

Forest growth strengthens diversity effects on multitrophic interactions

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Title: Forest growth strengthens diversity effects on multitrophic interactions

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Summary paragraph:

Positive effects of plant diversity on productivity increase over time through stronger complementarity among species¹. However, whether these temporal dynamics propagate across trophic levels towards higher-order ecosystem functions remains largely unexplored. Here we tested how tree diversity drives attack rates and trophic interactions of host-parasitoid communities over the course of a decade in a young large-scale forest experiment. We found that the effect of tree species richness on parasitism increased over time, driven both by accelerating stand productivity and changes in food web structure. Parasitism increasingly reflected an attenuation of consumer responses to accumulating resources and a shift towards tree and parasitoid

diversity-dependent regulation. The influence of parasitoid species richness on parasitism rose over time as generalist parasitoids concentrated interactions on shared hosts, increasing overall resource use and network robustness to species extinctions. Our results reveal that the functional benefits of biodiversity strengthen over time through shifts in the mechanisms linking trophic levels, underscoring the long-term value of diversity-focused restoration.

Main Text:

Forest restoration and reforestation have been recognized as key actions for addressing global loss of biodiversity and ecosystem functionality². Biodiversity–ecosystem functioning (B-E-F) research has broadly shown positive ‘diversity effects’ – the beneficial influence of species diversity on organisms and functions^{3,4} – providing a scientific basis for restoration strategies^{5,6}. Yet, how biodiversity effects change as ecosystems develop remains uncertain, as most biodiversity-functioning studies lack a long-term temporal component. This uncertainty is central to restoration, where ecosystem functioning emerges from feedbacks and the turnover of species and interactions unfolding over time.

In forests, higher tree species richness supports a multitude of primary ecosystem functions such as productivity, nutrient cycling, and temperature buffering^{7–9}. These diversity effects propagate beyond primary producers, shaping biodiversity at higher trophic levels and associated functions including herbivory, predation, and parasitism^{4,10}. Yet most evidence stems from snapshot studies lacking temporal replication, and little is known about how the mechanisms linking biodiversity to ecosystem functions change through time. Several studies have examined how plant diversity effects on productivity increase over time¹, but far fewer have explored the temporal dynamics of diversity effects across multiple trophic levels^{11,12}.

This may be particularly relevant in young forest stands, where tree growth drives the accumulation of plant biomass and deadwood, canopy closure, and a gradual increase in structural complexity¹³. These processes transform local habitat conditions, recruiting new species assemblages and reorganizing or modifying their interactions^{14,15}. Furthermore, biomass accumulation and structural development tends to accelerate in stands with higher tree diversity, reflecting greater resource partitioning (or “complementarity”) among tree species^{7,16–18}. Together, tree diversity and stand age are thus expected to exert strong, interactive effects on the regulation of biodiversity and ecosystem functioning across multitrophic food webs^{10,19,20}. Understanding these dynamics is necessary for predicting the long-term outcomes of forest restoration on higher trophic levels and ecosystem functions.

Parasites, kleptoparasites, and parasitoids – here collectively referred to as “parasitoids” – comprise a substantial proportion of all animal species and account for a large share of trophic interactions^{21,22}. By occupying higher trophic levels, parasitoids are especially sensitive to habitat change, as environmental filtering acts both directly on their own requirements and indirectly through host availability^{23,24}. Tree diversity can enhance parasitoids both directly by modifying habitat structure through increased stand biomass, and indirectly by promoting host abundance and diversity^{25,26}. The frequency of attacks by parasitoids – here “parasitism” – is a key higher-order ecosystem function that structures food webs by promoting species coexistence through top-down regulation of host populations^{27,28}. Higher parasitoid diversity may increase parasitism either through complementary niche partitioning, which improves resource-use efficiency, or by increasing the probability that communities include highly efficient consumer species²⁹. However, effects of tree diversity on parasitism may be ‘diluted’ when higher host abundance or diversity reduce encounter rates between parasitoids and their preferred hosts^{30,31}. Indeed, parasitism can remain relatively stable against plant species loss or habitat disturbance despite shifts in host and

parasitoid diversity^{29,32} or interactions³³, likely because of strong dilution effects counteracting bottom-up diversity pathways.

The relative strength of the mechanisms regulating parasitism are expected to change during forest growth. In very young stands, host and parasitoid communities may be constrained by limited or unstable resources^{34–36}. As forests develop, parasitoids may benefit from increasing tree diversity effects on biomass production, structural complexity, and resource availability and stability^{7,17,35}, while modified biotic interactions may facilitate higher parasitism^{37–39}. We therefore hypothesized that tree diversity effects on parasitism increase over time, mediated by two pathways (1) bottom-up benefits from accumulating stand biomass ascending across trophic levels, and (2) effects of parasitoid diversity on parasitism increasing over time from greater complementarity in resource use – consistent with what is generally observed for productivity of plant communities¹.

Here, using a decade of data from the world's largest forest biodiversity experiment, we tested how forest tree diversity shapes multitrophic interactions and parasitism during forest growth. The experiment comprises two forest sites established in 2009 and 2010 with a total of 566 plots covering a manipulated tree diversity gradient from 1 to 24 species⁴⁰. To test our predictions, we analyzed quantitative food webs of cavity-nesting bees, wasps and their parasitoids from 88 forest plots over ten years of young forest growth. From 2014 to 2023, we tracked the abundance, diversity, and antagonistic interactions among 75 host and 116 parasitoid species from more than 65,000 brood cells (Supplementary Tables 1 and 2), and assessed how stand age moderated the effects of tree, host, and parasitoid diversity on parasitism. We used generalized linear mixed models (GLMMs) to quantify interactions between diversity effects and forest stand age (4–14 years), and evaluated all multi-trophic pathways with path analyses. With this design, we investigate the temporal dynamics of

multitrophic diversity effects and assess the potential long-term benefits of restoring forests with high tree diversity on a higher-order ecosystem function.

