Canopy closure re-establishes ants in young tree plantations, while low soil pH limits ant diversity

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ABSTRACT

1. Tree species richness is known to enhance biodiversity and ecosystem functioning, but its effects across trophic levels during forest restoration remain insufficiently understood. In reforestation on complex terrain, habitat complexity may moderate the effect of canopy closure on animal community reassembly, a relationship further shaped by the abiotic environment.

2. Ants, as key functional organisms sensitive to vegetation structure and microclimate, provide an ideal system to test how tree species richness, canopy closure and abiotic environmental variables jointly influence animal communities in young plantations.

3. We examined ground ant diversity, community composition, and functional traits in subtropical tree plantations, using nearby secondary forest as a reference. No ant metric, including incidence, species richness, taxonomic or functional diversity, or community-weighted trait means, responded to tree species richness. Instead, canopy closure and soil pH explained variation in most metrics.

4. Canopy closure and topographical exposure shaped community composition, with canopy closure negatively influencing ant incidence and species diversity, while soil pH consistently had a positive effect on both across the observed range (4.1–5.2). More closed canopies favored leaf-litter-nesting ants, a higher proportion of predators, and communities with increased mandible length, indicating convergence toward forest-adapted predatory assemblages. Soil-nesting ants approached secondary forest values only where both canopy closure and tree species richness were high.

5. Early canopy closure appears to be the primary biotic environmental variable influencing ant community recovery in young plantations, which is further attenuated by the abiotic environment such as soil conditions. This highlights canopy development as a key mechanism of faunal recovery, beyond the effects of tree species richness alone, with increasing predator dominance suggesting potential functional restoration.

KEYWORDS

Biodiversity recovery, Early succession, Formicidae, Functional traits, Habitat complexity, Reforestation

INTRODUCTION

Reforestation is central to biodiversity conservation and climate mitigation. The last two decades have seen tree planting efforts on an unprecedented scale (Chen *et al.*, 2019), often accompanied by policies promoting species rich tree plantations with native and site-adapted species to restore ecosystem functioning (e.g., General Office of the State Council, 2021; Ministry of Environment and Forests, 2017). Tree species richness increases primary producer productivity (Grossman *et al.*, 2018), and there is evidence that positive effects of high tree species richness on biodiversity and ecosystem functioning propagate towards higher trophic levels (Schuldt *et al.*, 2019). However, the underlying mechanisms require further investigation to provide robust guidance for reforestation practices.

Theoretically, diverse tree stands increase habitat heterogeneity through variation in crown structure and phenology (Bauhus *et al.*, 2017), thereby supporting more functionally diverse faunal communities (Schuldt *et al.*, 2017; Li *et al.*, 2023). Tree-species-rich plantations may also stabilize ecosystem functioning via functional similarity, as the loss of functioning following tree species loss is more likely to be compensated (Yachi & Loreau, 1999; Eisenhauer *et al.*, 2023). Functional traits represent a valuable tool to assess shifts in animal communities in response to tree species richness and other environmental variables and infer on possible mechanisms and implications for ecosystem functioning (Gagic *et al.*, 2015).

Yet, during early forest succession, ecosystem functioning may be influenced more by productivity than by tree diversity (Grime, 1998; Lohbeck *et al.*, 2015). In young plantations, fast-growing light-demanding species typically contribute most to tree biomass, potentially diminishing the functional contribution of slower-growing, shade-tolerant species (Connell & Slatyer, 1977). A key indicator of this early structural development is canopy closure, which moderates temperature and moisture within the forest, creating favorable microclimate for forest-adapted species, and hence supporting ecosystem recovery (De Frenne *et al.*, 2019; Fornoff *et al.*, 2021). Convergence from reforested towards original habitats is therefore facilitated particularly by increased canopy closure, even in single-species stands (Palmer *et al.*, 1997). Compared to single-species stands, diverse plantations can begin to resemble secondary forests in structural complexity at an earlier age stage (Perles-Garcia *et al.*, 2021), but diversity effects may depend on interactions with canopy development. High canopy closure in single-species stands may suppress shade-intolerant flora and fauna (Viljur *et al.*, 2022). Species-rich mixtures, on the other hand, may simultaneously increase canopy closure and provide more varied microhabitats. Thus, the benefits of tree diversity in young plantations are expected to be most pronounced when diversity and canopy closure jointly enhance structural complexity.

Ants (Formicidae) are particularly well-suited to test expectations about the influence of environmental variables on animal communities in forests. Ants are ecologically dominant, responsive to environmental gradients, and strongly tied to ecosystem functions such as predation, scavenging, and nutrient cycling (Folgarait, 1998; Alonso & Agosti, 2000). Standardized trait frameworks, i.e. the standardized measurement of characteristics that can be related to the ecological attributes and functional roles of a species, make ants ideal organisms to study forest recovery and functioning (Parr *et al.*, 2017; Wong *et al.*, 2019). While many ants are generalist omnivores (Blüthgen *et al.*, 2003), predator species are particularly responsive to

habitat structure (Staab *et al.*, 2014b), and play a critical role in shaping the functional structure of forest ant communities (Silva & Brandão, 2010; Sosiak & Barden, 2021). Diverse tree stands may stabilize prey availability and thereby support predatory ant communities (Root, 1973; Staab & Schuldt, 2020), enhancing predation and scavenging functions.

Canopy closure and tree species richness mediate the response of ground-foraging ant communities to plantation structure through at least two complementary pathways. First, canopy closure influences ant community structure by buffering ground microclimate against desiccation and thermal extremes, thereby promoting conditions suitable for forest-dwelling ant species (Wiescher *et al.*, 2012; Parr & Bishop, 2022). Accordingly, several studies have shown the influence of different woody vegetation cover measurements on ant species composition (Gras *et al.*, 2016; Ahuatzin *et al.*, 2019; Brassard *et al.*, 2023), frequently noting increased presence of predatory ants in closed habitat (Parr *et al.*, 2012; Andersen, 2019). In contrast, species richness of ground-foraging ants is generally reported to decrease with woody vegetation cover in fragmented habitats (Parr *et al.*, 2012; Kendrick *et al.*, 2015; Brassard *et al.*, 2023). Second, tree species richness shapes the habitat of ground-foraging ants through leaf litter composition: Uniform litter in monocultures reduces habitat complexity and slows decomposition, subsequently decreasing nutrient availability (Getaneh *et al.*, 2022; Jin *et al.*, 2022), whereas mixed-species litter retains moisture more effectively (Zhou *et al.*, 2018) and promotes microbial and faunal activity (Blair *et al.*, 1990).

Isolating these biotic effects related to tree diversity from the underlying abiotic environment requires careful consideration of environmental covariates. Topographic features such as exposure and geomorphology modulate sunlight and water availability, particularly in complex terrain (Scholten *et al.*, 2017), while soil pH represents a further fundamental axis of environmental variation to which ground-foraging ants are sensitive (Staab *et al.*, 2014a; Ahuatzin *et al.*, 2019).

Here, we examine how tree species richness, canopy closure, and their interaction, alongside abiotic environmental conditions (soil pH, exposure, geomorphology), shape ant species diversity, community composition, and functional traits within the BEF-China forest biodiversity experiment. We hypothesized that tree species richness increases ant species richness and functional diversity by enhancing habitat heterogeneity, and that combined high tree species richness and canopy closure would particularly benefit predator and litter-nesting ants, as these groups depend on structurally complex, shaded environments. We further expected that trait shifts associated with predation and scavenging would signal enhanced ant-mediated ecosystem functions in structurally complex stands. To evaluate the re-establishment of ant communities in young plantations, we compared ant metrics (composition, total incidence, species richness, rarefied species richness, Shannon diversity, incidence fraction of functional groups, functional diversity, community weighted means of functional traits) with values from nearby naturally regenerating secondary forest.

MATERIALS AND METHODS

Study sites

The study was conducted at the BEF-China (Biodiversity-Ecosystem Functioning) research platform (www.bef-china.com) near Xingangshan, Jiangxi, Southeast China (117° 54′ E, 29° 07′ N), with a mean annual temperature of 17 °C and precipitation of 1800 mm (Yang et al., 2013).

For this study, 32 plots from the BEF-China tree diversity experiment were selected according to a broken-stick design, where all tree species are represented as single-species stands and randomly combined into higher diversity mixtures (resulting in 16 single-species stands, 8 two-species-stands, 4 four-species-stands, 2 eight-species-stands, and 1 sixteen and twenty-four-species stand, respectively) (Bruelheide *et al.*, 2014). The plots are 25.8 × 25.8 m

187 in size with the 1-24 tree species planted in 1.3 × 1.3 m grids and were established in 2010
188 following clear-cutting of conifer plantations. These plots are hereafter referred to as BEF
189 (Biodiversity-Ecosystem Functioning experimental) plots. The 32 BEF plots have a mean
190 elevation of 145 m (± 14 m SD, 119–182 m). Mean pairwise distance between BEF plot centers
191 was 315 m (± 170 m SD, 26–727 m) (Figure S1).

