Trophic interactions of ants are robust to tree species loss

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ABSTRACT

1. How changes in habitat conditions influence insect diversity has been intensively studied. However, whether trophic interactions of insects are also influenced by such changes is largely unknown. Higher habitat heterogeneity is often hypothesized to promote niche partitioning and complementarity in resource use among interacting species, yet evidence from animal interaction networks is sparse.

2. We tested in a biodiversity experiment how experimentally-manipulated tree species richness influences ant-nutrient interaction networks using a replicated and standardized set of nutrient baits. The structure of ant-nutrient networks was quantified with selected quantitative network indices representing diversity, redundancy and specialization of interactions.

3. Contrary to expectations, tree species richness had no direct or indirect effects on network complementarity. Instead, diversity of interactions declined slightly with increasing tree species richness, while network redundancy and specialization did not change. This indicates that higher tree diversity may influence the diversity of trophic links, possibly through altered competitive dynamics in more diverse ant assemblages, but not overall network structure.

4. These patterns are consistent with nutrient regulation theory predicting that foragers should concentrate interactions on resources that best satisfy the nutritional targets of colonies, reducing interaction diversity when nutritionally relevant resources are readily available. Our results suggest that for trophic networks of ants, habitat heterogeneity alters interaction frequencies rather than promoting complementarity or structural reorganization, indicating that ant trophic interactions are robust to tree species loss.

KEYWORDS

Formicidae; Habitat complexity; Nutrient baiting; Tree diversity experiment; Trophic network

INTRODUCTION

While the relationship between plant diversity and insect diversity has been frequently studied (Scherber *et al.*, 2010; Schuldt *et al.*, 2019; Wan *et al.*, 2020), evidence how trophic interactions are influenced by plant diversity is sparse (Petermann *et al.*, 2010; Fornoff *et al.*, 2019), with one notable exception being studies on flower visitors (Blüthgen & Klein, 2011; Kaiser-Bunbury *et al.*, 2017). The number of species in primary producers is hypothesized to increase the amount, diversity and heterogeneity of resources available to species in other trophic levels (Hutchinson, 1959; Siemann *et al.*, 1998). This greater resource heterogeneity, in turn, is expected to support more species in higher trophic levels, as a more diverse resource base allows a wider range of consumer niches to be filled (MacArthur & MacArthur, 1961; Haddad *et al.*, 2009). Consumer species occupying distinct dietary niches may complement one another in exploiting available resources, thereby increasing overall resource use efficiency and energy flux through a food web (Loreau *et al.*, 2001; Buzhdygan *et al.*, 2020). A common mechanism assumed to lead to complementarity in ecosystems is niche partitioning between different consumer species, which avoid competition by focusing on different resources (Tilman *et al.*, 2014).

Increased complementarity in resource use among insects may be directly influenced by tree species richness, which increases consumer richness through resource diversification (Schuldt *et al.*, 2019). Alternatively, the effects of tree species richness may be mediated less by resource diversity than by canopy closure and the development of a forest-like stand structure in young tree stands (Fornoff *et al.*, 2021). Diverse tree stands increase primary producer productivity (Huang *et al.*, 2018a) and promote a more stable forest microclimate compared to single-species stands (De Frenne *et al.*, 2019; Deng *et al.*, 2025). The multilayer structure of diverse tree stands may increase canopy and litter cover (Jucker *et al.*, 2015; Huang *et al.*, 2018b), thereby enhancing moisture retention (Zhou *et al.*, 2018) and increasing consumer richness in the leaf litter through increased habitat and resource availability (Grime, 1998; Siemann, 1998).

Biodiversity experiments are a valuable tool to test for the influence of plant diversity (Liu *et al.*, 2026). Within tree diversity experiments, investigating interaction networks can help to understand the mechanisms proposed above by revealing how tree species richness shapes trophic interactions. Among the many interactions an organisms establishes, trophic interactions are especially informative because they integrate patterns of resource use and species associations (Blüthgen & Staab, 2024), thereby helping to disentangle the pathways through which biodiversity may influence insect communities and ecosystem functioning (Scherber *et al.*, 2010; Wan *et al.*, 2020). Changes in networks are best captured by quantitative network indices, such as specialization, complementarity, and redundancy rather than by counting interacting species alone (Blüthgen *et al.*, 2006; Blüthgen & Staab, 2024). Trophic interaction networks can shift markedly across environmental gradients (Tylianakis & Morris, 2017). In networks including ants, tree species richness can increase generalization, whereas habitat fragmentation may increase specialization through species turnover (Fornoff *et al.*, 2019; Zhang *et al.*, 2023). Yet standardized quantitative network approaches have rarely been applied to ant foraging in a way that explicitly captures interactions between ant species and resources differing in nutritional composition.

Ants are ideal model organisms for studying trophic interactions, as they are dominant organisms that are sensitive to changes in the environment (Alonso & Agosti, 2000; Schultheiss *et al.*, 2022). Many ants also exhibit a degree of foraging plasticity, allowing them to respond quickly to changing food availability. At the same time, foraging is strongly shaped by competition, which influences how resources are discovered, exploited, and defended (Kolay *et al.*, 2020). Multiple studies have shown that diversity of herbivorous insects directly increases with tree species richness, thus diversifying prey and mutualistic partners for ants (Fornoff *et al.*, 2019; Schuldt *et al.*, 2019). From a top-down perspective, this may enable ant species across the trophic spectrum (from nectar feeders over generalists to predators) to coincide and complement each other in use of available resources (Blüthgen & Feldhaar, 2010). As central-place foragers, ant colonies balance nutritional demands according to their nutritional ecology and species-specific requirements (Feldhaar, 2014). Intense interspecific competition in diverse ant communities may reinforce the specialization of nutritional strategies by increasing niche differentiation in foraging (Davidson, 2005; Blüthgen & Feldhaar, 2010).

