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## **Multitrophic arthropod diversity mediates tree diversity effects on primary productivity**

Li, Yi ; Schmid, Bernhard ; Schuldt, Andreas ; Li, Shan ; Wang, Ming-Qiang ; Fornoff, Felix ; Staab, Michael ; Guo, Peng-Fei ; Anttonen, Perttu ; Chesters, Douglas ; Bruelheide, Helge ; Zhu, Chao-Dong ; Ma, Keping ; Liu, Xiaojuan

**Abstract:** Forests sustain 80% of terrestrial biodiversity and provide essential ecosystem services. Biodiversity experiments have demonstrated that plant diversity correlates with both primary productivity and higher trophic diversity. However, whether higher trophic diversity can mediate the effects of plant diversity on productivity remains unclear. Here, using 5 years of data on aboveground herbivorous, predatory and parasitoid arthropods along with tree growth data within a large-scale forest biodiversity experiment in southeast China, we provide evidence of multidirectional enhancement among the diversity of trees and higher trophic groups and tree productivity. We show that the effects of experimentally increased tree species richness were consistently positive for species richness and abundance of herbivores, predators and parasitoids. Richness effects decreased as trophic levels increased for species richness and abundance of all trophic groups. Multitrophic species richness and abundance of arthropods were important mediators of plant diversity effects on tree productivity, suggesting that optimizing forest management for increased carbon capture can be more effective when the diversity of higher trophic groups is promoted in concert with that of trees.

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1 **Multitrophic arthropod diversity mediates tree diversity effects on primary**  
2 **productivity**

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33

34 **Abstract**

35 Forests sustain 80% of terrestrial biodiversity and provide essential ecosystem services.

36 Biodiversity experiments have demonstrated that plant diversity correlates with both

37 primary productivity and higher trophic diversity. However, whether higher trophic

38 diversity can mediate the effects of plant diversity on productivity remains unclear.

39 Using five years of data on aboveground herbivorous, predatory and parasitoid

40 arthropods along with tree growth data within a large-scale forest biodiversity

41 experiment in southeast China, we provide evidence of multidirectional enhancement

42 among the diversity of trees and higher trophic groups, and tree productivity. We show

43 that the effects of experimentally increased tree species richness were consistently

44 positive for species richness and abundance of herbivores, predators, and parasitoids.

45 Richness effects decreased as trophic levels increased for species richness and

46 abundance of all trophic groups. Multitrophic species richness and abundance of

47 arthropods were important mediators of plant diversity effects on tree productivity,

48 suggesting that optimizing forest management for increased carbon capture can be more

49 effective when the diversity of higher trophic groups is promoted in concert with that

50 of trees.

51 **Main**

52 **Introduction**

53 Anthropogenic disturbance and climate change pose serious threats to biodiversity in  
54 forests and associated ecosystem functions<sup>1,2</sup>. Therefore, understanding the impacts of  
55 multiple biodiversity components on ecosystem functions such as primary productivity  
56 is critical for the effectiveness of management and conservation strategies. Previous  
57 experiments on biodiversity–ecosystem functioning (BEF) relationships have been  
58 limited to one (usually plants) or two trophic levels<sup>3</sup> and did not consider trophic  
59 interaction effects that occur through niche partitioning<sup>4</sup> and functional  
60 complementarity within and among trophic groups<sup>5-7</sup>. For example, the reduction in  
61 tree productivity that might follow increased herbivory can be negated by parallel  
62 changes in the structure and diversity of natural enemy communities (predators and  
63 parasitoids)<sup>8,9</sup>. Consequently, how biodiversity changes across trophic groups and how  
64 this impacts ecosystem functions remains poorly understood.

65 Ecosystem functions are affected by interactions between trophic groups via both  
66 bottom-up and top-down effects<sup>10,11</sup>. Bottom-up effects of lower on higher trophic  
67 levels tend to diminish in magnitude between each rank of the food web, both in  
68 freshwater<sup>12</sup> and terrestrial ecosystems<sup>13</sup>. Top-down effects of higher on lower trophic  
69 levels such as predation represents the inverse causality; but these effects may be  
70 weaker than bottom-up due to lower consumer efficiency<sup>14-17</sup>. Nevertheless, theory and  
71 empirical evidence suggests that plant productivity in the face of herbivory requires  
72 herbivore regulation processes (the ‘Oksanen-style pattern’<sup>18-21</sup> and ‘Green World  
73 Hypothesis’<sup>22</sup>). Therefore, advancing BEF understanding requires incorporation of  
74 multiple higher trophic feeding guilds and their bottom-up and top-down interactions.  
75 Recent experimental studies have shown that both plant richness and functional trait

76 means and diversity drive species richness and abundance of arthropods across trophic  
77 levels<sup>10,23</sup>. In turn, mechanisms by which arthropods impact plant performance include  
78 the induction of plant defenses<sup>24</sup> and control of herbivores<sup>25</sup>. In consequence, such  
79 interacting bottom-up and top-down effects may represent the mediating processes by  
80 which plant diversity drives ecosystem functioning<sup>26</sup>.

81 Such bidirectional regulatory effects vary temporally because stability in trophic  
82 interactions depends on the capacity of the ecosystem to sustain consumer abundance  
83 and prey populations, while top-down control can diminish in the absence of external  
84 perturbations<sup>27,28</sup>. This is addressed herein through two primary questions. First, how  
85 does the relationship between higher trophic groups and tree productivity change with  
86 tree diversity in species-rich forests? Second, how do such relationships vary among  
87 trophic groups over time? Answering these questions could help forest management,  
88 biodiversity conservation, and maintaining stability of ecosystem functions, because  
89 the presence of arthropod-mediated feedback effects on plant diversity–productivity  
90 relationships might be leveraged towards the mitigation of both species extinctions and  
91 climate change.

92 We assessed the relationship between multitrophic arthropod diversity (species  
93 richness and abundance) and tree productivity using an experimental tree species  
94 richness gradient (Fig. 1). We hypothesized that effects of tree species richness on  
95 diversity of multitrophic arthropod groups are consistently positive but weaken with  
96 increasing trophic level (H1); herbivore diversity negatively impacts tree productivity  
97 via consumption effects on tree biomass, whereas natural enemy (predator and  
98 parasitoid) diversity has positive effects on tree productivity through top-down controls  
99 on herbivores, leading to a net positive effect of multitrophic arthropod diversity on tree  
100 productivity (H2 and H3); and tree functional diversity (FD) and community-weighted

101 means (CWM) can also affect tree productivity via multitrophic arthropod diversity  
102 (H3). Furthermore, we predicted that the effects of herbivores and natural enemies on  
103 productivity would change over time due to changes in their diversity (Extended Data  
104 Fig. 1). We tested these hypotheses using extensive datasets on arthropods, tree growth,  
105 and functional traits from a large forest BEF experiment in subtropical China  
106 established in 2009 (BEF-China)<sup>29</sup>, including observations on 8,979 herbivorous  
107 Lepidoptera larvae, 8,831 Hymenoptera predators, 2,100 parasitoid wasps and tree  
108 growth records from 2015 to 2020 across manipulated tree diversities ranging from  
109 monocultures to mixtures with 24 tree species.

