



# Neighboring plants and core herbivores determine the importance of *Swietenia macrophylla* in the plant–herbivore network

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## Abstract

Species contribute differently to the structure and stability of networks of interacting species. However, species contributions to the importance of other species is usually neglected, thus limiting our understanding of species dynamics beyond the general network structure. We combined knowledge on diversity effects on focal species and network ecology to analyze the influence of plants and herbivores on big-leaf mahogany's (*Swietenia macrophylla*) importance in the plant–herbivore network. To this end, we built interaction networks using information from a large-scale tree diversity experiment and performed computer simulations of species removal with redistribution of interactions. We compared the importance of big-leaf mahogany in the observed networks to simulated networks where we removed: (a) tree species with similar beetle assemblages to mahogany, (b) the most interconnected (core) tree species and (c) the core beetle species. Removal of the core and similar tree species increased the importance of mahogany, whereas eliminating core beetle species decreased it. Interestingly, the effect of core tree species on mahogany's importance was mediated by core beetles ( $R^2 = 0.46$ ). Neither tree nor core beetle species' effects were contingent on tree species richness or abundance. These results indicate that highly connected tree and herbivore species jointly determine the role of mahogany in the plant–herbivore network. Likewise, these results provide insight into the effect of tree species composition and highly interactive herbivores in shaping the role of species in the herbivore network.

**Keywords** Mahogany · Coleoptera · Network importance · Core species · Polyculture

## Introduction

Research on ecological networks has helped to understand the ecological factors that shape species interactions (Delmas et al. 2019) and to gain insight into the resilience of ecological communities to disturbances (Solé and Montoya 2001; Ings et al. 2009). Traditionally, most studies have focused on quantifying descriptors of network complexity whereas the role of species identity effects in shaping networks has been comparatively less studied (e.g., Bascompte et al. 2003; Blüthgen et al. 2006; Lewinsohn et al. 2006). Recent work has provided a closer look and evaluation of the importance of species in the network. Such studies have identified species with particularly strong effects on network stability (i.e., keystone species; see Martín González et al. 2010) and in so doing, describe the role of species in structuring networks (e.g., Dáttilo et al. 2013) and subsets (e.g., modules) within the network (e.g., Dupont and Olesen 2009). However, evidence on how species in the network not only affect the network structure but also the role of other

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species within it, remains limited. Assessing and disentangling the relative contributions of species in the network to the associated interactions of a focal species can expand our knowledge of how species traits (e.g., specialization or network role) drive network characteristics at the species interaction level. Ultimately improving our understanding of ecological processes governing network structure and the individual role of the species in it (Bramon Mora et al. 2020).

At the same time, there is also good evidence that the broader plant community influences subsets of herbivore communities found on focal plant species and that the degree of influence depends on the diet breadth of herbivores (Barbosa et al. 2009). Empirical studies on so-called “associational effects” have shown that changes in plant species richness, phylogenetic diversity or composition (and associated traits; Castagneyrol et al. 2014) affect the interactions and associated herbivore faunas on focal plant species (Holmes & Barrett 1997, Barbosa et al. 2009), and that outcomes may also vary depending on herbivore traits such as diet breadth (i.e., generalist/specialist species; Jactel and Brockerhoff 2007; Barbosa et al. 2009). Within this context, network analyses have been a useful tool for describing patterns potentially driven by processes such as apparent competition or other types of associational effects. For example, the negative effects of an abundant bio-control agent on native herbivores through apparent competition (e.g., Carneiro et al. 2008), or the occurrence of secondary extinction events (e.g., Sanders et al. 2018). Through the construction of species removal simulations, network studies have allowed us to study theoretical associational effects that would otherwise be hard to evaluate under field conditions (e.g., Memmott et al. 2004; Pinheiro et al. 2019).

