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Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment

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Species and processes in ecosystems are part of multi-trophic interaction networks. Plants represent the lowest trophic level in terrestrial ecosystems, and experiments have shown a stabilizing effect of plant diversity on higher trophic levels. Such evidence has been mainly collected in experimental grasslands. Forests are structurally more complex than grasslands and support the majority of the global biodiversity, but studies on multi-trophic interaction networks are missing in experimental tree diversity gradients. In a forest diversity experiment in southeast China, we examined how tree diversity affects the structure of trophobiotic networks. Trophobioses are tri-trophic interactions between plants, sap-sucking Hemiptera and honeydew-collecting ants that can be subdivided into a largely mutualistic Hemiptera–ant and an antagonistic plant–Hemiptera network. We inspected almost 7000 trees in 146 plots ranging from monocultures to 16 tree species mixtures and found 194 trophobioses consisting of 15 tree, 33 Hemiptera and 18 ant species. We found that tree diversity increased the proportion of trees harboring trophobioses. Consistent with the prediction that mutualistic and antagonistic networks respond differently to changing environments, we found that the generality index of the mutualistic Hemiptera–ant but not the antagonistic plant–Hemiptera network increased with tree diversity. High generality, maintained by high tree diversity, might correspond to higher functional stability. Hence, our results indicate that tree diversity could increase via bottom–up processes the robustness of ant–Hemiptera associations against changing environmental conditions. In turn, the plant–Hemiptera network was highly complementary, suggesting that host-specific Hemiptera species may be vulnerable to co-extinction if their host plants disappear. Based on our results, we provide possible future research directions to further disentangle the bottom–up effect of tree diversity on the structure of trophobiotic networks.

Synthesis

It is now widely accepted that plant diversity promotes ecosystem functionality and stability. However, it is still largely unknown how plant diversity affects interactions between trophic levels and if different interaction types are affected differently. Using a tri-trophic study system consisting of plants, sap-sucking Hemiptera, and ants we provide evidence that increasing local plant diversity stabilizes the mutualistic Hemiptera–ant but not the antagonistic plant–Hemiptera networks. Our results suggest that bottom–up effects of plant diversity on trophic interactions might generally depend on the type of interaction (mutualistic versus antagonistic) considered.

Species assemblages in ecosystems form food webs consisting of multiple trophic levels, with producers such as plants representing the lowest level and various primary and secondary consumers representing the higher trophic levels. Plant diversity influences the complexity of multi-trophic interactions by affecting productivity and heterogeneity of plants, which can feed back on plant community structure and performance (Scherber et al. 2010).

These complex associations between species can be described in species interaction networks, and since the benchmark paper by Jordano (1987), the analysis of such networks has become a lively field in ecology (Bersier et al. 2002, Blüthgen et al. 2007, Dormann et al. 2009, Pocock et al. 2012). A network analysis considers single species as 'nodes' connected by 'links' which refer to the usually consumptive interactions between species in different trophic levels. The distribution of such links can subsequently be measured by manifold mathematical indices which allow characterizing the properties of a network (Bersier et al. 2002, Dormann et al. 2009). In parallel to the development of network analyses, the first large-scale biodiversity–ecosystem functioning (BEF) experiments started to investigate how the diversity of plants relates to ecosystem processes such as productivity (Tilman et al. 2001) or overall community stability (Hector et al. 2010). Network analyses have, however, rarely been considered in the context of BEF experiments, despite knowledge of multi-trophic interactions being important to understand the relationship between plant diversity and BEF processes (Balvanera et al. 2006, Hillebrand and Matthiessen 2009). The available studies in grassland experiments suggest that plant diversity has a stabilizing effect on food webs by, for example, providing more consistent and more heterogeneous resources to higher trophic levels (Petermann et al. 2010, Ebeling et al. 2011, Haddad et al. 2011). In this context, stability refers to the ability of a food web to resist changing habitat conditions. More stable food webs are more resistant to changes such as species extinction whilst less stable food webs are likely to be negatively affected.

In contrast to grasslands, forests are structurally much more complex habitats that are characterized by long-living plant individuals. As a biome, forests cover almost a third of the global land area, support approximately 80% of the terrestrial biodiversity and are critical for maintaining global physical processes (Bonan 2008, FAO 2010). The majority of network studies conducted in forests addressed either plant–frugivore (Albrecht et al. 2013) or extrafloral nectar plant–ant interactions (Rico-Gray et al. 2012, Dáttilo et al. 2013). While some of these studies focused on land use, such as logging, which might reduce tree diversity and found a reduced network complexity in modified landscapes (Albrecht et al. 2013), the pure effect of tree diversity alone has not yet been explored.