110

## 111 **Results and Discussion**

112 Species richness and abundance of herbivores, predators, and overall arthropods  
113 were all significantly positively (+) related to tree species richness, even after  
114 considering variability across years (species richness: herbivores  $F_{1,45} = 9.52+$ ,  $P =$   
115  $0.003$ , predators  $F_{1,45} = 3.64+$ ,  $P = 0.06$ , overall arthropods  $F_{1,45} = 13.57+$ ,  $P < 0.001$ ;  
116 abundance: herbivores  $F_{1,45} = 5.92+$ ,  $P = 0.02$ , predators  $F_{1,45} = 4.56+$ ,  $P = 0.04$ , overall  
117 arthropods  $F_{1,45} = 10.68+$ ,  $P = 0.002$ ; Fig. 2, Supplementary Table 4–5), whereas the  
118 effects of tree species richness on the species richness and abundance of parasitoids  
119 was not significant (species richness:  $F_{1,45} = 2.05+$ ,  $P = 0.16$ ; abundance:  $F_{1,45} = 1.48+$ ,  
120  $P = 0.23$ ; Fig. 2, Supplementary Table 4–5). Species richness and abundance of  
121 herbivores, predators and parasitoids increased (+) or decreased (–) over time (year as  
122 linear term; species richness: herbivores  $F_{1,185} = 6.84+$ ,  $P = 0.01$ , predators  $F_{1,185} =$   
123  $39.14-$ ,  $P < 0.001$ , parasitoids  $F_{1,185} = 26.78-$ ,  $P < 0.001$ ; abundance: herbivores  $F_{1,185}$   
124  $= 4.59+$ ,  $P = 0.03$ , predators  $F_{1,185} = 7.84-$ ,  $P = 0.01$ , parasitoids  $F_{1,185} = 39.91-$ ,  $P <$   
125  $0.001$ ; Fig. 2, Supplementary Table 4–5). These results are consistent with previous

126 studies that demonstrated the influence of plant diversity on species richness and  
127 abundance of single higher trophic groups<sup>13,23,30</sup> and highlight inter-annual variance in  
128 the responses, which thus far have not been considered in BEF experiments. Moreover,  
129 these findings parallel those from a large BEF experiment conducted in grassland,  
130 where positive plant diversity effects on other trophic groups also reduced with  
131 increasing trophic level<sup>13</sup>.

132 Tree productivity, as measured by the accumulated aboveground volume of tree  
133 stands, increased significantly with species richness and abundance of predators and  
134 parasitoids (species richness: predators  $F_{1,185} = 4.08+$ ,  $P = 0.04$ , parasitoids  $F_{1,186} =$   
135  $11.37+$ ,  $P < 0.001$ ; abundance: predators  $F_{1,188} = 5.97+$ ,  $P = 0.02$ , parasitoids  $F_{1,186} =$   
136  $11.73+$ ,  $P < 0.001$ ; Fig. 3, Supplementary Table 6–7), whereas tree productivity  
137 decreased with species richness and abundance of herbivores (species richness:  
138 herbivores  $F_{1,188} = 6.39-$ ,  $P = 0.01$ ; abundance: herbivores  $F_{1,187} = 5.77-$ ,  $P = 0.02$ ;  
139 Supplementary Table 6–7). Similar trends (although not significant) were also observed  
140 when considering species richness and abundance of higher trophic groups and the  
141 annual increase of aboveground tree stand volume (Supplementary Fig. 1, Table 8–9).  
142 The positive relationships between tree productivity and overall arthropod richness or  
143 abundance suggested that the latter might have had a beneficial effect on nutrient  
144 cycling, because for example arthropod remains and excreta are more readily available  
145 to plants than litter<sup>31</sup>. Considering the results of structural equation models (SEMs) as  
146 well (Fig. 4, more details below), our findings additionally suggest that top-down  
147 control of herbivores by predators and parasitoids in diverse tree communities can  
148 increase tree productivity. We thus infer that increases in the number of tree species  
149 provide more complex habitat structure and food resources (i.e., herbivore abundance  
150 and species richness itself) for natural enemies, enhancing predation or parasitism of

151 herbivores<sup>32</sup> which, in turn, enables increased tree productivity. Across years, the  
152 effects of herbivore species richness, herbivore abundance, and predator abundance on  
153 tree productivity increased, while those of parasitoid species richness, parasitoid  
154 abundance and predator species richness did not change (Supplementary Table 6–7).  
155 These findings suggest that top-down control decreased over time in the experiment<sup>27</sup>.

156 We note that our inferences were based on arthropods, the dominant higher trophic  
157 groups in our experiment<sup>33,34</sup>. Several studies have suggested that vertebrate predators  
158 such as birds may also benefit from tree diversity and increase tree productivity by  
159 predation on arthropods such as herbivorous caterpillars<sup>35,36</sup>. We therefore compared  
160 the predation rates of birds and arthropods on model caterpillars. We found that the  
161 predation rate of arthropods (mean  $\pm$  SD: spring,  $0.05 \pm 0.004$ ; summer,  $0.20 \pm 0.008$ )  
162 on model caterpillars was much higher than that of birds (spring,  $0.002 \pm 0.0007$ ;  
163 summer,  $0.007 \pm 0.002$ ; Extended Data Fig. 2a, b), and the predation rate of arthropods  
164 increased significantly with increasing tree diversity (Extended Data Fig. 2c, d). These  
165 results are consistent with general findings of a global study showing that arthropods  
166 drive overall predation rates in many low latitude forests<sup>37</sup>.

167 We statistically disentangled the possible causal connections among tree species  
168 richness, arthropod diversity and tree productivity using SEMs. We first tested two  
169 hypothetical frameworks with data pooled across years: i) a model of both bottom-up  
170 and top-down effects (i.e., arthropod diversity mediating tree diversity effects on tree  
171 productivity), and ii) a model with bottom-up effects only (i.e., tree productivity  
172 mediates tree diversity effects on arthropod diversity). Model i) was well supported by  
173 our data (Fig. 4a, c), whereas model ii) was not (Extended Data Fig. 3). To further  
174 delineate the role of diversity of different trophic groups, we divided arthropods into  
175 herbivores and their natural enemies (i.e., predators and parasitoids) and analyzed their



176 data annually. The results supported the hypothesis that top-down control of enemies  
177 on herbivores increased tree productivity (Fig. 4b, d). Furthermore, according to these  
178 SEMs the abundance of herbivores increased and the species richness and abundance  
179 of natural enemies decreased over the years. Combined with the result that some effects  
180 of higher trophic groups on tree productivity also changed over years (Supplementary  
181 Tables 6–7), this lends further support to the concept of temporal variation in trophic  
182 cascades<sup>27</sup>.

