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A tale of scale: Plot but not neighbourhood tree diversity increases leaf litter ant diversity

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Abstract

1. Diversity of producers (e.g. plants) usually increases the diversity of associated organisms, but the scale (i.e. the spatial area of plant diversity considered) at which plant diversity acts on other taxa has rarely been studied. Most evidence for cross-taxon diversity relations come from above-ground consumers that directly interact with plants.

2. Experimental tests of plant diversity effects on elusive organisms inhabiting the leaf litter layer, which are important for nutrient cycling and decomposition, are rare.

3. Using a large tree diversity experiment, we tested whether tree diversity at the larger plot (i.e. community) or the smaller neighbourhood scale relates to the abundance, species richness, functional and phylogenetic diversity of leaf litter ants, which are dominant organisms in brown food webs.

4. Contrary to our expectations of scale-independent positive tree diversity effects, ant diversity increased only with plot but not neighbourhood tree diversity. While the exact causal mechanisms are unclear, nest relocation or small-scale competition among ants may explain the stronger tree diversity effects at the plot scale.

5. Our results indicate that even for small and less mobile organisms in the leaf litter, effects of tree diversity are stronger at relatively larger scales. The finding emphasizes the importance of diverse forest stands, in which mixing of tree species is not restricted to small patches, for supporting arthropod diversity in the leaf litter.

KEYWORDS

ant functional traits, biodiversity–ecosystem functioning, biodiversity–ecosystem functioning-China, forests, Formicidae, phylogenetic diversity, species richness

1 | INTRODUCTION

Diversity at one trophic level affects the diversity in other trophic levels (Scherber et al., 2010) and can have wide-ranging implications for ecosystem functioning (Schuldt et al., 2018; Tilman, Isbell, & Cowles, 2014). While a general positive cross-taxon relationship between plant diversity and the diversity of other taxa is firmly established through biodiversity–ecosystem functioning (BEF) experiments for both grassland (Scherber et al., 2010) and forest ecosystems (Grossman et al., 2018), the scale (Wiens, 1989) at which plant diversity effects operate remains unclear (Bruelheide et al., 2019). While BEF experiments usually manipulate plot (i.e. community) diversity, it is theoretically expected that the biological mechanisms altered by changing plant diversity (e.g. resource heterogeneity) manifest themselves at the scale of plant individuals (i.e. local neighbourhood: Potvin & Dutilleul, 2009; Stoll & Weiner, 2000). For example, the positive tree diversity–productivity relationship in subtropical Chinese forests (Huang, Chen, et al., 2018) is driven by neighbourhood tree diversity and processes acting at this scale (Fichtner et al., 2017). Similar neighbourhood-scale diversity effects can be common in a wide range of ecosystems (McWilliam, Chase, & Hoogenboom, 2018), illustrating how small-scale variations in producer diversity have community-wide effects (see also Chen et al., 2016).

While richness–productivity relationships can be strongest at intermediate plot sizes (e.g. 30 m × 30 m in Lai, Mi, Ren, & Ma, 2009), it is an open question at which scale cross-taxon relationships are most prominent. More specifically, in BEF experiments, it is not known whether the diversity of organisms in other trophic levels is more strongly influenced by plant diversity at the neighbourhood or the plot scale (Setiawan et al., 2016). Likely, whether a taxon or guild of organisms is more strongly associated with neighbourhood or plot-scale plant diversity depends on its life history. Large and mobile organisms are expected to use resources at a larger spatial scale, which would imply stronger relationships with plot-scale plant diversity, while for small and less mobile (e.g. flightless) organisms, a stronger relationship with neighbourhood-scale plant diversity is expected. We address this by investigating leaf litter ants in a tree diversity experiment in subtropical China (Bruelheide et al., 2014). Ants are dominant arthropods in all sufficiently warm terrestrial ecosystems, easily sampled in a standardized way, and established ecological indicator organisms (Agosti, Majer, Alonso, & Schultz, 2000). In (sub)tropical forests, ants are abundant macroorganisms in the leaf litter, where they play important roles in brown food webs and can influence rates of nutrient cycling and decomposition (Frouz & Jilkova, 2008; McGlynn & Poirson, 2012). Trees provide the brown food web with its main source of detritus: leaf litter. This links trees (and tree diversity) to ants living in the leaf litter, for example, if tree diversity increases primary productivity and subsequently leaf biomass, litter fall (Huang, Ma, Niklaus, & Schmid, 2018) and decomposition (Trogisch, He, Hector, & Scherer-Lorenzen, 2016) increase, which can enhance the diversity of organisms associated with the leaf litter matrix (Gessner et al., 2010). Increased leaf input can also lead to more complex habitat structures and resources, which can drive ant diversity (Armbrecht, Perfecto, & Vandermeer, 2004; Siemann, Tilman, Haarstad, & Ritchie, 1998; Staab, Schuldt, Assmann, & Klein, 2014) following the habitat heterogeneity hypothesis (sensu Hansen & Coleman, 1998). Thus, more complex habitats with higher plant diversity are expected to have a higher diversity of ants.