Diversity effects increase over time

Parasitism increased with the experimentally-manipulated tree species richness and this relationship increased steadily over time (Fig. 1a,d). The difference in parasitism between monocultures and 16-species mixtures shifted from being negligible (-0.97% at age 4, CI = -4.5-2.6) to clearly positive after ten years of forest growth (6.5% at age 14, CI = 2.7-10.4, Fig. 1d). Our results thus extend earlier findings on BEF temporal dynamics by revealing that tree diversity not only accelerates productivity over time⁷, but also increasingly strengthens parasitism, associated with higher host suppression. Diversity effects on ecosystem functioning can become stronger over time either because of increasing performance in high-diversity communities, decreasing performance at low-diversity communities, or both⁴¹. Parasitism increased over time in 16-species mixture plots, remained relatively stable in 8-species mixtures, and decreased in 4- and 2-species mixtures and in monocultures (Fig. 1b,e). This suggests that forest tree diversity may promote host suppression by increasing parasitism while preventing the functional declines observed in tree species-poor stands. Following our hypothesis, the positive relationship between parasitoid diversity and parasitism also increased over time (Fig. 1c,f). The direct effect of naturally-assembling parasitoid species richness on parasitism approximately doubled during a decade of forest growth (two-fold increase in slope). Fourteen years after forest planting, parasitoids attacked an average of 67% (CI = 54-78%) of brood cells in the most diverse parasitoid communities (10 species), compared with 5% in single parasitoid species communities (CI = 3-7%). The temporal increase in parasitism was confined to high-richness parasitoid communities, while low-richness communities remained functionally static. In contrast, tree diversity effects on productivity and biomass accumulation increased over time

across the entire species richness gradient (but more so in high-richness communities)⁷.

Ecosystem functioning at higher trophic levels may thus be more dependent on high-diversity communities over the long term than primary production. Our results also suggest that the impacts of parasitoid species loss from food webs are likely higher than reflected by short-term studies.

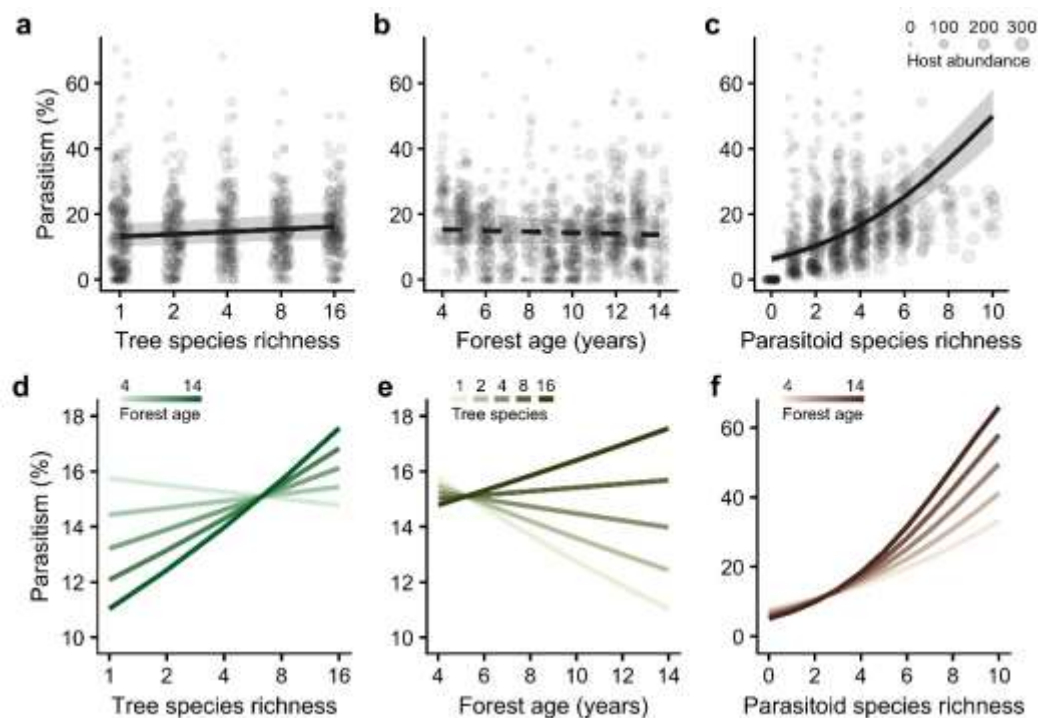


Fig. 1. Effect of tree diversity and parasitoid diversity on parasitism increase over time.

a, b, c, GLMM-predicted fixed marginal (net) effects of forest tree species richness, forest age, and parasitoid species richness on parasitism rate ($\pm$ 95% CI), and **d, f,** their increase in slope across five representative stand ages or **e,** across the tree species richness gradient. Note that **d** and **e** show the same interaction effect from different perspectives. Point size represents host abundance (number of brood cells constructed). Dashed line indicates non-significant relationship. Parasitism models without zeroes (no brood cells attacked) showed no qualitative differences.

Bottom-up benefits from tree richness

Accelerating accumulation of stand biomass resulting from increased complementarity among tree species⁷ had important bottom-up effects linking tree richness to multitrophic diversity and parasitism (Fig. 2a,b). Indeed, increased productivity as well as higher tree functional diversity from planting more tree species promoted the species richness of host communities, both directly or indirectly through increased abundance (brood cell production). Notably, host abundance exhibited moderate temporal autocorrelation across years, but with high uncertainty due to interannual variability (Extended Data Fig. 1). Despite this variation, both path analyses and mixed models showed consistent host community responses to tree FD and stand biomass (Supplementary Tables 3 and 4). Stand biomass partially affected host and parasitoid communities through the regulation of understory temperatures (Extended Data Table 1); an indication of how tree diversity can benefit forest communities in the long-term through greater temperature buffering⁹. Parasitoid species richness was subsequently positively associated with the availability and diversity of their hosts, and emerged as the primary driver of parasitism. Host richness was negatively associated with parasitism, potentially reflecting reduced encounter rates between natural enemies and suitable host species in more diverse host communities (dilution)³¹. Positive effects of multitrophic diversity on parasitism were thus offset by direct dilution effects from increased host richness. As such, we estimated that observed tree richness effects on parasitism were approximately 94% lower than expected in the absence of dilution effects from increased host richness (Extended Data Fig. 2). A negative association with host abundance indicated reduced per-host parasitism at higher host densities, consistent with negative density-dependence⁴², although this effect should be interpreted cautiously because it cannot be fully separated from the mathematical coupling between host density and proportional parasitism.

Crucially, accumulating stand biomass benefited parasitoid richness directly, independently of host-mediated pathways (Fig 2a). Results from GLMMs also suggested weak but significant direct effects of tree species richness on parasitoids independent of stand biomass accumulation (Supplementary Table 3). These patterns are consistent with expectations that natural enemies benefit directly from increased habitat complexity and structural heterogeneity²⁴. Stand structural complexity increased with tree richness at our study sites, a relationship that strengthened over time¹⁷. Such structural development creates additional microhabitats thereby providing complementary habitat-driven pathways – alongside bottom-up resource effects – through which parasitoids may have been supported in the developing forest⁴³. For instance, parasitoids directly benefited from reduced understory temperatures brought by increasing stand biomass (Extended Data Table 1). Although plant diversity effects are expected to weaken with increasing trophic level³, we found a comparable net effect of tree species richness on host and parasitoid richness (Fig. 2b and Extended Data Fig. 3), partly due to the direct association between parasitoids and stand biomass. Overall, tree richness had a significant net effect on parasitism (Fig. 1a and Fig. 2b), as benefits to and from parasitoids outweighed dilution from hosts. In contrast, a large-scale grassland experiment³² previously found no effect of plant diversity on parasitism, and analyses from the first year of our study (at 4-5 years after planting) detected no direct effects of tree diversity or stand biomass on parasitoids³⁴. This suggests that forests provide greater structural complexity compared to grasslands that supports parasitoid communities, and that long-term study designs and large datasets can capture weak multitrophic signals missed in approaches lacking sufficient temporal replication.