183 In natural ecosystems the numbers of species and individuals might not be  
184 independent, as a larger number of species give scope for more individuals to co-occur<sup>38</sup>,  
185 or a larger number of individuals increases the probability that there are more  
186 species<sup>39,40</sup>. Thus, we tested for abundance-independent effects of arthropod richness  
187 on productivity by analyzing rarefied species richness or by calculating SEMs including  
188 both arthropod abundance and species richness. The SEM results based on rarefied  
189 species richness were consistent with those based on species richness (Supplementary  
190 Fig. 2), indicating that the influence of arthropod richness on tree productivity was not  
191 simply the result of more individuals. When combining species richness and abundance  
192 in SEMs we obtained the best model fit when arthropod abundance was added as a  
193 mediator between arthropod species richness and plant productivity (Supplementary  
194 Fig. 3), whereas a model in which arthropod richness was a mediator of arthropod  
195 abundance effects on plant productivity had a poorer overall fit (based on a significant  
196 *P* value of the overall model fit). Removing the link between arthropod species richness  
197 and abundance yielded an unstable model (Supplementary Fig. 4, based on a significant  
198 *P* value of the overall model fit), providing further evidence for the non-independence  
199 of the numbers of species and individuals.

200 While SEMs can be used to explore causal hypotheses, the inclusion of data from

201 different study systems may provide broader insights. We therefore conducted similar  
202 analyses based on data from the Jena (Germany) grassland biodiversity experiment<sup>13</sup>,  
203 which also found effects of plant diversity on arthropod diversity cascading to plant  
204 biomass (Extended Data Fig. 4). Results for the grassland system were consistent with  
205 our findings for the forest system in that the plant diversity effects on higher trophic  
206 diversity did not depend on plant biomass<sup>13</sup>. However, for the grassland systems there  
207 were no negative effects of enemies on herbivores in trophic-resolved models  
208 (Extended Data Fig. 4c, d). The difference between these two ecosystems might be  
209 explained by the more rapid turnover of aboveground plant biomass in grasslands  
210 compared with forests and higher structural heterogeneity of the primary producers in  
211 the latter providing higher resource diversity for predators and parasitoids. Therefore,  
212 the top-down control of natural enemies and the negative effects on herbivores in forests  
213 may be stronger than in grassland. Generally, our results suggest that the diversity of  
214 multitrophic arthropod groups is a highly relevant mediator of both tree-diversity and  
215 functional-trait effects on primary productivity. Thus, biodiversity–ecosystem  
216 functioning relationships in plant species-rich forests could be partially driven by  
217 trophic interactions involving multiple trophic levels. These findings greatly enhance  
218 our mechanistic understanding of the ‘Oksanen-style pattern’<sup>18,19</sup> and ‘Green World  
219 Hypothesis’<sup>22</sup> and how they are affected by the species richness and traits of plant  
220 communities.

221 The positive association between multitrophic arthropod diversity and tree  
222 productivity detected in this study suggests that trophic complementary effects and top-  
223 down control are important mechanisms driving ecosystem functioning in species-rich  
224 forests, and indicates the necessity of considering higher trophic groups in the  
225 development of forest management and biodiversity conservation policies. Although

226 our inferences are based on the hypothetical causal relationships explored in the path  
227 analyses, our study provides an intriguing mechanistic interpretation how multitrophic  
228 interactions may underpin BEF relationships. These hypothetical causal relationships  
229 should eventually be tested using direct manipulations of higher trophic levels, however  
230 challenging they are for some groups of predators or parasitoids. Previous modeling  
231 work (e.g., Lotka–Volterra models) suggested that multiple trophic levels need to be  
232 considered to explain ecosystem processes because of the types of interactions  
233 described therein<sup>7,41</sup>. Moreover, our findings support a related study in the same  
234 experiment which found that reducing arthropods (i.e., herbivores and natural enemies)  
235 by insecticides had no significant effect on the relationship between tree species  
236 richness and tree productivity<sup>42</sup>. Therefore, our results suggest that a critical experiment  
237 would be to selectively exclude natural enemies of herbivores to reveal the potential  
238 impact of herbivores on plant productivity. However, that experiment would be difficult  
239 to engineer, given that methods typically used to remove enemies (e.g., insecticide  
240 application) would also affect herbivorous arthropods.

241 Understanding the mechanisms by which multitrophic communities drive BEF  
242 relationships is a central goal in community and ecosystem ecology. Although  
243 experimental manipulation of arthropod diversity is an insightful way to open the black  
244 box of trophic complexity, it is very difficult in the field because feeding relationships  
245 are often species-specific and cannot be experimentally randomized within or across  
246 diversity levels. Moreover, although we could not include all trophic taxonomic groups  
247 in our study logistical constraints, our work suggests direct relationships between  
248 multiple trophic groups and primary productivity in forests. We demonstrate that taking  
249 a multitrophic perspective can advance our understanding of the diverse mechanisms  
250 underlying BEF relationships. In further work, it will be interesting to test the wider

251 implications of these findings when including other groups of organisms such as  
252 mollusks, vertebrates, or microbes<sup>43</sup>. It is also necessary to include the dynamics of  
253 different trophic groups over time in such studies, to account for inter-annual variation  
254 in trophic cascades<sup>27</sup> and their relations with ecosystem functions such as primary  
255 productivity. Our study of multitrophic forest community dynamics emphasizes that  
256 tree diversity influences primary productivity through an interplay of bottom-up and  
257 top-down interactions, and it provides guidance for conserving those important  
258 processes in natural and constructed forest ecosystems.

259

## 260 **Methods**

261 **Study site and experimental design.** We conducted this study at the Biodiversity–  
262 Ecosystem Functioning Experiment China Platform (BEF-China, [www.bef-china.com](http://www.bef-china.com))  
263 at Xingangshan, Dexing, Jiangxi, China (29°08′–29°11′ N, 117°90′–117°93′ E). The  
264 study region is located in the subtropical zone with a mean annual temperature of  
265 16.7 °C and a mean annual precipitation of 1821 mm. In total, 566 study plots with an  
266 area of 25.8 × 25.8 m<sup>2</sup> (corresponding to the Chinese area unit 1 mu) were established  
267 at two sites (Fig. 1 A, site A: 271 mu, site B: 295 mu), planted in 2009 and 2010,  
268 respectively<sup>29</sup>. Plots were randomly distributed in rectangular grids across both sites.  
269 For each plot, 400 tree individuals were planted in 20 rows and 20 columns with tree  
270 species randomly assigned, which generated a total of 226,400 trees planted across all  
271 plots. For the tree species pool, 40 locally common tree species were selected  
272 (Supplementary Table 1). According to a “broken-stick” design, tree species richness  
273 of plots ranges from monocultures to mixtures of 2, 4, 8, 16, and 24 species (the 24-  
274 species mixtures are an additional treatment on top of the design).

