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Intra- and interspecific tree diversity promotes multitrophic plant–Hemiptera–ant interactions in a forest diversity experiment

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Abstract

Interactions between species of different trophic levels have long been recognized as fundamental processes in ecology. Although mounting evidence indicates that plant species diversity (PSD) or plant genetic diversity (PGD) can influence the plant-associated arthropod community, these two fundamental levels of biodiversity are not often manipulated simultaneously to assess their effects on species interactions. We used a large tree diversity experiment (BEF-China), which manipulates PSD and PGD in a crossed design to test individual and combined effects of PSD and PGD on multitrophic interaction networks and interaction partner species richness and occurrence. We focused on two tree species, on which sap-sucking Hemiptera and interacting ant species commonly occur. This tri-trophic interaction can be divided into the antagonistic plant–Hemiptera interaction and the mutualistic Hemiptera–ant interaction, known as trophobioses. Qualitative evaluation of tri-trophic interaction networks at different PSD and PGD combinations showed increased interaction partner redundancy at high PSD and PGD. This was supported by increased Hemiptera species richness at high PSD and PGD. Furthermore, the data indicate higher occurrence of Hemiptera and trophobioses and higher trophobiotic ant species richness with increasing PSD and PGD. As no plant diversity component alone caused an effect we conclude that the combined effect of high PGD and high PSD might be additive. In summary, as plant genetic diversity, especially at low species richness, seems to increase the interaction partner redundancy in interaction networks and the diversity of interacting communities, we suggest that genetic diversity should be considered in forest conservation and restoration programs.

Keywords: Tree genotype diversity, ant, Hemiptera, subtropical forest, BEF-China, multitrophic, interaction network, bottom-up, *Cinnamomum camphora*, *Idesia polycarpa*

Introduction

Plant biodiversity can increase species richness and abundance across trophic levels through bottom-up effects (Scherber et al. 2010). Likewise, biodiversity can stabilize ecosystem properties through complementarity of species or traits and via insurance effects (Ives, Cardinale, & Snyder 2005; Tilman, Isbell, & Cowles 2014; Yachi & Loreau 1999). The same effects are hypothesized to affect communities at multiple trophic levels (Scherber et al. 2010; Staab, Blüthgen, & Klein 2015). Most research in this field is conducted in biodiversity-ecosystem functioning (BEF) experiments which manipulate plant species richness (Bruelheide et al. 2014; Cardinale et al. 2012). However, plant intraspecific genetic diversity (PGD) is related to ecosystem functions (Crutsinger et al. 2006; Johnson, Lajeunesse, & Agrawal 2006) and effects of PGD, for example on arthropod communities, can be comparable to effects of plant species diversity (PSD) (Cook-Patton, McArt, Parachnowitsch, Thaler, & Agrawal 2011; Crawford & Rudgers 2013).

Previous studies have discussed increasing stability of species interactions with increasing PSD in grassland and forest experiments (Ebeling, Klein, & Tscharntke 2011; Haddad, Crutsinger, Gross, Haarstad, & Tilman 2011; Staab et al. 2015). In the context of species loss, the concept of stability is described as the resistance to perturbation; with the assumption that networks with higher interaction partner redundancy will exhibit higher robustness through resource heterogeneity and response complementarity of species or genotypes to perturbations (Ebeling et al. 2011; Haddad et al. 2011; Hooper et al. 2005).

Recently, increased species richness and abundance of insects were shown in response to increasing PGD (e.g. Müller, Klein, Scherer-Lorenzen, Nock, & Staab 2018), and insect community composition changed with the genotype of host plants (Barbour et al. 2016; Johnson 2008). Differences in heritable traits such as the concentration of chemical defence compounds could shape these observations (Barbour et al. 2016; Züst & Agrawal 2017). In combination with multitrophic responses to species richness of interaction partners, changes in PGD are expected to influence species interactions at different trophic levels (Barbour et al. 2016; Johnson 2008; Moreira & Mooney 2013; Staab et al. 2015). Only few studies have tested the potential interactive effects of PSD and PGD on plant-associated organisms (Campos-Navarrete, Munguía-Rosas, Abdala-Roberts, Quinto, & Parra-Tabla 2015; Cook-Patton et al. 2011; Crawford & Rudgers 2013), but none involved species interactions. Consequently, little is known about the relative importance of PSD and PGD as well as the potential interactive effects between PSD and PGD on multitrophic networks.