Biodiversity is often quantified as species richness, which represents just one component of organismal diversity. Functional (FD) or phylogenetic diversity (PD) is also important biodiversity measures describing diversity properties that are complementary and go beyond mere species numbers (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Diaz & Cabido, 2001; Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012; see also Materials and methods section below). For example, two ant communities with identical species richness may greatly differ in species identities and morphologies (i.e. FD) and their evolutionary relatedness (i.e. PD), which can have consequences for ecosystem functioning (Liu, Guenard, Blanchard, Peng, & Economo, 2016). Tree diversity may affect litter ant FD and PD, for example, if tree diversity or certain leaf types make the litter matrix unsuitable for certain ant lineages.
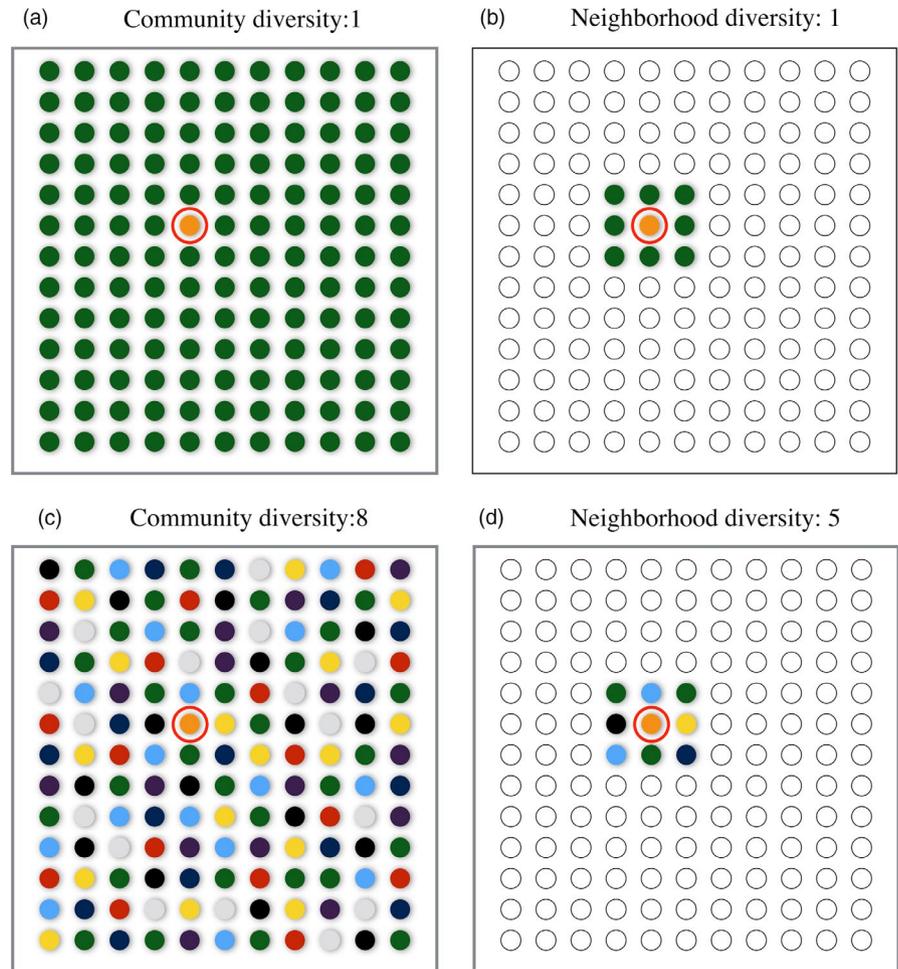
The general ecology of leaf litter ants has been the subject of many studies (e.g. Kaspari, 1996; McGlynn, Fawcett, & Clark, 2009; Woodcock et al., 2013), a number of which used observational approaches to explore how leaf litter ants react to small-scale environmental variation, including litter attributes and diversity (McGlynn et al., 2009; Silva, Bieber, Correa, & Leal, 2011). Yet, to our knowledge, the relationship between tree diversity and leaf litter ant diversity on either the plot or the neighbourhood scale has not been tested in the controlled setting of a tree diversity experiment, which allows for the assessment of diversity effects at different scales (i.e. the spatial area of plant diversity considered, compare Figure 1). Most typical litter ant taxa are small-bodied, live in relatively small colonies and have short foraging ranges (Hölldobler & Wilson, 1990), making them theoretically more dependent on the area directly surrounding the nest (i.e. neighbourhood scale) than on the wider tree stand (i.e. plot scale). Nevertheless, foraging behaviour can be plastic and even small species may use resources at larger scales, for example when nests are moved (McGlynn, 2012). Thus, tree diversity at the smaller neighbourhood and the larger plot scale is expected to increase ant diversity. Here, we test how tree diversity at both scales affects the abundance, species richness, FD and PD of leaf litter ants.