275

276 **Primary productivity.** We used accumulated stand volume ( $\text{m}^3 \text{ha}^{-1}$ ) per plot as a long-  
277 term proxy of primary productivity, accessed by directly measuring the basal diameter  
278 ( $BD$ ) and height ( $H$ ) of trees, both in meters (i.e., stand volume,  $V = H \times \pi(BD/2)^2$ ). The  
279 volumes were transformed into more accurate estimations by multiplication with a size-  
280 dependent correction factor developed in<sup>44</sup>. Tree individual data were measured yearly  
281 from 2015–2020 at sites A and B. The productivity of each plot for each year was  
282 estimated by pooling the volumes of 36 (monocultures and 2-species mixture plots) or  
283 144 (4, 8, 16 and 24-species mixture plots) surviving tree individuals in the central  
284  $15.49 \times 15.49 \text{ m}$  or  $7.74 \times 7.74 \text{ m}$  per plot, respectively. We also used annual stand  
285 volume increment ( $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ ) as a short-term proxy of productivity, i.e., the absolute  
286 difference of accumulated stand volume between two census years.

287

288 **Plant functional traits.** Leaf functional traits were measured from 2011–2012,  
289 including four traits that have been found to influence both tree growth and arthropod  
290 (especially herbivores): specific leaf area (SLA), leaf dry matter content (LDMC), leaf  
291 toughness (LT), leaf nitrogen (N) concentration (see Supplementary Table 3 for an  
292 overview of selected traits with explanations on their relationships with arthropods).  
293 More detailed information on leaf traits can be found in<sup>45-48</sup>. Leaf functional diversity  
294 (FD, indicated by functional dispersion) based on all traits and community-weighted  
295 mean (CWM) values for each trait were calculated for each plot weighted equally  
296 across different tree species because all tree individuals were planted in equal numbers  
297 per plot, with the R package “FD”<sup>49</sup>. In order to reduce the dimensionality of leaf traits,  
298 we subjected CWM trait values to a PCA using the R package “vegan”<sup>50</sup> and used the  
299 first axis of PCA scores (59% explained variance, Supplementary Table 11) to represent  
300 leaf functional CWM.

301

302 **Arthropod sampling.** The data used in this study were collected from 47 randomly  
303 distributed forest plots in 2015, 2017, 2018, 2019, and 2020, using different sampling  
304 methods to specific trophic groups: beating for herbivores (i.e., caterpillars) and trap  
305 nests for remaining groups (i.e., parasitoids and predators, Supplementary Table 2). Due  
306 to the broken-stick design, the numbers of sampled plots were 18, 13, 8, 4, 2, and 2 for  
307 the tree species richness levels of 1, 2, 4, 8, 16, and 24, respectively. Herbivore sampling  
308 was conducted by beating a fixed number (40 individuals in the first year and 80  
309 individuals in later years) of living trees from the first (southernmost) row of each plot  
310 at the time of peak herbivore abundance per year (April-May, June, and September). A  
311 white square sheet (1.5 m × 1.5 m) was used to collect all caterpillars dislodged from  
312 the tree crowns. This sampling regime covered all tree species and species richness  
313 levels of the random planting design. Caterpillars collected in 2015 were identified to  
314 species or morphospecies at family or genus level. DNA barcoding of the cytochrome  
315 oxidase 1 (CO1) was performed following standard protocols<sup>34</sup> to verify the  
316 classification in potentially ambiguous cases. Samples collected from 2017 and later  
317 years were mainly identified by DNA barcoding based on the CO1 gene. The Statistical  
318 Assignment Package (SAP) was used to identify herbivore samples via comparison  
319 with GENBANK, BOLD, and a local adult moth database<sup>51</sup>.

320 Parasitoids and predators were collected by using standardized trap nests. Trap  
321 nests provide nesting opportunities for solitary cavity-nesting Hymenoptera of various  
322 body sizes and have proven to be an effective sampling method<sup>52</sup>. Two wooden posts  
323 (1.5 m high) were deployed in each plot with four trap nests filled with reed (*Arundo*  
324 *donax*) internodes ranging from 0.2 cm to 2.0 cm in diameter. Trap nests were checked  
325 monthly between April and October every year, occupied internodes with Hymenoptera

326 nests were removed and replaced with empty internodes. Nests were brought to the  
327 laboratory, dissected, and reared at ambient temperature until specimens hatched. All  
328 trap nest samples were then identified to species or morphospecies<sup>33</sup>.

329

330 **Predation by birds and arthropods.** The data on predation rates were collected from  
331 different tree individuals. However, the experimental trees within each tree richness  
332 level were selected as mono- and heterospecific tree species pairs (a complete  
333 description of the design of tree pairs can be found in<sup>53</sup>). The number of tree replicates  
334 per richness level was six for monocultures, nine for two-species mixtures, and five for  
335 all other richness levels, caused by varying self-thinning between tree species in  
336 different richness levels. Predation estimation was conducted in spring (on 375 tree  
337 individuals) and mid-summer (on 383 tree individuals) of 2019 by checking the bite  
338 marks (arthropod or bird) on model caterpillars<sup>54,55</sup>. The model caterpillars (5 cm × 0.5  
339 cm) were made of green nontoxic, odorless modeling clay and placed on different tree  
340 branches. Six model caterpillars were placed per tree in two groups, i.e., three on higher  
341 branches and three on the lower branches (at least 50 cm away from each other). All  
342 model caterpillars were checked and estimated weekly and replaced with new ones if  
343 new bite marks were found.

344

345 **Statistical analyses.** We used R (v 4.0.5) for all statistical analyses ([http://www.R-](http://www.R-project.org)  
346 [project.org](http://www.R-project.org)). Prior to analyses, data on higher trophic-level species richness and  
347 abundance were pooled at the plot level by summing overall species numbers across  
348 different sampling methods, for multiple trophic groups, as well as herbivores,  
349 predators, parasitoids, respectively. Moreover, we calculated the rarefied species  
350 richness for each group to tease apart the effect of abundance<sup>39,50</sup>. In addition,

351 considering the different sampling methods of multiple trophic groups, we also  
352 calculated the diversity index of multitrophic species richness (i.e., overall species  
353 richness) by following the method described in<sup>56</sup>, by averaging the standardized values  
354 (based on the maximum species richness per group) for each trophic group. We did not  
355 find significant differences in the results based on two different calculation methods on  
356 multitrophic species richness (Supplementary Table 11-12). Therefore, we used the  
357 untransformed observed species richness and abundance (and not the diversity index)  
358 for downstream analyses.