Baiting experiments using basic nutrients represent a standardized approach to quantify trophic preferences of ants and have shown that environmental context modulates ant resource use (Peters *et al.*, 2014; Lasmar *et al.*, 2023; Moses *et al.*, 2023). Peters *et al.* (2014), for example, showed that the nutrient space exploited by ant communities increased with ant species richness in natural ecosystems but decreased slightly in managed ones. However, nutrient baiting studies have so far focused on foraging intensity and community-level preferences rather than the topology of ant-nutrient interaction networks. It therefore remains unknown how trophic complementarity and network structure among different ant species respond to tree species richness as proxy for resource diversity and habitat availability.

In this study, we examined whether increasing tree species richness in a diversity experiment (Bruelheide *et al.*, 2014) is associated with changes in how ground-foraging ants use different resources. Beyond a potential direct link between tree species richness and network topology, we also considered that tree species richness may shape complementarity in ant nutrient foraging indirectly by altering key habitat features, such as canopy and leaf litter cover, which in turn influence microclimate and resource availability. In single-species tree plantations, we expected ant communities to show greater overlap in nutrient foraging. In contrast, we expected increasing tree species richness to promote greater complementarity in nutrient use, thereby reducing overlap and increasing resource partitioning.

MATERIALS AND METHODS

Study sites

The study was conducted at the BEF-China (Biodiversity-Ecosystem Functioning) research platform located Southeast China in Jiangxi province near Xingangshan (117° 54′ E, 29° 07′ N). The regional climate is characterized by an annual mean temperature of 17 °C and a mean annual precipitation of 1800 mm (Yang *et al.*, 2013). The BEF-China tree diversity experiment spans two hilly sites: Site A, established in 2009, and Site B, established in 2010. The experiment comprises a total of 566 plots, each measuring 25.8 m × 25.8 m, with planted tree species richness levels ranging from 1 to 24 (Bruelheide *et al.*, 2014). Trees were planted in a 1.2 m × 1.2 m grid following the clear-cutting of former conifer plantations.

For this study, data was collected from 31 plots on Site A and 148 plots from Site B. Samples from three plots got lost during processing, resulting in data from a total of 176 plots, including 52 single-species stands, 51 two-species stands, 32 four-species stands, 22 eight-species stands, 16 sixteen-species stands, and 3 twenty-four-species stands. The sampled plots have a mean elevation of 151 m (± 28 m SD, 107 - 236 m).

Baiting experiment

Data was collected at Site A between September and October 2023 and at Site B between April and July 2024 by performing a standardized nutrient baiting experiment (Peters *et al.*, 2014). A set of six different baits containing sugar (C), salt (S), phosphate (P), amino acid (A), water (W) and oil (L) was used. All nutrient solutions, except for oil, which was pure rapeseed oil, were diluted with purified water. The purified water (W) also served as negative control. Sugar and oil represent energy sources for ants (Blüthgen & Feldhaar, 2010). The amino acid (Glycine) serves as a standardized proxy for protein (Peters *et al.*, 2014). Salt (non-iodized sodium chloride) targets sodium (Kaspari *et al.*, 2008), and phosphate (sodium dihydrogen phosphate) probes potential phosphorus demand (Kaspari *et al.*, 2016).

Baits were prepared as follows: the sugar solution and the amino acid solution were each mixed at a ratio of 200 g solute per 1 L water (20% weight/volume), while the salt solution and the phosphate solution were each mixed at a ratio of 40 g solute per 1 L water (4% weight/volume). Each bait consisted of 8 mL of nutrient solution placed in a 15 mL centrifuge tube (1.5 cm diameter). The solution was sealed with cotton wool to prevent leakage, while still allowing it to saturate the cotton. This ensured that ants could readily detect and access the nutrient solution for feeding (Figure S1). Each set of six different nutrient solutions served as one replicate, with four replicates per plot placed at the center of the edges of the 10 x 10 inner tree positions within a plot. Before placing the baits, the soil was gently leveled. Baits were then laid out in random order with about 1.5 cm distance to each other, with openings of vials pointing into the same randomly assigned direction (see Figure S1 illustrating the experimental setup). After three hours, baits including attending ants were collected by closing the tube lids. Ants were euthanized in a freezer at -20°C and subsequently stored in 90% ethanol.

Specimens were sorted into genera and identified to the species or morphospecies level using primary taxonomic literature and comparison to reference material (e.g., Staab *et al.*, 2014; Skarbek *et al.*, 2020). As ant abundances in baiting surveys are not comparable because of differences in foraging behavior among species, we calculated all analyses on incidence data only. While in some species single individuals or small groups forage together, others can mass recruit within short time spans (Lanan, 2014).

Environmental covariates

In addition to the experimental treatment variable tree species richness, ant-nutrient interactions may also depend on further biotic and abiotic environmental variation (Supplement Table S1). To describe the terrain and thus the abiotic environmental variation among plots we used mean slope curvature (Evans, 1980). This variable quantifies terrain convexity/concavity based on a digital elevation model (Scholten *et al.*, 2017). Slope curvature data for three plots was not available and extrapolated as the mean value of the directly adjacent plots.

Canopy cover per plot was estimated on plot level using elevation-normalized LiDAR point clouds collected by a UAV-based LiDAR scanner (Hesai Pandar 40P, Hesai Group, Shanghai, China) in 2023 and 2024, as the proportion of ground covered by forest canopy. The UAV flew at an average altitude of 100 m above the ground and at a velocity of 8 m s^{-1}, resulting in an average point density > 105.9 points m^{-2}. Most flight lines overlapped > 50% and the maximum scan angle was ± 15° (Deng *et al.*, 2025).