2 | MATERIALS AND METHODS

2.1 | Study site and plot-scale tree diversity

The data were collected at the Biodiversity and Ecosystem Functioning China (BEF-China) experiment, a large tree diversity experiment in South-East China (Bruelheide et al., 2014). This region has a subtropical climate with a mean annual temperature and precipitation of, respectively, 16.7°C and 1,821 mm. All months are

FIGURE 1 Conceptual representation of plot- and neighbourhood-scale tree diversity at two different levels of tree diversity. The encircled orange dot represents the target tree around which leaf litter ants were sampled. Plot (a) and neighbourhood (b) tree diversity are 1 and identical in monoculture plots. In the exemplary plot with eight tree species, however, plot (c) and neighbourhood tree diversity (d) differ. Therefore, neighbourhood tree diversity may vary at constant plot diversity when plot diversity is >1

(a) Community diversity:1 (b) Neighborhood diversity: 1 (c) Community diversity:8 (d) Neighborhood diversity: 5

humid with highest rainfall in June and July. The natural vegetation is mixed evergreen broad-leaved forest, but many forests have been converted to conifer monocultures.

The BEF-China experiment consists of two sites (A planted in 2009 and B planted in 2010) with a total of 566 plots, each covering 25.8 × 25.8 m (665.64 m²). Per plot, 400 tree individuals were planted in a regular 20 × 20 grid, with trees planted approximately 1.3 m apart in horizontal projection. The plots have a tree diversity gradient of 1, 2, 4, 8, 16 and 24 species. The spatial location of plots in the respective study site and the position of tree individuals within a plot were randomized. A more detailed description of the experiment can be found in Bruelheide et al. (2014). Our sampling was conducted in April and May 2015 (before the start of the monsoon) at Site A (29°07′29″N/117°54′31″E), which is a hilly watershed of 18.4 ha ranging in elevation from 105 to 275 m and in slope from 0 to 45 degrees. During the sampling period, there is a peak in arthropod activity and the average daily temperature is between 14 and 22°C with about 150 mm precipitation per month (compare Kröber, Zhang, Ehmig, & Bruelheide, 2014).

2.2 | Ant sampling

We selected eight target tree species under which to sample leaf litter for ants: *Castanea henryi, Choerospondias axillaris, Liquidambar* *formosana, Nyssa sinensis* (deciduous); *Castanopsis sclerophylla, Cyclobalanopsis glauca, Lithocarpus glaber, Schima superba* (evergreen). These species were well-established 6 years after planting, which ensured that the litter originated from the target trees and not from herbs or grasses.

To reduce potential influences from adjacent plots, only trees in the central 7 × 7 planting positions of a plot were sampled, and sampled trees were separated by at least two individuals. For each tree species, we sampled leaf litter for ants under four tree individuals in plots with 1, 2, 4, 8 and 16 tree species. For each tree diversity level × target tree species combination, three plots were sampled as replicates, summing up to 60 samples per tree species (4 trees × 3 plots × 5 diversity levels) and 480 samples in total (analyses restricted to 479 data points, one sample lost during processing). Tree species identity was not related to ant diversity (99.1% of pairwise contrasts with tree species identity not significant; Figure S1; compare also Donoso, Johnston, & Kaspari, 2010).