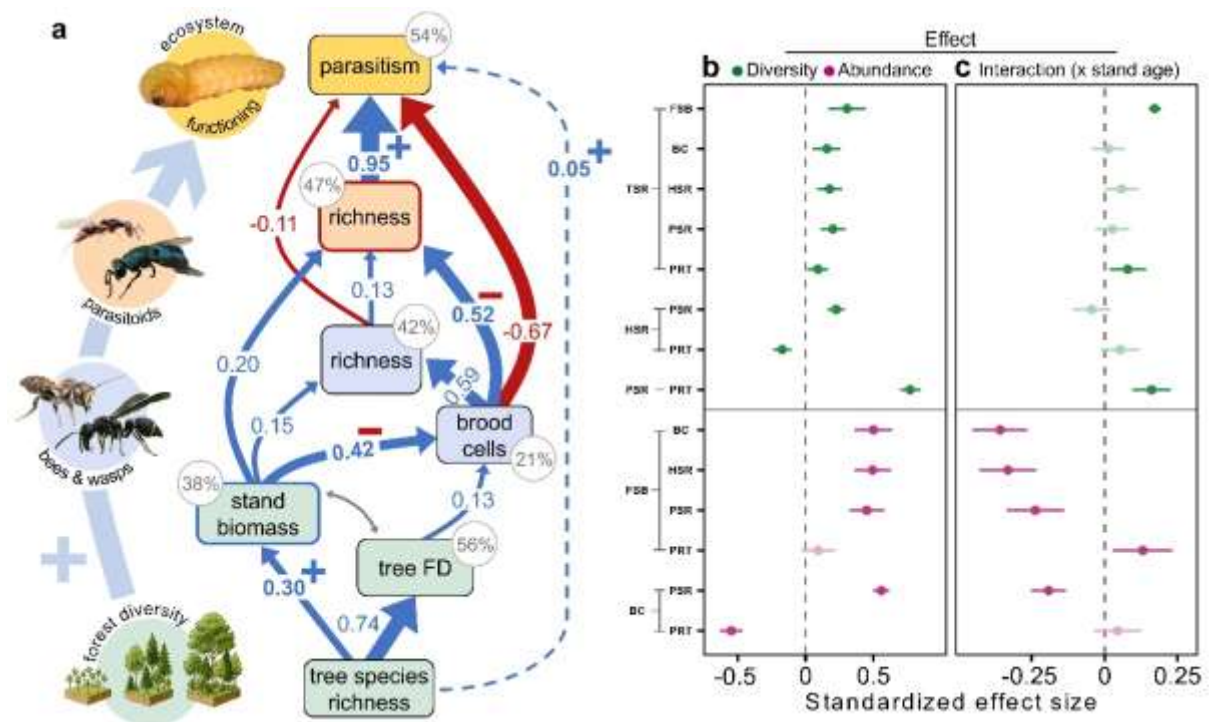


Fig. 2. Bottom-up pathways and their temporal change across trophic levels. **a** path model of direct and indirect effects of tree diversity (tree species richness), tree functional diversity (FD), stand biomass, cavity-nesting host abundance (brood cells) and species richness, and parasitoid species richness on brood-cell parasitism during 10 years of observations ($n = 792$, Fisher's $C = 21.3$, $df = 16$, $p = 0.17$). Positive effects are shown in blue and negative effects in red. Arrow width is scaled by standardized path coefficients. Dashed arrow shows non-significant pathway. Bold path coefficients indicate a significant interaction with forest age, accompanied by the sign of direction of the interaction (increasing or decreasing path strength). Highlighted nodes in blue or red show significant fixed effect of stand age. A partial correlation shown as a gray bidirectional arrow was added to account for the relationship between stand biomass and biomass-weighted tree FD, improving model fit. Percentage values show the marginal explained variance of endogenous variables. **b** standardized net effects of tree species richness (TSR), forest stand biomass (FSB), host abundance (brood cells, BC), host species richness (HSR), and parasitoid species richness (PSR) on higher-level abundance, richness, or parasitism (PRT) from GLMMs ($\pm 95\%$ CI). **c**

interaction effects with stand age (4 – 14 yrs), representing the yearly rate of change. Green points indicate diversity-based predictors (tree, host, and enemy richness), and purple points indicate quantity-based predictors (stand biomass and host abundance).

From abundance to diversity regulation

We hypothesized that the temporal increase of tree diversity effects on parasitism may be explained by accelerated stand biomass production. For instance, parasitism may increase over time when parasitoids progressively benefit from greater host diversity or availability and increased stand structural complexity²⁴. Indeed, productivity accelerated in stands with more tree species and was directly associated with increasing host and parasitoid species richness (Fig.2a). However, we found that the positive effect of tree species richness on both host and parasitoid richness did not change during a decade of forest growth (Fig. 2c), indicating that increasing tree diversity effects on parasitism were not explained by amplified effects on higher trophic levels.

Our results show a progressive weakening of host abundance effects on parasitoids, and of stand biomass effects on both hosts and parasitoids. Stand biomass played a strong role in the regulation of host and parasitoid diversity in young forests, but its effects declined over time (Fig. 2b,c). This was mainly due to a weakening of the effect of stand biomass on host abundance, and of host abundance on parasitoid richness (Fig, 2a). Other relationships, including the direct effects of stand biomass on host and parasitoid species richness, and the positive association between host and parasitoid species richness did not change systematically through time. As a result, the density-dependent pathway linking stand biomass to host and parasitoid richness progressively weakened. Consumers are predicted to be primarily governed by the amount of available resources⁴⁴, and while we did not quantify host resources such as pollen or herbivorous arthropod prey, direct and indirect trophic

dependencies with trees are expected^{25,34}. However, our results reveal diminishing effects of stand biomass on host abundance and of host abundance on parasitoids over time, consistent with saturating consumer responses to increasing resource quantity⁴⁵. This suggests that as forests grow, the structure of host and parasitoid communities becomes increasingly shaped by tree diversity and stand structural complexity per se rather than by the abundance of resources. The net effect of stand biomass on parasitism increased over time, but this was fully mediated by the weakening relationship between biomass and host abundance (Fig. 2a,c). Overall, our results suggest that increasing tree richness effects on parasitism were only partially driven by accelerated primary productivity, as abundance-driven pathways emerging from increasing stand biomass weakened over time. Notably, parasitoid richness showed a negative association with stand age once stand biomass- and host-mediated pathways were accounted for (Fig. 2a). Yet increasing parasitism in highly-diverse tree and parasitoid communities suggested an underlying temporal shift in the functional organization of host-parasitoid interactions that was not captured by diversity patterns alone.

