % neighbouring pine, spruce and birch cover. Results from LMMs (Table 2) shown as follows: solid lines = significant trends ($p < 0.05$), dashed lines = marginally significant trends ($0.05 \leq p < 0.1$), dotted lines = non-significant trends ($p \geq 0.1$). †Monoterpenes and sesquiterpenes data given as summed peak area μg^{-1} dried needles analysed.

leaf area (SLA) to species diversity in 12 tree species, but found no clear link between shade-tolerance and the degree of trait responses. In addition to shade tolerance, pine and spruce differ in their growth patterns and resource requirements, which could help explain variation in their responses to different growing conditions (Forrester 2014, Pretzsch 2014).

Neighbour identity further shaped tree responses to diversity. Pines in neighbourhoods with birch exhibited reduced growth and elevated needle monoterpene and sesquiterpene concentrations. In contrast, neighbouring spruce was positively correlated with pine DBH but had no influence on terpene content, highlighting the significance of neighbouring species identity in determining the direction of diversity effects.

Finally, stand density influenced several trait responses, however this was independent of the effect of tree species diversity. Spruce DBH was lower in high density (unthinned) plots than in thinned plots, consistent with patterns seen through density-driven competition for light and resources (Mäkinen and Isomäki 2004). However, pine DBH was low in both thinned and unthinned pine–birch mixtures as compared to stands of other tree species composition, suggesting that for pine the effects of tree species composition can override the benefits of thinning in mixed stands.

Local versus plot-level diversity effects

Recent research demonstrates that tree species diversity effects tend to be stronger and more predictable at smaller spatial scales (Davrinche and Haider 2021, Proß et al. 2025). Additionally, assessing immediate neighbours can reveal whether trait variation in species mixtures arises from an increase in heterospecific neighbours or a reduction in conspecific competition (Bellone et al. 2020). While low sample sizes prevented a direct comparison of plot-level and immediate neighbourhood-level diversity effects within the same statistical model, the comparison of plot-level and immediate neighbourhood-level effects in our study still provides several noteworthy findings.

For spruce, the only needle trait influenced by plot-level species composition was dry needle mass, which was lowest in spruce monocultures. The negative association between spruce cover and dry needle mass on a local neighbourhood level suggests that this trend was driven by intraspecific competition for light in densely packed spruce monocultures (Gebauer et al. 2011). This is supported by the absence of any trend between spruce dry needle mass and pine cover or birch cover, as both form more open canopies than spruce (Petersson 2019).

For pine, neighbourhood-level models revealed diversity effects not detected at the plot scale: increased pine cover was associated with decreased monoterpene and sesquiterpene concentrations, while birch cover was associated with marginally higher monoterpenes. Although statistical support for these trends was weak, even small shifts in secondary metabolite concentrations can have important ecological consequences, potentially influencing herbivore deterrence and pathogen resistance (Gershenzon and Dudareva 2007). These local-scale effects likely reflect fine-grained variation in abiotic drivers of terpene synthesis such as light, temperature, water