In plant–Hemiptera–ant networks, Hemiptera extract plant sap and excrete honeydew, which provides nutrition to ants (Davidson, Cook, Snelling, & Chua 2003). The ants protect Hemiptera from natural enemies in exchange for honeydew (Blüthgen, Mezger, & Linsenmair 2006; Ivens, von Beeren, Blüthgen, & Kronauer 2016). Hence, this tri-trophic network can be subdivided into an antagonistic plant–Hemiptera and a mutualistic Hemiptera–ant network, of which the latter is known as trophobiosis. Trophobioses are common in many ecosystems and have attracted much research (Blüthgen et al. 2006; Johnson 2008; Mooney & Agrawal 2008; Moreira & Mooney 2013; Moreira Mooney, Zas & Sampedro 2012; Staab et al. 2015). Here we use trophobioses to test for the effect of PSD and PGD on specialized antagonistic and generalized mutualistic interaction networks (Blüthgen et al. 2006; Staab et al. 2015) in a forest BEF experiment manipulating PSD and PGD independently and simultaneously (Hahn et al. 2017).

We expect increasing occurrence and species richness of Hemiptera with, both, increasing PSD and PGD, but with stronger responses to PSD. Hemiptera species are known for their high degree of plant specificity (Blüthgen et al. 2006; Forister et al. 2015; Staab et al. 2015), but are likely less specialized on plant genotypes. This is explained by higher interspecific than intraspecific variation expected for traits of Hemiptera relevant for utilizing plant resources, and plant defence traits deterring sucking herbivores (Campos-Navarrete et al. 2015; Cook-Patton et al. 2011). Further, we expect ant species richness and abundance responses to be weaker than the potential Hemiptera responses, due to the opportunistic interaction of ants with Hemiptera and their mostly indirect association to the plant level (Moreira & Mooney 2013; Staab et al. 2015). Moreover, as shown for plant–Hemiptera–ant interactions in response to PSD, we expect interaction networks to increase in interaction partner redundancy due to complementary provision of resources or complementary expression of traits by plants and Hemiptera at locally increased levels of PSD and PGD (sensu Staab et al. 2015).

Material and methods

Study site

The sampling was conducted at the Biodiversity-Ecosystem Functioning (BEF)-China experiment (www.bef-china.de), located near Xingangshan Township (29.08–29.11 N, 117.90–117.93