For sampling, we used Winkler extraction, which is a quantitative and representative collection method for leaf litter ants (Agosti et al., 2000). All samples were taken between 8:00 and 18:00 under dry weather conditions. The leaf litter of one square metre (with the target tree trunk in the centre) including the first few mm of top soil was sifted (mesh size 7 mm) to remove coarse debris. The sieved organic material was placed for 48 hr in

mini-Winkler extractors (details in Agosti et al., 2000). For each sample, the leaf litter cover (in %) of the sifted square metre was estimated in the field to obtain a measure of leaf litter availability that constitutes the main habitat matrix for leaf litter ants. As the trees had been planted 6 years before the sampling, no thick litter layer had yet developed, which makes litter cover a suitable estimate of total litter availability. The diameter at breast height (DBH) of the target tree was recorded as a measure of tree size. Ant specimens were identified to species or morphospecies (referred to as species) with taxonomic literature and comparison with reference material (Staab, Blüthgen, & Klein, 2015; Staab, Hita Garcia, Liu, Xu, & Economo, 2018; Staab et al., 2014). As ant abundance, we use the sum of individuals per samples. As 'rare', we consider all species that were found in <1% of all samples (four or fewer samples).

2.3 | Functional and phylogenetic diversity

We quantified a range of continuous and categorical traits (Parr et al., 2017) for up to seven individuals per ant species (continuous: head length, head width, mandible length, scape length, eye width, mesosoma length, hind femur length; categorical: nest site, diet, worker polymorphism; see Table S1). Continuous traits were measured through a stereomicroscope equipped with an ocular micrometre, and categorical traits were based on published information and the long-standing expertise of the senior author on ants in the study area. FD per sample was quantified as Rao's quadratic entropy weighted by species abundances (Rao Q) with the 'dbFD' function in the R-package 'FD' (Laliberté & Legendre, 2010).

We built a phylogeny for all sampled ant species by rooting species with equal branch length (see Liu et al., 2016) into their respective genera of the comprehensive genus-level phylogeny of Blanchard and Moreau (2017). Per sample, the full phylogeny was pruned to contain only the present species, and 'mean phylogenetic distance' (MPD) weighted by species abundances was calculated using the R-package 'PICANTE' (Kembel et al., 2010; see Supporting Information). Thus, MPD describes the average pairwise distance on the phylogeny between all pairs of individuals in a sample.

The same FD and PD indices were also calculated based on presence–absence data. In this case, the respective values describe the average pairwise functional and phylogenetic distance between all pairs of species per sample. To test whether observed FD and PD are influenced by potential deviation from null expectations, we calculated null models (10,000 iterations) for each sample and used the difference between null and observed values as alternative response variables.

2.4 | Neighbourhood-scale tree diversity

The size of the neighbourhood scale in this study is 6.76 m^2 and comprises nine trees, the target tree and its eight direct neighbour trees (Figure 1, compare to plot scale of 665.64 m^2 with 400 trees). Neighbourhood tree diversity and density were calculated using tree survey data from 2015 (Fichtner et al., 2017; Huang, Chen, et al., 2018). Each tree in the planting grid has a unique ID, enabling identification of all eight direct neighbours of each target tree. Neighbourhood tree diversity is necessarily correlated with plot diversity (Spearman's ρ = .44). Some trees had died as saplings after planting, which we took into account by calculating 'neighbour density', that is the number of living neighbour trees surrounding the target tree. Total (sum) 'neighbour DBH' was calculated as a proxy for neighbourhood biomass, which could influence litter availability and quality at the neighbourhood scale.

2.5 | Environmental covariates

To describe the terrain and thus the abiotic environmental variation among plots (e.g. insolation, slope, aspect, elevation, soil properties), we used geomorphons (Jasiewicz & Stepinski, 2013) that delineate landscape units and have been calculated for the BEF-China experiment from a digital elevation model by Scholten et al. (2017). Geomorphons include the land units 'hollow', 'ridge', 'slope', 'spur' and 'summit', with the main land unit of each plot used to describe that plot. This approach allows us to comprehensively account for the abiotic environmental variability among plots, as demonstrated by Scholten et al. (2017).

2.6 | Statistical analysis

All analyses were conducted with R 3.5.0 (R Core Team, 2018) on the level of individual samples (Skarbek et al., 2019). To test whether ant abundance, species richness, FD and PD (response variables) are related to tree diversity at the plot and neighbourhood scale, we used generalized linear mixed-effects models with either Poisson (abundance, species richness) or Gaussian (FD, PD) errors in the R-package 'LME4' (Bates, Maechler, Bolker, & Walker, 2015). Fixed effects in all models were 'plot diversity', 'neighbour diversity', 'neighbour density', 'litter cover', 'target tree DBH', 'neighbour DBH' and 'geomorphons' (Table 1). All fixed effects were selected a priori, and no model selection was carried out.