Host-parasitoid interactions

We hypothesized that the increasing effect of tree diversity on parasitism partly reflects higher complementarity among parasitoid species, mirroring what is consistently observed in plant communities¹. Although fully separating effects of consumer richness and species composition requires factorial designs^{11,46}, quantifying multitrophic interactions can serve as an alternative approach in determining the contribution of complementary resource use towards increased functioning^{47–49}. Under this expectation, a strengthening diversity-parasitism relationship over time would be associated with declining niche overlap among parasitoids, as gradual niche partitioning reduces interspecific competition and increases complementary resource use⁵⁰. To test this, we quantified realized host-use overlap among

co-occurring parasitoid species based on quantitative interaction frequencies, after accounting for network size.

Results contradicted our initial expectations. Niche overlap among parasitoids increased with tree species richness, and this relationship strengthened over time (Fig. 3a), indicating progressive convergence of interactions onto shared hosts. Networks were small and consistently top-heavy, containing more parasitoid than host species, and this imbalance increased at higher levels of tree species richness (Extended Data Fig. 4). Thus, stands with higher tree species richness supported parasitoid assemblages organized around a comparatively restricted base of host-resource diversity. Rather than promoting niche partitioning, this network structure may intensify shared host use and favor communities structured by differences in parasitoid performance on shared hosts⁵¹.

Our second path analysis suggests that the temporal amplification of the parasitoid diversity-parasitism relationship was linked to parasitoid community assembly favoring a small set of highly effective generalist species (Fig. 3b). Over time, more diverse tree and parasitoid communities became increasingly likely to contain species whose co-occurrence shifted networks towards greater niche overlap, increasing shared host use (Fig. 3b,c). This pattern was reflected in the growing presence of four parasitoids – *Amobia auriceps* (Baranov), *Chrysis principalis* Smith, *Lycogaster violaceipennis* Chen, and *Melittobia sosui* Dahms – which collectively accounted for 70% of all observed interactions and were associated with both higher niche overlap and higher parasitism (Fig. 3b and Extended Data Fig. 5). Critically, niche overlap remained directly associated with higher parasitism after controlling for parasitoid species richness and generalist co-occurrence (Fig. 3b and Supplementary Tables 5 and 6), indicating that convergence on shared hosts translated into intensified attack pressure beyond simple changes in network size or parasitoid species identity (Extended Data Figure 6).

Our results contrast with the common expectation that strengthening biodiversity effects arise primarily from increased resource partitioning^{50,52}. Instead, we found that biodiversity effects strengthened through increasing convergence in resource use among functionally-similar consumers. High niche overlap can intensify interspecific competition when shared resources are limiting⁵⁰. However, in our host-parasitoid food webs only 15% ($\pm$ 11.5 SD) of brood cells were attacked on average across plots and years, suggesting that shared host resources remained incompletely exploited. This may have reduced the importance of competitive differences among parasitoid species⁵³, allowing convergence on common hosts, such as the mason wasp *Anterhynchium flavomarginatum* (Smith), to increase parasitism without necessarily preventing coexistence (Extended Data Fig. 6). Although niche overlap is generally expected to stabilize ecosystem functioning through space or time⁴⁸, our findings show that functionally-similar species can also increase its magnitude. This aligns with recent empirical evidence that niche overlap in antagonistic networks can promote ecosystem multifunctionality⁵⁴.

Sensitivity analyses were consistent with our interpretations: including generalist co-occurrence as a covariate in the models largely accounted for temporal changes in community-wide niche overlap and attenuated the interaction effects of both tree richness and parasitoid richness with stand age (Fig. 3d and Supplementary Tables 6 and 7). Nonetheless, parasitoid species richness retained a direct positive association to parasitism (Fig. 3b,d), indicating that additional diversity-mediated pathways beyond the ones explicitly tested here still contributed to parasitism but did not vary systematically over time. Niche overlap between parasitoid species was also negatively associated with network specialization and positively associated with network robustness to random host species extinctions (Extended Data Fig. 7). This suggests that functionally-similar parasitoid species may have buffered parasitism against strong temporal fluctuations in host availability (Extended Data Fig. 1),

contributing to the maintenance or increase of parasitism in forests with higher tree and parasitoid diversity.