Here we study in a recently established forest BEF experiment (Bruelheide et al. 2014) if tree diversity affects tri-trophic interactions between plants, various groups of sap-sucking Hemiptera (dominated by aphids) and ants (Fig. 1). These so-called trophobioses consist of two essentially different trophic interactions: the exploitation of plants by Hemiptera (antagonism), and the largely mutualistic Hemiptera–ant relationship. In exchange for the carbohydrate-rich honeydew excreted by the Hemiptera, ants usually provide protection against natural enemies (Way 1963). Trophobioses are common in forests, especially after habitat disturbance (Crist 2009), and contribute significantly to fluxes of matter and energy to dominant canopy ants (Davidson et al. 2003). Due to their simplicity and commonness trophobioses have been studied in many ecosystems (Blüthgen et al. 2004, 2006, Moreira et al. 2012). Blüthgen et al. (2006) showed that the antagonistic plant–Hemiptera networks are usually more specialized and more complementary (i.e. on average a species in one trophic level only interacts with few species in the other trophic level) than the mutualistic Hemiptera–ant networks which are more generalized (i.e. on average a species in one trophic level interacts with many species in the other trophic level).

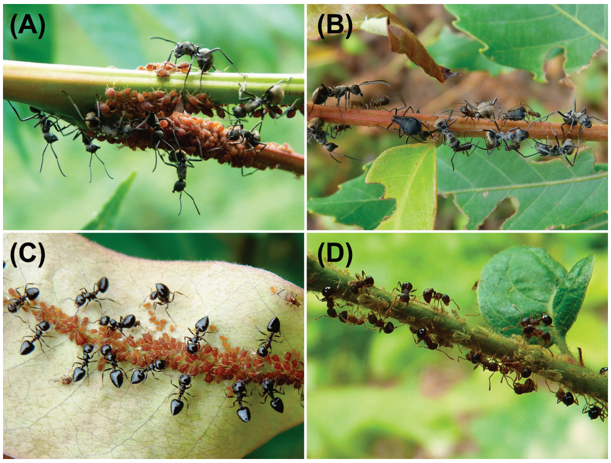

Figure 1. Exemplary trophobioses found in this study illustrating the diversity of participating ants, Hemiptera, and plants. (A) *Polyrhachis dives* (ant 12) tending *Toxoptera* sp. CN01 (Hemiptera 30) on *Choerospondias axillaris* (plant 3), (B) *P. dives* tending *Lachnus tropicalis* (Hemiptera 16) on *Quercus serrata* (plant 12), (C) *Crematogaster cf. nawai* (ant 4) tending *Aphis odinae* (Hemiptera 1) on *Schima superba* (plant 15), and (D) *Pristomyrmex punctatus* (ant 15) tending *Cervaphis quercus* (Hemiptera 8) on *Q. fabri* (plant 11). Numerical codes refer to Supplementary material Appendix 1 Table A1 and are identical to Fig. 2 and Fig. A1.

Comparing plant–pollinator and plant–herbivore networks Thebault and Fontaine (2010) found that antagonistic and mutualistic networks are structured differently: most antagonistic networks are much more complementary and less generalized than mutualistic networks (e.g. compare Blüthgen et al. 2007 and Schleuning et al. 2012 with Morris et al. 2014). For our study system we hypothesize that Hemiptera–ant associations are relatively generalized, and increasing tree diversity further increases the generality of the partners which, from the ant's perspective, may stabilize their resource availability. In turn, we predict that plant–Hemiptera networks are more complementary and specialized, and consequently Hemiptera species may not benefit from an increase in tree diversity. Changes in plant diversity may thus affect trophic interaction networks in complex ways with different effects on antagonistic and mutualistic networks.