192 To enable comparison between experimental plantations and naturally regenerating
193 secondary forest, comparative study plots (30 × 30 m) were established in 2008 within the
194 nearby Gutianshan National Nature Reserve (GNNR; 118°27′–118°11′ E, 29°08′–29°17′ N;
195 about 20 km distance from the BEF plots), Zhejiang Province (Bruelheide et al., 2011). These
196 plots spanned a recovery gradient from 20 to over 100 years since abandonment of forestry
197 (typically clear-cutting). For the present study, nine young plots with a regeneration age of 20-
198 40 years since abandonment were selected and are hereafter referred to as CSP plots
199 (Comparative Study Plots in secondary forest). In the present study, the CSP plots serve as a
200 comparative reference for assessing ant community re-establishment in the BEF plots. They
201 represent the most comparable secondary forest stands available, as mature and old-growth
202 secondary forests are very rare in the region and situated in high elevation with different ant
203 communities (Staab *et al.*, 2014a). The nine CSP plots are located at moderate elevations
204 between 251 and 679 m (mean = 439 ± 158 m SD). Mean annual precipitation at the GNNR is
205 1,964 mm, with a mean annual temperature of 15 °C (Geißler et al., 2012). Mean pairwise
206 distance between CSP plots was 4623 m (± 3025 m SD, 250–8960 m) (Figure S1).
207

208 Ant sampling

209 Ants in the 32 BEF plots were collected in 2016 using four standardized pitfall traps per plot
210 (plastic cups, diameter 8.5 cm, height 15 cm), placed at the corners of the central 10 m × 10 m
211 square. Traps were filled with Renner solution (40% ethanol, 30% water, 20% glycerol, 10%

212 acetic acid, plus detergent) and emptied every two weeks between July and September, yielding
213 five sampling periods. In six cases, one collection period had no ant specimens (four did not
214 yield any ants, two were lost during processing). Data from the five sampling periods was
215 aggregated on trap level leading to a total of 128 samples (32 plots × 4 traps). For comparison
216 with secondary forest communities, we used pitfall data from nine CSP plots collected with
217 identical methods in 2009 (4 traps per plot, placed in the central 10 m × 10 m square), restricting
218 analyses to the matching July-September period (Staab et al., 2014). The CSP data were used
219 solely as a reference and were not included in formal statistical analyses. Nevertheless, because
220 sampling occurred seven years apart, unaccounted temporal variation may affect these
221 qualitative comparisons. Ant specimens were identified to species or morphospecies using
222 taxonomic literature and reference material (Staab et al. 2014, Skarbek et al., 2020). Because
223 pitfall traps do not provide reliable abundance estimates, all analyses were based on incidence
224 data (Alonso & Agosti, 2000), with a maximum of 5 incidences possible per species and trap.
225 In addition to total incidences, we calculated the fraction of incidences attributable to functional
226 groups (nesting and foraging ecology: nest site: litter, soil; diet: predator; full set of categorical
227 traits see Table S2) and to dominant species (the four species contributing most incidences:
228 *Pheidole nodus*, *Tetramorium wroughtonii*, *Tetramorium smithi*, and *Ectomomyrmex astutus*)
229 to characterize shifts relevant to ecosystem functioning, as preliminary exploration suggested
230 functional-group patterns could be influenced by dominant species.
231
232 Functional and life history traits
233 To functionally characterize ant communities, we measured seven continuous traits - head
234 length and width, mandible length, scape length, eye length, Weber's length, and tibia length -
235 using a Leica S6E microscope and a Keyence VHX-5000 (Leica, Wetzlar, Germany; Keyence
236 Deutschland GmbH, Neu-Isenburg, Germany). These classical functional traits relate to

species' interactions with their environment, e.g., head length to feeding mode, head width to habitat preference, mandible length to diet, scape length to sensory capabilities, eye length to feeding habit and habitat preferences, Weber's length to body size, and tibia length to locomotion and foraging type (Table S1; Hoenle et al., 2023; Parr et al., 2017; Sosiak & Barden, 2021). Continuous morphological traits were analyzed as follows: Weber's length, averaged per species, served directly as a measure of body size, while all other traits were expressed as residuals from linear regressions against Weber's length to account for allometric scaling, then averaged per species prior to analysis (Hoenle *et al.*, 2023). Categorical life-history traits - nest site, colony size, diet, and polymorphism - were included from literature and own observation (Table S2). These categorical traits complement measured continuous traits to infer on mechanisms and potential implications of ant community shifts. Community-weighted means (CWMs) of traits were computed using the R package FD (Laliberté & Legendre, 2010; Laliberté *et al.*, 2014).

Functional diversity was quantified as Rao's quadratic entropy (Rao Q), integrating species incidence with pairwise trait differences and suitable for mixed (continuous and categorical) trait data (De Bello *et al.*, 2010). Standardized effect sizes (SES) of Rao Q were calculated using the R-package *picante* (Kembel *et al.*, 2008) based on Gower dissimilarity, comparing observed communities to 1000 randomized communities (independent swap algorithm). Negative SES indicates narrower trait compositional space than expected by chance, positive SES a wider space (Nooten *et al.*, 2021).

Environmental variables

A set of environmental variables (Table S3) was compiled for the BEF plots to test relations with ant community metrics. From the CSP plots, only ant data were included as a reference to qualitatively evaluate ant community recovery in the BEF plots, as key environmental variables

were measured using different protocols and therefore are not ecologically comparable (Bruelheide *et al.*, 2011).

Canopy closure was measured at two points separated by 11 m from each other along a SW-NE diagonal in the center of the plot. Hemispherical pictures were taken in October 2015 at 1.3 m above ground with a 140-mm fisheye lens. Canopy closure was calculated as percentage of black pixels of total image size using image J (www.imagej.net) and the mean of both values per plot was used in analysis (Fornoff *et al.*, 2021).To describe the terrain and thus the abiotic environmental variation among plots (e.g. insolation, slope, aspect, soil properties), we used eastness, northness (Roberts, 1986), and geomorphons (Jasiewicz & Stepinski, 2013) derived from a digital terrain model with a resolution of 5 m (available at https://data.botanik.uni-halle.de/bef-china/datasets/126). Eastness and northness are trigonometric transformations of aspect: eastness = sin(aspect), and northness = cos(aspect). These variables quantify the directional orientation of slopes, allowing to capture variation in solar exposure and microclimate related to topography. Geomorphons delineate landform types such as 'hollow', 'ridge', 'slope', 'spur' and 'summit'; the dominant land unit was assigned to each plot. This approach enables a comprehensive assessment of abiotic environmental variability among plots, as demonstrated by Scholten *et al.* 2017.

Soil pH at 0-5 cm depth was measured in H_20 using an inolab pH-meter with Sentix 81 electrodes (WTW, Weilheim, Germany), following the method described in Scholten *et al.* (2017); pH data were originally collected in 2014 and previously reported in Li *et al.* (2019). We included pH because acidity/alkalinity can strongly influence soil chemistry (nutrient availability, cation exchange), microbial activity, and litter decomposition, all of which affect habitat quality for ants. For example, soil pH has been shown to influence ant community composition in the region (Staab *et al.*, 2014a), with more ant species found on less acidic soil (Staab *et al.*, 2014b).

Statistical analyses

All statistical analyses were performed in R 4.3.2 (R Core Team, 2023). Sampling completeness for the full dataset and functional groups was assessed using sample-based species accumulation curves (10,000 permutations) and the first-order jackknife species richness estimator with the R-package *vegan* (Oksanen et al., 2024; Figure S2). In addition to raw ant species richness we calculated rarefied ant species richness based on the smallest incidence (11) per trap, and Shannon diversity (the exponentiated Shannon index (Jost, 2006) with *vegan*. Rarefied ant species richness helps to identify if patterns in raw species richness are influenced by incidence. Shannon diversity weighs species richness by species incidence, thereby capturing both the number of species and their relative abundance, and reducing disproportionate influence of rare species on diversity estimates while remaining sensitive to changes in community structure.

Differences in species composition based on incidence and trait composition based on community weighted means of continuous and categorical traits (CWMs) were visualized using two-dimensional NMDS (non-metric multidimensional scaling) (plot level: 32 BEF plots (plantations), 9 CSP plots (secondary forest); *vegan* function *metaMDS*). For species composition, ordinations used Bray-Curtis dissimilarities while for trait composition, Gower distance was applied. A Procrustes analysis was performed to test the correspondence between the species-based and trait-based ordinations (*vegan* function *protest*, 10,000 permutations). Procrustes rotation optimally superimposes two ordinations by rotation and scaling, with the resulting correlation coefficient indicating the degree of correspondence between them: here, whether sites that are similar in species composition are also similar in trait composition. Group differences in multivariate dispersion for species and trait matrices were tested using *betadisper* and *permutest* (*vegan*, 10,000 permutations) to compare dispersion of BEF plots and CSP plots

312 in species and trait compositional space. To identify which environmental variables structure
313 ant community composition at the BEF plots, correlations between the first two NMDS axes
314 and the numeric variables tree species richness (log2-transformed), canopy closure, soil pH,
315 northness and eastness were assessed using *envfit* (10,000 permutations), with the strength and
316 direction of correlation determined from the fitted vectors. All numeric variables were centered
317 and scaled. CSP plot ant data served as reference points in ordination analyses.

318 To test for the relationships between the response variables ant species incidence,
319 incidence fractions of functional groups and dominant species, ant species richness, community
320 weighted means of functional traits, functional diversity and the environmental variables (fixed
321 effects), we fitted generalized linear mixed-effects models (GLMM) to the BEF data at the trap
322 level (128 observations, 4 per plot; *lme4*) (Bates *et al.*, 2015). Gaussian errors were assumed
323 for rarefied richness, Shannon diversity, Rao Q SES, and CWMs; Poisson errors for total
324 occurrences and raw richness; and binomial errors for fractions of dominant ants and functional
325 groups.