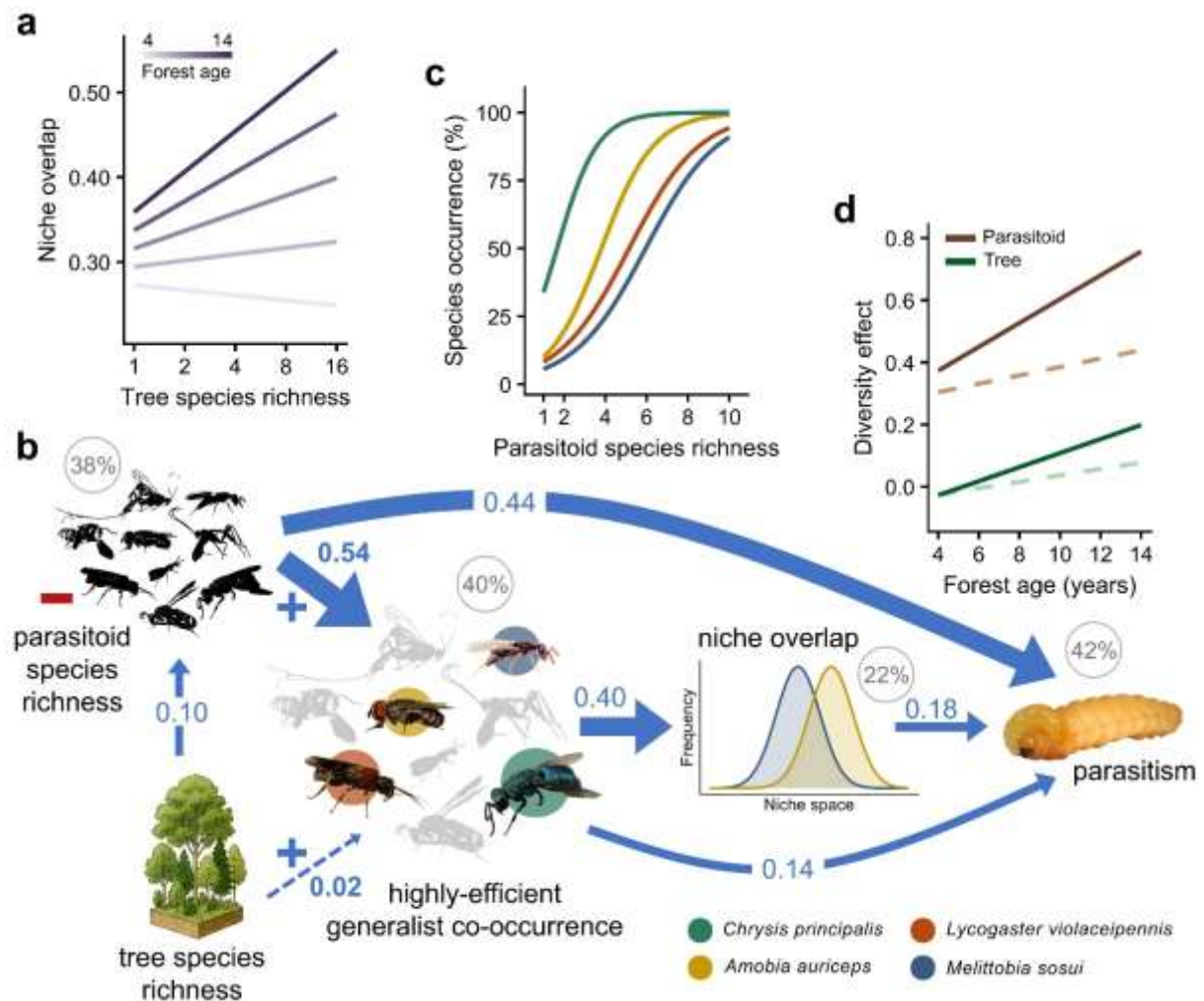


Fig. 3. Altered host-parasitoid food webs drive the increasing diversity-ecosystem functioning relationship. **a**, host-parasitoid interactions become more functionally similar (i.e. higher niche overlap) in response to tree species richness and time. **b**, Path model of direct and indirect effects of tree diversity and parasitoid diversity on parasitism, mediated by increased co-occurrence of four highly-efficient and dominant generalist parasitoid species, and resulting changes in network structure during ten years of forest growth ($n = 448$, Fisher's $C = 11.4$, $df = 10$, $p = 0.32$). All component models additionally included host richness and host abundance as covariates to account for variation in network size and

resource availability. Blue arrows indicate positive effects. Arrow width is scaled by standardized path coefficient. Dashed arrow shows non-significant pathway. Bold path coefficients indicate a significant interaction with stand age. Positive blue signs or negative red signs indicate temporal increase or decrease of pathways or nodes. Percentage values show the marginal explained variance of endogenous variables. **c**, probability of occurrence of four dominant parasitoid species increases in more diverse parasitoid communities. **d**, Sensitivity analyses on the temporal increase of tree richness and parasitoid richness effects on parasitism. Full lines represent significant GLMM-predicted positive interactions of diversity and stand age. Dashed lines represent non-significant effects when models accounted for the co-occurrence of the four dominant species. Analyses for **c** and **d** included all plot-years ($N = 792$).

Conclusion

Our results show that biodiversity effects on ecosystem functioning intensify over time through shifts in the mechanisms linking trophic levels. As young forest stands develop, host regulation transitions from resource-quantity limitation to being driven by species diversity and the structure of interaction networks. In these young forest stands, species-rich tree communities increasingly favored the co-occurrence of highly effective generalist consumers, reorganizing food webs towards a more concentrated use of shared resources and thereby strengthening top-down control. These findings reveal that the ecological benefits generated by tree diversity strengthen across trophic levels and over time during forest growth. Forest restoration with high tree diversity promotes not only biomass accumulation but also the emergence of trophic structures that enhance host suppression over time and increased the robustness of the food web to species extinctions. The benefits of biodiversity

thus extend beyond productivity, supporting the recovery of higher-order ecosystem functions. Our results suggest that losses of natural enemies from the ongoing biodiversity crisis may carry delayed but disproportionate impacts on the regulation of host populations – an “ecosystem function debt” that is unlikely to be captured in short-term studies. More broadly, the full ecological value of biodiversity in recovering ecosystems, and the costs of its loss, may only become apparent over years or even decades.

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Methods

Study sites

This study was conducted in the BEF-China experiment, located in subtropical southeast China near Xingangshan, Jiangxi province (117°54' E, 29°07' N)^{1,2}. This region is characterized by a humid subtropical climate with a mean annual temperature and precipitation of 16.7°C and 1821 mm³. The surrounding hilly landscape is covered by diverse secondary forest or conifer plantations (mostly *Pinus massoniana* or *Cunninghamia lanceolata*) on the slopes, and small-scale agricultural fields in the valleys. Detailed descriptions of the region and local forest tree compositions are given by Bruelheide *et al.*⁴. The BEF-China experiment includes two replicated field sites (A and B) situated 4 km apart from each other, approximately 20 ha each, and is currently the largest forest tree diversity

experiment worldwide⁵. Across the experiment, 566 study plots were established by planting seedlings from a pool of 40 native tree species in 2009 (site A) and 2010 (site B). Each plot measures 25.8×25.8 m in orthogonal projection (equivalent to 1/15 ha, or 1 mu, a traditional Chinese area unit) and contains 400 trees planted in a 20×20 grid, with 1.29 m spacing between individuals. At each site, a tree diversity gradient of 1, 2, 4, 8, 16 and 24 coexisting species was established between plots. All species are equally represented at all richness levels by splitting three overlapping 16-species pools at each site into non-overlapping species mixtures of lower tree diversity². The highest tree diversity level was created by combining 24 species from these pools. Plots of different tree species richness are randomly distributed within each field site. The BEF-China Main Experiment is described comprehensively by Yang *et al.*³, Brulheide *et al.*², and Huang *et al.*¹.