Material and methods

Study site

The study site was located in southeast China, a region that is characterized by a typical seasonal subtropical monsoon climate with hot and humid summers contrasted by cool and relatively dry winters. Mean annual temperature is 16.7°C and mean annual precipitation 1821 mm (Yang et al. 2013). The study area is on sloped land (mean slope 26° ± 6° [SD]) on 100–300 m a.s.l. The potential natural vegetation is a diverse mixed evergreen broad-leaved forest that is numerically dominated by evergreen tree species but deciduous species contribute to about half of the total tree species richness (Bruelheide et al. 2011). In old growth forests *Castanopsis eyrei* (Fagaceae; species authorities not mentioned in the main text are listed in Supplementary material Appendix 1 Table A1), *Cyclobalanopsis glauca* (Fagaceae), and *Schima superba* (Thecaceae) are the most abundant canopy tree species. In the shrub layer *Loropetalum chinensis* (Hamamelidaceae), *Quercus serrata* (Fagaceae), *Rhododendron* sp. (Ericaceae) and *Camellia* sp. (Thecaceae) are most abundant (Bruelheide et al. 2011). Nowadays, forests are restricted to steeper slopes and most natural forests have been converted to commercial monocultures of the conifers *Pinus massoniana* (Pinaceae) and *Cunninghamia lanceolata* (Cupressaceae) or to agricultural land.

Near Xingangshan, Dexing County, Jiangxi Province (117°54′E, 29°07′N) the BEF-China project (<www.bef-china.de>) established what is currently the largest tree diversity experiment in the world (Bruelheide et al. 2014).

Using a total of 42 naturally occurring tree species including all locally common canopy species, 566 experimental plots were established on two different sites that were planted in 2009 and 2010 respectively. Every plot has a size of 25.8 × 25.8 m in horizontal projection which corresponds to the traditional Chinese area unit of 1 mu. On each plot 400 tree individuals were planted in 20 × 20 regularly arranged columns and rows, with a distance of 1.29 m among trees. As the main objective of the BEF-China Experiment is to investigate the influence of tree diversity on ecosystem processes and functions, the plots span a tree diversity gradient from 1, 2, 4, 8, 16 to 24 tree species. The spatial location of plots in a site was randomized as was the position of individuals of each tree species in a plot. For a comprehensive description of the BEF-China Experiment, including maps, elevation profiles, and a full list of planted tree species we refer to Yang et al. (2013) and Bruelheide et al. (2014).

Data collection

We sampled trophobioses from 21 May to 20 August 2011 on the site that was planted in 2009, 25 months before the start of the sampling. The site is located on the hillsides of a narrow valley and plots are directly bordering each other. Most of the 24 planted tree species were established well (Yang et al. 2013) and had a height of 100 cm or more. We selected in total 146 plots from tree diversity level 1, 2, 4, 8 and 16 (see Table 1 for number of plots per diversity level). Because there are only two plots with tree diversity 24, we did not study the highest available tree diversity level. The proportion a single tree species had in the sampling was similar for that tree species across all diversity levels. As the abundance of a tree species in a plot decreases with increasing tree diversity, we increased the number of sampled trees per plot accordingly (Table 1), summing up to a total of 10 359 trees which were sampled once each. By only sampling the central area in each plot there was always a spatial distance of over 10 m between the closest sampled trees in two directly adjacent plots, reducing possible effects of the tree community of neighboring plots on the sampling.

On each tree, 20 randomly selected young leaves and the attached branch sections were visually inspected for the occurrence of sap-sucking Hemiptera and honeydew-collecting ants. Voucher specimens of each trophobiosis were collected with soft insect forceps and stored in 70% ethanol. Hemiptera were grouped into morphospecies and sent to taxonomic experts (see Acknowledgements) for further identification. Non-ant-tended Hemiptera were also recorded but not further identified. Ants were first assorted to genera with Bolton (1994) and then identified to species level whenever possible with primary taxonomic literature and the Antweb Database (<www.antweb.org>). In a few cases Hemiptera and ants could only be identified to morphospecies, which we also refer to as species (see also Supplementary material Appendix 1 Table A1).

Data analyses

Data were analyzed with the software package R 3.0.2 (<www.r-project.org>). In all analyses we used the occurrence of trophobioses as the smallest data unit, i.e. every interaction between a Hemiptera and an ant species observed on an individual tree was only counted once, regardless of the number of individuals involved (Blüthgen et al. 2006, 2007). This conservative approach rules out potential biases of abundances, as several Hemiptera species are capable of very rapid population growth by reproducing asexually in parts of their life cycles (Blackman and Eastop 1994). However, if one Hemiptera species was tended on the same tree by two different ant species, or if one ant species tended two different Hemiptera species, we counted them as two separate trophobioses.