Leaf litter cover was visually estimated as the proportion of ground surface at four rectangular 1 x 1 m areas near the placed baits that was covered by leaf litter (see supplement Figure S1). For analysis, mean leaf litter cover was calculated at the plot level.

Data analysis

All statistical analyses were performed in R 4.5.2 (R Core Team, 2025). Interactions of ant species with different baits were evaluated by bipartite interaction networks (Blüthgen & Staab, 2024) based on the incidence of each species at each bait across replicates per plot, meaning that a single species could be assigned a maximum incidence of four at a specific nutrient bait on plot level. An overall networks for data pooled across all plots was calculated to obtain a general overview of interactions. In turn, plot-level networks facilitated testing for the influence of tree species richness and environmental covariates on network characteristics.

Indices that describe characteristics of a network were calculated and network visualization was generated with the R-package *bipartite* (Dormann *et al.*, 2009). To assess complementarity in resource use, a range of quantitative network indices was calculated. H2′ quantifies weighted complementary specialization (in the following: network specialization) by measuring how strongly species partition their interactions across resources relative to a null expectation of random resource use (Blüthgen *et al.*, 2006). Higher values of network specialization indicate less overlap in resource use among species and increased trophic complementarity. Due to constraints imposed by small network sizes, H2′ could be calculated for 138 out of 176 plot level networks.

Additional indices were calculated to discriminate mechanisms of trophic complementarity. Shannon diversity of interactions (in the following: interaction diversity) reflects how broadly the ant community as a whole uses available resources. Interaction diversity complements network specialization as it allows insight into whether interactions are spread across many links or are dominated by a few (Blüthgen *et al.*, 2006). Generality (in the following: forager generality) describes the average breadth of resource use at the species level, i.e. how many different bait types every species exploits on average, weighted by interaction frequency (marginal totals). Increased forager generality combined with stable network specialization may point towards complementarity, even though species are not strictly specialized. In contrast, vulnerability (in the following: bait attractiveness) captures the same concept from the resource perspective, indicating how many species, on average, are attracted to a given bait type, weighted by interaction frequency (marginal totals). Bait attractiveness allows changes in complementarity to be linked to patterns of resource sharing, whereas forager generality reflects consumer behavior (Bersier *et al.*, 2002).

For dominant species, defined as the three species with the highest total bait visitation, average d’ (in the following: species specialization, Blüthgen *et al.*, 2006) was computed across plots as a measure of species level specialization. This metric quantifies how strongly the interactions of a species with the different baits deviates from random expectation given overall resource availability and interaction frequencies. Specifically, species specialization increases when a species concentrates its interactions on a subset of resources rather than using resources in proportion to their availability in the network.

Before analysis, the experimental treatment variable tree species richness was log2-transformed. To test direct and indirect pathways of tree species richness on the characteristics of ant trophic interactions (i.e. the four network indices), we used path analyses (Shipley, 2009). Component models were fitted as linear mixed-effects models with a random intercept for site using *lmer* from the *lme4*-package (Bates *et al.*, 2015) and assembled using *piecewiseSEM* (Lefcheck, 2016) to evaluate fit and to obtain standardized path estimates.

An a priori model structure was deduced from published literature and ecological theory (Supplement Table S1). For each network index (network diversity, forager generality, bait attractiveness, network specialization), a separate path model was calculated. Apart from a direct path from tree species richness to network indices, indirect paths via environmental variables describing ant habitat were tested (Supplement Table S2). Terminal endogenous variables were the network indices, while tree species richness and slope curvature were exogenous predictors. As intermediate exogenous predictors we included canopy cover, litter cover, and network size. Canopy cover and litter cover are closely related to habitat quality for ground-foraging ants. The numerical formulation of all evaluated network indices (except H2') is not independent of the number of nodes in a network. Hence, we explicitly account for this dependency by including network size as a covariate (Blüthgen & Staab, 2024). Network size was defined as the number of ant species in the network, as the lower level (nutrient baits) was fixed and thus did not contribute to variation in the number of nodes. All continuous variables were standardized (mean 0, SD 1) prior to modeling to facilitate comparison of effect sizes. To evaluate the overall fit of the hypothesized model structure for each network index, we calculated Fisher's C and directed separation tests (Shipley, 2009).

Potential multicollinearity (Dormann *et al.*, 2013) among variables was assessed with variance inflation factors (VIF) of models calculated with the *vif* function from the *car* package (Fox *et al.*, 2001). No collinearity (VIF < 3) was detected. For each component, we inspected residual histograms and residuals vs fitted values to check homoscedasticity and normality, which were always met.

RESULTS

In total, 47 ant species visited the baits cumulating to 1575 ant-bait interactions (Figure 1; Supplement Table S3). The mean number of species visiting the baits was 3.4 ± 1.5 on plot level. The sugar bait attracted 35%, the oil bait 27%, the salt bait 15%, the phosphate bait 8%, the amino acid bait 8%, and the water bait 6% of all incidences respectively. *Carebara altinodus* (Species specialization d' = 0.15 ± 0.24), *Pheidole nodus* (d' = 0.16 ± 0.26), and *Nylanderia picta* (d' = 0.26 ± 0.32) were the three most frequent species accounting for 70% of all incidences. Mean network specialization per plot (H2') was 0.14 ± 0.2 and the specialization of the overall network was H2' = 0.07.