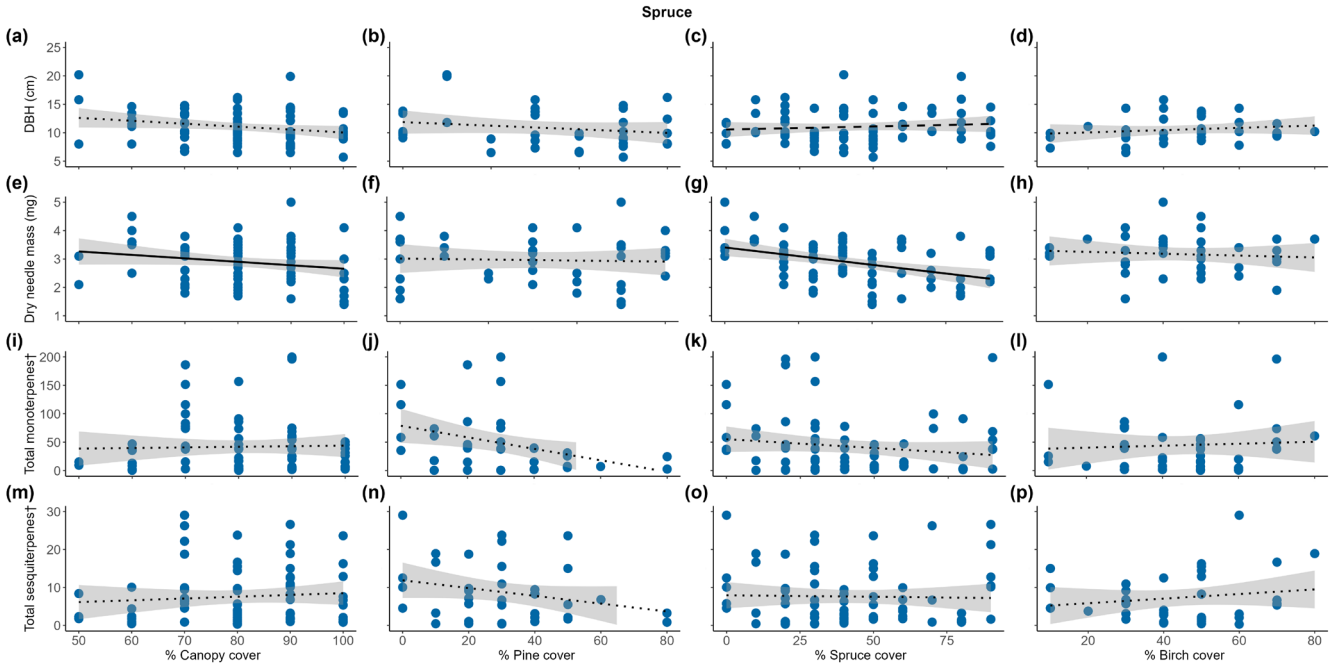

Figure 5. Relationships between Norway spruce traits (DBH, needle mass, and terpene concentration), overall neighbouring tree canopy cover and % neighbouring pine, spruce and birch cover. Results from LMMs (Table 2) shown as follows: solid lines = significant trends ($p < 0.05$), dashed lines = marginally significant trends ($0.05 \leq p < 0.1$), dotted lines = non-significant trends ($p \geq 0.1$). †Monoterpenes and sesquiterpenes data given as summed peak area μg^{-1} dried needles analysed.

and nutrient availability (Turtola et al. 2003, Kopaczyk et al. 2020), that are modified by nearby tree species (Zhang et al. 2022, Beugnon et al. 2024). Birch litter decomposes rapidly compared with the waxy, lignin-rich needles of conifers and can enrich surface soils (Felton et al. 2016, Huuskonen et al. 2021). The marginally positive influence of birch cover on monoterpene concentrations in pine may therefore reflect increased nutrient availability, which has in some cases been associated with elevated terpene production in Scots pine (Björkman et al. 1991, 1998), although the evidence is inconsistent (Koricheva et al. 1998, Kopaczyk et al. 2020). Conversely, reduced nutrient availability in pine-dominated neighbourhoods may explain the negative relationship between pine cover and terpene concentrations. Differences in rooting depth between pine and spruce could also promote nutrient partitioning in mixtures (Lutter et al. 2021), which

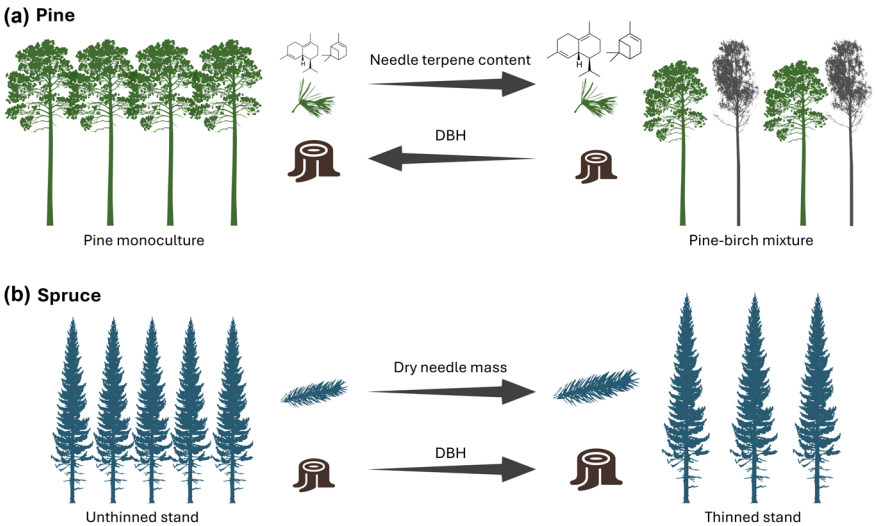

Figure 6. Summary of the main sources of trait variation for each focal species. (a) In Scots pine, needle monoterpene and sesquiterpene concentrations increased in the presence of birch, coinciding with reduced DBH. (b) In Norway spruce, both dry needle mass and DBH were higher in thinned plots compared to unthinned plots.

may explain why spruce cover did not suppress terpene concentrations as pine cover did. Interestingly, canopy cover was negatively correlated with pine sesquiterpenes but not monoterpenes – possibly reflecting differences in the light sensitivity of their biosynthetic pathways (Kopaczyk et al. 2020). As litter decomposition and nutrient feedbacks are driven by soil and microhabitat conditions around individual trees, these effects are plausibly more detectable at the local neighbourhood scale than when averaged across plots.