359 To test hypothesis 1 (H1), we analyzed relationships between species richness and  
360 abundance of multiple trophic groups and tree species richness by using linear mixed-  
361 effects models (LMMs) with plot as a random term. The impacts of the following fixed  
362 effects were tested on higher trophic species richness: tree species richness, year (as  
363 continuous variable, i.e. as a linear term in all linear mixed-effects models, and as a  
364 factor term for visualization by using linear models), and the interaction between tree  
365 species richness and year.

366 To test hypothesis 2 (H2), we analyzed relationships between species richness and  
367 abundance of multiple trophic groups and primary productivity (response variable)  
368 using LMMs. We used species richness or abundance across trophic groups (i.e.,  
369 herbivores, pollinators, parasitoids, predators and overall groups), year (as continuous  
370 variable, i.e. a linear term in all models, and as a factor term for visualization), and their  
371 interactions as fixed effects and the same random effect as mentioned above. Tree  
372 species richness was log<sub>2</sub>- transformed in all models. We performed log- (species  
373 richness and abundance) and square-root (tree productivity) transformation to  
374 normalize residuals for all response variables. For all explanatory variables, species  
375 richness and abundance of higher trophic arthropods were log-transformed, and the year



376 was centered. LMMs were fitted with the “lme4” package in R<sup>57</sup>.

377 We applied a structural equation model (SEM) framework to test our third  
378 hypothesis (H3, Extended Data Fig. 1) by including the pathways that tested for effects  
379 of tree species richness, leaf functional traits (FD and CWM), and multitrophic  
380 arthropod diversity on primary productivity. SEMs based on mixed effects models  
381 (package piecewiseSEM) were used to test the support for and relative importance of  
382 our hypothesized pathways<sup>58</sup>. Through these SEM analyses, we were able to  
383 disentangle how higher trophic arthropods mediate the impacts of tree species richness  
384 on primary productivity and how these effects differ across trophic groups. Given the  
385 potential for temporal variance across trophic group (i.e., year), we first used average  
386 data of 5 years to analyze the effect of overall arthropod diversity on productivity (Fig.  
387 S2a). Further, we used yearly data for trophic-resolved SEMs (Fig. S2b). Models were  
388 simplified by removing non-significant paths step by step and compared using both  
389 Akaike Information Criterion (AICc,  $\Delta AICc > 2$ ) values and Fisher’s C statistic ( $P >$   
390 0.05). In all SEMs, tree species richness was log<sub>2</sub>- transformed, and the other variables  
391 were also transformed in the same way as in the models in the first two steps. For all  
392 SEMs we used the same random effect, i.e., (1|plot) as mentioned above. In addition,  
393 to explore whether similar results can be observed for ecosystems other than forests,  
394 we performed the similar SEM analysis (but without plant functional traits) on  
395 aboveground data from the Jena (Germany) grassland biodiversity experiment<sup>13</sup>.

396

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412

#### 413 **Author contributions**

414 X.L. conceived the study. X.L., K.M., S.L., Y.L., A.S., M-Q.W., F.F., M.S., P-F.G., P.A.,  
415 and C-D.Z. were responsible for data collection. Y.L. and X.L. performed statistical  
416 analyses with contributions from B.S., A.S. and M.S. The initial manuscript was  
417 prepared by Y.L. and X.L. with contributions from B.S., A.S., M.S., D.C., H.B. and  
418 K.M. All co-authors helped improve the manuscript.

419

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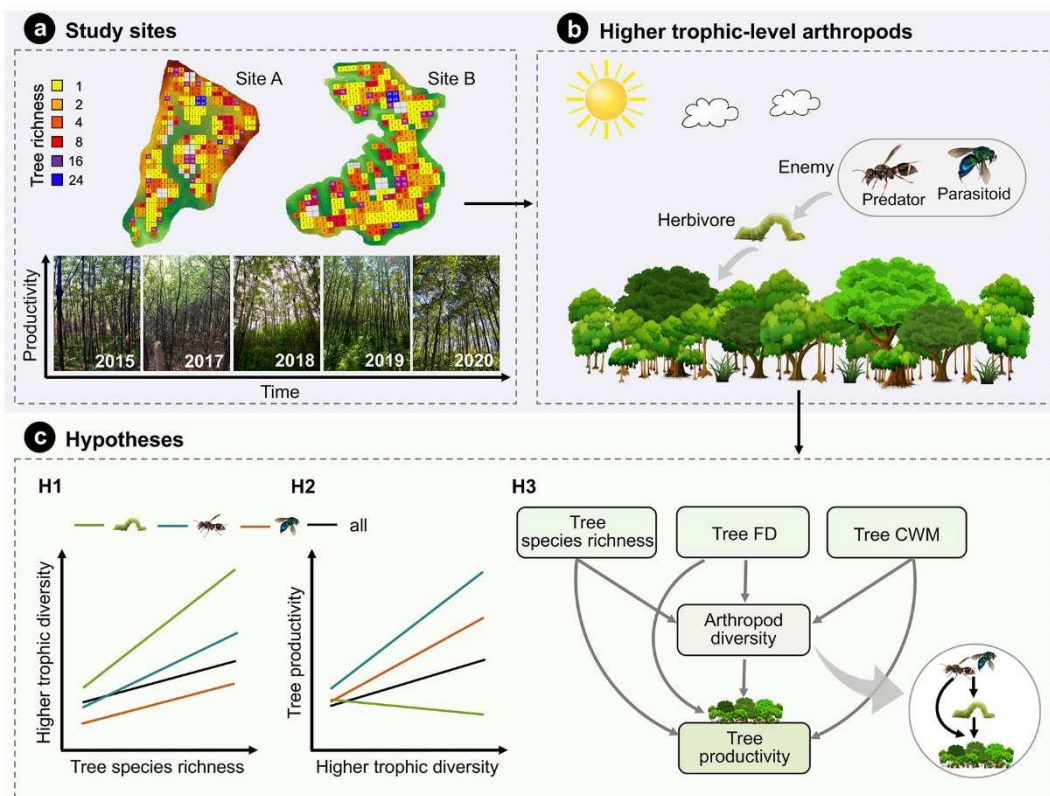
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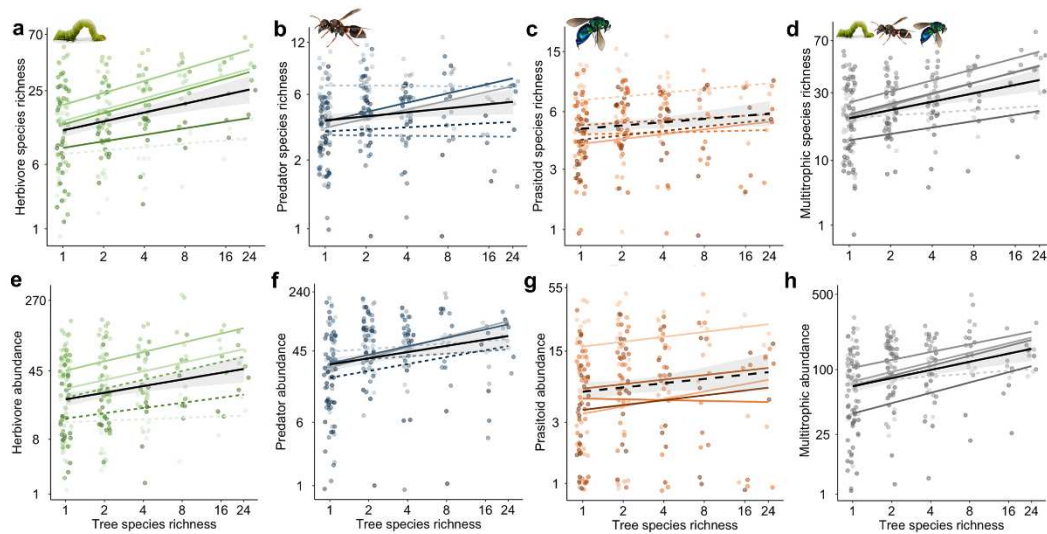