326 Fixed effects were tree species richness, canopy closure, eastness, northness, soil pH,
327 geomorphon, and an interaction term between tree species richness and canopy closure. Tree
328 species richness and canopy closure were included to test for both independent and interactive
329 effects of tree diversity and forest structural development on ant communities. Eastness and
330 northness served as proxies for slope orientation and associated microclimatic variation,
331 geomorphon described local landform characteristics, and soil pH represented an important
332 component of soil chemistry. Due to the hierarchical data with multiple samples per plot, we
333 used 'plot ID' as random intercept. BoBiQA optimizers were used to facilitate model
334 convergence. To address model uncertainty, all possible model combinations were generated
335 using *dredge* (*MuMIn*), and models within ΔAICc ≤ 2 were averaged (*model.avg*) (Bartoń,

2024). If the best model had an AICc value more than 2 units lower than the second-best model, no averaging was applied.

Model assumptions were checked using residual diagnostics and goodness-of-fit statistics from the *DHARMa* package (Hartig, 2016). Model residuals were inspected for normality and homoscedasticity, which were met (DHARMa KS test p-values for Gaussian models: 0.287-0.781, Table S4). Overdispersion in Poisson models was assessed using the *check_overdispersion* function from the *performance* package (Lüdecke et al., 2021). No overdispersion was detected for either model ("Total incidence": dispersion ratio = 0.759, Pearson's χ^2 = 87.257, p = 0.975; "Raw ant species richness": dispersion ratio = 0.587, Pearson's χ^2 = 67.489, p = 1). Fixed effects were assessed for collinearity using two approaches: (1) pairwise Spearman correlations (Table S5), where variables with $|r| > 0.7$ were considered highly correlated (Dormann *et al.*, 2013), and (2) Generalized Variance Inflation Factors (GVIF, Table S6) calculated with the *vif* function from the *car* package (Fox & Weisberg, 2019). No variables were collinear (Table S5), and VIF diagnostics indicated that multicollinearity was not present (Table S6; GVIF < 3.16; Dormann et al., 2013). To test for potential spatial autocorrelation, we calculated Moran's I coefficients (10,000 permutations) based on residuals of all models using an inverse geographic distance matrix as a spatial weight, implemented in the R package *ape* (Paradis *et al.*, 2002). Moran's I tests revealed no significant spatial autocorrelation in the residuals of any model (Moran's I range: -0.019 to -0.074, all p > 0.26; Table S7).

RESULTS

Sampled ant community

Sampling at the 32 BEF (Biodiversity-Ecosystem Functioning) experimental plots yielded a total of 55,864 ant individuals and 3,499 incidences belonging to 7 subfamilies, 38 genera, and

77 species (Table S8). Four species occurred over 300 times, and were classified as dominant ants, accounting for 49% of all incidences: *Pheidole nodus*, *Tetramorium wroughtonii*, *Tetramorium smithi*, and *Ectomomyrmex astutus*. Fourteen species occurred only once across traps and sampling periods (18%) and 8 species only twice (10%). The ant community was sufficiently sampled, with 84% of the expected total species number collected (jackknife1 species richness estimator: 89 ± 4, Figure S1). The dominant ant species were part of the shared species pool of BEF plots and CSP (Comparative Study Plots in secondary forest) (Table S8).

Ant community composition

Ant species composition was not related to any environmental variable (Table S9). Dispersion in species composition was significantly higher in the CSP than in the BEF plots (Figure 1; permutation test for homogeneity of multivariate dispersions (PERMDISP): $F = 6.05$, $p = 0.017$). In contrast, trait composition was significantly related to canopy closure ($R^2 = 0.303$, $p = 0.005$) and aspect eastness ($R^2 = 0.184$, $p = 0.048$) (Table S9). However, neither canopy closure nor eastness resulted in an alignment of the BEF ant community with the CSP ant community in trait composition (Figure 1). Dispersion in trait composition did not differ between the BEF and the CSP ants (PERMDISP: $F = 1.18$, $p = 0.292$; Figure 1). A symmetric Procrustes rotation (Procrustes correlation = 0.709, $p < 0.001$) indicated correspondence between the species composition and trait composition ordinations.

Abundance and richness metrics

Total ant incidence decreased with higher canopy closure ($b = -0.105 \pm 0.026$, $z = -4.056$, $p < 0.001$), indicating a 3% reduction in expected ant incidence for each 0.1-unit increase in canopy closure (Figure 2A, Table 1), and increased with soil pH ($b = 0.054 \pm 0.025$, $z = 2.128$, $p =$

0.033; Table 1); both predictors were retained as significant following model averaging across all top-ranked models (ΔAICc ≤ 2). Ant Shannon diversity (b = -0.958 ± 0.279, z = -3.43, p < 0.001) and raw ant species richness decreased with canopy closure (b = -0.094 ± 0.026, z = -3.558, p < 0.001) (Table 1); these effects represent model-averaged parameter estimates across the candidate model set (ΔAICc ≤ 2). However, the effect of canopy closure disappeared when rarefied ant species richness was used as the response, as canopy closure was not significant in the final averaged model for this metric (Table 1). Soil pH had a consistently positive effect across the averaged models on Shannon diversity (b = 0.864 ± 0.279, z = 3.094, p = 0.002; Figure 3), ant species richness (b = 0.07 ± 0.026, z = 2.702, p = 0.007), and rarefied ant species richness (b = 0.255 ± 0.091, z = 2.797, p = 0.005) (Table 1). Ant functional diversity (Rao Q SES) was not related to any environmental variable.

Functional groups and traits

The fraction of leaf litter-nesting ant incidence increased with canopy closure (b = 0.154 ± 0.058, z = 2.664, p = 0.008). (Figure 2B, Table 1). Likewise, the fraction of predator ant incidence increased with canopy closure, converging towards secondary forest (Figure 2C, Table 1). An increase in canopy closure from 0 to 0.1 was associated with a 4% increase in the fraction of predator ant incidence (b = 0.161 ± 0.062, z = 2.596, p = 0.009). In addition to canopy closure, the fraction of predator ants was influenced by exposure, increasing with aspect eastness (b = 0.137±0.06, z = 2.277, p = 0.023) and declining with aspect northness (b = -0.128±0.062, z = -2.071, p = 0.038) (Table 1).

The interaction between tree species richness and canopy closure was significant only in the final model of the fraction of soil-nesting ant incidence (Figure 2F, Table 1). Here, the negative effect of canopy closure was reduced at medium tree species richness levels and reversed in single-species stands, where the fraction of soil-nesting ant incidence increased with

410 increasing canopy closure (b = -0.143 ± 0.069, z = -2.063, p = 0.039). At the community level,
411 the CWM of mandible length increased with canopy closure (b = 0.013 ± 0.003, z = 4.189, p <
412 0.001; Figure 2E, Table 1), surpassing secondary forest values. The remaining community-
413 weighted mean morphological traits (mesosoma length, scape length, tibia length, head width,
414 and head length) showed no significant response to any environmental variable. For each of the
415 traits, model selection identified the intercept-only model as the best-supported model.
416

417 Dominant species

418 Analyses for the four dominant species revealed that the increase in fraction of predator ant
419 incidence was accompanied by an increase in the fraction of the large-bodied predator
420 *Ectomomyrmex astutus* that converged towards secondary forest (b = 0.253 ± 0.086, z = 2.924,
421 p = 0.003; Figure 2D, Table 1). Removing *Ectomomyrmex astutus* from the dataset eliminated
422 the significant effects on predator ant fraction and CWM mandible length. For the remaining
423 dominant ant species (*Pheidole nodus*, *Tetramorium wroughtonii*, *Tetramorium smithi*), the
424 final models did not contain significant variables.
425

426 DISCUSSION

427 Contrary to our expectations, we found that canopy closure, not tree species richness, was the
428 primary biotic variable influencing ant community composition, ant functional diversiry and
429 functional traits in young subtropical plantations. As expected, the abiotic environment
430 independently influenced ant metrics, with a low soil pH decreasing ant species richness
431 metrics, and predatory ants exhibiting sensitivity to exposure. While we hypothesized
432 independent or interactive effects of tree species richness and canopy closure, tree species
433 richness alone had no significant relationship with any ant metric. In contrast, canopy closure

explained variation in incidence, trait composition, and functional group prevalence, highlighting the critical role of canopy closure together with soil conditions in shaping ant communities and likely ant-mediated ecosystem processes in regenerating forests. These results align with prior studies demonstrating that canopy closure has stronger effects on arthropod communities than other biotic habitat variables (Queiroz & Ribas, 2016; Ahuatzin *et al.*, 2019) and suggest that early structural recovery may be more important than tree species richness for re-establishing faunal communities.