E), Dexing City of Jiangxi Province, China. The region is typical for the Chinese subtropics with a mean annual temperature of 16.7 °C and a mean annual precipitation of 1821 mm (Yang et al. 2013). The BEF experiment was established at two sites (site A and site B) in 2009 and 2010, respectively, to investigate effects of tree and shrub species richness and also genetic diversity on ecosystem functioning with a pool of 42 local tree species planted on 566 experimental plots. Each plot has a size of 25.8 m × 25.8 m in orthogonal projection and 400 tree individuals are planted in a 20×20 regular grid, with a distance of 1.29 m among closest neighbouring trees (Bruelheide et al. 2014). Within site B, a PSD × PGD experiment was installed, using four tree species from the main experiment, on a total of 23 plots (Hahn et al. 2017). The experimental design includes all factorial combinations of 1 or 4 tree species (PSD) and 1 or 4 seed families (PGD), from now on called ‘diversity treatments’ with the levels: 1/1-PSD/PGD, 4/1-PSD/PGD, 1/4-PSD/PGD and 4/4-PSD/PGD. The replication of each diversity treatment is shown in Table 1. Monoculture subplots were taken as individual replicates (Table 1), thus the number of planted trees per genotype was kept constant throughout all PSD and PGD combinations. The species pool includes two deciduous trees, *Alniphyllum fortunei* (Hemsley) Makino (Styracaceae) and *Idesia polycarpa* Maximowicz (Flacourtiaceae), and two evergreen trees, *Cinnamomum camphora* (L.) J. Presl. (Lauraceae) and *Daphniphyllum oldhamii* (Hemsley) Rosenthal (Daphniphyllaceae). For plot tree establishment, seeds were collected from different mother trees, which form distinct genetic seed families of half-sibs for each mother tree. Mother trees were chosen in a larger area around Gutianshan National Nature Reserve (29°10 ′19″N, 118°03 ′50″E), Zhejiang Province, China. As all tree species are insect pollinated, seed family diversity represents intraspecific genetic diversity. Although this genetic diversity experiment aimed to use the same number of genotypes for each tree species, in fact, 8 genotypes for *I. polycarpa*, 9 genotypes for *A. fortunei* and *C. camphora*, and 15 genotypes for *D. oldhamii* were planted, due to limited availability of seeds per mother tree (see Hahn et al. 2017). For tree monoculture plots, each plot was subdivided into 4 subplots (quarters) of equal size and tree abundance. Within each tree monoculture subplot or polyculture plot, the genotypes were assigned randomly to the planting positions.

Data collection

From the tree species pool in the PSD × PGD experiment, only the two tree species *C. camphora* and *I. polycarpa* are known to harbour trophobioses, whereas *A. fortunei* and *D. oldhamii* were never recorded harbouring trophobiotic Hemiptera species (Fornoff unpublished data investigating 600 and 300 tree individuals, respectively). Thus, this study is based on 19 genetic plots (excluding four monoculture plots (1/1-PSD/PGD) of *A. fortunei* and *D. oldhamii* and one plot (4/1-PSD/PGD) with extraordinary mortality of tree saplings). In total, 2396 living trees of *C. camphora* and *I. polycarpa* were inspected in April (early growing season during leaf flushing) and September/October (end of growing season with full foliage and expected maximum insect abundances) 2015. We recorded all trophobioses and Hemiptera known to be tended by ants by visually inspecting a total of 20 leaves from three randomly chosen branches. We counted a trophobiosis when a Hemiptera species was tended by an ant species at the unit of one leaf regardless of the insects' absolute individual numbers, to avoid potential biases of abundance owing to rapid population growth (Ben-Dov & Hodgson 1997). If an observed Hemiptera species was tended by more than one ant species (or an ant species tended more than one Hemiptera species), we scored interactions separately. Voucher specimens of each trophobiosis were collected with soft insect forceps and preserved in 70% ethanol for further identification. All species were identified to species or morphospecies level.

Data analysis

All data analyses were conducted in R 3.3.1 (R Development Core Team 2016). Prior to testing responses of trophobioses to PSD and PGD, samples were pooled per plot or subplot, representing replicates for each combination of tree PSD and PGD. Then we calculated the proportion of trees occupied by Hemiptera (including non-ant-tended) and trophobioses. Tree establishment success varied between plots leading to different sampling effort between plots. To correct for this, we calculated rarefied species richness of Hemiptera and ants, using the 'rarefy' function of the vegan-package (Oksanen et al., 2017). Hemiptera and trophobiosis occurrence was used to calculate the proportion of trees within each treatment plot that harboured Hemiptera or trophobiosis. The effects of PSD and PGD on rarefied species richness and proportion of trees with Hemiptera or trophobiosis were tested using linear and generalized linear mixed effect models, respectively, with a random intercept on plot identity, accounting for non-independence of sub-plots. The proportion data were analysed with a binomial error distribution, with prior weights given by the number of sampled trees, and including an observation level random effect to account for overdispersion (Bolker et al., 2009). Rarefied species richness was analysed using a normal distribution as residual plots showed no strong patterns suggesting a log transformation. Significant effects were tested using pairwise comparisons, computed with the R-package 'lsmeans' (Lenth 2016) applying the Tukey (HSD) method to correct for multiple comparisons.