557 **Figures**

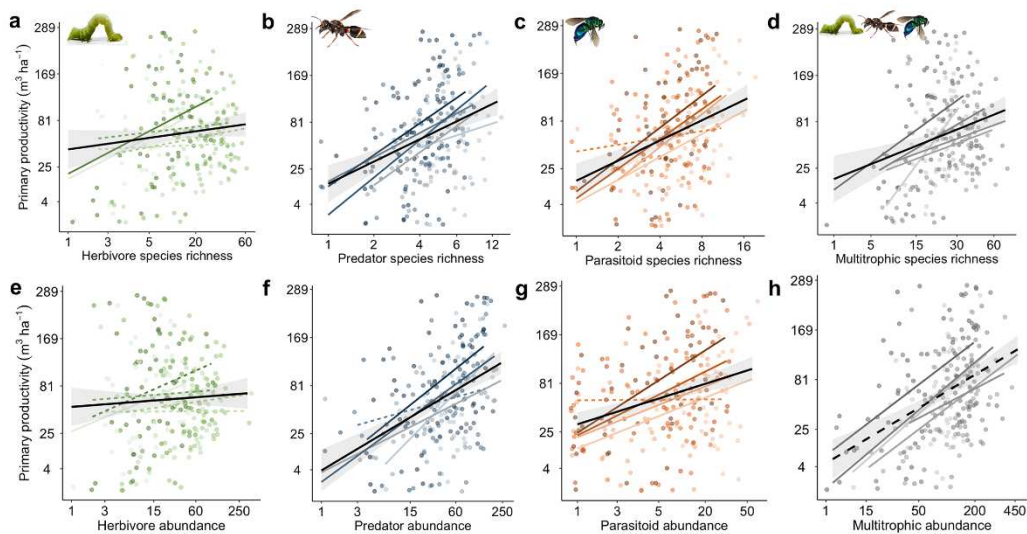
558 **Fig. 1 | Graphical illustration of the research framework and hypotheses.** **a**, Study  
559 sites; **b**, Higher trophic-level arthropods; **c**, Hypotheses. We collected data on  
560 arthropods and tree growth from the BEF-China biodiversity experiment from 2015 to  
561 2020 to test three hypotheses (H1-H3). First, we predicted (H1) that effects of tree  
562 diversity on higher trophic diversity are consistently positive and dampen with  
563 increasing trophic level. Second, we predicted (H2) that herbivore diversity negatively  
564 affects tree productivity via consumption on tree biomass, whereas enemy (i.e.,  
565 predator and parasitoid) diversity has a positive effect on tree productivity through top-  
566 down control on herbivores, leading to an overall positive effect of multitrophic  
567 arthropod diversity on tree productivity. Lastly, we predicted (H3) that tree functional  
568 diversity (FD) and community-weighted means (CWM) can also affect tree  
569 productivity via multitrophic arthropod diversity.



571 **Fig. 2 | Relationships between tree species richness and species richness and**  
572 **abundance of higher trophic groups.** Each point represents one plot. Regression lines  
573 represent the slope of linear models that show change in species richness (a-d) and  
574 abundance (e-h) according to trophic group with tree species richness across year (a, e,  
575 herbivores; b, f, predators; c, g, parasitoids; d, h, overall arthropods). In a-h, raw data  
576 points and regression lines are shaded according to year, with lighter shading indicating  
577 earlier years. Black lines represent samples from all years. Solid lines show significant  
578 ( $P < 0.05$ ) or marginally significant ( $0.05 \leq P < 0.1$ ) effects, and dashed lines show non-  
579 significant ( $P > 0.1$ ) relationships. The grey-shaded zone covers the 95% confidence  
580 interval. The axes are on a log<sub>2</sub>-scale for tree species richness and log-scale for higher  
581 trophic richness and abundance. All tests were two-sided and can be found in  
582 Supplementary Table 4–5.



584 **Fig. 3 | Relationships between species richness and abundance of higher trophic**  
585 **groups and primary productivity.** Each point represents one plot. Regression lines  
586 represent the slope of linear models that show change in primary productivity ( $\text{m}^3 \text{ha}^{-1}$ )  
587 with species richness (a-d) and abundance (e-h) according to trophic group across year  
588 (a, e, herbivores; b, f, predators; c, g, parasitoids; d, h, overall arthropods). In a-h, raw  
589 data points and regression lines are shaded according to year, with lighter shading  
590 indicating earlier years. Black lines represent samples from all years. Solid lines show  
591 significant ( $P < 0.05$ ) or marginally significant ( $0.05 \leq P < 0.1$ ) effects; dashed lines  
592 show non-significant ( $P > 0.1$ ) relationships. The grey-shaded zone covers the 95%  
593 confidence interval. The axes are on a square-root scale for productivity and log scale  
594 for higher trophic-level species richness and abundance. All tests were two-sided and  
595 can be found in Supplementary Table 6–7.