Opposed to our hypothesis, tree species richness was not consistently related to network characteristics. Tree species richness had a small negative direct effect on network diversity ($\beta = -0.09$, $p = 0.048$). As mathematically expected, network diversity, forager generality, and bait attractiveness were strongly positively correlated with ant species richness ($\beta = 0.31$-0.81, all $p < 0.001$). The path models for each network index (network diversity, forager generality, bait attractiveness, network specialization) had acceptable fits (Fisher's C = 4.54-9.74, p = 0.045-0.119; Table S4).

Direct pathways from canopy and litter cover to network indices were generally weak and non-significant (Figure 2; Table S4). The pathway from tree species richness to canopy cover was positive ($\beta = 0.34$-0.37, all $p < 0.001$), as was the pathway from canopy cover to litter cover ($\beta = 0.57$-0.58, all $p < 0.001$). Slope curvature was positively associated with litter cover ($\beta = 0.15$-0.18, $p < 0.01$).

The overall path model structure explained a large fraction of variation in network diversity (marginal $R^2 = 0.74$) and bait attractiveness (marginal $R^2 = 0.62$), but little in network specialization (marginal $R^2 = 0.01$) and forager generality (marginal $R^2 = 0.11$; Table S4).

DISCUSSION

Contrary to our expectations, tree species richness neither directly nor indirectly influenced complementarity in ant resource use, indicating that niche partitioning in resource use among ant species is insensitive to tree species loss. Rather, network diversity declined slightly, indicating a more unequal distribution of interactions across resource types despite stable ant species richness.

The diversity of ants can be relatively robust to habitat change (Belshaw & Bolton, 1993; Yeeles *et al.*, 2017; Hoenle *et al.*, 2022), as long as alterations, for example due to land use, are not too severe and as long as non-native invasive ants are absent. This is also the case in the BEF-China Experiment, which is covered by an early successional experimental forest of equal age and where no invasive ants have so far been found (Skarbek *et al.*, 2020; Staab *et al.*, 2023; Spitz *et al.*, 2026). In the ant-nutrient networks recorded by us, network topology was robust to changes in tree species richness and was not affected by slope curvature. These findings partly contradict earlier studies from the same sites (Fornoff *et al.*, 2019) and several studies on the influence of plant diversity on trophic interaction networks. For example, in many plant-flower visitor networks, an increase in plant species richness is associated with higher network complementarity and flower visitor generality, which is often mediated by a positive effect of plant diversity on flower visitor diversity (e.g., Ebeling *et al.*, 2008; Weiner *et al.*, 2011; Kaiser-Bunbury *et al.*, 2017). A positive association between consumer (ant) species richness and network diversity, forager generality and bait attractiveness was also found in the generalist interactions studied by us. This suggests that also in ant-nutrient networks the diversity of the interacting species is an important predictor of network topology, particularly when interactions are not specialized (Thébault & Fontaine, 2010).

The low specialization in nutrient use means that ant species are not dependent on particular resource types and their nutrient foraging is therefore robust to changes in resource diversity associated with varying tree species richness. This contrasts with niche-based coexistence theory, which predicts that resource differentiation should be a primary stabilizing mechanism (Chesson, 2000), and suggests that interaction structure is maintained through mechanisms other than nutritional niche partitioning. Notably, the dominant ant species in the community were also among the most generalistic foragers. In ground-foraging ant communities, coexistence can be structured by dominance hierarchies in which dominant species monopolize resources through interference competition, while subordinate species persist through spatiotemporal segregation, foraging in different microhabitats or under different microclimatic conditions to cope with dominant competitors (Fellers, 1987; Andersen, 1992; Cerdá *et al.*, 1998). Under this framework, species do not require distinct nutritional niches to coexist; instead, the timing, location, and competitive context of resource access determine interaction structure independently of resource type (Parr & Gibb, 2009; Arnan *et al.*, 2011). This asymmetry in access to resources, rather than inherent dietary specialization, may therefore be the primary driver of any variation in individual species' interactions across the ant community. The low specialization even of the otherwise largely predatory *Carebara altinodus* is consistent with this interpretation. Even though this species is expected to focus on protein-rich food objects, it did not prefer the amino acid solution in our resource choice experiment but foraged at all offered baits. This broad resource use suggests that *Carebara altinodus*, and likewise the other dominant ant species, is not limited by nutritional preferences. Instead, competitive exclusion from preferred resources or opportunistic exploitation of whatever resources are accessible within its foraging range may override nutritional preferences (Blüthgen & Fiedler, 2004). When all dominant ants in a community are nutritional generalists that are also not constrained by biotic and abiotic environmental conditions, this can result in highly generalistic interaction networks that are not influenced by changes in resource heterogeneity or other environmental variables (Blüthgen & Feldhaar, 2010).

However, the absence of nutritional niche partitioning does not preclude more subtle shifts in interaction frequencies. The decline in interaction diversity with higher tree species richness may suggest that competitively constrained foragers can nonetheless concentrate effort on nutritionally preferred resources when their availability increases (Simpson & Raubenheimer, 2012), potentially due to increased encounter rates with high-quality resources in more diverse habitats. Diverse tree plantations likely contain more arthropod prey (Staab & Schuldt, 2020), and mutualist partners such as trees with extrafloral nectaries and aphids (Staab *et al.*, 2015, 2016), increasing the availability and diversity of food resources in sites with higher tree species richness. This higher constituent nutrient availability could reduce the need to forage for additional complementary nutrient sources, potentially decreasing the risk of resource (co-)limitation (Sperfeld *et al.*, 2016), thereby concentrating interactions at few nutrient baits and lowering overall interaction diversity. Previous studies provide insight into the potential underlying mechanisms. For example, Fornoff *et al.* (2019) observed increased generality in ant-Hemiptera networks with higher tree species richness , attributed to greater hemipteran diversity and abundance, which likely increases the encounter rates with a high-quality energy source of carbohydrates and amino acids. This allows the ants to broaden trophobiont associations as a buffer against the loss of valuable mutualist partners (Fornoff *et al.*, 2019), thereby reducing the need to forage on alternative nutrient types. The ability to concentrate foraging on a few high-quality resources may reinforce the competitive asymmetries that structure the community. Albeit speculative, if dominant species secure reliable access to preferred resources, the relative frequency of subordinate species interactions with those same resources may decrease (Blüthgen & Fiedler, 2004), lowering the number of interactions across resource types and leading to the decline in network diversity with increasing tree diversity.

