



# Tree diversity promotes predatory wasps and parasitoids but not pollinator bees in a subtropical experimental forest

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## Abstract

From regional to global scales, anthropogenic environmental change is causing biodiversity loss and reducing ecosystem functionality. Previous studies have investigated the relationship between plant diversity and functional insect communities in temperate and also in tropical grasslands and forests. However, few studies have explored these dynamics in subtropical forests. Here, cavity-nesting Hymenoptera and associated parasitoids were collected across a controlled tree diversity experiment in subtropical China to test how predatory wasps, bees and parasitoids respond to tree species richness. Abundance and species richness of predatory wasps and parasitoids were positively correlated with tree species richness, while bee abundance and bee species richness were unrelated to tree species richness. Our results indicate that tree species richness increases the abundance and species richness of important communities such as predators and parasitoids. Moreover, the results highlight the importance of subtropical forests in maintaining abundance and species richness of key functional insect groups.

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## Introduction

Human-caused global change is altering the composition of ecosystems worldwide, resulting in species extinctions and the loss of ecosystem services at multiple scales (Hooper et al., 2005; Mora et al., 2011; Newbold, 2018;

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Newbold et al., 2015; Schuldt et al., 2019; Tschardt et al., 2012). Studies predict that the consequences of biodiversity loss will be enormous, reducing ecosystem functioning and services to humanity's detriment (Cardinale et al., 2012; Huang et al., 2018; Isbell et al., 2018; Loreau et al., 2001; Mommer et al., 2018). Plant diversity has a large impact on terrestrial ecosystem functioning (Grime, 1998; Isbell et al., 2017; Schuldt et al., 2018; Tilman, Wedin & Knops, 1996; Wang et al., 2019), for example, by altering functions such as herbivory in a grassland ecosystem (Knops et al., 1999).

It is generally assumed that arthropod diversity at different trophic levels is related to plant diversity (Basset et al., 2012; Haddad et al., 2009; Zhang et al., 2016). A range of studies show that arthropods play important roles in maintaining ecosystem functions (Duffy et al., 2007), and that arthropods respond to changes in plant diversity (Borer, Seabloom & Tilman, 2012; Fornoff, Klein, Blüthgen & Staab, 2019; Haddad et al., 2009; Johnson, Lajeunesse & Agrawal, 2006; Knops et al., 1999). Even at the global scale, we can see relationships between insects such as bees and the plants that they rely on (Orr et al., 2021). At a smaller scale, the abundance and species richness of arthropods increased with plant diversity in some long-term grassland experiments (Dinnage, Cadotte, Haddad, Crutsinger & Tilman, 2012; Scherber et al., 2010). Nevertheless, evidence from another grassland experiment shows that arthropod abundance is not necessarily correlated with plant species richness (Perner et al., 2005) and this relationship is likewise not unequivocal in forests (Staab & Schuldt, 2020). There is some general agreement on the positive relationship between plant diversity and arthropod diversity, but it is still not clear for arthropod abundance. For example, different climate types can lead to contrasting results (Staab & Schuldt, 2020). Most studies about the relationship between plant diversity and arthropod diversity in forests focus on temperate or tropical forests (Moretti, Duelli & Obrist, 2006; Slade, Mann, Villanueva & Lewis, 2007). Meanwhile, few studies have been done at the intersection of these environments, in subtropical forests, and even fewer on the relationships between tree diversity and arthropod diversity there (Fornoff et al., 2019; Schuldt et al., 2015; Staab et al., 2016).