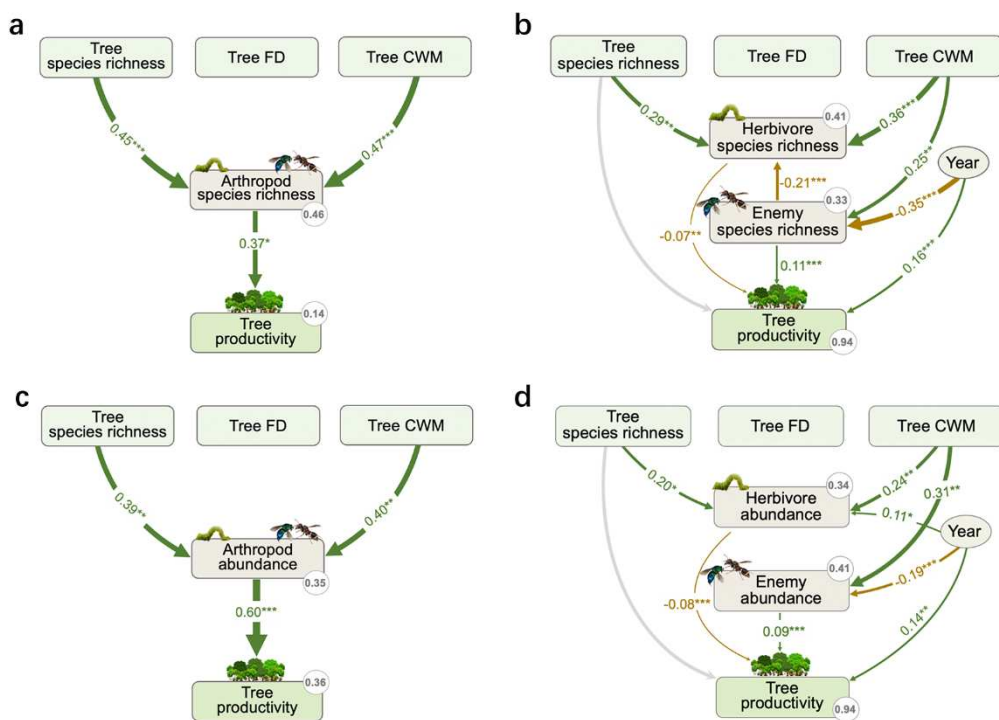


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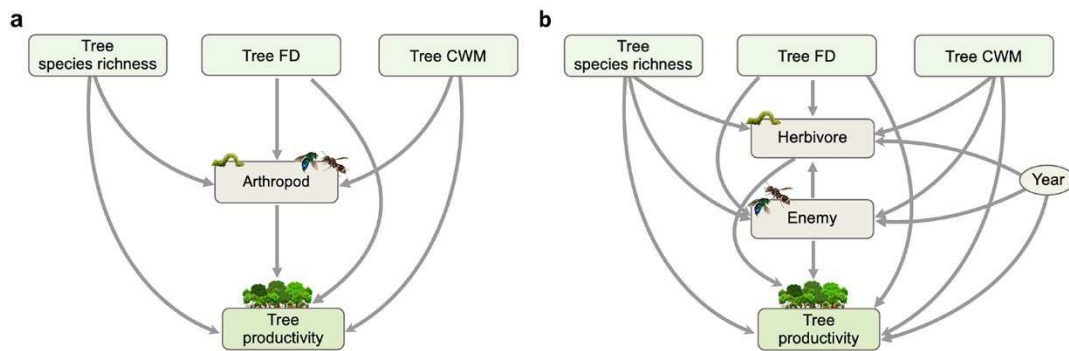
599 **Fig. 4 | Structural equation models (SEMs) of tree species richness, functional**  
600 **traits (tree FD and CWM), year, and overall arthropod or herbivore and enemy**  
601 **species richness or abundance explaining tree productivity.** a and c SEMs based on  
602 overall arthropod data averaged over the five years of observation using arthropod  
603 richness (a, Fisher's C = 2.57,  $P = 0.632$ , DF = 4, AIC = 16.570) or arthropod abundance  
604 (c, Fisher's C = 4.798,  $P = 0.309$ , DF = 4, AIC = 18.798). b and d SEMs based on yearly  
605 data and arthropods separated into herbivores and enemies using herbivore and enemy  
606 species richness (b, Fisher's C = 8.089,  $P = 0.232$ , DF = 6, AIC = 44.089) and herbivore  
607 and enemy abundance (d, Fisher's C = 12.078,  $P = 0.148$ , DF = 8, AIC = 46.078). Green  
608 lines show significant ( $P < 0.05$ ) positive relationships and brown lines show negative  
609 significant relationships, while grey lines show marginally significant relationships  
610 ( $0.05 \leq P < 0.1$ ). Standardized path coefficients are shown in each path with asterisks  
611 indicating significance (\*  $P < 0.05$ , \*\*  $P < 0.01$ , and \*\*\*  $P < 0.001$ ). Percentage values  
612 (i.e., conditional  $R^2$ ) are shown next to the corresponding variables. Arrow widths are  
613 scaled by the absolute values of the standardized path coefficients.