Several environmental variables were expected to influence network structure but did not do so. Neither slope curvature, nor litter cover, nor canopy cover were correlated with any network property, suggesting that ant trophic interactions are not only robust to changes in tree species richness and correlated habitat properties, but also to the abiotic environment. This suggests that, while ants in forests may prefer less topographically exposed locations (Kaspari & Weiser, 2000) with high leaf litter cover (Bastos & Harada, 2011), their nutrient foraging is independent of fine-scale variation in the abiotic environment and habitat availability, and instead is structured by resource diversity (cf. Moses *et al.*, 2023) and competitive hierarchies (Parr & Gibb, 2009; Mottl *et al.*, 2021).

To summarize, our results indicate that ant trophic interactions are largely robust to tree species loss. If there is any influence of tree species richness on network topology it appears to be via the frequency distribution of interactions (i.e. network diversity) rather than on the complementarity of resource use. This response appears to be influenced by encounter-rate-mediated shifts in foraging effort toward nutritionally preferred resources as resource availability for ground-foraging ants increases with tree species richness. Where species lack strong nutritional specialization, changes in resource availability reshape how often interactions occur without restructuring which interactions are possible, such that subtle shifts in network diversity can arise from changes in encounter rates and competitive contexts without fundamental reorganization of network topology. If confirmed by direct functional measurements, these findings imply that ant-mediated ecosystem functions, including predation, scavenging, plant defense, and nutrient cycling (Folgarait, 1998), may be broadly maintained also in forests with comparatively few tree species such as young secondary forest. As the spatial scale of our study was limited, and as plots with few and many tree species were adjacent to each other, we caution against transferring the results to large scale homogenous tree monocultures.

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FIGURES

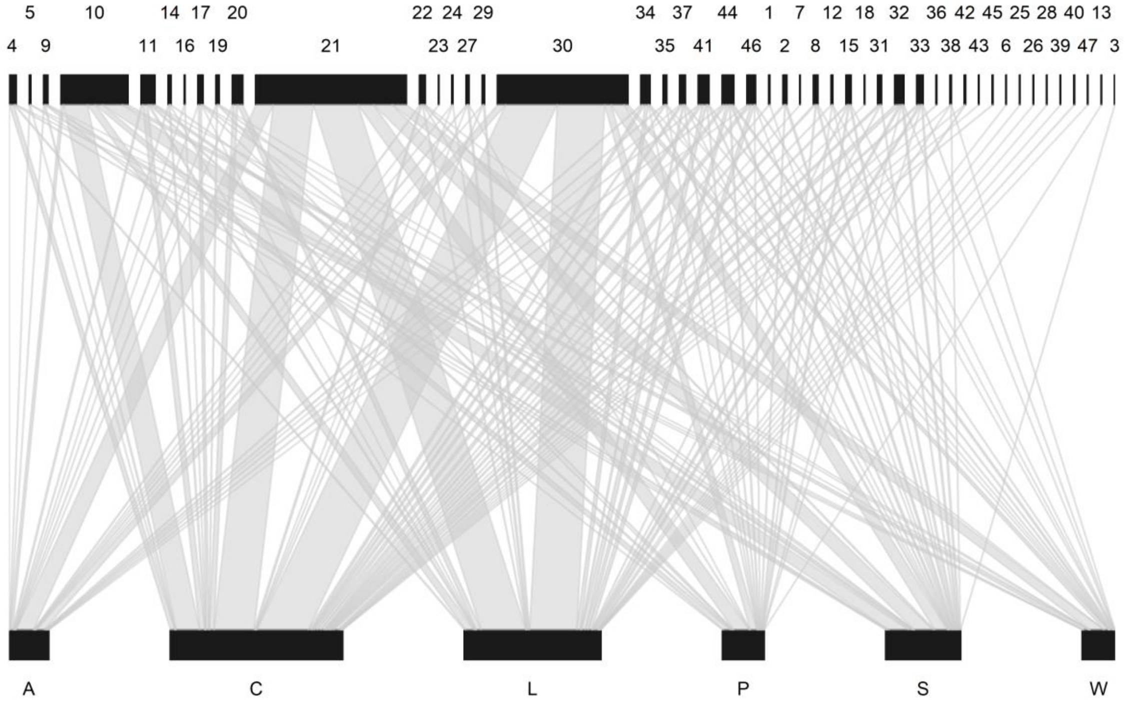

Figure 1. The overall bipartite network illustrating interactions between ants (higher level) and nutrient baits (lower level) based on total incidence across all plots. Node widths are proportional to total interaction frequency, and link widths represent number of interactions between trophic levels. Ant species are coded by numbers (Table S3). Nutrients are coded as letters (A = amino acid, C = carbohydrate, L = lipid, P = phosphate, S = salt, W = water. Overall network specialization was low (H2′ = 0.07).