We pooled the total number of Hemiptera occurrences, i.e. the number of trophobioses and the number of untended Hemiptera occurrences to one value each per tree diversity level. We then calculated for every tree diversity level the proportion of trees that were occupied by Hemiptera and the proportion of trees that harbored trophobioses. Analyses are based on the number of living trees only; dead trees were excluded. We tested for the completeness of our sampling for the entire data and for the data per tree diversity level with the jackknife 1 (jack1) species richness estimator. Species richness estimation extrapolates the number of species that are expected with infinite sampling effort and indicates no bias of differing sample effort per tree diversity level if similar estimated species numbers are retained. For these analyses, plots were taken as sample units and calculations were done in the R-package 'vegan' (<www.cran.r-project.org/package=vegan>). While species richness estimation for Hemiptera and ants is a measure of the number of species we may expect with very high sampling effort, for the plant level the total species richness in all diversity levels was 24. Thus we interpret species richness estimation for the plant level as a measure of the possibility that additional plant species had trophobioses which were not detected by us.

We also pooled all trophobioses for each of the five tree diversity levels to obtain one network each. Pooling was

Table 1. Details of sampling per tree diversity level. The number of plots sampled, the number of trees sampled per plot, the total number of sampled trees, the number of trees with Hemiptera, and the number of trees with trophobioses are shown. Values in parentheses refer to the proportion of living trees per level.

Tree diversity	No. of plots	Trees per plot sampled	Total live trees	Trees with Hemiptera	Trees with trophobioses
1	41	36	1146	119 (10.4%)	23 (2.0%)
2	42	36	1094	102 (9.3%)	11 (1.0%)
4	27	81	1368	136 (9.9%)	41 (3.0%)
8	20	144	1931	190 (9.8%)	56 (2.9%)
16	16	144	1445	153 (10.6%)	52 (3.6%)
Total	146		6984	700 (10.0%)	183 (2.6%)

necessary as network analyses require a minimal network size to work reliably (Dormann et al. 2009), which was not the case in our raw data as several plots had no or very few trophobioses. Consequently, we had only one data point per diversity level, which was too low for formal statistical testing, a common problem in ecological network analyses (Blüthgen 2010). Properties of trophobiotic networks per tree diversity level were analyzed and visualized with the R-package 'bipartite' (<www.cran.r-project.org/package=bipartite>). Out of the variety of available network indices (reviewed by Dormann et al. 2009) we choose the weighted 'generality' index to describe interactions between trophic levels. This index is a robust measure of the connectivity and thus the stability of networks. Hence it is suitable to address our main question, if and how tree diversity affects trophobiotic interactions. In a bipartite network, weighted generality is defined as the weighted mean effective number of species in the lower trophic level per species in the higher trophic level, with each species weighted by the number of trophobioses in which it was found (marginal row sums) (Bersier et al. 2002, Dormann et al. 2009).

$$G_{\mathrm{qw}} = \sum_{j=1}^{J} \times \frac{A_j}{m} e^{H_j} \qquad (1)$$

G_{qw} (Eq. 1) is calculated with J being the number of species in the higher trophic level, A_j the total number of interaction of species j from the higher trophic level, m the total number of interactions for all species, and H the Shannon diversity of interactions for the higher trophic level (Dormann et al. 2009). The index G_{qw} is 1 if each Hemiptera species has only a single host plant species or each ant species has only a single Hemiptera partner. Higher G_{qw}, suggests higher redundancy, which is thought to contribute to higher stability. G_{qw} may increase with the species' abundances, overall diversity and the total number of interactions between trophic levels (Blüthgen 2010, Albrecht et al. 2013). We discuss whether these two parameters may explain the change in weighted generality. Lastly, to test if the observed values for G_{qw} are different from random interactions of the species, we calculated for each network null models based on the Patefield algorithm with 10 000 random model runs (Blüthgen et al. 2006, Dormann et al. 2009).

Results

In total, 700 of 6984 living trees were occupied by Hemiptera, including 183 trees (Table 1) with 194 trophobioses (Fig. 1). The proportion of trees with Hemiptera was around 10% and similar for all tree diversity levels. However, the proportion of trees with trophobioses was higher in the higher tree diversity levels compared to the lower levels and increased from 2% in tree diversity level 1 to 3.6% in tree diversity level 16 (Table 1).