TABLE 1 Summary information on ant communities and continuous explanatory variables used in the statistical analyses

Variable	Min–Max	Mean ± SD
Ant abundance	0–506	25.9 ± 36.0
Ant species richness	0–13	4.4 ± 2.4
Plot diversity	1–16	6.2 ± 5.5
Neighbour diversity	0–8	2.2 ± 1.5
Neighbour density	0–8	5.0 ± 2.7
Target tree DBH (mm)	3–130	40.9 ± 24.8
Neighbour DBH (mm)	0–703	127.4 ± 110.9
Litter cover (%)	10–95	55.0 ± 23.7

Note: DBH, diameter at breast height; SD, standard deviation of the mean.

Predictors were not collinear (ρ < .7, following Dormann et al., 2013; see Table S2 for a correlation matrix). As the data were hierarchical with multiple samples per plot, we used 'plot ID' as random effect. 'Target tree species identity' was included as a further random effect crossed with 'plot ID', since we are interested in tree diversity rather than species identity effects (compare Figure S1). For Poisson models, an 'observation level random effect' was added to account for overdispersion. Fixed effects were centred and scaled to allow comparison of parameter estimates. Plot diversity was log_2-transformed. Significance tests refer to marginal effects, with all other fixed effects in the model held constant at their mean.

3 | RESULTS

In total, 12,416 individual ants from 38 genera and 72 species were collected (Table S3). The most abundant species were *Carebara altinoda* (14%), *Temnothorax* sp. (12%) and *Tetramorium wroughtonii* (9%), which are all members of the subfamily Myrmicinae. In 14 samples, no ants were found. Invasive ant species were absent.

We found weak evidence that plot-scale tree diversity had a positive effect on ant abundance, species richness and PD but not FD (Figure 2, full statistical details in Tables 2 and S4). The exclusion of rare species did not affect the abundance results (Table S5). Our models predict, for example, an increase in ant species richness from an average of 3.9 species in monocultures to 5.4 species in plots with 16 tree species, which corresponds to approximately 5.5% more ant species for each doubling of tree diversity within the levels of tree diversity investigated. Relative increases of ant abundance (10%) and PD (8.4%) showed similar but statistically more moderate trends. Neighbourhood tree diversity, in turn, showed a negative parameter estimate in all four models. However, this was only significant for PD (Figure 2). When using only presence-/absence-based measures for FD and PD, the results did not change (Table S6). Likewise, FD and PD results were invariant to using the differences from the null expectations as response variables (Table S7).

Leaf litter cover increased each component of ant diversity, and this relationship was significant except for FD. The other fixed effects (neighbour density, neighbour DBH, target tree DBH, geomorphons) were not related to the response variables except for geomorphons in the FD model (Table 2).

4 | DISCUSSION

4.1 | Relationships between ant and plot versus neighbourhood-scale tree diversity

Contrary to our expectations of scale-independent positive relationships between ant and tree diversity, leaf litter ant abundance and diversity (species richness, PD) increased with plot but not neighbourhood tree diversity. This indicates that for positive cross-taxon effects of tree diversity, the plot scale is more important than the neighbourhood scale with regard to enhancing the diversity of functionally important organisms in the brown food web. Thus, our results show that diversity effects at the plot scale cannot necessarily be extrapolated from local neighbourhoods, likely because different mechanisms related to tree diversity shape ant diversity at smaller compared with larger scales.

Other BEF studies showed that the diversity of herbivorous arthropods (in particular dietary specialists) on trees is usually positively related to tree diversity, often via increased resource heterogeneity when larger and more diverse food resources increase herbivore diversity with effects transcending to predators (Scherber et al., 2010; Zhang et al., 2016). However, this association is less clear for leaf litter ants that are not dependent on the litter of particular tree species (Donoso et al., 2010) and have a broad range of dietary niches. While it was previously assumed that most leaf litter ant taxa are omnivorous, stable isotopes indicate that leaf litter ants are often predominantly predators (Pfeiffer, Mezger, & Dyckmans, 2014), as is the case for many ant genera in our dataset. Leaf litter ants are indirectly associated with tree diversity, as they do not directly consume leaf litter, but rather depend on organisms in the brown food web that feed on litter. For the same study site, Huang, Ma, et al. (2018) showed that plot tree diversity increases total litter production and stabilizes litter fall throughout seasons, resulting in a more constant and higher litter supply in plots with more tree species. Thus, plot tree diversity may also be a suitable descriptor of the leaf litter encountered at a given m^2, potentially explaining the positive relationships between ant diversity and plot tree diversity. Furthermore, decomposition (Trogisch et al., 2016) and energy flows within the leaf litter habitat are positively related to plot tree diversity, leading to more and more diverse organisms including ants (Kaspari, O'Donnell, & Kercher, 2000; McGlynn et al., 2009). By allowing the coexistence of more ant nests per area (Kaspari, 1996; Kaspari et al., 2000), a higher leaf litter cover increases ant abundance and species richness. These relationships seem more likely for common species, as the exclusion of rare ants did not change the abundance results.