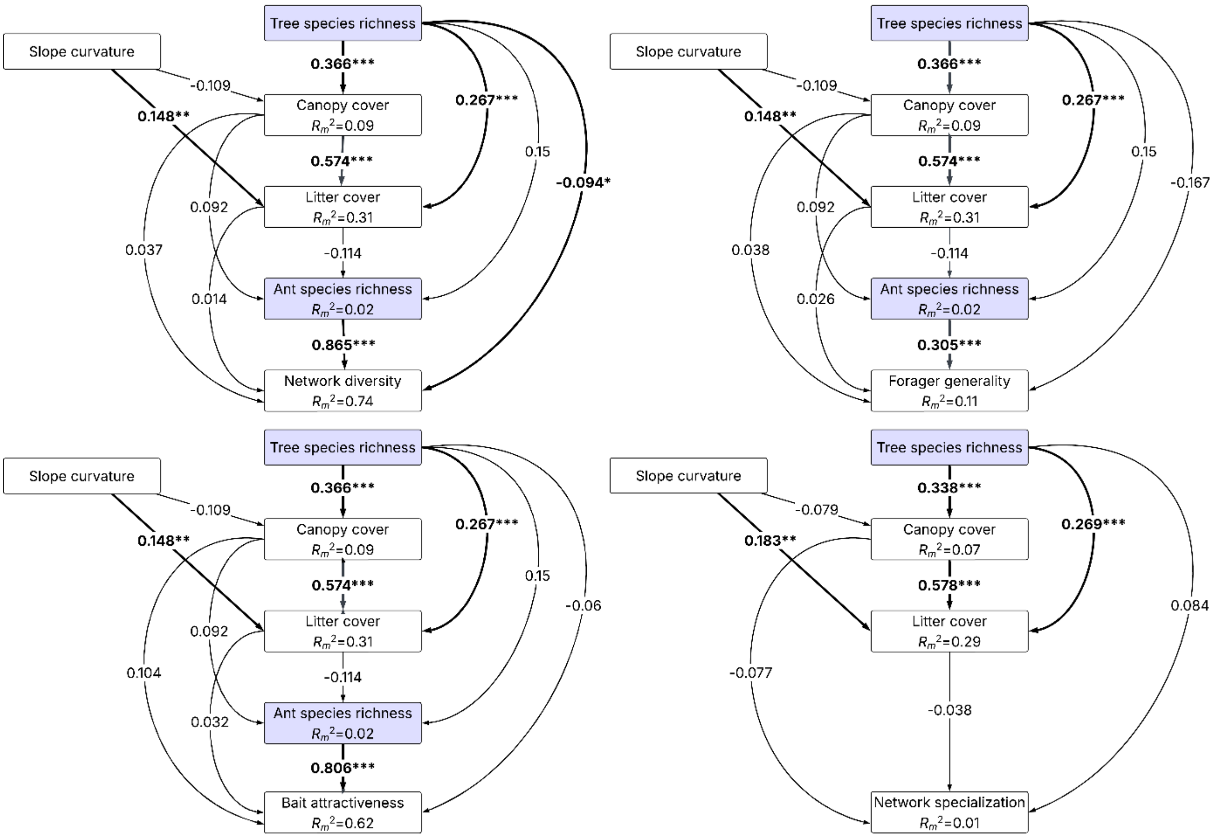

Figure 2. Path diagrams for the four models (A-D) on network diversity, forager generality, bait attractiveness, and network specialization. The design variable tree species richness and the assumed mediator ant species richness are colored light blue to highlight the hypothesized driver of nutritional complementarity in ants (tree species richness) and its assumed mediating pathway (ant species richness). Tree species richness and slope curvature are exogenous variables and thus have no incoming arrows. Labels next to arrows show standardized coefficients with significant p-values indicated by asterisks ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)). Significant coefficients and corresponding arrows are printed bold. Marginal R² values (R_m^2) are reported for each model and represent the proportion of variance explained by the fixed effects alone.