Predators, pollinators and parasitoids are representative functional groups vital to and indicative of arthropod communities. Recent studies showed that plant diversity drives consumer communities, including predators and parasitoids (Fornoff et al., 2019; Schuldt et al., 2019). Evidence from a fairly well-studied subtropical forest ecosystem suggests that the abundance and species richness of spiders, as predators, are negatively correlated with plant diversity (Schuldt et al., 2011). However, the diversity of predatory ants in the same subtropical forest ecosystem is positively correlated with plant diversity (Skarbek et al., 2020; Staab, Schuldt, Assmann & Klein, 2014). A temperate forest management study showed that plant diversity promotes parasitoid abundance and diversity (Rodriguez, Pohjoismaki & Kouki, 2019). Conversely, evidence from a tropical tree diversity

experiment showed tree diversity had no effect on parasitoid diversity (Abdala-Roberts et al., 2016b). A few studies addressing plant–pollinator diversity correlates in temperate grasslands found positive relationships (Orford, Murray, Vaughan & Memmott, 2016; Venjakob, Klein, Ebeling, Tschardt & Scherber, 2016). A study from temperate agricultural ecosystem, however, found that pollinator diversity is not affected by plant diversity (Uyttenbroeck, Piqueray, Hatt, Mahy & Monty, 2017). Given somewhat conflicting evidence, additional studies are needed to improve our knowledge of the effects of tree species richness on predators, parasitoids and functionally vital pollinators.

The hyper-diverse insect order Hymenoptera includes myriad representatives of these important ecosystem service providers, including bees, predatory wasps and many types of parasitoids. Cavity-nesting bees and predatory wasps and associated parasitoids can be influenced by biotic and abiotic factors across habitats (Fründ, Dormann, Holzschuh & Tschardt, 2013; Klein, Steffan-Dewenter & Tschardt, 2006; Morris, Sinclair & Burwell, 2015; Sobek, Tschardt, Scherber, Schiele & Steffan-Dewenter, 2009; Staab, Pufal, Tschardt & Klein, 2018). However, there is a lack of study on the effect of tree diversity on these groups in subtropical forest ecosystems. Hence, it is important to fill this knowledge gap to better understand and preserve ecosystem functionality in these understudied areas.

The ecosystems of subtropical southeastern China are of special conservation interest, as they are critically threatened due to agriculture and urbanization (Su et al., 2017). In our study, cavity-nesting Hymenoptera, consisting of predators, pollinators and parasitoids, were assessed across a tree species richness gradient spanning from monocultures to 24-species mixtures in subtropical southeastern China. We hypothesized that the abundance and species richness of bees, predatory wasps and associated parasitoids will be positively influenced by tree species richness as there are probably more stable and abundant food and nest material resources available in subtropical forests with higher tree species richness.

## Materials and methods

### Study site

This study was conducted within the BEF-China experimental framework, the largest tree-diversity experiment worldwide, located in subtropical southeastern China near Xingangshan Town, Jiangxi Province (117°54' E, 29°07' N). The experiment consists of two experimental sites (A and B), separated by 4 km, comprising a total area of 50 ha. Plots at both sites comprise a tree diversity gradient (1, 2, 4, 8, 16, 24) using a total species pool of 40 native, broad-leaved tree species planted in 2009 (site A) and 2010 (site B). A total of 566 plots were established, each planted with 400 tree seedlings in a 20 × 20 grid system with 1.3 m

distance between seedlings that were completely randomly assigned to the planting positions within each plot of 25.8 × 25.8 m in an orthogonal projection. The total number of tree individuals per plot was divided equally among the planted species. For a comprehensive description of the BEF-China Main Experiment design, see [Bruelheide et al. \(2014\)](#) and [Yang et al. \(2013\)](#).

## Sampling

In total, 88 plots including 24, 16, 16, 12 and 4 plots for the richness levels of 1, 2, 4, 8, 16, and 24 tree species, respectively, were selected (Supplementary material; Fig. S1). Average distance among selected plots per site are 324.3 m for Site A and 314.2 m for Site B. Sampling used standardized trap nests ([Staab et al., 2018](#)) deployed in the plots from September 2015 to September 2016 and from June 2018 to June 2019. Two wooden posts (1.5 m) with four trap nests consisted of a random mix of reed (*Arundo donax*) internodes ranging from 0.2 cm to 2.5 cm in diameter were placed in each plot to offer nesting possibilities for a broad size range of Hymenoptera. Occupied reeds with Hymenoptera nests were removed and replaced with empty reeds each month. Reeds with Hymenoptera nests were dissected and the number of bee and predatory wasp brood cells, the number of brood cells parasitized by natural enemies, as well as host and parasitoid morphospecies were counted. Nests were reared at ambient temperature in individual glass test tubes until specimens emerged. All individuals were identified to species or morphospecies by taxonomists (see Acknowledgements). Specimens that could not be identified to species-level were assigned to morphospecies within higher taxonomic levels (minimally family). More information on sampling can be found in the Supplementary material.