At least one Hemiptera occurrence was found on 23 out of the 24 possible tree species, with 15 tree species supporting trophobiosis (Supplementary material Appendix 1 Table A1). These trophobioses consisted of 33 Hemiptera species that were tended by 18 ant species. Trophobioses were most common on tree species of the family Fagaceae, on which 68.0% (132 interactions) of all trophobioses were found whilst Fagaceae only contributed 48.5% (3390 trees) to all inspected tree individuals (Supplementary material Appendix 1 Table A1). The three *Quercus* species – *Q. acutissima*, *Q. fabri* and *Q. serrata* – had 51.6% (100 interactions) of all trophobioses while only accounting for 14.3% (999 trees) tree individuals. Among the Hemiptera, true aphids (Aphididae) represented 82.0% (159) of all trophobioses, and the 15 aphid species 45.5% of the 33 total Hemiptera species. *Cervaphis quercus* and *Diphyllaphis quercus* were the most common trophobiotic aphid species (each 15.5%). Treehoppers (family Membracidae) were most common (15 interactions) after Aphididae. The ant community consisted of species of the subfamilies Dolichoderinae, Formicinae and Myrmicinae. A single species, *Polyrhachis dives* (Formicinae) participated in most trophobioses (106 or 54.6%), followed by two species of *Crematogaster* (38 or 19.6%) (Supplementary material Appendix 1 Table A1).

The jack1 species richness estimator suggests that our sampling collected over two-thirds of the predicted species pool involved in trophobioses. Compared to the richness estimates, our 15 tree species recorded with trophobionts represented 79% of a total estimated 19 ± 2 tree species, 33 collected Hemiptera species represented 67% of the totally estimated 49 ± 5 Hemiptera species, and the 18 collected ant species represented 69% of the estimated 26 ± 3 ant species. The observed but not the expected number of plant species having trophobioses was higher at higher tree diversity levels as was the sampling efficiency (Table 2). The number of trophobiotic Hemiptera species showed a similar trend; however jack1 species richness estimation indicated a consistently moderate sampling efficiency of ca 60% for all tree diversity levels. Observed ant species richness was independent of the tree diversity level. The sampling efficiency for ants was similar to Hemiptera (Table 2).

Table 2. Properties of trophobiotic networks per tree diversity level. The number of trophobioses as well as the number of tree, Hemiptera and ant species that were observed and expected (based on the jack1 estimator ± SE; in parentheses) in trophobioses are shown. The generality index G_{qw} is shown for the plant–Hemiptera (p-H) and for the Hemiptera–ant (H-a) level. G_{qw} values in brackets are derived from Patefield null models with 10 000 randomizations. p-values indicate if G_{qw} of observed and randomized networks differ. Significant p-values are in bold. See main text for definition of G_{qw} and for description of null models.

Tree diversity	Trophobioses	Tree richness	Hemiptera richness	Ant richness	G_{qw} p-H	$p_{\mathrm{p\text{-}H}}$	G_{qw} H-a	$p_{\mathrm{H\text{-}a}}$
1	25	7 (12 ± 2)	12 (22 ± 4)	9 (14 ± 2)	1.14 (2.34)	**< 0.001**	3.20 (4.05)	**0.05**
2	11	5 (8 ± 2)	7 (12 ± 2)	4 (7 ± 1)	1.00 (1.77)	**0.002**	2.27 (3.06)	**0.007**
4	43	9 (14 ± 2)	14 (23 ± 4)	9 (15 ± 2)	1.20 (3.24)	**< 0.001**	5.03 (7.07)	**< 0.001**
8	61	9 (11 ± 1)	15 (25 ± 4)	10 (14 ± 2)	1.70 (3.67)	**< 0.001**	5.13 (6.87)	**< 0.001**
16	54	11 (14 ± 2)	18 (29 ± 6)	9 (13 ± 2)	1.44 (3.87)	**< 0.001**	4.67 (6.46)	**< 0.001**
Total	194	15 (19 ± 2)	33 (49 ± 5)	18 (26 ± 3)	1.79 (5.81)	**< 0.001**	9.16 (11.45)	**< 0.001**