Network analyses can provide a powerful approach for assessing how the importance of a focal plant species in the network is affected by other plant and herbivore species in the network, ultimately advancing our understanding of the mechanisms that govern ecological communities (Bramon Mora et al. 2020). To address the importance of species in a network, species are usually described in terms of the number of interactions they establish or their position in the network. Broadly, the higher the number of interactions, the greater the importance of a species in the network (see Martín González et al. 2010). Based on this, species can be classified as core species or peripheral species. The former are generalist species that interact with most of the species in the network (constituting the network’s core of generalist interacting species), whereas peripheral species interact with a minor group of species (i.e., the network’s periphery; Dáttilo et al. 2013). Correspondingly, core species have disproportionately strong effects on overall network structure (e.g., Nuwagaba et al. 2017) and stability (e.g., Luviano et al. 2018), whereas

peripheral species have marginal effects. The effects of species with different traits can also extend beyond the structure of whole network and affect other species interactions in the network. For example, core plant species could attract insects away from other plant species, affecting their importance in the plant–herbivore network (Barbosa et al. 2009). Likewise, core herbivores could determine the focal plant species’ effects on overall networks, and are also more likely to mediate associational effects among plant species as they are frequently shared by multiple host plants (Jactel and Brockerhoff 2007). This effect is one that has not been widely studied to date.

We address these gaps by studying the effect of tree and beetle species on the importance of a tree focal species in a plant–herbivore interaction network recorded in a long-term tree diversity experiment in Yucatan, Mexico (UADY Tree Diversity Experiment; <https://treedivnet.ugent.be/ExpUADY.html>). We used a network analysis approach by which we constructed a plant–insect herbivore network based on data of phytophagous beetles associated with the tree species planted in polycultures. Our focal species was big-leaf mahogany (*Swietenia macrophylla* King, Meliaceae), a highly valued timber species in tropical forestry and high conservation priority (CITES 2003). Likewise, Coleoptera, were selected as a highly diverse, generalist and dominant herbivore insect group (Erwin 1982; García-Robledo et al. 2020) whose presence in mahogany has seen to be affected by tree diversity (Campos-Navarrete et al. 2015a).

Previous work in the UADY experiment has reported variations in insect herbivory level and abundance across taxonomic groups associated with mahogany between monocultures and polycultures (Campos-Navarrete et al. 2015a, b; Abdala-Roberts et al. 2015, 2016; Quinto et al. 2021). They also report stronger effects of diversity on specialist (Abdala-Roberts et al. 2015) and variable responses in generalist species (Campos-Navarrete et al. 2015a; Abdala-Roberts et al. 2016). Meanwhile, Quinto et al. (2022) showed that the annual plant-beetle networks of the experiment are significantly nested (weighted nestedness) but not modulated across years and seasons (dry and rainy). This pattern means that most beetle species were densely connected with several tree species at once. Authors also observed that hub tree species vary across years and seasons when analyzing the network of the whole experiment. Overall, *Enterolobium cyclocarpum* (Jacq.) Griseb, *Swietenia macrophylla*, *Piscidia piscipula* (L.) Sarg and *Tabebuia rosea* (Bertol.) were hub species in at least one season or year of study. Similarly, they observed that beetle species from different taxonomic groups (Elateridae, Apionidae, *Diaphalulaca* and *Epitrix*) as well as *Platyomus zebra* (Champion), *Rhopalohora yucatanana* Giesber & Chemisak and *Isorrhinus undatus* (Champion) played a role as hub species at least in one year during the study (Quinto et al. 2022).

Based on the observed differences in response to the diversity of the mahogany herbivore assemblage, and the presence of different interconnected species in the plant-beetle network, we tested how neighboring host plants and dominant beetle species affect the interactions on this focal tree species. First, we calculated beetle abundance on mahogany, the relative importance of this species calculated as the normalized degree (how many species of beetles feed on mahogany), and the relative interaction weights of mahogany or species strength (how strong is the dependency of the beetle community on mahogany when considering the number of individuals feeding on the species). Second, we conducted simulations to test for the influence of tree and beetle herbivore species on the importance of big-leaf mahogany in the network. Specifically, we computationally removed (a) the core tree species, (b) tree species with a similar herbivore community to mahogany, and (c) the core herbivore. In each case we recalculated mahogany's importance in the network and compared the value with the observed network to test the influence of these species on mahogany-associated interactions. Finally, we tested if core beetle species mediated the effect of tree species on the importance of big-leaf mahogany.