To explore the effects of intraspecific genetic diversity on the structure of interaction networks, we treated each tree genotype as a 'node in the network' (i.e. tree species × seed family). Each diversity treatment of PSD and PGD had originally been planned to contain 8 genotypes of each tree species and, hence, 16 tree 'nodes' in total. However, 1/1-PSD/PGD and 4/1-PSD/PGD had 15 and 13 tree genotypes, respectively, due to natural mortality and different availability of seeds. For exploring interaction network responses, we pooled all trees found in plots representing the same PSD and PGD combination. This was necessary for allowing each tree species and seed family to be present in each interaction network and to increase network size and confidence of network indices (Dormann, Fründ, Blüthgen, & Gruber 2009). The resulting four communities of each diversity treatment (1/1-PSD/PGD, 1/4-PSD/PGD, 4/1-PSD/PGD, 4/4-PSD/PGD) showed different tree abundance, due to unequal mortality of trees prior to the sampling. In order to account for different field sampling effort, we randomly sampled 173 trees (the lowest number of trees found in any of the four diversity treatments) without replacement from each diversity treatment 1000 times by using the 'sample' function of the 'base' R-package. Accordingly, the network analyses (see below) were based on 1000 subsets containing 692 trees (4 times 173 trees) out of 2396 originally inspected trees.

Consequently, each diversity treatment has only one data point, which cannot be compared statistically. Properties of trophobiotic networks per diversity treatment were numerically represented and visualized with the R-package ‘bipartite’ (Dormann et al. 2009). Among the variety of network indices reviewed in Dormann et al. (2009), two indices derived from Shannon entropy, ‘weighted generality’ (G_{qw}) (Bersier, Banašek-Richter, & Cattin 2002) and ‘complementary specialization’ (H_2') (Blüthgen et al. 2006) were selected to describe the interaction partner redundancy and interaction specialization at the network level. In a bipartite network, G_{qw} is defined as weighted mean effective number of interaction partners in the lower trophic level per species in the higher trophic level (Bersier et al. 2002). In our case, it describes the weighted mean of all ant species’ Shannon diversity of Hemiptera tended by each ant species, and the weighted mean of all Hemiptera species’ Shannon diversity of plant interaction partners. Weighted generality (G_{qw}) is by definition larger than 1. A higher G_{qw} reflects a higher level of redundant interaction partners or function providers, which is supposed to increase the robustness of the interaction to a perturbation and thus suggests higher stability of a bipartite network (Blüthgen 2010; Yachi & Loreau 1999). Complementary specialization (H_2') reflects the extent of deviation of observed interactions from the expected probability distribution of the interactions (Blüthgen , Menzel, & Blüthgen 2006) and quantitatively describes the level of specialization of an entire bipartite network, ranging from 0 (extreme generalization) to 1 (extreme specialization). For example, high specialization is achieved when each species of the higher level (e.g. Hemiptera) interacts only with its specific partner (e.g. tree) and no overlap between hosts (e.g. trees) exists. In contrast, if for example, each ant species interacts with multiple Hemiptera species and there is host (Hemiptera) overlap between different ant species, then H_2' approximates 0. Therefore H_2' and G_{qw} are inversely correlated, but describe similar structural changes in interaction networks, and inform about resource (lower level species) redundancy. In our analysis for each diversity treatment in each random sampling run, a respective G_{qw} and H_2' of the antagonistic plant–Hemiptera and the mutualistic Hemiptera–ant network was calculated based on a subset containing 173 randomly sampled trees. After 1000 random sample runs, we calculated the mean value of each index (G_{qw} and H_2'). By this, we did not change the number of replicates but accounted for unequal sample sizes.