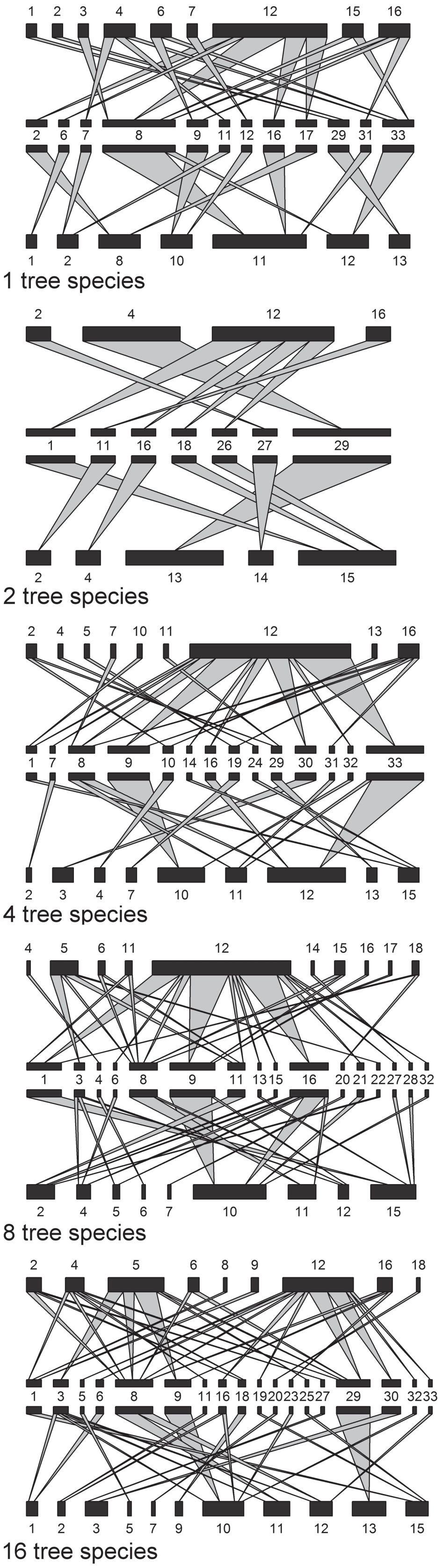

Figure 2. Quantitative tri-trophic food webs based on the occurrences of trophobioses along the tree diversity gradient. For each food web, lower bars represent plants, middle bars represent Hemiptera, and upper bars represent ants. Width of bars indicates number of occurrences per species, width of arrows indicates the number of interactions between two species in two adjacent trophic levels. The most narrow bars and arrows indicate a single interaction per tree diversity level. *Quercus acutissima*, *Q. fabri*, and *Q. serrata* are plant species 10, 11, and 12 respectively. *Polyrhachis dives* is ant species 12. Numerical codes refer to species names given in Supplementary material Appendix 1 Table A1.

The tri-trophic interaction network of the complete dataset (Supplementary material Appendix 1 Fig. A1) revealed that the plant–Hemiptera network had a low generality ($G_{qw} = 1.79$), suggesting that each Hemiptera species had on average less than two 'effective' host tree species. In contrast, the Hemiptera–ant network had a much higher generality ($G_{qw} = 9.16$) (Table 2) suggesting more than nine 'effective' Hemiptera partners per ant species. For plant–Hemiptera networks, the low generality was consistently found across the five tree diversity levels, as G_{qw} was only slightly increasing with higher tree diversity (Table 2). A maximum G_{qw} of 1.70 in diversity level 8 indicates that even in higher tree diversity levels every Hemiptera species had always fewer than two 'effective' host plants. In contrast, G_{qw} of the Hemiptera–ant networks was 1.8-fold higher when four or more tree species were planted in a plot (Table 2). The differing patterns for each network are illustrated in the tri-trophic network graphs for each tree diversity level (Fig. 2). The null-model analyses revealed that the G_{qw} values of the complete network and of all tree diversity level specific networks were significantly different from chance. In all cases, G_{qw} was lower than it would have been expected if interactions between species were only driven by random processes (Table 2). For both networks, lowest G_{qw} values were found for tree diversity level 2 which had, however, only few trophobioses.

As described above the estimated species richness of plants, Hemiptera, and ants was not influenced by tree diversity and, thus, the increase of G_{qw} in the Hemiptera–ant network not caused by species numbers of Hemiptera and ants. However, the proportion and thus also the number of trees harboring trophobioses was higher in higher tree diversity levels. This increase in the number of trophobioses in higher tree diversity levels corresponds directly to the observed increase in G_{qw}, which was considerably larger for the Hemiptera–ant than for the plant–Hemiptera networks (Table 2).