## Environmental variables

Because of the heterogeneous topography of our two study sites, plot-level data on mean elevation, slope, aspect northness (cosine-transformed radian values of aspect) and aspect eastness (sine-transformed radian values of aspect) were used as fixed effects in addition to tree species richness. Topographic data were measured by a 5 m resolution digital elevation model that was established based on differential GPS measurements when the experiment was established ([Bruelheide et al., 2014](#)).

## Statistical analyses

All analyses were conducted with R 3.5.3 (<https://www.r-project.org/>). Prior to analyses, the insect data from the two trap nests per post were pooled and treated as statistical replicates nested in the same plot. We used the package iNEXT

([Hsieh, Ma & Chao, 2016](#)) to assess sampling completeness for bees, predatory wasps and parasitoids (Supplementary material; Figs S2, S3 and S4, respectively).

To improve normality and homoscedasticity of the models, tree species richness was log-transformed. To account for the two different sites where our samples were taken, we included two field sites (levels = A and B) in all models. Moreover, all continuous predictors were standardized (mean = 0, standard deviation = 1) prior to the analyses for direct comparisons of model estimates. All models contained aspect eastness, aspect northness, elevation, slope, study site and tree species richness as fixed effects. Plot identity was included as a random factor in all models to account for plot-specific environmental variation and for the hierarchical structure of the data. The correlations among all fixed effects and variance inflation factors (VIF) of our statistical models were tested with the package car (<https://www.cran.r-project.org/package=car>). Pairwise correlation of all fixed effects was below 0.2 (Pearson's correlation coefficient) ensuring that the analyses were not affected by multicollinearity ([Dormann et al., 2013](#); Supplementary material; Fig S5). Plot identity was included as a random factor in all models to account for the hierarchical structure of the data.

We used generalized linear mixed models (GLMMs) to analyze the relationship between fixed effects and the response variables: abundance (brood cell number) and species richness of bees, predatory wasps and parasitoids. A Poisson distribution was used for the count data on abundance and species richness. A single-level observation random factor was used to avoid possible overdispersion to improve model fits ([Harrison, 2014](#)). All possible models were calculated based on the fixed effects of the full models and ranked them by lowest Akaike information criterion. All equally likely candidate models within two AICc units of the model with the lowest AICc were averaged ([Grueber, Nakagawa, Laws & Jamieson, 2011](#)) in package MuMIn to explain the response variables.

## Results

A total of 21,551 brood cells constructed by 53 cavity-nesting, solitary Hymenoptera species belonging to six families were found. Twelve species were pollinators (bees) and 41 species were predators (predatory wasps). The percentage of brood cells parasitized was 11.9% (2569 brood cells) and the parasitoid community consisted of 55 parasitoid species belonging to Coleoptera (five brood cells/one species), Diptera (897/17), and Hymenoptera (1667/37). More detailed descriptions of bee, predatory wasp and parasitoid communities are given in the Supplementary material, table S2 and S3.

Although bee abundance and species richness were unrelated to tree species richness ([Table 1](#), [Fig 1A](#) and [B](#)), bee abundance and species richness were both lower at site B ([Table 1](#)).

**Table 1.** Summary results of the averaged generalized linear mixed models (within two AICc units of the model with the lowest AICc) for abundance, species richness of trap-nesting bees, wasps and their parasitoids across a tree species richness gradient. Shown are standardized parameter estimates (with standard errors, z and p values) for the significant variables and the relative importance of variables retained in the averaged models. Detailed output of averaged models can be found in the Supplementary material, Table S4.