Results

In total, 2396 living trees were inspected, of which 473 (19.7%) were occupied by Hemiptera, including 305 (12.8%) trees with 408 trophobioses. In these trophobioses, 19 Hemiptera species were tended by 13 ant species (Appendix A: Table 1). In a comparison of PSD and PGD diversity treatments, we found no significant effects of the diversity treatments on the occurrence of Hemiptera and trophobiosis (Fig. 1A). The single significant response was higher Hemiptera species richness for 4/4-PSD/PGD compared to 1/4-PSD/PGD (Fig. 1B and Table 2). However, across the whole dataset there was a trend of increasing Hemiptera and ant species richness and proportion of trees with Hemiptera and trophobioses occurrence, with lowest values at 1/1-PSD/PGD and highest at 4/4-PSD/PGD. This trend showed an increase of the median from 13% to 36% and from 7% to 28% for Hemiptera and trophobioses occurrence from 1/1 to 4/4-PSD/PGD treatment levels, respectively (see Fig. 1A and Appendix A: Table 2). Although statistically not yet supported, the box-plots indicate stronger responses to PSD than to PGD for insect species richness (Fig. 1B and Table 2).

Quantitative interpretation of the networks showed that generality (G_{qw}) of the antagonistic plant–Hemiptera interaction was higher and specialization (H_2') lower at high PGD, both in PSD monocultures and polycultures (Fig.2 and Table 3). However, in the mutualistic Hemiptera–ant network, G_{qw} was slightly lower at high PGD in PSD monocultures but higher in PSD polycultures, while H_2' was lower at high PGD in PSD polycultures (Table 3). The value of H_2' in Hemiptera–ant networks at 1/1-PSD/PGD is unknown because of the on average too small network size inhibiting reliable index calculation. Comparing 1/1-PSD/PGD and 4/4-PSD/PGD, high PSD resulted in high G_{qw} for both, antagonistic and mutualistic interactions, while H_2' remained constant in all diversity treatments and was generally lower for the mutualistic compared to the antagonistic interaction (Table 3).

Discussion

Our results show that PSD and PGD can affect multitrophic interactions bottom-up by increasing interaction partner species richness. At high PSD and PGD, interaction networks were more generalistic and less specialized, indicating increased resource redundancy. Thus, the interaction among PSD and PGD might promote the stability of tri-trophic plant–Hemiptera–ant networks against tree diversity loss. In general, the diversity treatment of high PSD combined with high PGD could pose a stronger influence on interacting insect communities than each component of diversity alone. To the best of our knowledge, this is the first study to indicate positive combined effects of PSD and PGD on species interactions.

We observed a positive bottom-up effect of PSD on the species richness of trophobiotic Hemiptera. As we cannot exclude a potential contribution of PGD and as mechanistic explanations are shared between PSD and PGD we discuss both simultaneously as potential drivers. In support of this, increased insect species richness in response to PGD was found by Crawford and Rudgers (2013) and Müller et al. (2018) and in response to PSD by Staab et al. (2015). Complementary resource provision of different plant species or genotypes could increase Hemiptera species richness, for example, by the complementary expression of traits increasing resource heterogeneity and niche diversity. Additionally, a positive diversity-productivity relationship has been documented for global forests (Liang et al. 2016; Zhang, Chen, & Reich 2012). Although not significant, we found an up to three-fold increase in Hemiptera occurrence at high PSD and PGD compared to low PSD and PGD. Accordingly, increased Hemiptera species richness could be a result of increased Hemiptera occurrence, which might be related to more productive tree communities providing more resources (e.g. biomass, Crutsinger et al. 2006) in more genotypic and species diverse plots (following the 'more individuals hypothesis', Srivastava & Lawton 1998). A similar trend was indicated for interacting ant species richness. For ants, Hemiptera could provide higher quantities of honeydew and honeydew with more complementary nutrients (Blüthgen & Fiedler 2004; Pringle, Novo, Ableson, Barbehenn, & Vannette 2014; Staab et al. 2015). Honeydew is the most commonly used energy resource for vegetation-foraging ants (Davidson et al. 2003). Therefore, ants might be sensitive to changes in Hemiptera species richness. The lack of significance in this trend could indicate that ants were not affected by changes in the Hemiptera and plant level due to the small variations in Hemipteran species richness and hence potential traits relevant for Hemiptera-ant interactions.