Being small organisms (mean mesosoma length 0.627 ± 0.220 mm in our samples; compare Donoso, 2014) with likely limited foraging distances, we initially expected that leaf litter ant diversity would be also positively related to the smaller neighbourhood tree diversity and not only to plot tree diversity. One possible reason may be that, although the foraging range of an individual colony at a given time is limited to few square metres, litter ants may frequently relocate their nests (McGlynn, 2012). Typical relocation distances for leaf litter ant nests are several metres and thus extend beyond the neighbourhood scale in our study (McGlynn, Carr, Carson, & Buma, 2004; Smallwood, 1982; Tsuji, 1988). This could explain why litter ants benefit more from plot tree diversity, as relocation increases the size of the effective required habitat, rendering small-scale diversity of the local neighbourhood less important for litter ants than tree
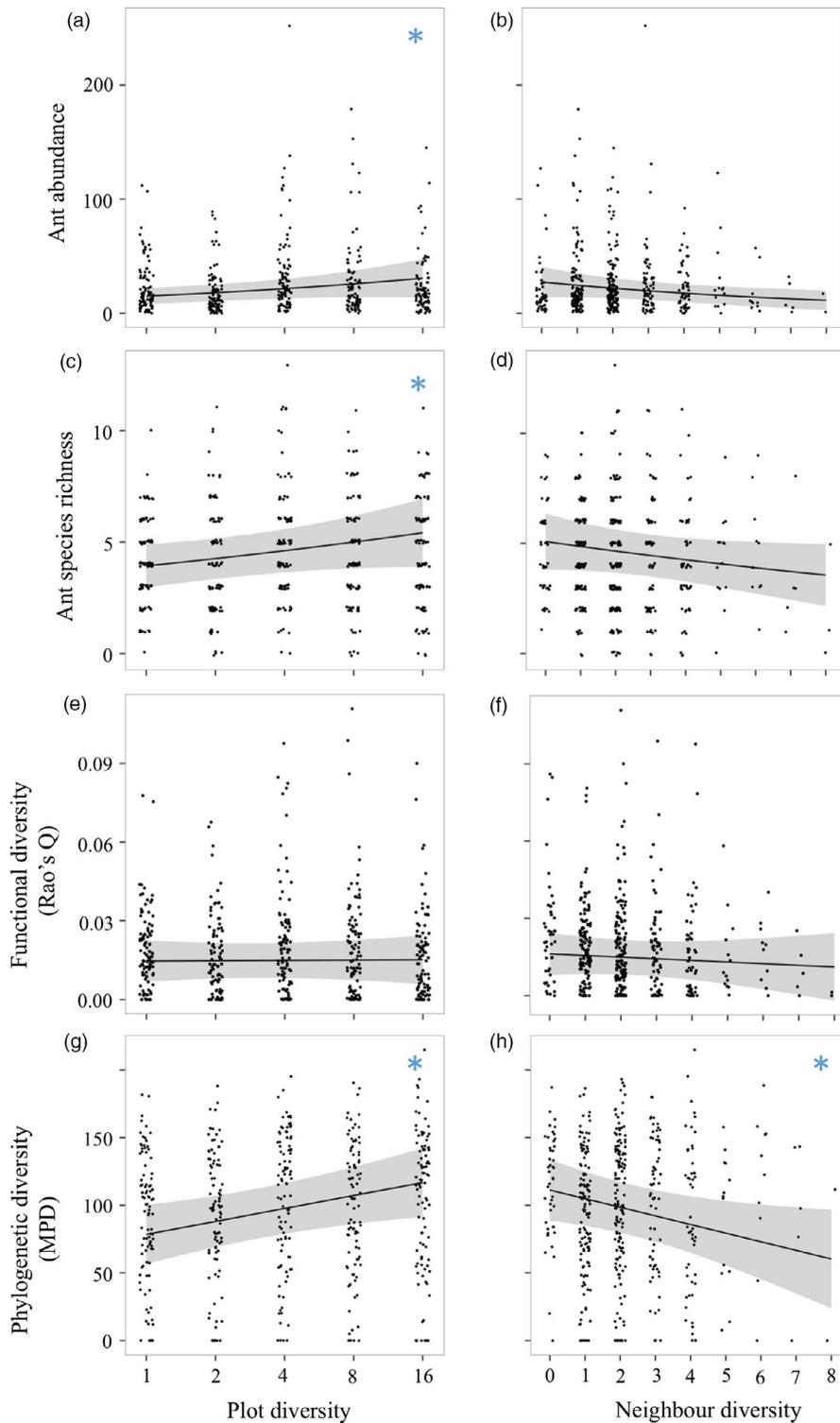
FIGURE 2 Relationships between plot (left column) and neighbourhood tree diversity (right column) and ant abundance (a, b), ant species richness (c, d), functional diversity (e, f) and phylogenetic diversity (g, h). Results are illustrated as 'effect plots', showing the predicted effects (solid line; 95% CI indicated with grey shading) of tree diversity on ant response variables with all other explanatory variables held constant at their mean effect. Significant relationships are denoted with an asterisk (see Tables 2 and S4 for details)