Variable	Est.	SE	Z-value	p-value	RI
Bee species richness					
Site B	−0.657	0.132	4.987	<0.001	1.00
Bee abundance					
Site B	−1.137	0.262	4.338	<0.001	1.00
Predatory wasp species richness					
Tree species richness (log)	0.112	0.035	3.168	0.002	1.00
Predatory wasp abundance					
Tree species richness (log)	0.156	0.063	2.489	0.013	1.00
Elevation	−0.189	0.087	2.167	0.030	0.63
Site B	−0.349	0.168	2.083	0.037	0.63
Parasitoid species richness					
Tree species richness (log)	0.127	0.048	2.658	0.008	1.00
Parasitoid abundance					
Tree species richness (log)	0.167	0.075	2.219	0.027	1.00

RI is Relative Importance.

Abundance ( $p = 0.013$ ) and species richness ( $p = 0.002$ ) of predatory wasps significantly increased with tree species richness (Table 1, Fig 1C and D). Predatory wasp abundance was negatively related to elevation ( $p = 0.030$ , Table 1).

Parasitoid abundance ( $p = 0.027$ ) and species richness ( $p = 0.008$ ) were positively correlated with tree species richness (Table 1, Fig 1E and F). While parasitoid abundance declined with elevation ( $p = 0.058$ , Supplementary material Table S4), there was no correlation between parasitoid species and elevation.

## Discussion

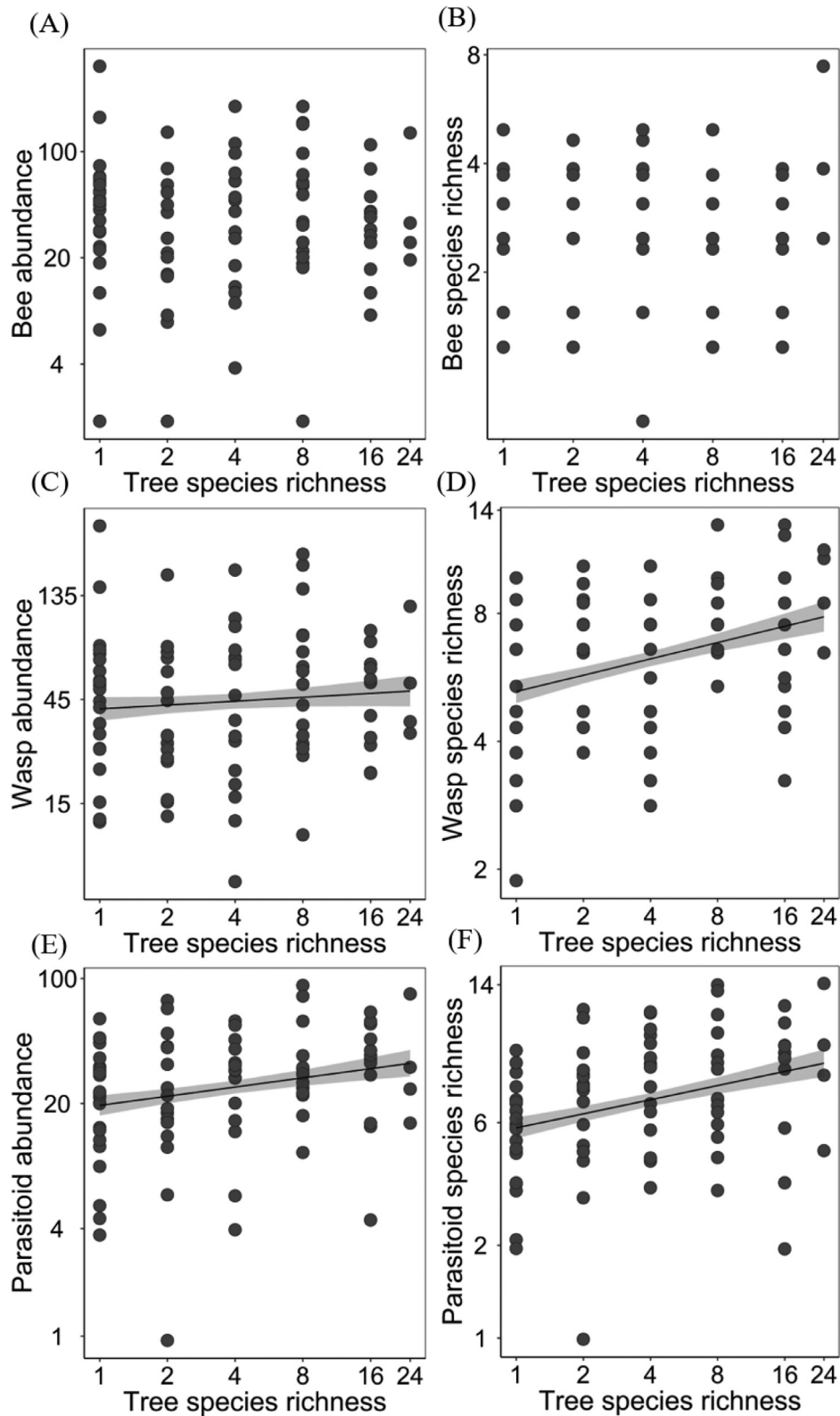
Our study demonstrates the complexity of the relationships between tree species richness and other abiotic environmental variables with the abundance and species richness of cavity-nesting solitary Hymenoptera and their natural enemies. Of particular importance, we show that the abundance and species richness of predatory wasps and parasitoids increased with tree species richness, while abundance and species richness of pollinator bees were not correlated with tree species richness.