Sampling design

We used standardized trap nests to provide nesting sites for naturally occurring solitary bee (pollinators) and wasp (arthropod hunters)⁶ and parasitoid communities (parasites, parasitoids, and kleptoparasites) in 88 forest plots from 2014 to 2023. At each site (A and B), eight plots of each tree species richness level (1, 2, 4, 8, 16) were randomly selected for placing trap nests. Because only two 24-species plots were established per site, these plots were grouped with the 16-species mixtures to maintain balanced replication across the tree species mixture levels. Eight additional plots were sampled in site B such that all site-specific monocultures would be included⁷. This resulted in 40 plots sampled in site A (five tree species richness levels $\times$ eight plots), and 48 plots in site B. In each plot, two poles holding two trap nests each were installed in 2014, 11 m apart from each other (along a SW-NE diagonal) and 9 m away from the nearest adjacent plots. Each trap nest was held at 1.3 m off the ground and consisted of a PVC tube (12.5 cm diameter $\times$ 22 cm length) filled with 75 ± 9 (SD) internodes of *Arundo donax* L. of 20 cm length and diameters ranging between 1

mm and 20 mm⁷. Each trap nest thus provided approximately 150 cavities for bee and wasp nest establishment. Traps were checked monthly for nests from August 2014 to September 2016, and from April 2018 to November 2023, yielding data from nine calendar years over a 10-year period. Occupied *A. donax* internodes were directly replaced with others of the same diameter and the nests were reared in glass test tubes in ambient conditions. We identified all reared hosts and natural enemies to species or morphospecies based on reference specimens (Supplementary Table 1, vouchers kept at the Institute of Zoology, Chinese Academy of Sciences, Beijing). We jointly categorize as parasitoids all insects that fed or parasitized on host individuals, including kleptoparasites.

Trap nests provide a standardized measure of reproductive activity and host-parasitoid interactions in cavity-nesting Hymenoptera^{6,8}. Because nests are recorded only after females select a nesting site, construct brood cells, and provision offspring, the method captures realized reproductive use rather than transient activity⁹. The required proximity of nesting cavities, larval and adult food resources, and suitable microclimatic conditions contribute to species' sensitivity to local habitat changes⁸, also at comparatively small plot scales^{7,10}. Sampling plots within the same forest sites minimized broad-scale variation in climate, biogeography and species pools, allowing tree richness and stand structural effects to be evaluated within site-level host and parasitoid metacommunities. Although experimentally-supplied cavities may not reproduce the full spatial distribution of natural nesting sites, standardized trap-nest design and sampling across plots and years provide a robust basis for testing diversity effects across space and time⁶.

Plot-level habitat variables

We calculated annual stand volume as a measure of accumulated, aboveground forest plot biomass production. Tree height and basal diameter were measured annually at the end

of the growing season from 2014 to 2023. To avoid edge effects, the central 12 x 12 trees were measured for each plot in the 4, 8, 16, and 24 species mixtures, while a smaller group of 6 x 6 trees were measured for monocultures and 2 species mixtures. Individual tree wood volume was calculated as $ba \times h \times f$, where ba is the basal area, h the tree height, and f a fixed form factor of 0.5 that accounts for tree taper, based on average values for the young subtropical trees in the experimental sites¹. We summed the wood volume for all trees and scaled to one ha accounting for plot size (665.64 m²) and the area in which trees were measured, to derive the annual estimate of forest stand volume as a proxy of stand biomass (m³ha⁻¹).

We calculated plot-level tree functional diversity (or tree FD) to test direct and indirect effects of primary resources on cavity-nesting bees, wasps, and their natural enemies. Specifically, we selected a combination of chemical and morphological plant leaf traits that have been proven to influence the community structure of arthropod herbivores directly by nutritional conditions, and arthropod predators both indirectly by nutrient transmission or directly by determining microhabitat structure^{11–13}. These traits included specific leaf area (SLA), leaf dry matter content (LDMC), leaf toughness (LT), leaf carbon (C) concentrations, and the ratio of leaf carbon to nitrogen (C:N). These traits have been related to herbivore and predator arthropods that are the main food resources of the studied predatory wasps^{14–17}. All traits were measured on at least five individuals of sun-exposed leaves per tree species following standard protocols¹⁸. Rao's Q, or quadratic entropy¹⁹, was calculated as a fixed indicator of tree FD as the mean pairwise distance in trait values among tree species, weighted by tree volume¹⁷. We considered adding tree mean phylogenetic diversity (MPD) as a potential covariate in the models, but it was previously shown to be highly correlated with both tree species richness (Pearson's $r = 0.78$, $p < 0.001$) and tree FD ($r = 0.86$, $p < 0.001$) in the BEF-China experiment¹³. Tree FD was less strongly correlated with tree diversity in our

study ($r = 0.57$, $p < 0.001$). To avoid over-complicating our models, we did not include tree phylogenetic diversity in our analyses, as its variation was already well reflected by tree diversity and functional diversity.

We considered potential effects of abiotic environmental variables on host populations by using plot means of slope, elevation, ‘eastness’ (sine-transformed radian values of aspect), and ‘northness’ (cosine-transformed radian values of aspect) to characterize heterogeneity of the study plots. Furthermore, stand age was calculated as the number of years elapsed since stand establishment (accounting for the one-year delay between site A and B). Finally, in a subset of 56 plots representing all levels of tree species richness, below-canopy microclimate was recorded hourly from January 2015 to November 2023 using HOBO data loggers installed at 1m height above ground in the center of the plots²⁰. Mean annual temperature and relative humidity were thus calculated to be used for analyses on the nested dataset.

Statistical analyses

All statistical analyses were performed in R v.4.5.1²¹. Only brood cells from which bees, wasps, or parasitoids successfully emerged were considered, while other brood cells, e.g. when larvae had died prematurely, were excluded from analyses due to uncertainty in species identification. To discern interannual BEF dynamics in the cavity-nesting community, monthly samples were pooled by plot and year for statistical analyses, yielding a total of 792 plot-year replicates ($88 \text{ plots} \times 9 \text{ calendar years}$). All nesting bees and wasps per plot-year were considered as one (host) community, and all parasitoids as a second community to test general responses of species richness and abundance (number of constructed brood cells, corresponding to individual chambers within nests where single eggs are laid). We assessed sampling completeness for hosts and parasitoids using species accumulation curves and

sample coverage based on the number of occupied nests^{22,23}. Curves were randomly calculated over 1000 permutations²⁴. The same random nest sequence was applied to both hosts and parasitoids to allow direct comparison. Both hosts and parasitoids were sampled adequately, and no bias in sampling completeness was detected among environmental variables (Extended Data Fig. 8 and Supplementary Table 8).

To test how tree diversity and growth influenced host and parasitoid communities and parasitism rate over the 10-year sampling period, we fitted generalized linear mixed models (GLMMs) using the package ‘glmmTMB’²⁵. Separate models were constructed for host abundance (or total brood cells constructed), host richness, parasitoid richness, parasitoid abundance (or realized parasitism, i.e. the total number of brood cells attacked) and parasitism rate. Abundance and richness models used generalized Poisson distributions. Identical models for richness and abundance were fitted with Poisson or negative binomial distributions (respectively) to perform sensitivity tests and compare variance partitioning (Supplementary Table 7). Using Generalized Poisson improved model fit and residual distributions in all tests, with results remaining qualitatively unchanged. Parasitism rate was modelled as a beta-binomial response defined by the number of parasitized and non-parasitized brood cells (‘success’ vs ‘failure’). Since parasitoid communities with high richness (more than 10 species) were sparse ($n = 4$), we binned these together with the 10-species communities to avoid imprecise model estimates. All models included random effects for plots nested within sites (site/plot) and for sampling year (factor with nine levels) to account for non-independence in space and time.