## Material and methods

### Study system and sampling

The study was conducted at the UADY Tree Diversity Experiment, a long-term diversity experiment established in December of 2011 at the Sitio Experimental Uxmal (20°24'44" N, 89°45'13" W) owned by INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias) and located 70 km southwest of Merida (Yucatan, Mexico). The system consists of 74 plots of 21 m by 21 m, with 64 plants within each plot and 3-m spacing among plants ( $N=4780$  plants); and 6 m between plots. Big-leaf mahogany is present in 59 of these plots in 32 monocultures and 27 polycultures (for more details see Abdala-Roberts et al. 2015). Polycultures are comprised of 16 randomly distributed mahogany trees, and 48 ( $16 \times 3$ ) individuals of three out of the following five native tree species that co-occur with big-leaf mahogany in the tropical dry forest of the Yucatan Peninsula: *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae), *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), and *Cordia dodecandra* A. DC. (Boraginaceae). These species were selected because they exhibit substantial differences in attributes such as growth rate and leafing phenology which are expected to increase ecological complementarity (Abdala-Roberts et al. 2015). The experiment can be viewed as a simplified version

of the natural tropical forest where there is not a consistent distance between trees and both tree and understory diversity are higher. At the same time, the study design allows us to control for multiple biotic and abiotic drivers, enabling us to study ecological processes and changes in tree-insect interactions in a more tractable fashion.

We used data on beetle communities on mahogany and the other tree species planted in polyculture plots collected by Campos-Navarrete et al. (2015a, b) and (Quinto et al. 2021, 2022). Data were collected six months after the establishment of the experiment between May 2012 and September 2013. At the start of sampling plants were all the same ontogenetic phase and height (nine months old saplings, around 60 cm height). Species showed similar height during the sampling period. The sampling proved to be adequate as it exhibited a sample coverage higher than 78% in all samplings (Quinto et al. 2021). Surveys consisted of 25 min of direct catches per tree species (six species grow in plots of four species, 300 samplings per year, 50 samplings per species per year). For a total of 1250 min per species ( $25 \times 50$  across all sampling events) within 18 polyculture plots randomly selected in each sampling. The 18 polycultures plots were sampled four times for a total of 72 observations from which 54 were made in plots where mahogany was grown. All beetles occurring or feeding on the tree tissues were placed in pots of 70% ethanol. The specimens were subsequently identified (to species) by specialist taxonomists (see acknowledgments). Herbivore diets were classified based upon morphological aspects such as their mouthparts, direct observations in the field, natural history information and expert advice. The dataset consists of a herbivore community of 84 species and 493 individuals of herbivorous Coleoptera belonging to 13 families (Quinto et al. 2022). For this study, we selected the twelve quantitative networks (out of the 54 observations) that included mahogany and have records for at least three out of the four tree species growing in each plot ( $N=12$ ). This network selection allows us to make network analyses robust to random observations and reduce the effect of small network size (see Jordano 2016). The representation of other tree species in the networks were as follows: *T. rosea* was present in 6/12 networks, *C. pentandra* in 8/12, *E. cyclocarpum* in 6/12, *P. piscipula* in 8/12 and *C. dodecandra* in 3/12 networks.

### Mahogany-associated insect herbivore communities

Big-leaf mahogany (*Swietenia macrophylla*, Meliaceae), is a self-compatible, long-lived perennial tree that grows in moist and dry tropical forests from the southern Mexico to Bolivia (Pennington and Sarukhán 2005). In the neotropics, current management mainly consists of harvesting and its subsequent reintroduction to the forest (e.g., Verwer et al. 2008; Negreiros Castillo et al. 2014). In South America,

mahogany's natural populations have been highly reduced due to overharvesting (Grogan et al. 2010) regardless of the species being listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2003). The main insect herbivores of this species in tropical forest are leaf chewers (e.g. Coleoptera and Lepidoptera, Norghauer et al. 2010) while in managed systems are *Hypsipyla grandella* (Lepidoptera: Pyralidae) a stem-boring caterpillar, *Phylocnistis meliacella* (Lepidoptera: Gracillariidae) a leaf miner caterpillar and generalist leafhoppers (Cicadellidae; Abdala-Roberts et al. 2015). At the UADY Tree Diversity Experimental site, the following taxonomic groups have been observed on big-leaf mahogany: Coleoptera, Hemiptera, Lepidoptera, Orthoptera and Tysanoptera. Among these groups Coleoptera and Hemiptera are the most abundant herbivores, however, 82.5% of the leafhoppers belong to *Oncometopia* sp., with Coleoptera showing much higher evenness and species richness (Campos-Navarrete et al. 2015b; Quinto et al. 2021).