Our results suggest an abundance-driven pattern, i.e. compared with herbs and shrubs, trees are longer-lived, providing more stable resources for predatory wasps (e.g. nest materials and prey objects) in both time and space, and this may explain why higher richness and abundance were observed with higher tree diversity. This is commonly termed a ‘more individuals mechanism’ following the corresponding hypothesis of [Srivastava and Lawton \(1998\)](#). Previous studies have demonstrated that plant diversity ([Schuldt & Staab, 2015](#)), climate ([Hoffman & Aviles, 2017](#); [Pitta, Zografou, Poursanidis & Chatzaki, 2019](#)) and different

habitat types ([Klein et al., 2006](#); [Melliger, Braschler, Rusterholz & Baur, 2018](#)) can influence predatory spiders, ants, and wasps, but without specifically testing highly-controlled experimental tree species richness gradients. The study highlights that tree species richness is the most important factor for predatory wasps, but that this is not the case for bees even though they are using the same nest sites.

In prior studies, parasitoid abundance and species richness increased with ([Sperber, Nakayama, Valverde & Neves, 2004](#)) or were unrelated to ([Staab et al., 2016](#)) tree species richness. It may be that inconsistent evidence results from additional confounding factors prevalent in more complex natural systems ([Staab & Schuldt 2020](#)). For other studies on host-parasitoid systems, such as leaf-miner parasitoids ([Fenoglio, Srivastava, Valladares, Cagnolo & Salvo, 2012](#)), plant species loss reduces parasitoid diversity, generally agreeing with our results. Our finding that tree species richness contributed significantly to increasing parasitoid abundance and species richness indicates that high-trophic-level parasitoids in a forest stand also depends on niche space and resource availability, and thus support a more diverse community of host that would promote more diverse parasitoids. A recent study showed that tree phylogenetic diversity better explains variation in parasitoid abundance than tree species richness ([Staab et al., 2016](#)). However, our study has not yet tested the effects of tree phylogenetic diversity on parasitoids.