Discussion

Our results showed that experimental manipulation of tree diversity was associated with changes in tri-trophic interactions. The proportion of trees harboring trophobioses increased with higher tree diversity, which had a stabilizing effect on the mutualistic Hemiptera–ant networks as suggested by the higher effective number of Hemiptera species tended by each ant species (i.e. the generality of the Hemiptera–ant networks). In contrast, the antagonistic plant–Hemiptera networks remained at low generality and the effective host plant spectrum attacked by each Hemiptera species along the tree diversity gradient increased only little. All network patterns in our study were not influenced by random processes, indicating that actual tree diversity is causing the observed changes in the networks.

So far, the studies investigating the relationship between producer diversity and network structure in grasslands found an association of network stability and complexity with plant diversity (Ebeling et al. 2011, Haddad et al. 2011). In a broader context it has been shown that the complexity and structure of networks is strongly dependent on a variety of habitat properties such as successional age (Albrecht et al. 2010), geographical latitude (Schleuning et al. 2012), local microclimate (Rico-Gray et al. 2012) or land use (Albrecht et al. 2013, Vanbergen et al. 2014). In principle, biodiversity and other factors can directly or indirectly affect networks via top–down or bottom–up processes (Hunter and Price 1992). Both effects are known to alternate in a trophic cascade when interactions between different levels are studied (Petermann et al. 2010). Scherber et al. (2010) showed in a grassland experiment a positive bottom–up effect on multi-trophic interactions, which we confirm in our study. This supports the findings of Moreira et al. (2012) and Moreira and Mooney (2013) from smaller scale experiments. Equivalently, Schuldt et al. (2010) found in a close-by secondary forest an increase of folivore herbivory with tree diversity. Taken together, these findings suggest a general positive effect of tree diversity on trophic interactions.

In our study, the higher generality was not simply evoked by a higher species richness of Hemiptera and ants in plots with high tree diversity, as the estimated richness of species was roughly similar for all tree diversity levels. Instead, the proportion of trees harboring trophobioses, and consequently the absolute number of trophobioses, increased with tree diversity. Generality measures the average interaction density between two trophic levels and hence a positive relationship between generality and the number of trophobioses is expected (Dormann et al. 2009). Thus, the higher proportion of trees harboring trophobioses and higher absolute number of trophic interactions recorded in higher tree diversity levels likely explains the higher generality. In addition, we cannot completely exclude that lower generality in the two lowest tree diversity levels might partly reflect the somewhat lower sampling effort. However, we think that such a bias is unlikely. Our dataset for every tree diversity level is based on a large number of sampled tree individuals. With the exception of level 8, sampling effort varied less than 25% between diversity levels while the observed differences in generality of the ant–Hemiptera network were considerably higher.

The increased generality is in accordance to the predictions of the diversity–stability hypothesis (reviewed by McCann 2000) which suggests that producer diversity can have a stabilizing effect on trophic-interactions in higher trophic levels. In contrast, the primary consumer level (Hemiptera) was not affected by tree diversity in our study. Both, the proportion of trees with Hemiptera and the generality of the Hemiptera–ant network were similar between plots of varying tree diversity.

Most Hemiptera species are, with a few polyphagous exceptions, specialized feeders restricted to a single plant genus or family (Blackman and Eastop 1994). In order to feed, most Hemiptera need to distinctly pierce a delicate single phloem vessel, a task that requires specific behavioral and morphological adaptations (Walling 2008). Plants are chemically and morphologically well defended against herbivores including Hemiptera, resulting in a strong co-evolutionary arms race. The continuously low generality of the plant–Hemiptera network in our study can be considered a direct consequence of high host-plant specialization. The Hemiptera–ant network is, in turn, a largely mutualistic interaction. Trophobiotic ants are only in very few striking cases associated with an exclusive set of Hemiptera species (Maschwitz and Hänel 1985). Honeydew excreted by most Hemiptera can be collected by a broad range of ant species that are characterized by a joint set of behavioral and morphological traits (Oliver et al. 2008), explaining the wide generalization of trophobiotic networks observed here and in other studies (Blüthgen et al. 2004, 2006). Our results are also congruent with the prediction that diversity should influence the stability of mutualistic but not antagonistic networks (Thebault and Fontaine 2010, Sauve et al. 2014). This prediction is supported by two recent meta-analyses: Morris et al. (2014) revealed that antagonistic networks had consistently a high degree of specialization across host guilds and latitudes while the generality was only related to network size and the diversity of the interacting species. For mutualistic networks, Schleuning et al. (2012) showed that specialization of pollination and seed-dispersal networks decreased, while the generality increased, from temperate to tropical latitudes. The authors of the latter study suggested that this gradient is mediated by the higher plant diversity in tropical regions.