We expected a positive effect of both PSD and PGD on the occurrence of Hemiptera and trophobioses, due to increased plant trait diversity and plant productivity (e.g. Hughes, Inouye, Johnson, Underwood, & Vellend 2008; Hutchinson 1959). In a similar tri-trophic system, Johnson (2008) showed that genotype specific plant traits caused large variations in Hemiptera density and together with Hemiptera abundance affected trophobiotic ant abundance. For our experimental forest system, two studies found that the aboveground productivity of trees was not related to PGD (Hahn et al. 2017; Zeng, Durka, & Fischer 2017). Hence, the large variance in our occurrence data could be explained by the variance introduced by different plant genotypes, and the lack of increased plant productivity might explain the non-significant differences in Hemiptera occurrence.

To disentangle the effect of PSD and PGD on higher trophic levels further studies combining larger species- and genetic diversity gradients are a promising approach. In this study, we were limited in replications of treatment diversity levels, tree species and sampling turns but still observed trends resembling ecological expectations on the effects of PSD and PGD on multitrophic interactions. However, plant traits vary more strongly among species than within species and therefore, complementarity effects of PSD can be expected to more strongly influence consumer species richness (e.g. Cook-Patton et al. 2011), and are hence more easily detected experimentally.

The described trends within the four diversity treatments do not exclude a positive combined effect of PSD and PGD on the occurrence and species richness across consumer levels. The mechanisms discussed for PSD and PGD might act simultaneously and additively result in the observed positive relationship (but see Campos-Navarrete et al. 2015). Therefore, we conclude that higher trophic level communities and the interactions with their resources might benefit from a combination of intra- and interspecific diversity. This is also indicated by our network analyses, which show higher values of generality in the plant–Hemiptera network at high local diversity of plant genotypes: Hemiptera utilized a higher number of interaction partners (e.g. feed on different tree genotypes). This increased redundancy might suggest that the stability of interaction networks is positively related to PGD. Moreover, indicated by the high level of generality observed at 4/4 PSD/PGD in plant–Hemiptera and Hemiptera–ant networks, we assume combined effects of PSD and PGD on the stability of trophic networks.

Antagonistic networks are frequently more complementary and specialized than mutualistic networks (Blüthgen et al. 2006; Morris, Gripenberg, Lewis, & Roslin 2014; Staab et al. 2015). However, in our study, the antagonistic plant–Hemiptera network was more generalized than the mutualistic Hemiptera–ant network, which is a result of treating different genotypes of the same plant species as individual hosts 'nodes' in the networks. The distinction between genotypes was only possible at the plant level in this study, but may generally be important for herbivore-plant and ant-Hemiptera interactions (Barbour et al. 2016; Züst & Agrawal 2017). Furthermore, the low generality of the mutualistic network might be related to the limited number of different Hemiptera partners for ants, which reduced the redundancy of the respective interaction network for mathematical reasons.

In summary, we directly linked PGD to species interactions, and demonstrated that both PSD and PGD may increase the number of interacting species among trophic levels, network redundancy and thus the robustness of trophic interactions. While the exact mechanisms how PSD and PGD affect species interactions in a combined way are as yet unclear, our study indicates that PSD and PGD simultaneously influence ecosystem structure across trophic levels. Therefore, studying the effects of species and genetic diversity on trophic interactions is a promising field for further ecological research. Finally, as plant genetic and species diversity positively influence the diversity and interactions of organisms in other trophic levels, both plant diversity components should be considered in forest conservation and restoration.