Influence of biotic variables

Among the biotic variables examined, canopy closure influenced ant community most consistently. However, the negative effect of canopy closure on ant species richness disappeared when sample sizes were standardized. While earlier studies already found a decrease in ground foraging ant incidence and species richness, our results suggest that the effect of canopy closure on ant species richness may be mediated by ant incidence. Comparison with secondary forest values and other studies indicate that ground-foraging ants often occur less in complex shaded habitat, as long as habitat disturbance is not severe (Parr *et al.*, 2012; Kendrick *et al.*, 2015; Brassard *et al.*, 2023). The reason for this finding in the context of the plantations could be that soil nesting ant species preferentially occur in forest gaps, likely because of improved nesting conditions (Andersen, 2019). In closed complex woody habitat, the leaf litter layer may be thicker and more continuous, increasing the difficulty for soil nesting ants to establish their nests (Huang *et al.*, 2018; Elliott-Vidaurri *et al.*, 2023). This is indicated by our results, where soil nesting ant prevalence tended to decrease with canopy closure, the only exception being single species stands. Only when tree species richness was high an increase in canopy closure led to a low soil nesting ant prevalence comparable to that of secondary forest. On the other hand, leaf litter ant prevalence and predator ant prevalence

459 increased with canopy closure. Both leaf litter ants and predator ants are associated with
460 complex ground habitats and comparatively high demands regarding microclimate (temperature
461 and moisture, preferring warm but not hot and moist but not wet environments) (Kaspari, 2000;
462 Parr & Bishop, 2022).
463
464 Influence of abiotic variables
465 Beyond canopy closure, only predator ants (which were largely a subset of litter ants)
466 additionally responded to exposure as abiotic variable. South-east facing slopes, which warm
467 earlier in the day but are less exposed to late-afternoon heat, were associated with greater
468 predator ant prevalence. The combined effects of canopy closure and exposure may improve
469 habitat conditions for predator ants by creating warm and moist conditions and increased litter
470 cover, which possibly suits requirements of predator ants themselves (cf. Parr & Bishop, 2022)
471 and is likely linked to greater prey availability (Ma *et al.*, 2025). This highlights the
472 vulnerability of predator ants to environmental change (Parr & Bishop, 2022), whereas leaf
473 litter nesting ants have often been found to be relatively resistant towards disturbance (Belshaw
474 & Bolton, 1993; Woodcock *et al.*, 2013).
475 In general, ant species richness was high in the plantations, even surpassing secondary
476 forest values. However, differential effects of soil pH and canopy closure on ant species
477 richness metrics revealed distinct mechanisms influencing sampling results. The positive effect
478 of soil pH on ant species diversity persisted after rarefaction, whereas the effect of canopy
479 closure did not. This suggests that soil acidity is constraining the emergence of ant species in
480 the context of the tree diversity experiment, as had been shown before for the CSP (Comparative
481 Study Plots in secondary forest) (Staab *et al.*, 2014a). Small-scale changes in parent rock
482 material and decomposition of vegetation likely modulate soil pH in the young plantations,

given the complex topography and different tree composition (Sayer, 2005; Scholten *et al.*, 2017).

Soil pH may influence ant communities through both direct and indirect pathways. When soil pH decreases below 5.0, Al^{3+} is solubilized and released into the soil (Kochian *et al.*, 2005). Al^{3+} ions preferentially bind to negatively charged biological components including phospholipids in the plasma membrane, glutamate and aspartate residues in proteins, and phosphate residues in nucleic acids, interfering with membrane functioning and enzyme activity (Panda & Matsumoto, 2007). Such toxicity may propagate through the food web, for example negatively affecting ant larvae that consume contaminated prey. Indirectly, low soil pH may lead to reductions in microbial diversity (Rousk *et al.*, 2010) cascading upward through soil food webs to affect higher trophic levels including microbivorous invertebrates (Ma *et al.*, 2025), ultimately reducing prey availability for ants.

Community reassembly in young plantations

Distinct ant communities between plantation and secondary forest in taxonomic and functional composition suggest slower recovery for ground-dwelling ants compared to more mobile taxa such as bees and wasps (Fornoff *et al.*, 2021). Similar delays in community reassembly are well known for soil arthropods, whose richness may recover faster than composition (Cole *et al.*, 2016). In line with this, plantations showed higher prevalence of soil-nesting ants and a single litter-nesting species shaped the rise in predator ant prevalence. Yet predator ant prevalence remained below secondary forest levels. Notably, functional composition diverged from secondary forest along similar environmental trajectories as the increase in predator ant prevalence. The high values in community weighted means of mandible length, surpassing secondary forest values with canopy closure, are indicative for the separation in trait composition between plantations and secondary forest. We attribute this to the high prevalence

508 of opportunist soil nesting ants in the plantations increasing community weighted mean of
509 mandible length, while their relative absence in secondary forest increases the influence of
510 nectar feeding arboreal nesting ants with short mandibles on community weighted mean values.
511 Both the increase in predator ant prevalence and the increase in the community weighted
512 mean of mandible length were associated with an increase in *Ectomomyrmex astutus* prevalence
513 in the plantations. The increase in *Ectomomyrmex astutus* as a forest colonizer highlights the
514 early state of recovery, where competitively superior species recolonize first (Connell &
515 Slatyer, 1977). As a generalist predator, it indicates the broad recovery of the litter invertebrate
516 prey base and the availability of suitable nesting microhabitats both of which relate to
517 improving habitat structural complexity in recovering plantations. The dominance of
518 *Ectomomyrmex astutus* may cause temporary impoverishment of the ant community, which
519 may explain the low dispersion in species composition in the plantations (Parr & Gibb, 2009).
520 However, dominant species may also facilitate others, especially under heterogeneous ground
521 conditions (Gibb, 2011). Limited dispersal abilities of other forest ants may explain the current
522 absence of tree-species-richness effects on ant community, which may emerge later (Chazdon,
523 2003; Skarbek *et al.*, 2020). The relative scarcity of army ant incidence (Dorylinae) in
524 plantations for example reflects limited dispersal due to wingless queens (Gotwald, 2019).
525 Dispersal constraints, landscape connectivity, and legacy effects can slow full community re-
526 establishment for decades (Hoenle *et al.*, 2022).
527
528 Implications for forest ecosystem restoration
529 Our findings demonstrate that canopy closure is central to reestablishing forest-dwelling ants
530 in young plantations. Rapid canopy closure can be promoted by selecting site-adapted, fast-
531 growing tree species, but single-species stands may hinder reestablishment goals by favoring
532 soil ants, which were more prevalent in plantations compared to secondary forest. Simplified

ground habitats in such stands may further facilitate colonization by invasive species such as the soil-nesting *Solenopsis invicta* (Grodsky *et al.*, 2018). Reforestation strategies should therefore incorporate complementary tree species mixtures and management practices that maintain structurally complex forest floors. Diverse tree stands produce greater litter fall (Huang *et al.*, 2018), and may improve canopy development through facilitative interactions among species with contrasting growth and allocation strategies (Li *et al.*, 2024). While ant species richness was relatively high across sites, its dependence on soil pH suggests that on severely degraded, strongly acidic soils, soil restoration may be a prerequisite for ant community recovery and the ecosystem functions ants provide, warranting further investigation.

As canopy closure increases, the associated increase in predator ant prevalence may enhance predation on forest-floor arthropods, reducing herbivory (e.g., caterpillars) and influencing leaf litter decomposition (e.g., via termite regulation). This functional shift is further supported by the observed increase in the community-weighted mean of mandible length, indicative of a more predatory community composition (Sosiak & Barden, 2021). In secondary forest, high predator ant prevalence suggests increased predation pressure on detritivores such as termites, springtails, and mites (Dejean et al., 2025). Through top-down control, predator ants may prevent competitive dominance within these groups, maintaining a more functionally diverse decomposer community and hence decomposition and soil fertility (Saleem et al., 2012, Lienau et al., 2025). The sensitivity of predator ants to exposure suggests that their recovery is connected to improved microclimate, underscoring the importance of rapid canopy closure particularly on open sun-exposed restoration sites.

CONCLUSION

Our study shows that even young tree plantations can support high ant diversity, underscoring their early biodiversity potential. Predator ants, however, appear to depend on stand development and the emergence of a forest-like microclimate, highlighting the importance of fast-growing tree species to achieve canopy closure and create suitable conditions for forest-floor communities. To disentangle underlying mechanisms, experimental approaches such as canopy thinning or litter manipulations, combined with standardized monitoring and trait measurements will be essential. Such efforts can inform plantation designs that balance rapid structural development with long-term functional resilience, supporting both ecological function and conservation in reforestation landscapes.

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FIGURES

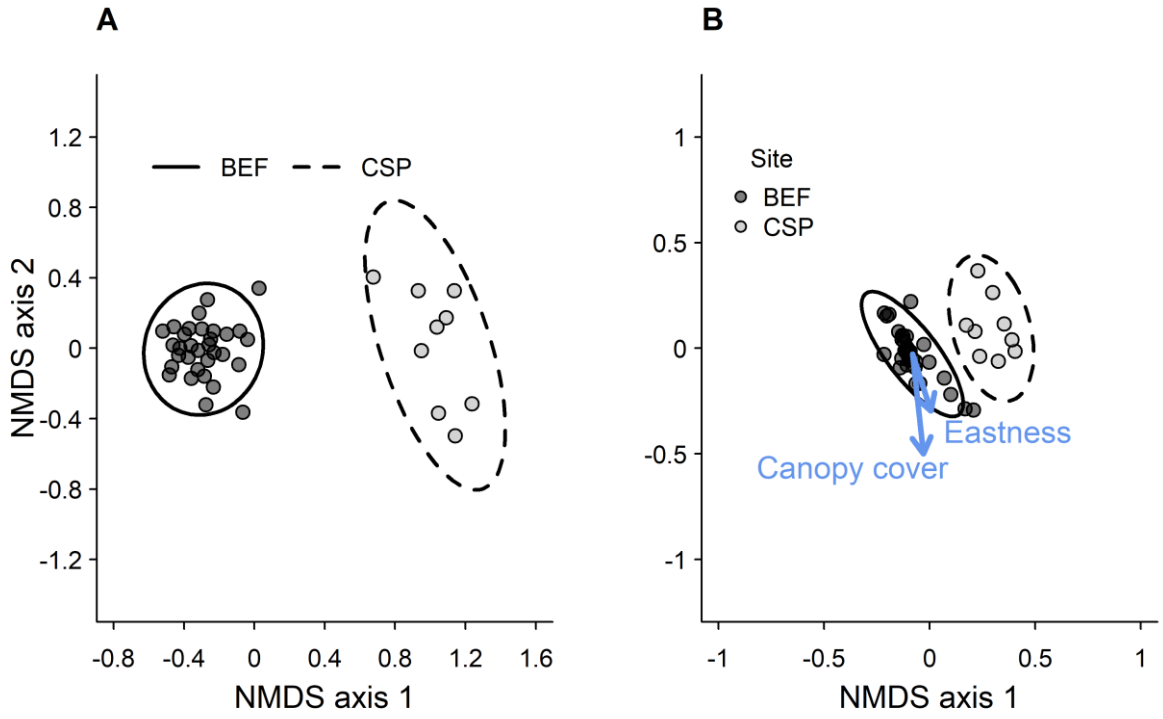

Figure 1 Non-metric multidimensional scaling (NMDS) plots in two dimensions. (A) NMDS of ant species composition (stress = 0.1) based on Bray-Curtis dissimilarity, comparing plot-level communities from the BEF (Biodiversity–Ecosystem Functioning) experimental plots to