614

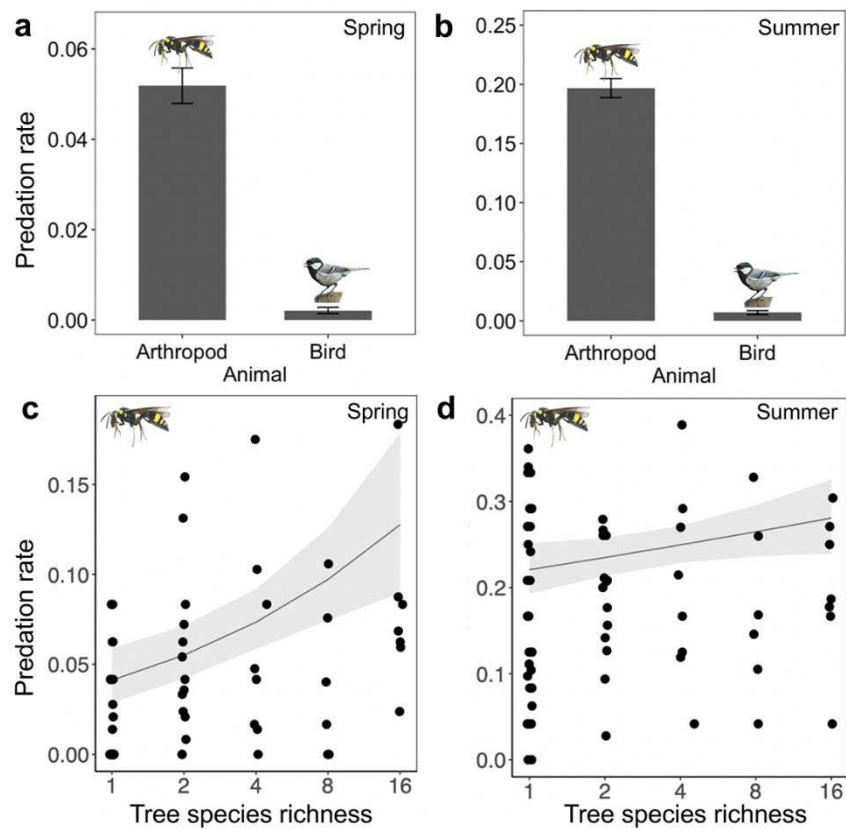
615 **Extended Data Figures**

616 **Extended Data Fig. 1 | Hypotheses framework for relationships among tree species**  
617 **richness, functional traits (indicated by tree functional diversity, FD; and**  
618 **community-weighted mean, CWM), arthropod (indicated by their species richness**  
619 **and abundance), and tree productivity.** Model (a) was constructed based on averaged  
620 overall arthropod data. Model (b) was constructed based on 5-year trophic-resolved (i.e.,  
621 herbivores and natural enemies are partitioned) data, in which we included ‘year’ as a  
622 linear predictor. The framework is based on theoretical expectations and correlations  
623 among multiple variables. Grey arrows indicate hypothesized causal relationships.



624

625 **Extended Data Fig. 2 | Predation rate of model caterpillars by arthropods and**  
626 **birds.** Predation rate of arthropods and birds on model caterpillars in spring (a, n = 383)  
627 and summer (b, n = 375); relationships between predation rate of arthropods on model  
628 caterpillars and tree species richness in spring (c) and summer (d). Grey bars indicate  
629 the averaged predation rate on model caterpillars by arthropods and birds, and black  
630 error bars represent the standard deviation. Solid lines show significant ( $P < 0.05$ )  
631 effects. The grey-shaded zone covers the 95% confidence interval. All tests were two-  
632 sided. The x-axes are on a log<sub>2</sub>-scale for tree species richness.

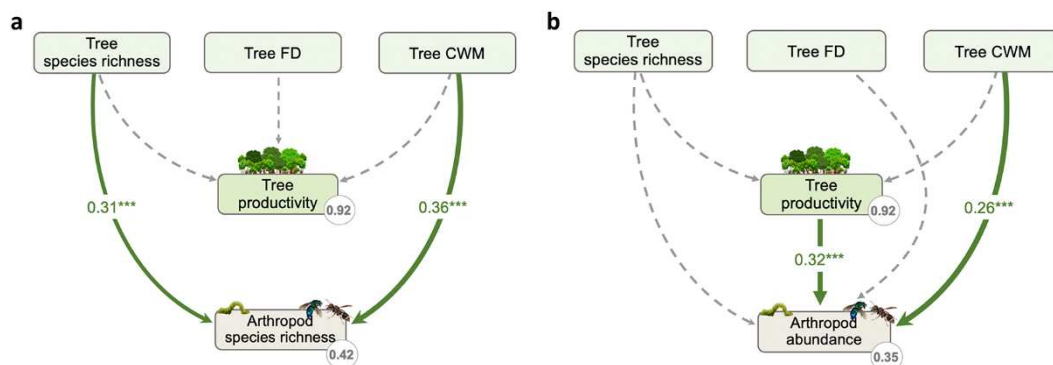


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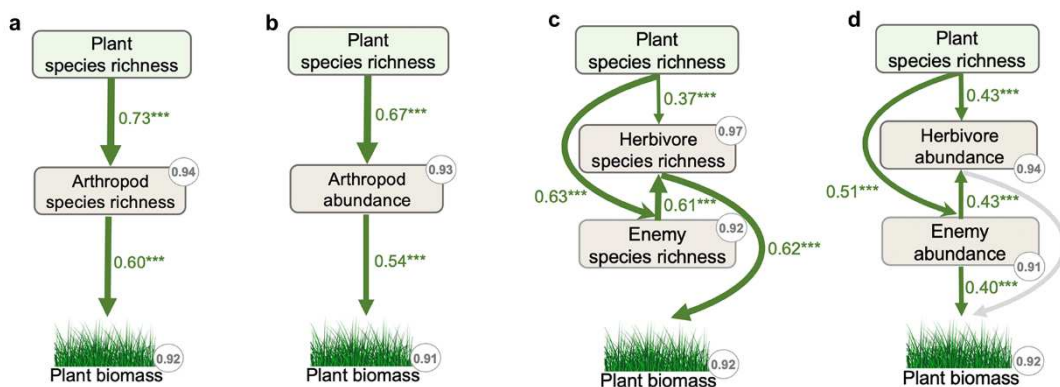


635 **Extended Data Fig. 3 | Structural equation model testing if tree species richness**  
636 **and functional traits affect arthropod species richness and abundance through**  
637 **tree productivity.** The model fit for both models (model a: Fisher's C = 4.09, P = 0.394,  
638 DF = 4, AIC = 26.090; model b: Fisher's C = 0.299, P = 0.861, DF = 2, AIC = 24.299)  
639 suggested that tree diversity effects on arthropod species richness (a) or abundance (b)  
640 are not mediated through tree productivity. Green lines show significant (P < 0.05)  
641 positive relationships, and brown lines show significant negative relationships, while  
642 grey lines show marginally significant relationships (0.05 ≤ P < 0.1). Standardized  
643 path coefficients are shown in each path with asterisks indicating significance (\* P <  
644 0.05, \*\* P < 0.01, and \*\*\* P < 0.001). Percentage values (conditional R2) are shown  
645 below the corresponding variables. Arrow widths are scaled by the absolute values of  
646 the standardized path coefficients.



647

648 **Extended Data Fig. 4 | Structural equation model testing how plant species**  
649 **richness, arthropod species richness or abundance explaining plant biomass, using**  
650 **the data collected from the Jena biodiversity experiment.** Model (a) (Fisher's C =  
651 5.249, P = 0.072, DF = 2, AIC = 21.249) and (b) (Fisher's C = 8.247, P = 0.016, DF =  
652 2, AIC = 24.247) were constructed based on overall arthropod species richness and  
653 abundance. Model (c) and (d) were constructed based on trophic-resolved (herbivores  
654 and enemies partitioned) data (c: Fisher's C = 3.876, P = 0.144, DF = 2, AIC = 31.876;  
655 d: Fisher's C = 3.042, P = 0.219, DF = 2, AIC = 31.042). Green lines show significant  
656 ( $P < 0.05$ ) positive relationships, and grey lines show marginally significant paths ( $0.05$   
657  $\leq P < 0.1$ ). Standardized path coefficients are shown next to each path with asterisks  
658 indicating significance (\*  $P < 0.05$ , \*\*  $P < 0.01$ , and \*\*\*  $P < 0.001$ ). Percentage values  
659 (conditional R<sup>2</sup>) are shown below the corresponding variables.



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