Supplementary material

Trophic interactions of ants are robust to tree species loss

Contents

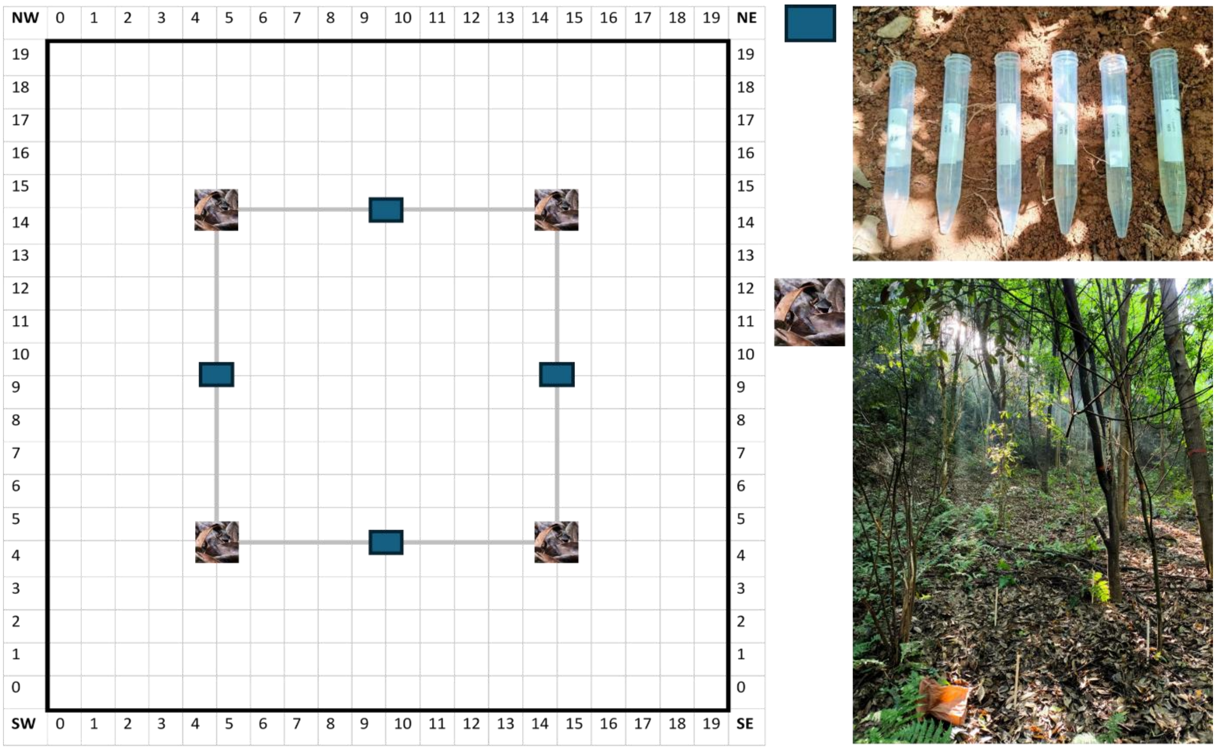

Figure S1 Experimental setup. Left side: Schematic plot overview. In each plot 20 × 20 trees were planted. The panel shows the position of the nutrient baiting experiment (blue rectangle) in the middle of the edges of the inner 10 × 10 planting positions (North, West, South, East). Litter cover was visually estimated in 1 m^2 corners of the inner 10 × 10 planting positions (litter quadrat). Top right side: Nutrient baits laid out on the ground in random order, pointing into the same randomly assigned direction. Bottom right side: Estimation of litter cover in the field.

Table S1 A priori path model. Summary of the hypothesized relationships included in the a priori path model (see Figure 2), with the theoretical rationale and empirical support for each proposed path. For each relationship, the expected direction of effect and key references informing the hypotheses are provided.

Path	Direction	Rationale	Evidence type	References
Complementarity ~ Canopy cover	+	Canopy cover improves microclimate benefiting ants, resulting in more foragers and complementary resource use	Theory; empirical	Edney 1977, Parr & Bishop 2022, Fornoff *et al.* 2021
Complementarity ~ Litter cover	+	Litter cover increases ant habitat, resulting in more foragers and complementary resource use	Theory; empirical	Arrhenius 1921, Bastos & Harada, 2011
Complementarity ~ Ant species richness	+	Except network specialization, indices correlate to visiting ant species richness, which needs to be accounted for	Methodological	Blüthgen & Staab 2024
Complementarity ~ Tree species richness	+	Tree species richness increases resource diversity, resulting in more foragers and complementary resource use	Theory; empirical	MacArthur 1984, Skarbek *et al.* 2020
Canopy cover ~ Topography	-	Concave topography accumulates water and nutrients, increasing plant productivity and canopy cover	Theory; empirical	Beven & Kirkby, 1979, Whittaker 1956
Canopy cover ~ Tree species richness	+	Tree species richness promotes a layered tree stand, increasing canopy cover	Theory; empirical	Pretzsch 2014, Deng *et al.* 2025
Litter cover ~ Canopy cover	+	Canopy cover increases litter cover	Theory; empirical	Bray & Gorham 1964, Majasalmi & Rautiainen 2020

Litter cover ~ Topography	-	Concave topography promotes litter accumulation	Theory	Beven & Kirkby 1979
Litter cover ~ Tree species richness	+	Tree species richness promotes litter fall	Theory; empirical	Pretzsch 2014, Huang *et al.* 2018
Ant species richness ~ Canopy cover	+	Canopy cover improves microclimate benefiting forest ants	Theory; empirical	Edney 1977, Parr & Bishop 2022, Fornoff *et al.* 2021
Ant species richness ~ Litter cover	+	Litter cover increases habitat of ground-foraging ants	Theory; empirical	Arrhenius 1921, Bastos & Harada, 2011
Ant species richness ~ Tree species richness	+	Tree species richness increases resource diversity for ants	Theory; empirical	MacArthur 1984, Skarbek *et al.*, 2020

Table S2 Environmental covariates considered in addition to the experimental design variable tree species richness

Variable	Range	Median	Mean ± SD
Topography (Mean curvature after Evans, 1980)	-7.7-7.3	0.9	0.7 ± 3.3
Canopy cover (%)	29-99	83	80 ± 12
Litter cover (%)	0.3-98.5	72.4	63.6 ± 29.7

Table S3 Sampled ant species. Given is the total incidence across all plots. Numerical codes in associate with codes in Figure 1.

Species ID	Subfamily	Genus	Species	Total incidence
1	Dolichoderinae	*Iridomyrmex*	*anceps*	3
2		*Tapinoma*	*melanocephalum*	12
3		*Technomyrmex*	*brunneus*	1
4		*Technomyrmex*	*obscurior*	23
5	Formicinae	*Camponotus*	*albosparsus*	4
6		*Camponotus*	*pseudoirritans*	1
7		*Camponotus*	*vitiosus*	1
8		*Lepisiota*	cf. *capensis*	14
9		*Nylanderia*	*flavipes*	13
10		*Nylanderia*	*picta*	211
11		*Nylanderia*	sp.3	44
12		*Nylanderia*	sp.6	5
13		*Nylanderia*	sp.8	1
14		*Nylanderia*	*yaeyamensis*	9
15		*Paraparatrechina*	*neela*	16
16		*Paraparatrechina*	*sauteri*	2
17		*Paratrechina*	*umbra*	15
18		*Polyrhachis*	*dives*	1
19		*Prenolepis*	*naoroji*	10
20	Myrmicinae	*Aphaenogaster*	sp.1	32
21		*Carebara*	*altinodus*	476
22		*Crematogaster*	cf. *biroi*	18