### Quantifying the importance of big-leaf mahogany in the plant–herbivore network

We quantified the importance of mahogany in the plant–herbivore network as (a) the number of beetle individuals observed on mahogany (abundance), (b) the relative importance of mahogany measured as the normalized degree of mahogany in the plant–herbivore network, and (c) the relative interaction weights measured as the species strength of mahogany in the network. Normalized degree is the number of species that *species i* interacts with, divided by the total number of species in the network (see Martín González et al. 2010). Normalized degree ranges from 0 (lowest importance of the species in the networks) to the maximum value of 1 (highest importance). This metric is standardized by species richness in the network, so it is appropriate to compare networks of different sizes (see Pocock et al. 2011). Species strength is a quantitative metric that measures the sum of dependencies of each species (relative interaction weights) within the network. It aims to quantify a species' relevance across all its partners, or its contribution to the other trophic level (Bascompte et al. 2006). We consider the observations of beetles feeding or occurring on a plant species as an interaction.

### Testing the influence of tree species on the importance of big-leaf mahogany in the plant–herbivore network

We tested whether other tree species influence the importance of big-leaf mahogany in the plant–herbivore network in terms of beetle abundance, relative importance and relative weight of interactions of mahogany. We first identify

tree species that could potentially have the greatest impact on the importance of mahogany in the plant-beetle network. Species that due to associational effects among tree species (apparent competition, associational susceptibility; Barbosa et al. 2009) could affect the beetle assemblages of mahogany via spillover effects. We identified two types of species: (a) tree species with a substantial overlap with mahogany in their beetle herbivore assemblage, i.e., similar beetle species composition, and (b) tree species that interact with the largest number of beetle species in the network, i.e., the core tree species in the network. We then simulated the removal of each of the tree species identified from the network and evaluated changes in the importance of mahogany. The identification of tree species with overlapping beetle communities and core tree species was done independently for each network.

### Identifying tree species with a similar beetle community to mahogany

To identify species with the highest overlap in beetle species composition to mahogany, we adapted the quantitative version of the Morisita index, which measures dissimilarity in species composition among N-communities (see Chao et al. 2006) by subtracting the index value from 1 to calculate similarity. The Morisita index is useful for detecting similarity based on common species, and is substantially less biased in the face of under sampling or unequal sample sizes (Barwell et al. 2015). We calculated the index using the package *vegan* (Oksanen et al. 2019) in R version 4.0.2 (R Core Team 2020).

### Identifying the core tree species in the plant–herbivore network

We consider core species as the most generalist or interconnected species in the network as defined by the generalist core index (GC) (Dáttilo et al. 2013). This index is based on the difference between the observed number of links for a given species (i.e., tree species) and the mean number of links for all species from the same trophic level divided by the standard deviation of the number of links for species from the same trophic level. A value of  $GC > 1$  indicates species with a larger number of interactions than other species of the same trophic level, therefore constituting the generalist core. The analyses were performed using the software R version 4.0.2 (R Core Team 2020).

### Simulation of tree species removal

Species removal simulations consisted of reallocating interactions from the removed species and assigning them to the remaining plant partners of each beetle species, taking into



account the host preference of the beetle species (e.g., Morrison et al. 2020). We define host preference as the probability that individuals of a given beetle species feeding on the removed species choose another tree species present in the plot (Fig. 1). We calculated the probability, dividing the number of interactions of a given beetle species with each of its host trees in the plot by the total of its interactions observed in the plot. We removed the unique interactions of the removal species without replacement. The reallocation of interactions was restricted to interaction partners observed within each network because the realization of an interaction

between two species depends on a suite of abiotic and biotic factors that are context-dependent (Brosi and Briggs 2013; Morrison et al. 2020). We discarded the density-dependent effect could affect the host preferences, given that in the UADY experiment, all trees species grow in equal numbers within the plots (Abdala-Roberts et al. 2015). Finally, we calculated the abundance of beetles and the relative importance of big-leaf mahogany for each network after the species removal and compared the value with the observed network.