In the time of global change, food webs are predicted to be heavily affected by rapidly changing environmental conditions (Barnosky et al. 2012). The extinction of a species in a complex food web can have cascading effects on other species (secondary extinctions), thus altering the entire food web (Dunne and Williams 2009, Cardinale et al. 2012). More generalized food webs with higher redundancy will be buffered against secondary extinctions (Dunne et al. 2002, Blüthgen 2010). In our case, secondary extinctions of Hemiptera may be likely if their host plants disappear while the high generality of the Hemiptera–ant food webs, especially in higher tree diversity levels, may stabilize this part of the network.

While we showed a positive bottom–up effect of tree diversity on the Hemiptera–ant network, we can only speculate about the exact underlying mechanisms. Tree diversity increases tree productivity (Zhang et al. 2012b) which was confirmed by a study conducted in a nearby secondary forest (Baruffol et al. 2013). Accordingly, we suspect that the young trees in our study site are in high diversity plots likewise more productive, thus being more attractive hosts for trophobiotic Hemiptera (Powell et al. 2006). It could be that Hemiptera feeding on relatively more productive plants perform better and thus excrete qualitatively and quantitatively more attractive honeydew, which might also explain the higher proportion of ant-tended Hemiptera in higher tree diversity levels. As trophobiotic ants are able to detect small differences in honeydew composition (Blüthgen and Fiedler 2004) and to select a diet that maximizes longevity (Dussutour and Simpson 2012), the effect of tree diversity on the Hemiptera–ant food web could be mediated bottom–up by honeydew quality and quantity. Testing these assumptions would be a promising direction for further research. Alternatively, higher interspecific genetic diversity might have a direct positive bottom–up effect on Hemiptera performance and thus the number of trophobioses, as suggested by the findings of Moreira and Mooney

(2013) for the effects of intra-specific diversity. Lastly, higher tree diversity might also have non-trophic effects on Hemiptera, e.g. by providing more suitable microhabitats, which could also feed back to Hemiptera performance and ant-tending, as indicated by the higher proportion of ant-tended compared to non-ant-tended Hemiptera in higher tree diversity levels.

Outlook

Although the trees in our study site were not yet forming a closed canopy at the time of sampling, we expect that the bottom–up effects of tree diversity will stay similar or become even more pronounced in more mature forest stands. As a forest matures, the primary production and thus the resource availability per area increases which will increase the number of trophobioses irrespective of tree diversity. At the same time we expect the effects of tree diversity on trophobiotic interactions outlined above will be preserved, resulting in relatively more trophobioses and thus more generalized Hemiptera–ant networks in more diverse forests. Our study only begins to explore for the bottom–up effect of tree diversity on the proportion of trees harboring trophobioses and on tri-trophic network structure. Trophobioses have been regarded as ecological key-stone interactions that contribute significantly to fluxes of matter and energy in (sub)tropical forest canopies by fueling the abundance and prevalence of ants (Davidson et al. 2003). Moreover, trophobioses can have community-wide effects e.g. by influencing the arthropod community on the forest floor (Zhang et al. 2012a). Our data showed a clear and distinct trend, but we acknowledge that future studies should repeatedly sample the same study sites, both inside and between different years, to confirm possible bottom–up effects of tree diversity. Increased sampling effort will also help to reveal if the low number of trophobioses in two-tree-species plots is an artefact of our study or a consistent pattern. Ideally, studies on trophobioses will also include phylogenetic information of plants, Hemiptera and ants. Trophobioses are evolutionary old interactions as inclusion fossils of Hemiptera and ants in amber demonstrate (LaPolla et al. 2013). The network patterns we observe today may at least partially be explained by evolutionarily conserved relationships (sensu Pellissier et al. 2013).

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Supplementary material (available online as Appendix oik.01723 at <www.oikosjournal.org/readers/appendix>). Appendix 1.