those from the CSP (Comparative Study Plots in secondary forest). (B) NMDS of community-weighted mean morphological and categorical trait composition (stress = 0.1) based on Gower dissimilarity. Continuous ellipses (95% CI around group centroids) represent BEF communities, while dashed ellipses represent CSP communities. Environmental variables were fitted to BEF plot level data using the *envfit* function (see Table S9 for *envfit* results), with only significant (at $p<0.05$) relationships shown.

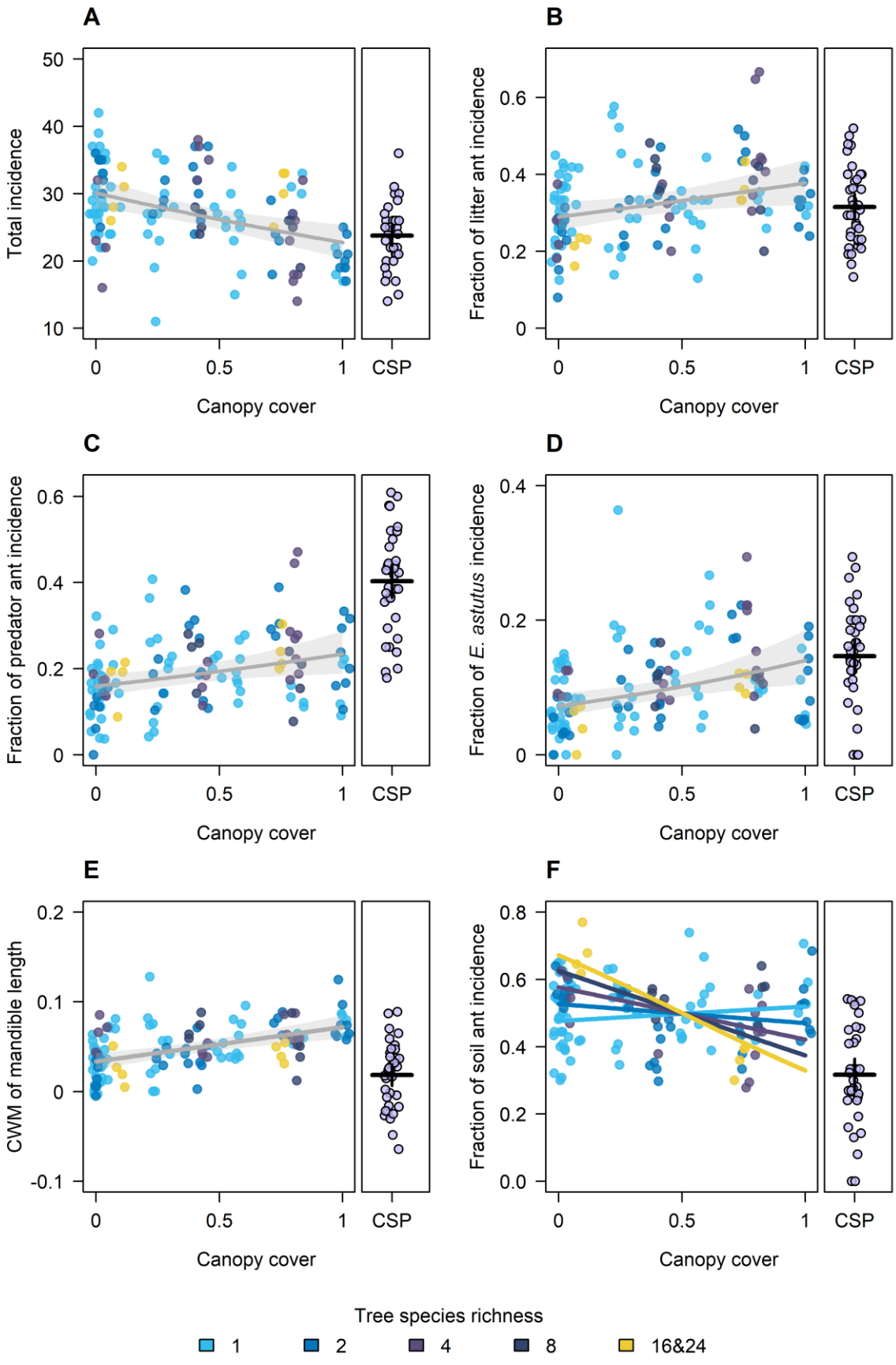
A
B
C
D
E
F
Total incidence
Fraction of litter ant incidence
Fraction of predator ant incidence
Fraction of E. astutus incidence
CWM of mandible length
Fraction of soil ant incidence
Canopy cover
CSP
Tree species richness
1
2
4
8
16&24

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Figure 2 Model plots of significant relationships (at $p<0.05$) of ant community metrics with canopy closure for the BEF (Biodiversity-Ecosystem Functioning) experimental plots. The points show raw data on trap level. For the BEF tree species richness is color-coded from light blue (1 species) to dark blue (8) and yellow (16 and 24 species). CSP (Comparative Study Plots in secondary forest) values are in light grey and shown for comparison only. For the BEF, the line indicates predictions from (generalized) linear mixed-effects models, with 95% confidence intervals (except for interaction plot in F); see Table 1 for full model details). Total ant incidence (A) declined with canopy closure, converging toward CSP values. Fraction of leaf litter-nesting ant incidence (B) increased with canopy closure but remained within the CSP range. Fraction of predator ant incidence (C) and that of the predator *Ectomomyrmex astutus* (D) increased with canopy closure, also converging toward CSP values. Community-weighted means of mandible length increased with canopy closure, surpassing CSP values (E). Only fraction of soil-nesting ant incidence (F) showed a significant interaction: it decreased with canopy closure in high-diversity plots to converge towards CSP values but increased in single-species stands.