23		*Crematogaster*	cf. *nawai*	1
24		*Crematogaster*	cf. *rogenhoferi*	3
25		*Crematogaster*	sp.5	1
26		*Mayriella*	*granulata*	1
27		*Monomorium*	*chinense*	9
28		*Monomorium*	*intrudens*	1
29		*Pheidole*	*laevithorax*	7
30		*Pheidole*	*nodus*	412
31		*Pheidole*	*pieli*	12
32		*Pheidole*	*rabo*	28
33		*Pheidole*	*roberti*	19
34		*Pheidole*	*vulgaris*	28
35		*Pristomyrmex*	*punctatus*	11
36		*Recurvidris*	*glabriceps*	2
37		*Recurvidris*	*recurvispinosa*	17
38		*Solenopsis*	sp.1	4
39		*Tetramorium*	*nipponense*	1
40		*Tetramorium*	*shensiense*	2
41		*Tetramorium*	*smithi*	33
42		*Tetramorium*	sp.11	3
43		*Tetramorium*	sp.13	1
44		*Tetramorium*	*wroughtonii*	37
45	Ponerinae	*Brachyponera*	*chinensis*	2
46		*Ectomomyrmex*	*astutus*	27

47	*Hypoponera sauteri*	1

Table S4 Standardized path coefficients and p-values for all structural paths across the path models (Network diversity, Forager generality, Bait attractiveness, Network specialization). Beta: Standardized path coefficient. P-value: Two-sided p-value for the path coefficient test. Marginal (R_m^2) and conditional (R_c^2) coefficients of determination are given for endogenous variables. Each path model's overall d-separation test fit is given together with Fisher's C summary statistics. df: degrees of freedom. AIC: Akaike Information Criterion. K: total number of free parameters estimated in the path model. N: Sample size used to fit the path model.

Response ~ Predictor	Beta ± SE	P-value	R_m^2	R_c^2
Network diversity				
Fisher's C = 9.743, df = 4, p-value = 0.045, AIC = 1674.3, K = 24, N = 176				
Canopy cover ~			0.09	0.6
Slope curvature	-0.109 ± 0.063	0.086		
Tree species richness	0.366 ± 0.064	<0.001		
Litter cover ~			0.31	0.68
Canopy cover	0.574 ± 0.065	<0.001		
Slope curvature	0.148 ± 0.054	0.007		
Tree species richness	0.267 ± 0.059	<0.001		
Ant species richness ~			0.02	0.11
Canopy cover	0.092 ± 0.100	0.445		
Litter cover	-0.114 ± 0.101	0.304		
Tree species richness	0.150 ± 0.086	0.087		
Network diversity ~			0.74	0.74
Canopy cover	0.037 ± 0.044	0.671		
Litter cover	0.014 ± 0.049	0.834		
Ant species richness	0.865 ± 0.039	<0.001		
Tree species richness	-0.094 ± 0.045	0.048		
Forager generality				
Fisher's C = 8.605, df = 4, p-value = 0.072, AIC = 1890.875, K = 24, N = 176				
Canopy cover ~			0.09	0.57
Slope curvature	-0.109 ± 0.063	0.086		
Tree species richness	0.366 ± 0.064	<0.001		
Litter cover ~			0.31	0.68

Canopy cover	0.574 ± 0.065	<0.001		
Slope curvature	0.148 ± 0.054	0.007		
Tree species richness	0.267 ± 0.059	<0.001		
Ant species richness ~			0.02	0.11
Canopy cover	0.092 ± 0.100	0.445		
Litter cover	-0.114 ± 0.101	0.304		
Tree species richness	0.150 ± 0.086	0.087		
Forager generality ~			0.11	0.11
Canopy cover	0.036 ± 0.083	0.822		
Litter cover	0.025 ± 0.092	0.842		
Ant species richness	0.304 ± 0.074	<0.001		
Tree species richness	-0.165 ± 0.084	0.065		
Bait attractiveness			0.62	0.67
Fisher’s C = 7.330, df = 4, p-value = 0.119, AIC = 1735.9, K = 24, N = 176				
Canopy cover ~			0.09	0.57
Slope curvature	-0.109 ± 0.063	0.086		
Tree species richness	0.366 ± 0.064	<0.001		
Litter cover ~			0.31	0.68
Canopy cover	0.574 ± 0.065	<0.001		
Slope curvature	0.148 ± 0.054	0.007		
Tree species richness	0.267 ± 0.059	<0.001		
Ant species richness ~			0.02	0.11
Canopy cover	0.092 ± 0.100	0.445		
Litter cover	-0.114 ± 0.101	0.304		
Tree species richness	0.150 ± 0.086	0.087		
Bait attractiveness ~			0.62	0.67
Canopy cover	0.104 ± 0.063	0.151		
Litter cover	0.032 ± 0.063	0.635		
Ant species richness	0.806 ± 0.047	<0.001		
Tree species richness	-0.060 ± 0.054	0.270		

Network specialization				
Fisher's C = 4.536, df = 2, p-value = 0.103, AIC = 1090.1, K = 17, N = 138				
Canopy cover ~			0.07	0.6
Slope curvature	-0.079 ± 0.07	0.259		
Tree species richness	0.338 ± 0.071	<0.001		
Litter cover ~			0.29	0.72
Canopy cover	0.578 ± 0.075	<0.001		
Slope curvature	0.183 ± 0.061	0.003		
Tree species richness	0.269 ± 0.066	<0.001		
Network specialization ~			0.01	0.11
Canopy cover	-0.079 ± 0.116	0.592		
Litter cover	-0.038 ± 0.114	0.769		
Tree species richness	0.085 ± 0.099	0.396		

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