diversity at larger scales. However, it should be noted that in plots with highest tree diversity, the maximum number of tree species in a neighbourhood of eight tree individuals was always lower than the number of planted tree species. While we accounted for this in the statistical analyses by treating all predictors at a common data scale, the higher maximum plot diversity might superimpose potential neighbourhood-scale diversity effects under field conditions.

4.2 | Potential mechanisms behind the opposed relationships between ant PD and tree diversity at both scales

In addition to increasing ant abundance and richness, our results indicate that plot-scale tree diversity may also increase the number of ant lineages present in a sample and not only benefit common generalist ant taxa. This increases the probability that a sample contains

an evolutionary distinct lineage. Ants likely evolved in the soil and litter (Lucky, Trautwein, Guenard, Weiser, & Dunn, 2013), and almost all contemporary species from basal ant lineages inhabit leaf litter

TABLE 2 Results of mixed-models testing for the relationship of the response variables ant abundance (Poisson error distribution), ant species richness (Poisson), functional diversity (Rao Q, Gaussian) and phylogenetic diversity (MPD, Gaussian). Significant (at $p < .05$) predictors are printed in bold. See Table S4 for model summaries

Predictor	Estimate ± SE	F/X^2	p
Abundance (Poisson; $R^2_m = .102/ R^2_c = .262$)			
Plot diversity	**0.253 ± 0.113**	**5.021**	**.025**
Neighbour diversity	−0.168 ± 0.089	3.546	.060
Neighbour density	0.136 ± 0.101	1.806	.179
DBH neighbours	−0.005 ± 0.049	0.008	.928
DBH target tree	0.087 ± 0.068	1.639	.201
Litter cover	**0.235 ± 0.056**	**17.635**	**<.001**
Geomorphons	–	9.460	.051
Species richness (Poisson; $R^2_m = .110/R^2_c = .288$)			
Plot diversity	**0.114 ± 0.058**	**3.892**	**.049**
Neighbour diversity	−0.067 ± 0.045	2.190	.140
Neighbour density	0.050 ± 0.051	0.952	.329
DBH neighbours	<−0.001 ± 0.026	<0.001	.992
DBH target tree	0.023 ± 0.029	0.633	.426
Litter cover	**0.142 ± 0.029**	**24.153**	**<.001**
Geomorphons	–	7.378	.117
FD: Functional diversity (Linear; $R^2_m = .068/ R^2_c = .190$)			
Plot diversity	0.001 ± 0.001	0.486	.486
Neighbour diversity	<0.001 ± 0.001	0.011	.915
Neighbour density	−0.001 ± 0.001	0.829	.363
DBH neighbours	<0.001 ± 0.001	0.007	.934
DBH target tree	<0.001 ± 0.001	0.163	.687
Litter cover	0.001 ± 0.001	3.479	.062
Geomorphons	**–**	**14.445**	**.006**
MPD: Phylogenetic diversity (Linear; $R^2_m = .048/R^2_c = .194$)			
Plot diversity	**13.589 ± 5.212**	**6.799**	**.010**
Neighbour diversity	**−9.633 ± 4.211**	**5.233**	**.022**
Neighbour density	6.313 ± 4.697	1.806	.179
DBH neighbours	1.198 ± 2.363	0.257	.612
DBH target tree	−2.597 ± 2.741	0.898	.343
Litter cover	**7.344 ± 2.613**	**7.903**	**.005**
Geomorphons	–	1.175	.884