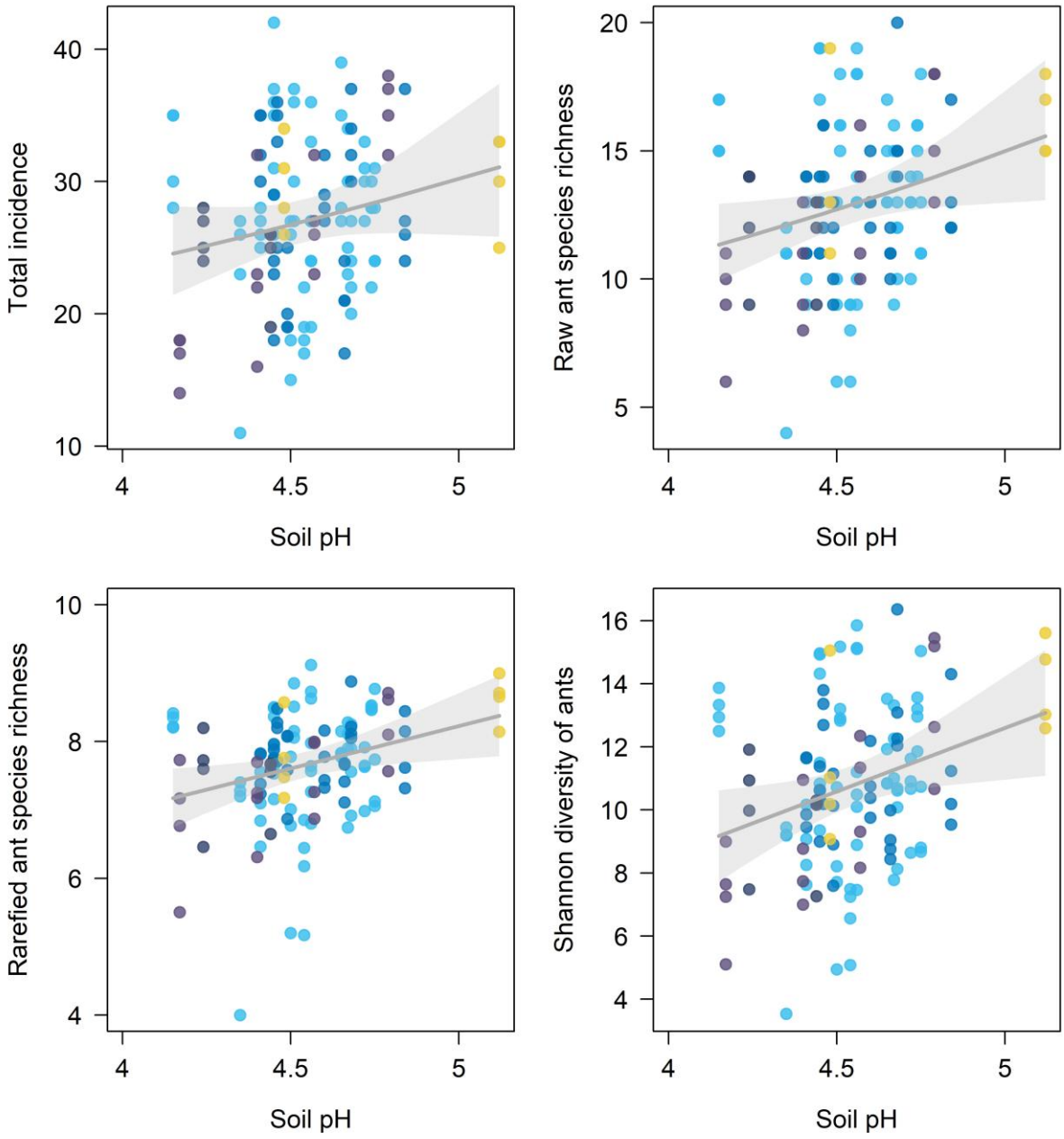

Figure 3 Model plots showing significant relationships ($p < 0.05$) between total ant incidence and species diversity metrics and soil pH for the BEF (Biodiversity-Ecosystem Functioning) experimental plots. Points represent raw trap-level data; tree species richness is color-coded from light blue (1 species) to dark blue (8) and yellow (16 and 24 species). Lines indicate predictions from (generalized) linear mixed-effects models, with 95% confidence intervals.

Table 1 Full averages of (generalized) linear mixed-effects models for ant metrics from BEF (Biodiversity-Ecosystem Functioning) experimental plots. Fixed effects are ranked by the absolute value of their z-values. Models with a single best fit (no model averaging applied) are indicated by an asterisk (*). Models without any selected variables in model averaging (i.e., intercept only models) are omitted for simplicity; these included the fraction of dominant ants in most cases (*Pheidole nodus, Tetramorium wroughtonii, Tetramorium smithi*), community-weighted means (CWM) of head length, head width, scape length, eye length, Weber's length, tibia length, as well as functional diversity (Rao's Q standardized effect sizes)).

Variable	Estimate±SE	z	p
Total incidence (Poisson)			
Canopy closure	**-0.105±0.026**	**-4.056**	**<0.001**
Soil pH	**0.054±0.025**	**2.128**	**0.033**
Northness	0.012±0.022	0.536	0.592
Tree species richness	0.006±0.017	0.375	0.708
Eastness	-0.003±0.013	-0.262	0.793
Raw ant species richness (Poisson)			
Canopy closure	**-0.094±0.026**	**-3.558**	**<0.001**
Soil pH	**0.07±0.026**	**2.702**	**0.007**
Tree species richness	0.012±0.021	0.541	0.588
Tree species richness : Canopy closure	0.01±0.022	0.431	0.666
Eastness	0.002±0.01	0.147	0.883
Rarefied ant species richness (Gaussian)			
Soil pH	**0.255±0.091**	**2.797**	**0.005**
Canopy closure	-0.166±0.132	-1.255	0.209
Shannon diversity (Gaussian)*			
Canopy closure	**-0.958±0.279**	**-3.43**	**<0.001**
Soil pH	**0.864±0.279**	**3.094**	**0.002**

Fraction of litter ant incidence (Binomial)

Canopy closure	**0.154±0.058**	**2.664**	**0.008**
Tree species richness : canopy closure	0.127±0.076	1.670	0.095
Eastness	0.101±0.064	1.574	0.115
Soil pH	-0.068±0.067	-1.023	0.307
Northness	-0.064±0.066	-0.971	0.331
Tree species richness	-0.054±0.061	-0.887	0.375

Fraction of soil ant incidence (Bionomial)

Tree species richness : canopy closure	**-0.148±0.07**	**-2.103**	**0.035**
Canopy closure	-0.061±0.053	-1.157	0.247
Tree species richness	0.063±0.053	1.186	0.236
Soil pH	-0.05±0.057	-0.876	0.381
Eastness	-0.017±0.037	-0.449	0.653
Northness	0.013±0.034	0.384	0.701

Fraction of predator ant incidence (Binomial)

Canopy closure	**0.161±0.062**	**2.596**	**0.009**
Eastness	**0.137±0.06**	**2.277**	**0.023**
Northness	**-0.128±0.062**	**-2.071**	**0.038**
Soil pH	-0.02±0.045	-0.451	0.652

Fraction of E. astutus *incidence (Binomial)*

Canopy closure	**0.253±0.086**	**2.924**	**0.003**
Soil pH	-0.058±0.082	-0.701	0.483
Eastness	0.037±0.072	0.519	0.604
Northness	-0.017±0.05	-0.330	0.741
Geomorphon ridge	0.088±0.275	0.321	0.749
Geomorphon slope	0.072±0.231	0.312	0.755

Geomorphon summit	0.089±0.297	0.299	0.765
Geomorphon valley	0.028±0.151	0.188	0.851
Geomorphon spur	0.01±0.143	0.073	0.942
CWM mandible length (Gaussian)*			
Canopy closure	**0.013±0.003**	**4.189**	**<0.001**

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Supplementary material

Canopy closure re-establishes ants in young tree plantations, while low soil pH limits ant diversity

Contents

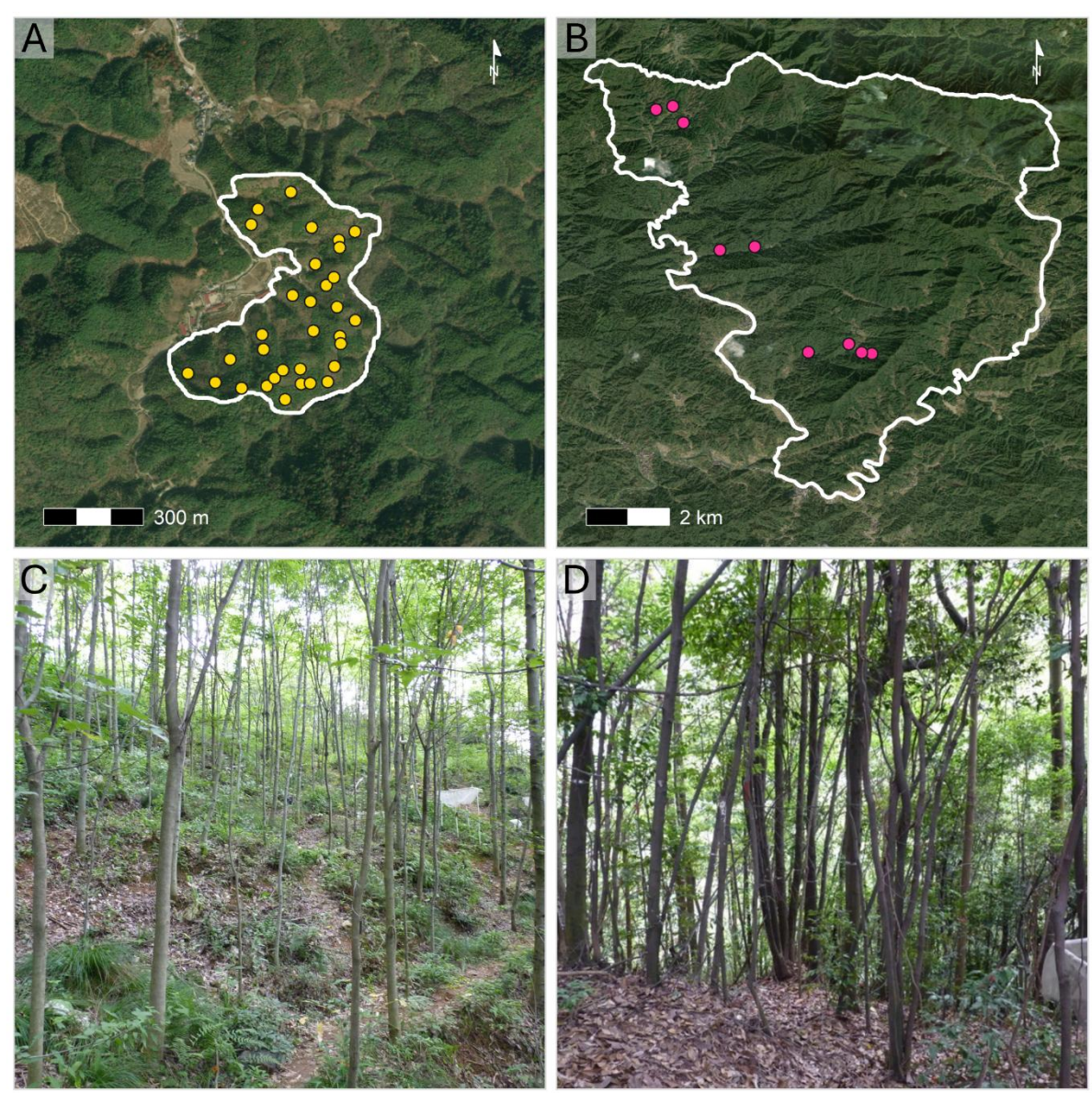

Figure S1. (A) Location of the BEF (Biodiversity–Ecosystem Functioning) experimental plots (yellow points) within the boundary of BEF-China Site B (white) (coordinates: 29°5'13.9"N, 117°55'46.3"E). (B) Location of the comparative study plots in secondary forest (CSP, red points) within the boundary of the Gutianshan National Nature Reserve (white) (coordinates: 29°14'47.9"N, 118°6'51.1"E). Basemap imagery © Esri and contributors (World Imagery; accessed via the R package *maptiles* (Giraud, 2020), 2026-02-26). GNNR boundary © OpenStreetMap contributors (downloaded 2026-02-26). BEF-China Site B boundary derived from the extent of a digital elevation model (DEM) provided/processed by Karsten Schmidt

and Thorsten Behrens (University of Tuebingen). (C) BEF plot photograph (2019; © Michael Staab). (D) Early-successional CSP plot photograph (2011; © Michael Staab).