It has been previously suggested that plant diversity positively and indirectly promoted cavity-nesting bee abundance and diversity ([Ebeling, Klein, Weisser & Tschardtke, 2012](#)). We expected that bee abundance and species richness would be more positively related to tree species richness than other environmental variables. However, when considered along with study site, elevation, and aspect northness, tree species richness was not a significant predictor for bee species



**Fig. 1.** Relationships between tree species richness and abundance (left column), and species richness (right column) of bees (A, B), predatory wasps (C, D) and parasitoids (E, F). Regression lines (with 95% confidence bands) show significant ( $p \leq 0.05$ ) relationships. Note that axis values are on a log-scale.



richness and abundance. This is not entirely surprising, as recent work found that plant productivity and richness were positively associated with bee species richness only when discounting areas with many trees (Orr et al., 2021). At the local scale, there are several additional potential reasons for our results. First, bees from our study are almost exclusively leaf-cutter bees, which build their nests with leaves from relatively diverse sources, likely based on the local flora available (Kambli et al., 2017; MacIvor, 2016). Second, even if there were some required resources lacking from specific plants, bees are less negatively influenced by plant loss than other herbivorous insects because of their higher movement capacity and longer foraging distances (Traveset, Castro-Urgal, Rotllan-Puig & Lazaro, 2018). Further, bees are potentially foraging on understory plants around our study sites instead of specific planted trees in plots (most of which do not yet flower), so it may be that only a few species are important to them for resources and that just having trees around as nesting resources is sufficient to them, without regard to species. There were fewer bees in site B than in site A, potentially as human activity is more frequent in the vicinity of site B. This site is located adjacent to a small village, where domesticated honey bees (*Apis cerana*) are commonly kept, which may compete with wild bees for pollen and nectar, thus locally lowering their abundance and species richness (Cane & Tepedino, 2017).

The effect of elevation on abundance of predatory wasps suggests a pronounced influence of microclimate. In this study, the abundance of predatory wasps declined with increasing elevation, despite the narrow elevational range (140 m). This suggests that elevation of the study plots relates to topographic features such as exposure, which can influence cavity-nesting predatory wasps via the microclimate their offspring will experience. Higher plots are on hill-tops and thus in full sunlight, and lots of heat can get in the young forest stands, which is likely not favorable for cavity-nesting predatory wasps (Everaars, Strohbach, Gruber & Dormann, 2011; Taki, Viana, Kevan, Silva & Buck, 2008). Another alternative explanation that may better explain these patterns is that the lower elevation areas around the sites are planted with crops such as *Brassica rapa* (Free & Nuttall, 1968), which can provide food resources to adult predatory wasps, enhancing their activity.

## Conclusions

Here, we provide evidence from a controlled tree diversity experiment in subtropical China that tree species richness is a significant predictor of the abundance and species richness of predatory wasps and parasitoids. However, the abundance and species richness of bees showed no relationships with tree species richness. It may have been impossible to explore and disentangle these relationships if not for the highly-controlled nature of the BEF-China experimental platform.

A recent subtropical forest study shows that the positive relationship between the diversity of insect herbivores and tree species richness enables a better insight in the assembly of communities (Wang et al., 2019). However, studies on higher trophic levels such as predators and parasitoids in subtropical forests remain comparatively limited (Staab et al., 2016). Hence, future work should incorporate more functional insect communities across trophic levels to disentangle the mechanisms behind the bottom-up effects of tree species richness. Additionally, to tease apart potential finer-scale interactions, we need to carry out more experiments in the BEF-China platform to explore whether specific tree species might contribute more to unique ecosystem functions than others.

## Authors' contributions

C.-D. Z. and A.-M. K. conceived the idea for the manuscript; C.-D.Z., G.-H. C. and A.-M. K. designed the research; P.-F. G., M.-Q. W., M. O., Y. L., J.-T. C., Q.-S. Z., N.-L. Z., collected and/or contributed data and advice; P.-F. G., M.-Q. W., M. S. and F. F. conducted data analyses. P.-F. G. wrote up the manuscript, combining inputs from all authors.

## Declaration of Competing Interest

None

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.03.007.

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