### Testing the influence of beetle species on the importance of mahogany in the plant–herbivore network

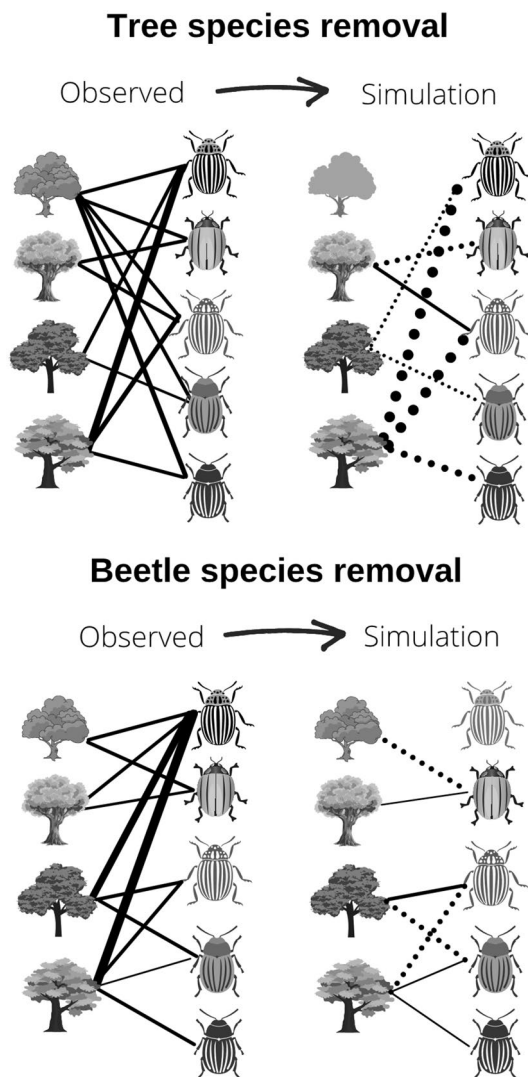
To test how beetle species influence the importance of big-leaf mahogany in the plant–herbivore network, we identified beetle species whose plant–herbivore interaction to mahogany can be influenced by other tree species. Specifically, we focused on the influence of the most generalist beetle species since generalist species are the most likely herbivore group to move from one host to another according to host availability (Barbosa et al. 2009). For each network, we identified the most generalist species as the most interconnected or core generalist beetle species as defined by the GC index as we did for the core tree species (Dáttilo et al. 2013).

#### Simulation of core beetle species removal

Similarly, to the tree species removal simulation, we reallocated the lost links across the other beetle species according to their similarities in host preferences. We assumed that beetle interactions to tree species are density-dependent and limited by the presence of highly generalist beetle species. We determined the degree of similarity in host preferences by comparing the number of host tree species shared between the core beetle species and the rest of the beetle species. We proportionally added the lost links to the rest of the beetle species interactions according to the similarity in host preferences to the core beetle and abundance of the species (Fig. 1). For instance, if two beetle species have the same host preferences as the core beetle, we assume that the more abundant beetle species was more likely to replace the removed species (Fort et al. 2016). We also restricted the reallocation of interactions to interaction partners observed within each network as explained in the simulations of tree species removal.