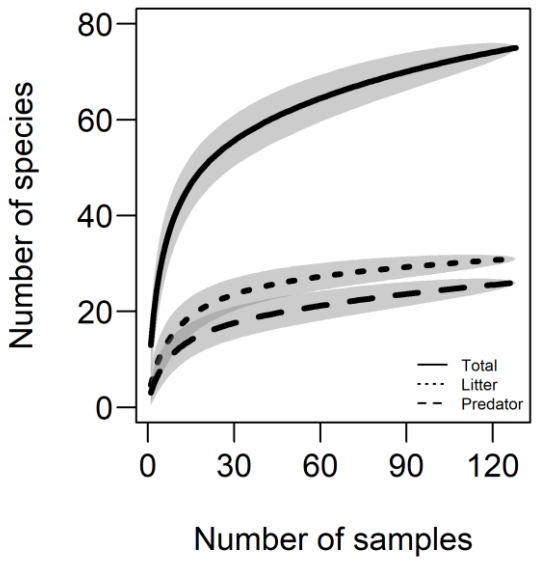

Figure S2. Sample-based species accumulation curves for BEF (Biodiversity-Ecosystem Functioning) experimental plots. The solid line represents the total ant community, the dotted line litter nesting ants, and the dashed line predator ants. Curves are based on 10,000 permutations, and shaded areas give 95% confidence intervals. Estimated sampling efficiency for the total ant community: 84% of the expected total species number (jackknife1 species richness estimator: 89 ± 4). Estimated sampling efficiency for the litter ant community: 86% of the expected total species number (jackknife1 species richness estimator: 36 ± 2). Estimated sampling efficiency for the predator ant community: 79% of the expected total species number (jackknife1 species richness estimator: 33 ± 3).

Table S1 Morphological (continuous) traits used for characterizing ant community (adapted from Hoenle et al., 2023).

Trait	Characteristics
Weber's length	Closely related to body size and linked to metabolism (Gibb *et al.*, 2018) and microclimate (Kaspari, 1993)
Head length	Indicator of diet, longer head length in predators (Weiser & Kaspari, 2006)
Head width	Correlates positively with bite force (Rühr *et al.*, 2024), can be indicative of feeding mode (Weiser & Kaspari, 2006)
Mandible length	Length of mandibles relates to diet, with predators typically having longer mandibles (Gibb & Cunningham, 2013; Sosiak & Barden, 2021)
Scape length	Sensory abilities: longer scapes facilitate following of pheromone trails (Weiser & Kaspari, 2006); shorter scapes in complex environments; predators have, on average, shorter scapes (Sosiak & Barden, 2021); higher environmental complexity might select for shorter scapes (Kaspari & Weiser, 1999)
Tibia length	Indicative of foraging speed (Feener *et al.*, 1988); predators often have shorter legs (Sosiak & Barden, 2021); longer legs enable thermoregulatory strategy (Sommer & Wehner, 2012); higher environmental complexity might select for shorter legs (Kaspari & Weiser, 1999), but see (Guilherme *et al.*, 2019)

Table S2 Categorical traits used for characterizing ant community. Categories based on Hölldobler & Wilson 1990, Brown 2000, Blüthgen & Feldhaar 2009 and applied according to Brown 2000, Hölldobler & Wilson, and own observations by the senior author Michael Staab.

Trait	Value	Characteristics
Nest site (Brown, 2000; Blüthgen & Feldhaar, 2009)	Leaf litter	Nest in the leaf litter at the soil-atmosphere interface
	Soil	Nest in mineral soil
	Bivouac	Temporary nest formed by worker aggregation
	Arboreal	Nest in the tree canopy
	Deadwood	Nest in decaying wood
Colony size (Hölldobler & Wilson, 1990)	<100	Colony typically contains under 100 workers
	<1000	Colony typically contains between 100 and 1000 workers
	>1000	Colony typically contains between 1000 and 10000 workers
	>10000	Colony typically contains more than 10000 workers
Diet (Brown, 2000; Blüthgen & Feldhaar, 2009)	Generalist	Opportunist omnivores
	Sugar feeder generalist	Opportunist omnivores, but able to exploit additional sugar sources such as extrafloral nectaries and sugary excretions by other insects
	Predator	Hunters and scavengers, mostly on arthropods.
Polymorphism (Hölldobler & Wilson, 1990)	Monomorphic	Workers cannot be separated into morphologically distinct worker castes
	Dimorphic	Colony has two morphologically distinct worker castes (minors and majors)
	Polymorphic	Colony has a continuous range of worker sizes

Table S3 Environmental variables measured in the 32 BEF (Biodiversity-Ecosystem Functioning) experimental plots in addition to the experimental design variable tree species richness

Variable	**Range**	**Median**	**Mean ± SD**
Canopy closure (%)	0-100	35	38±35
Northness	-0.9-0.9	-0.1	-0.1±0.6
Eastness	-0.9-1	-0.2	-0.1±0.6
Soil pH	4.2-5.1	4.5	4.5±0.2
Geomorphon (factor)			6 levels: hollow, ridge, slope, spur, summit, valley

Table S4 Kolmogorov-Smirnov test p-values assessing goodness-of-fit for Gaussian models via DHARMa simulated residuals. Values above 0.05 indicate adequate fit.

Model	**KS p**
Rarefied ant species richness	0.287
Shannon diversity	0.781
CWM mandible length	0.679

Table S5 Spearman's rank correlation coefficients (ρ) among environmental predictor variables at the BEF (Biodiversity-Ecosystem Functioning) experimental plots. None of the variable pairs were collinear ($|\rho| > 0.7$; Dormann et al., 2013).

	Tree species richness	**Canopy cover**	**Northness**	**Eastness**	**Soil pH**
Tree species richness	1	0.34	-0.3	0.09	-0.09
Canopy cover	0.34	1	0.1	0.12	0.08
Northness	-0.3	0.1	1	0.13	0.19
Eastness	0.09	0.12	0.13	1	-0.04
Soil pH	-0.09	0.08	0.19	-0.04	1

Table S6 Generalized variance inflation factors (GVIF^(1/(2×Df))) for each predictor (rows) across the nine response models (columns). All values fell well below the threshold of concern (> 3.16), indicating no multicollinearity issues.

Predictor	**Total incidence**	**Raw ant species richness**	**Rarefied ant species richness**	**Shannon diversity**	**Fraction of litter ant incidence**	**Fraction of soil ant incidence**	**Fraction of predator ant incidence**	**Fraction of E.astutus incidence**	**CWM mandible length**
Tree species richness (log2)	1.3	1.31	1.29	1.29	1.3	1.29	1.31	1.31	1.29
Canopy closure	1.17	1.18	1.16	1.16	1.18	1.17	1.17	1.16	1.16
Northness	1.09	1.09	1.1	1.1	1.08	1.08	1.09	1.09	1.1
Eastness	1.16	1.16	1.14	1.14	1.14	1.15	1.14	1.1	1.14
Soil pH	1.33	1.36	1.33	1.33	1.34	1.33	1.36	1.32	1.33
Geomorphon	1.14	1.15	1.15	1.15	1.14	1.14	1.15	1.14	1.15
Tree species richness : canopy closure	1.17	1.19	1.18	1.18	1.18	1.17	1.19	1.2	1.18

Table S7. Moran's I statistics and permutation-based p-values testing for spatial autocorrelation in plot-level conditional residuals of model-averaged mixed-effects models for each response variable. No significant spatial autocorrelation was detected in any model.