Full host abundance and richness models included tree species richness, tree FD, stand biomass, and stand age along with the topographic covariates as predictors. To test whether tree diversity effects changed over time and to capture forest growth dynamics, we added interactions between tree richness and stand age, and between stand biomass and stand

age. To account for temporal auto-correlation in brood-cell production within plots, we modelled year-specific residual variation using a first-order autoregressive covariance structure, AR(1), within each plot nested in site. We assumed host abundance to influence host species richness, as populations with more individuals are expected to support more species²⁶. We therefore included host abundance as a predictor of host species richness to determine independent direct effects of habitat variables. The parasitoid richness model incorporated host community variables to capture bottom-up trophic effects. This model thus included tree richness, tree FD, stand biomass, and stand age as forest-level predictors, as well as host abundance and species richness as additional fixed effects. Plot topographical variables had no effects on parasitoids and were therefore excluded to reduce the number of covariates. We included interactions between tree richness, stand biomass, host variables, and stand age to assess temporal dynamics. The ‘parasitoid abundance’ model further included an interaction between parasitoid richness and stand age to assess temporal dynamics of parasitoid richness effects on the total number of brood cells attacked, after accounting for the diversity and availability of host resources. We tested our assumption that microclimate was partially mediating effects of stand biomass on hosts and parasitoids with a nested subset of 56 plots and 8 sampling-years (2015-2023) for which mean temperature and relative humidity were calculated. To do so, we compared stand biomass effects in models with and without understory temperature included as a covariate. The parasitism model included tree richness, tree FD, stand biomass, host richness, host abundance, parasitoid richness, and stand age as predictors. Interactions between parasitoid richness, host richness, and host abundance with stand age were included to evaluate temporal trends of diversity and dilution effects. The model also included an interaction between host abundance and host species richness to test whether the dilution effect from host richness was related to host density²⁷. Additionally, an interaction between parasitoid richness and stand biomass was included, as habitat

structural complexity can moderate parasitoid diversity effects on parasitism through either reduced or increased search efficiency^{28–30}. Non-significant interactions were removed from all global models for parsimony. To isolate baseline (net) relationships between hosts, parasitoids, and parasitism with only the experimental design variables, we also fitted two partial models including only the predictors of tree richness or tree richness and stand biomass (respectively), and interactions with stand age. Finally, we implemented a hierarchical model-comparison framework to evaluate the sequential contribution of predictors and interaction terms to each model. Nested models were compared using Type I analysis of deviance based on likelihood-ratio χ^2 tests, with changes in AIC used to assess improvements in model fit (Supplementary Table 6).

We assessed model robustness by conducting sensitivity tests, such as those to different model distribution families. Because temporal dynamics in communities or populations may be nonlinear³¹, we fitted additional models including quadratic terms for stand age. Host richness, host abundance, and parasitism showed some support for nonlinear temporal trends; however, the inclusion of quadratic terms did not qualitatively change the direction or interpretation of the main effects and interactions (Supplementary Table 7). We therefore retained the linear stand-age specification in the main models to preserve parsimony, improve interpretability of interaction terms, and maintain comparability among all models. Finally, since the parasitism model response is defined by the number of parasitized and non-parasitized brood cells, we assessed sensitivity to the exclusion of host abundance as a predictor.

We developed an S.E.M. framework to investigate how forest tree diversity and accumulating biomass enhances parasitism during succession via direct or indirect pathways mediated by multitrophic community relationships. We confirmed our hypothesis by including direct pathways that tested for effects of tree species richness, tree FD, and stand

biomass on parasitism that are mediated via host abundance and richness and parasitoid richness. As the experimental manipulation of tree species richness may have a direct effect on tree community functional diversity and on above-ground wood production^{1,2}, we included a pathway from tree species richness to tree FD, as well as from tree species richness to stand biomass. We assessed bottom-up pathways by including pathways connecting host species richness and abundance to parasitoid richness. We further included direct pathways from host richness and abundance, tree richness and FD, stand biomass and tree richness to parasitism to test for direct effects not mediated by parasitoids. Finally, we tested for direct effects of stand age on all endogenous variables and for moderating effects on all pathways. We used the ‘piecewiseSEM’ package³² to test for the support and relative importance of these hypothesized pathways. We performed a step-wise removal of non-significant predictors while assessing model fit improvements using AICc.

We quantified interaction network structure using realized niche overlap among parasitoid species using the “bipartite” package³³, calculated from quantitative host-parasitoid interaction frequencies within each plot-year network. Specifically, niche overlap (N.O.) was calculated as

$$NO = \frac{2 \sum_{i < j} 1 - d(x_i, x_j)}{S(S - 1)}$$

with S indicating parasitoid richness, and $d(x_i, x_j)$ being the Morisita-Horn dissimilarity³⁴ between parasitoid species i and j based on the abundances of their host species. Niche overlap thus reflects the extent to which co-occurring parasitoids exploit shared host resources, accounting for differences in interaction strength. Higher values indicate more similar feeding interactions, hence more competition for resources and thus less complementary trophic niches. Analyses were restricted to networks containing at least two host species, two parasitoid species, and two trophic links ($n = 448$), as network metrics

derived from very small networks can be unreliable. To test how tree diversity propagates through multitrophic pathways to influence parasitism, we implemented a second path analysis linking tree species richness to parasitoid richness, network structure (niche overlap), and parasitism. To test for potential “selection” (or dominance) effects, we included the co-occurrence (species richness) of the four most abundant generalist parasitoid species (accounting for 70% of all interactions) as a mediating node between parasitoid richness and network structure. All component models included host richness and host abundance as covariates to account for variation in network size and resource availability. We also tested for direct effects of stand age on all endogenous variables and for moderating effects on all pathways. While we cannot exclude the possibility that network composition and structure are mutually-reinforcing, the directionality implied by our path analysis is consistent with community assembly as a primary driver of changes in interactions and ecosystem functioning³⁵.

We assessed multicollinearity among raw predictors using Spearman’s rank correlations to avoid including redundant variables in the models. All variables were at most moderately correlated ($\rho < 0.7$, Extended Data Fig. 9). Parasitoid richness and abundance approached this threshold, supporting an exclusion of parasitoid abundance from the main parasitism model. Continuous predictors were mean-centered and standardized (divided by one standard deviation) using the ‘scale’ function in R; tree species richness was log₂-transformed prior to scaling. Path analyses were based on a series of nested GLMMs with Gaussian error distributions. All explanatory and intermediate response variables were therefore transformed to approximate normal distributions and scaled prior to SEM modelling. Residuals from all models were checked for normality and homogeneity of variances. All models showed no significant under- or over-dispersion, and variance inflation factors (VIFs) for predictors and interactions were low.