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Figures

Fig. 1. Proportion of trees occupied by Hemiptera and trophobioses (A) and rarefied species richness per plot of Hemiptera and interacting ants (B) in response to experimental diversity treatments. The diversity treatments represent combinations of PSD (2 target and 2 non-target tree species) and PGD (17 seed families within the target species). Boxes and whiskers represent the data distribution about the median, filled circles represent extreme values and diamonds represent mean values. Significant differences between treatments are indicated by different letters and presented in Table 2 and Appendix A: Table 2.

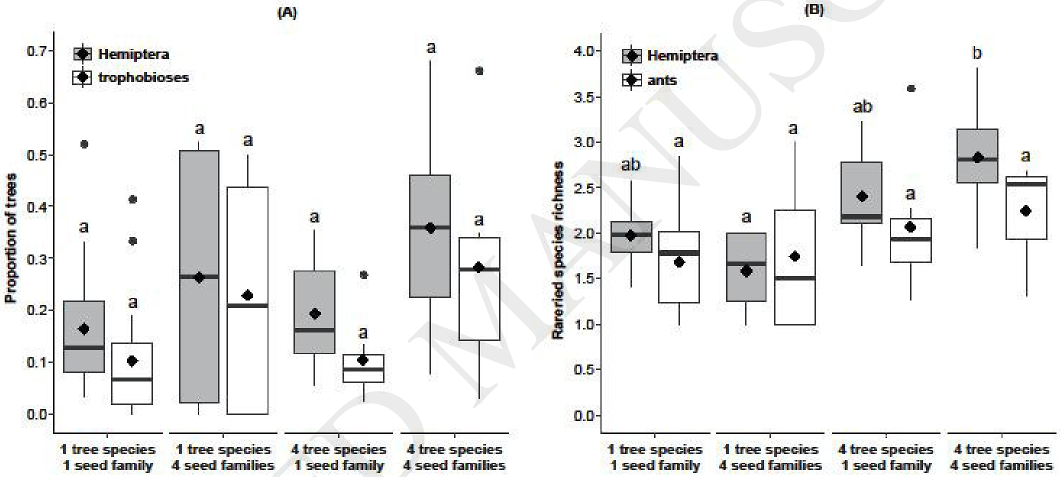
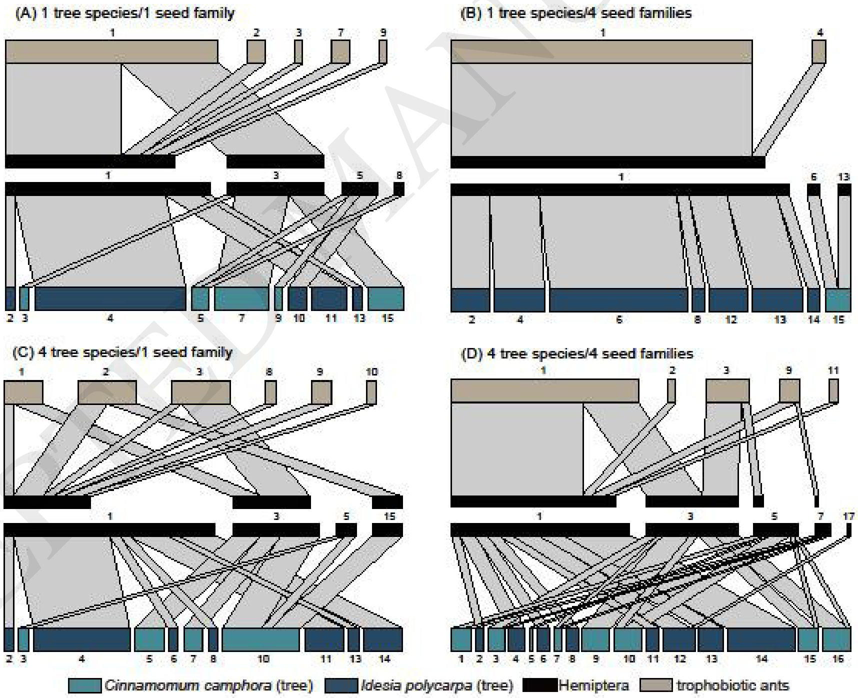