Patterns in tree growth mirrored several of the needle traits responses to tree species diversity. Pine DBH was highest in pine–spruce mixtures and lowest in pine–birch mixtures, while increasing birch cover locally corresponded with reduced DBH and elevated terpene content, suggesting a potential growth–defence tradeoff under competitive shading between the two light-demanding species (Valkonen and Ruuska 2003, Hynynen et al. 2010). In contrast, spruce growth was only influenced by plot density, which was also a major driver of variation of dry needle mass. Although previous studies have reported species-specific composition effects on spruce growth (Aldea et al. 2021, Bianchi et al. 2021), we did not detect such effects here, possibly because Norway spruce, as a late-successional species, is still in an early, slow-growth phase at this stage of the experiment (Koricheva et al. 2025).

Taken together, our results indicate that plot-level and local-neighbourhood measures of diversity capture complementary but distinct ecological processes. While plot-level analyses reveal general compositional effects, local neighbourhood-scale approaches uncover the species-specific and density-dependent interactions that shape individual tree responses. Recognising these cross-scale dynamics is essential for understanding the context dependence of diversity–trait relationships and their implications for forest functioning (Ratcliffe et al. 2017, Felix et al. 2023).

Implications for ecosystem functioning

Trait variation among trees has broad implications for ecosystem functioning, and influences tree productivity, carbon storage, nutrient cycling, and biotic interactions. In this study, we found that both local and plot-level neighbourhood composition shaped tree growth and defence-related needle traits, linking species diversity to several functional outcomes.

Scots pines growing near birches contained higher concentrations of monoterpenes and sesquiterpenes. One potential implication of this is that pines in pine–birch mixtures may be better protected against certain herbivores, as terpenoids can deter herbivore feeding or attract natural enemies when released as volatile organic compounds (VOCs) (Manninen et al. 1998, Mumm and Hilker 2006, Iason et al. 2011). However, VOCs are not universally protective and can also serve as host-location cues for specialised herbivores (Ali and Agrawal 2012, Achotegui-Castells et al. 2013) making the net effects of diversity-mediated changes in terpene production on herbivory difficult to predict. Beyond their defensive roles, elevated terpene concentrations in foliage and litter may influence nutrient cycling and soil–atmosphere carbon exchange by altering microbial activity and decomposition dynamics, as terpenes can suppress or stimulate specific fungal and bacterial groups and thereby affect soil community composition and carbon sequestration (Paavolainen et al. 1998, Kainulainen and Holopainen 2002, McBride et al. 2020).

Pines growing in the presence of birch also exhibited reduced growth, diminishing their aboveground carbon sequestration capacity and potential timber yields (Valkonen and Ruuska 2003). This contrasts with general patterns observed across forest ecosystems, where higher tree diversity often enhances productivity and carbon storage (Warner et al. 2023, Yang et al. 2023) through facilitative interactions and niche partitioning among species that improve resource availability and growing conditions (Fichtner et al. 2017, Wright et al. 2017, Liu et al. 2022). The observed reduction in pine growth in birch mixtures therefore suggests that competitive shading outweighed potential facilitative effects in this combination. These growth–defence tradeoffs highlight the potential for contrasting effects of species interactions on different ecosystem functions: while increased terpene production may enhance resistance to biotic stress, reduced growth can constrain productivity and carbon sequestration. Notably, pine DBH was not reduced in pine–spruce–birch mixtures, suggesting that higher species richness may buffer or offset such tradeoffs in more diverse stands (Grossiord 2020).

In contrast to pine, spruce leaf traits and growth were largely unaffected by plot-level composition or immediate neighbours and were most responsive to plot density. This highlights that differences in life-history strategy may explain why the strength and direction of BEF relationships vary across forest types and environments.

Overall, our findings emphasise that tree species diversity effects on forest functioning are highly context dependent, shaped by focal and neighbouring species identity, stand density, and the spatial scale at which diversity is quantified. Understanding these contingencies is essential for establishing mixed-species forests that balance productivity, resilience, and carbon storage under changing environmental conditions.

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Juri Felix Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead); **Phillip**

Stevenson Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting); **Julia Koricheva** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from Zenodo: https://zenodo.org/records/16738987 (Felix et al. 2025).

Supporting information

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

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