Note: p-values are based on Wald–chi-square tests for Poisson and Wald–F tests for linear models. Degrees of freedom (*df*) for significance tests have been approximated with the Kenward–Roger algorithm. Each continuous variable accounted for 1 *df* in the nominator (5 *df* for the categorical variable 'geomorphons', see Table S4 for regression coefficients). Marginal and conditional R^2 values (R^2_m, R^2_c) are given for each model.
DBH, diameter at breast height; *SD*, standard deviation of the mean.

(Ward, 2014). These species are often rarely collected (e.g. cryptic species) and characterized by specialized life histories (Staab et al., 2018). However, plot tree diversity also seems to be beneficial for these ants, because abundance-weighted and presence-/absence-based FD and PD results were congruent.

We found that in contrast to plot tree diversity, neighbourhood tree diversity had a negative effect on ant PD. This may be due to high competition among ants at small scales (Parr & Gibb, 2010) when habitats are of high quality, that is neighbourhood tree diversity is high and resources are plentiful (Blüthgen & Feldhaar, 2010). All behaviourally dominant ant species in our study belong to a single subfamily, the Myrmicinae (M. Staab, unpublished data), and are thus more closely related to each other than to the less dominant species in other subfamilies. As competitive interactions between distantly related species can be common and shape species occurrences (Beaudrot et al., 2013), the presence of a dominant Myrmicinae species may exclude phylogenetically distant species and lower ant PD per sample (sensu Arnan et al., 2018; Parr, 2008). If competitive species benefit from high-quality habitats, then high neighbourhood-scale tree diversity may decrease PD. To examine this thought, we correlated the presence of *T. wroughtonii* (9% of all specimens), the most dominant species whose influence on trophic and non-trophic interactions of other species is largest when local tree diversity is high (Schuldt, Fornoff, Bruelheide, Klein, & Staab, 2017) with ant abundance, richness, FD and PD. As expected, the presence of *T. wroughtonii* reduced PD (Figure S2), indicating competitive exclusion of phylogenetically distinct species.

4.3 | Implications for forest plantings

Litter ants are an oft-cited example of organisms that are relatively resistant to land use change, as their diversity is only little affected by habitat change as long as disturbance is not too severe (e.g. Belshaw & Bolton, 1993; Woodcock et al., 2013; but see Ross, Hita Garcia, Fischer, & Peters, 2018). We show that even planted early successional forests composed of native tree species can recover diverse leaf litter ant communities already after 6 years. Considering that ant diversity correlates with the diversity of many taxa (Agosti et al., 2000) and that the brown food web is tightly connected to the green food web (Zou, Thebault, Lacroix, & Barot, 2016), similar recoveries for other organisms are likely. The positive association between plot tree diversity and litter ant diversity indicates that diverse tree mixtures increase ant abundance and diversity, which may have far-reaching consequences, for example by enhancing ant-mediated ecosystem functions including nutrient cycling (Folgarait, 1998; Griffiths et al., 2018) and by stabilizing trophic interactions (Schuldt et al., 2017; Staab et al., 2015). As trees are actively planted in reforestation and plantation forestry (as in BEF experiments), our results suggest that diversifying tree mixtures in young forests can promote species diversity and positive diversity effects across trophic levels without reducing carbon stocks (Liu et al., 2018) or lowering potential future harvest (Huang, Chen, et al., 2018). It would be interesting

to see whether the effects revealed by our study remain in more mature forest stands.

5 | CONCLUSIONS

The exact causal mechanisms driving the associations we found remain elusive, and further research is necessary to fully understand the scale dependency of tree diversity effects on leaf litter ants. For example, it would be valuable to quantify the scales at which ants interact with their habitat and whether habitat use, foraging distances and nest relocation depend on tree diversity. From the present data, we can conclude that mixed forest stands are superior to monocultures in promoting litter ant diversity, particularly when stand diversity is high and mixed planting is not restricted to small patches, as biodiversity effects are more prominent at larger scales.

AUTHOR CONTRIBUTIONS

M.S. designed research; M.N. conducted fieldwork; H.B., W.H., G.v.O., T.S. and S.S. contributed data; C.J.S. and M.S. analysed data and wrote the manuscript; all authors revised the manuscript.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.v5s547r (Skarbek et al., 2019).

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