Data availability:

All data supporting the findings of this study are deposited on the Figshare digital repository

Code availability

Code for statistical analyses is archived on Zenodo and maintained in a public GitHub repository, available at: <https://doi.org/10.5281/zenodo.20179542>

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Author contributions:

MM, FF, CDZ, and AMK conceptualized the study. AMK, CDZ, XL, AL secured funding. FF, MSt, PFG, SKG, GAC, and JJY contributed towards the investigation. MM, QSZ, SL, XS, and AL were responsible for data curation. MM, FF, FR and MQW conducted the formal analysis. MM, FR, FF, and AMK contributed towards data visualization. MM, FF, FR wrote the original draft. All authors revised the manuscript and contributed towards the final version.

Competing interests:

The authors declare no competing interests.

Additional information:

This manuscript contains supplementary information including Supplementary Tables 1-8

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Extended data figure legends:

Extended Data Fig. 1: Random effects and temporal autocorrelation parameters of host abundance. **a**, Model-estimated interannual variation and **b**, plot-to-plot variation in host abundance (total brood cells constructed per plot-year, $N = 792$) after accounting for fixed effects ($\pm$ SE). Horizontal dashed lines in **a**, **b** indicate the global model mean. **c**, Variance of group-level random effects on autocorrelated dispersion of host abundance; bars show variance of the random effect in the AR(1) dispersion model, indicating heterogeneity in residual spread across groups. **d**, Estimated temporal autocorrelation coefficient (ρ) for host abundance ($\pm$ 95% CI). While point estimates in **c**, **d** indicate moderate persistence of host abundance within the same plots and sites from year to year, confidence intervals reflect large uncertainty due to high interannual variability.

Extended Data Fig. 2: Dilution from host species richness buffers the net positive effect of tree species richness on parasitism. Observed and expected net effect of tree species richness on parasitism rate with and without direct dilution effects incurred from increasing host richness. Full line represents the net effect of tree species richness estimated from the path analysis. Dashed line represents the estimated net effect of tree richness when the direct negative pathway from host richness to parasitism is ‘switched off’ (std. effect set to 0).

Extended Data Fig. 3: Comparable net effect of tree species richness on host and parasitoid species richness. Predicted richness of hosts and parasitoids across the tree species richness gradient, derived from a GLMM fitted to both groups simultaneously, with trophic group, tree species richness, and their interaction as predictors, and plot and year as random effects. Predictions are expressed relative to communities at intermediate diversity (four tree species) to account for differences in baseline richness. Shaded areas represent 95% confidence intervals.

Extended Data Fig. 4: Top-heavy host-parasitoid interaction networks. **a**, Interaction networks had consistently more parasitoid species than host species; dashed line indicates 1:1 ratio. **b**, marginal effect ($\pm 95\%$ CI) of tree species richness, independent of stand volume or forest age, on the ratio between parasitoid and host species (log scale); the imbalance of species richness between trophic levels increased slightly along the tree diversity gradient ($p = 0.01$). Points in **a**, **b** represent individual interaction networks pooled by plot and year that consisted of at least two host species, two parasitoid species, and two interactions ($n = 448$).

Extended Data Fig. 5: Tree species richness and forest age alter host-parasitoid networks. **a**, Predicted probabilities from a binomial GLMM modelling the number of focal parasitoid species (*A. auriceps*, *C. principalis*, *L. violaceipennis*, and *M. sosui*) present per community (0–4, $N = 792$) as a function of tree species richness, forest age, and their interaction. Points represent observed proportions of focal species present (0–4). **b**, GLMM-predicted marginal effect of tree species richness in interaction with forest age on network niche overlap, measured as the mean similarity in interaction pattern between parasitoid species in a plot-year (Horn-Morisita, $n = 448$); after controlling for host abundance, host species richness and parasitoid species richness.

Extended Data Fig. 6: Parasitoid community niche overlap is associated with higher parasitism rates of shared host species. Line shows GLMM-predicted marginal effect ($\pm$ 95% CI) of niche overlap on the parasitism rate of the most abundant and shared host species *A. flavomarginatum*, after accounting for tree, host, and parasitoid species richness as well as co-occurrence of the four highly efficient species *A. auriceps*, *C. principalis*, *L. violaceipennis*, and *M. sosui*. Point size indicates number of *A. flavomarginatum* brood cells available to parasitoids.

Extended Data Fig. 7: Relationships between niche overlap and other network metrics after accounting for network size. Points show residual variation after regressing each metric against network size; point size indicates host abundance (total number of constructed brood cells). Lines show linear fits with 95% confidence intervals. Spearman's ρ ("rho") and associated P values are shown within each panel ($n = 448$). Linkage density is calculated as the marginal totals-weighted diversity of interactions per species. H2 represents the overall level of specialization of all interacting (host and parasitoid) species in the network. Mead d' indicates the mean parasitoid species-level specialization, which expresses how specialized a given species is in relation to what hosts are available. Interaction evenness quantifies how balanced the distribution of interactions is across species, based on Shannon's diversity. Robustness was calculated as the area below the secondary extinction curve while randomly removing host species, mean value from 999 repetitions per network. All metrics were measured using the 'bipartite' R package. We refer to the package documentation for detailed descriptions of each network metric and formulas used.

Extended Data Fig. 8. Species accumulation curves and sample coverage of host and parasitoids. **a, b** Host species accumulation curves and sample coverage based on sampled nests within each tree species richness level (grey bars) and sampling year. Mean sample coverage per plot-year replicate (N = 792) was 92% for host and 80% for parasitoid communities. Results from GLMM showed no influence of tree richness, tree functional diversity, stand volume, or forest age on sample coverage for either community. **c** Overall species accumulation curves for hosts and parasitoids. Shown are the observed number of species (solid lines), the ± 1 SD of the accumulation curves from 1,000 random permutations (shading), and the expected number of species $\pm$ SE based on jack1 estimators (solid and dashed horizontal lines, respectively). Approximately 93% (75 species) of the total expected host species, and 77% (116 species) of the total expected parasitoid species were sampled.

Extended Data Fig. 9: Pairwise rank correlations among measured variables. The triangular heatmap shows correlation coefficients (Spearman's ρ) between all variables at plot-year level used in path analyses and mixed-effects models. Red indicates positive and blue negative associations; color intensity reflects correlation strength.

Extended data table legends:

Extended Data Table 1: Direct marginal effects of aboveground stand biomass on host abundance (brood cells) and on host and parasitoid species richness are partially mediated by lower average annual understory temperatures (°C).

Supplementary Files

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