Fig. 2. Examples of quantitative tri-trophic networks for 4 PSD and PGD diversity treatments. Networks among plant species and genotypes (lower bars), Hemiptera (middle bars) and ants (upper bars) are based on randomly sampled communities (173 trees) after pooling all trees of each diversity treatment ((A) 1/1 PSD/PGD, (B) 1/4 PSD/PGD, (C) 4/1 PSD/PGD, (D) 4/4 PSD/PGD). Accordingly, some plant genotypes, Hemiptera and ant species may not be included in the networks. Note that plant genotypes without Hemiptera occurrence are not included in these networks as no interactions can be depicted or analysed. Width of bars represents number of occurrence of corresponding species (or tree genotypes). Width of links indicates number of interactions between two species in adjacent trophic levels. All plant genotypes, Hemiptera and ant species are coded by numbers (see Appendix A: Table 1). The two tree species studied are indicated by different intensities of blue in the lower bar.



Note to the editor: this figure can be produced in gray scale for the printed issue.

Tables

Table 1. Number of replicates per PSD and PGD diversity treatment.

PSD (tree species)	PGD (genotype(s) per tree species)	Plot/subplot size	Replicates (subplot/plot)
1	1	¼ × 625 m^2	32 (32 × ¼ × 625 m^2 = 8 × 625 m^2)
1	4	¼ × 625 m^2	8 (8 × ¼ × 625 m^2 = 2 × 625 m^2)
4	1	1 × 625 m^2	8 (8 × 1 × 625 m^2 = 8 × 625 m^2)
4	4	1 × 625 m^2	6 (6 × 1 × 625 m^2 = 6 × 625 m^2)

Table 2. Results of the pairwise comparisons for rarefied species richness of Hemiptera and trophobiotic ants among 4 PSD and PGD diversity treatments (e.g. 1_4 indicates the diversity treatment of 1 PSD and 4 PGD) using linear mixed-effects models (LMM) and subsequent Tukey (HSD) tests.

Contrast	Rarefied species richness of Hemiptera				Rarefied species richness of ants			
	Estimate±SE	df	t.ratio	p	Estimate±SE	df	t.ratio	p
1_1 - 1_4	0.386±0.446	13.05	0.867	0.822	-0.064±0.497	9.95	-0.129	0.999
1_1 - 4_1	-0.429±0.326	13.60	-1.315	0.569	-0.380±0.373	11.73	-1.019	0.742
1_1 - 4_4	-0.859±0.336	13.75	-2.554	0.095	-0.558±0.388	12.20	-1.440	0.500
1_4 - 4_1	-0.815±0.420	14.07	-1.939	0.256	-0.316±0.491	13.27	-0.643	0.916
1_4 - 4_4	-1.246±0.429	14.14	-2.907	0.050*	-0.494±0.503	13.51	-0.984	0.761
4_1 - 4_4	-0.431±0.302	16.10	-1.428	0.501	-0.178±0.381	19.92	-0.468	0.965

Note: Significance is indicated by asterisks, with $p < 0.05$ (*).

Table 3. The values of H_2' and G_{qw} of trophobiotic networks per PSD and PGD diversity treatment (e.g. 1_4 indicates the diversity treatment of 1 PSD and 4 PGD). G_{qw} (weighted generality) could be directly translated as the effective number of lower level interaction partner richness for each species at the higher trophic level, hence interaction partner redundancy. H_2' decreases with decreasing complementary specialization on unique interaction partners (range 0-1) at the network-level.

Diversity	H_2'(p–H)	G_{qw}(p–H)	H_2'(H–a)	G_{qw}(H–a)
1_1	0.83	2.63	0.37	1.69
1_4	0.75	4.99	NA	1.00
4_1	0.80	3.59	0.69	1.26
4_4	0.76	5.38	0.49	1.88

Note: ‘p–H’ indicates the antagonistic plant–Hemiptera network and ‘H–a’ indicates the mutualistic Hemiptera–ant network.