Model	**Observed**	**Expected**	**SD**	**p-value**
Total incidence	0.02	-0.032	0.039	0.173
Raw ant species richness	-0.033	-0.032	0.038	0.993
Rarefied ant species richness	-0.087	-0.032	0.038	0.15
Shannon diversity	-0.071	-0.032	0.037	0.303
Fraction of litter ant incidence	-0.027	-0.032	0.038	0.898
Fraction of soil ant incidence	-0.028	-0.032	0.038	0.911
Fraction of predator incidence	-0.077	-0.032	0.038	0.237
Fraction of *E. astutus* incidence	0.016	-0.032	0.038	0.207
CWM mandible length	-0.071	-0.032	0.038	0.303

Table S8. Ant species sampled at BEF (Biodiversity-Ecosystem Functioning) experimental plots and CSP (Comparative Study Plots in secondary forest), their incidence and categorical traits assigned based on literature and own observation (see Table S1)

Subfamily	**Genus**	**Species**	**Incidence BEF**	**Incidence CSP**	**Nest**	**Workers**	**Diet**	**Polymorphism**
Dolichoderinae	*Iridomyrmex*	*anceps*	106	0	soil	>1000	sugar feeder generalist	monomorphic
	Ochetellus	*glaber*	20	0	arboreal	<1000	generalist	monomorphic
	Tapinoma	cf. *indicum*	8	0	litter	<100	generalist	monomorphic
	Tapinoma	*melanocephalum*	30	0	arboreal	<1000	sugar feeder generalist	monomorphic
	Technomyrmex	*antennus*	0	2	soil	<1000	generalist	monomorphic
	Technomyrmex	*brunneus*	32	0	arboreal	<1000	sugar feeder generalist	monomorphic
	Technomyrmex	*obscurior*	38	55	soil	>1000	generalist	monomorphic
Dorylinae	*Aenictus*	*bobaiensis*	37	8	bivouac	>10000	predator	monomorphic
	Aenictus	*fuchuanensis*	2	1	bivouac	>10000	predator	monomorphic
	Aenictus	*gutianshanensis*	0	1	bivouac	>10000	predator	monomorphic
	Aenictus	*henanensis*	1	0	bivouac	>10000	predator	monomorphic
	Aenictus	*hodgsoni*	23	13	bivouac	>10000	predator	monomorphic
	Dorylus	*orientalis*	1	0	bivouac	>10000	predator	polymorphic
Ectatomminae	*Stictoponera*	*quadrutinodules*	2	3	soil	<100	predator	monomorphic
Formicinae	*Camponotus*	*albosparsus*	129	0	soil	<1000	sugar feeder generalist	polymorphic
	Camponotus	*pseudoirritans*	41	106	arboreal	>1000	sugar feeder generalist	polymorphic

Camponotus	*rubidus*	0	1	deadwood	>1000	sugar feeder generalist	polymorphic
Camponotus	*vitiosus*	18	0	arboreal	<100	sugar feeder generalist	polymorphic
Formica	*japonica*	0	27	soil	>100	sugar feeder generalist	monomorphic
Lepisiota	cf. *capensis*	95	0	arboreal	<100	sugar feeder generalist	monomorphic
Nylanderia	*bourbonica*	1	0	soil	>1000	generalist	monomorphic
Nylanderia	*emmae*	2	0	soil	<1000	generalist	monomorphic
Nylanderia	*flavipes*	2	0	NA	<1000	generalist	monomorphic
Nylanderia	*picta*	69	1	litter	<1000	generalist	monomorphic
Nylanderia	sp.1	2	0	NA	<1000	generalist	monomorphic
Nylanderia	sp.3	39	3	NA	<1000	generalist	monomorphic
Nylanderia	sp.6	1	5	arboreal	<1000	generalist	monomorphic
Nylanderia	sp.9	3	0	NA	NA	generalist	monomorphic
Paraparatrechina	*sauteri*	3	0	litter	>1000	generalist	monomorphic
Paraparatrechina	*neela*	1	0	NA	NA	generalist	monomorphic
Paratrechina	*umbra*	19	5	litter	<1000	generalist	monomorphic
Plagiolepis	sp.2	1	0	NA	<100	generalist	monomorphic
Polyrhachis	*demangei*	0	2	arboreal	<1000	sugar feeder generalist	polymorphic
Polyrhachis	*dives*	139	3	arboreal	>10000	sugar feeder generalist	polymorphic
Polyrhachis	*fellowesi*	0	1	arboreal	<1000	sugar feeder generalist	polymorphic

	Polyrhachis	*illaudata*	2	74	arboreal	<1000	sugar feeder generalist	polymorphic
	Polyrhachis	*lamellidens*	0	8	arboreal	<1000	sugar feeder generalist	polymorphic
	Polyrhachis	*shixingensis*	0	14	arboreal	>1000	sugar feeder generalist	polymorphic
	Polyrhachis	sp.4	0	1	arboreal	<1000	sugar feeder generalist	polymorphic
	Prenolepis	*naoroji*	1	8	NA	<1000	generalist	monomorphic
Myrmicinae	*Aphaenogaster*	sp.1	170	63	soil	>1000	generalist	monomorphic
	Aphaenogaster	sp.2	0	5	soil	>1000	generalist	monomorphic
	Aphaenogaster	sp.3	0	1	soil	>1000	generalist	monomorphic
	Cardiocondyla	*kagutsuchi*	7	0	soil	<100	generalist	monomorphic
	Carebara	*altinodus*	47	0	litter	>10000	predator	dimorphic
	Carebara	*vespillo*	13	4	bivouac	>10000	predator	polymorphic
	Carebara	sp.6	1	0	litter	>1000	predator	dimorphic
	Crematogaster	cf. *rogenhoferi*	97	0	arboreal	>10000	sugar feeder generalist	polymorphic
	Crematogaster	sp.5	0	1	soil	>1000	generalist	monomorphic
	Dilobocondyla	*fouqueti*	0	1	arboreal	<100	predator	monomorphic
	Kartidris	*galos*	0	3	litter	>100	predator	monomorphic
	Monomorium	*chinense*	29	0	soil	<1000	generalist	monomorphic
	Monomorium	*intrudens*	3	0	arboreal	<1000	generalist	monomorphic
	Myrmecina	*sauteri*	1	0	litter	<100	predator	monomorphic

Pheidole	*laevithorax*	8	0	litter	<1000	generalist	dimorphic
Pheidole	*nodus*	587	71	soil	>10000	generalist	dimorphic
Pheidole	*pieli*	14	0	litter	>1000	generalist	dimorphic
Pheidole	*rabo*	39	0	litter	<1000	generalist	dimorphic
Pheidole	*roberti*	111	0	soil	>1000	generalist	dimorphic
Pheidole	sp.11	15	0	soil	NA	generalist	dimorphic
Pheidole	*tumida*	0	2	soil	>10000	generalist	dimorphic
Pristomyrmex	*punctatus*	27	0	bivouac	>10000	generalist	monomorphic
Recurvidris	*recurvispinosa*	11	0	litter	<1000	generalist	monomorphic
Solenopsis	sp.1	27	0	litter	<1000	generalist	monomorphic
Solenopsis	sp.2	3	0	litter	<1000	generalist	monomorphic
Strumigenys	*canina*	3	0	litter	<100	predator	monomorphic
Strumigenys	*feae*	11	0	litter	<100	predator	monomorphic
Strumigenys	*leptothrix*	1	0	litter	<100	predator	monomorphic
Temnothorax	*argentipes*	2	0	litter	<100	generalist	monomorphic
Temnothorax	sp.3	56	0	litter	<100	generalist	monomorphic
Temnothorax	sp.5	1	0	litter	<100	generalist	monomorphic
Tetramorium	*nipponense*	9	13	arboreal	<1000	generalist	monomorphic
Tetramorium	*parvispinum*	10	0	litter	<100	generalist	monomorphic

	Tetramorium	*shensiense*	17	25	litter	<1000	generalist	monomorphic
	Tetramorium	*smithi*	341	0	litter	<100	generalist	monomorphic
	Tetramorium	sp.13	1	0	NA	NA	generalist	monomorphic
	Tetramorium	*wroughtonii*	459	7	soil	>10000	sugar feeder generalist	monomorphic
Ponerinae	*Anochetus*	*risii*	55	5	soil	<100	predator	monomorphic
	Brachyponera	*luteipes*	18	34	litter	<1000	predator	monomorphic
	Brachyponera	*chinensis*	14	68	litter	<1000	predator	monomorphic
	Cryptopone	sp.2	9	0	litter	<100	predator	monomorphic
	Ectomomyrmex	*annamitus*	0	5	litter	<100	predator	monomorphic
	Ectomomyrmex	*astutus*	338	123	litter	<100	predator	monomorphic
	Ectomomyrmex	*javanus*	9	3	litter	<100	predator	monomorphic
	Euponera	*sharpi*	32	0	litter	<100	predator	monomorphic
	Hypoponera	sp.1	5	0	litter	<100	predator	monomorphic
	Hypoponera	sp.4	1	0	litter	<100	predator	monomorphic
	Leptogenys	*kitteli*	8	42	bivouac	>10000	predator	monomorphic
	Odontomachus	*monticola*	18	30	soil	<100	predator	monomorphic
	Discothyrea	*banna*	2	0	litter	<100	predator	monomorphic
	Discothyrea	*sauteri*	0	2	litter	<100	predator	monomorphic
	Proceratium	*bruelheidei*	1	0	soil	<100	predator	monomorphic

Pseudomyrmecinae	*Tetraponera*	*convexa*	0	6	arboreal	<100	sugar feeder generalist	monomorphic

Table S9 Results of a permutation-based correlation analysis using *envfit* between environmental variables and NMDS axes representing ant species composition and functional trait composition. Each scaled environmental variable is correlated with the two NMDS axes. The squared correlation coefficient (R^2), and the significance of the relationship (*p*) based on 10,000 permutations are shown.

Variable	**NMDS1**	**NMDS2**	**R^2**	**p**
Species composition				
Tree species richness	0.991	0.132	0.02	0.749
Canopy cover	0.876	0.482	0.16	0.077
Northness	-0.997	-0.075	0.123	0.149
Eastness	0.791	-0.612	0.05	0.479
Soil pH	-0.995	-0.097	0.002	0.967
Trait composition				
Tree species richness	0.969	0.246	0.026	0.685
Canopy cover	**-0.488**	**-0.873**	**0.303**	**0.005**
Northness	-0.995	0.104	0.116	0.162
Eastness	**0.982**	**0.189**	**0.184**	**0.048**
Soil pH	-0.995	-0.1	0.075	0.324

Permutation test based on 10,000 unrestricted permutations.

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