#### Data analysis

We used linear mixed-effects models to compare the beetle abundance and the network importance of mahogany (normalized degree and species strength) between the original



**Fig. 1** Example of the average simulation of species removal performed across simulation types for tree and beetle species removal. Left: tree species removal. Right: beetle species removal. Species removed are shown as disconnected in the simulation. Solid lines are the observed interaction among tree species and beetle species. Pointed lines are the re-distributed interaction based on the probability of the pairwise interaction. Size of the line is proportional to frequency of interaction

networks and the networks from each of the species removal simulations. We considered the type of network i.e., species removal simulation or observed network, as a fixed effect and sampling date and network id (plot) as random effects. To account for the networks' non-independence, we included the network id effect nested under sampling date (Zuur et al. 2009). We did not consider tree height since all saplings were of similar height during the sampling period (see “Material and methods”). We tested the normality distribution of the variables using a Shapiro–Wilk analysis and the variance homogeneity of the residuals visually. In the beetle abundance analysis, the model was built using a *poisson* error distribution of the residuals. Models were fitted using the R packages *lme4* (Bates et al. 2015). We conducted Post-hoc analyses using Tukey tests in the package *multcomp* (Hothorn et al. 2008; R Core Team 2020).

To avoid a confounding effect due to a change in species richness in the network, we compared the beetle abundance, relative importance, and relative interaction weights of mahogany from each simulation and the observed network to the value calculated from networks where we randomly removed a tree or a beetle species. We followed the same reallocation of interactions for tree species removal simulation and beetle species removal simulation, respectively. We tested for significant differences between the simulations and between the observed vs random species removal simulation, using the same approach as for the comparison between the non-random species removal and observed networks. In all cases, we calculated the effect size of the treatment ( $\delta_T$ ) following the method of Hedges (2007) and reported likelihood confidence intervals (95% CI).

### Testing the mediating effect of core beetle species on the importance of big-leaf mahogany

To test if the influence of tree species on the importance of mahogany is mediated by the core beetle species, we analyzed if there was a relationship between the importance of mahogany and the number of beetle species interacting on an identified tree species group (similar or core), in both the observed network and the networks where the core beetle species was removed. To avoid confounding effects with species richness, we only performed the analysis with the tree species group that showed a significant effect on mahogany independent of plant species richness. Similarly, we only performed the analysis for the mahogany's importance measure significantly affected by both beetle and tree species. In both the observed networks and in the core beetle species removal simulations, we used linear mixed effect models to test for a possible relationship. We considered herbivore species richness on the tree species as a fixed effect and sampling date as a random effect. We  $\log(x + 1)$  transformed the number of interacting species to meet the assumption

of normality. We tested for normality of the residuals with Shapiro–Wilk analysis and checked for the homogeneity of the variance visually.

## Results

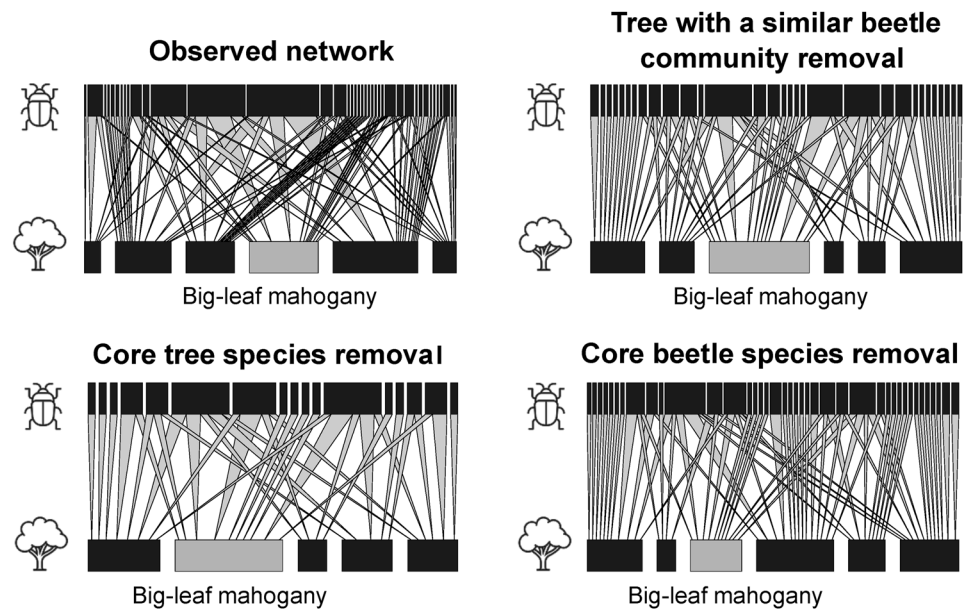
The beetle community was comprised of 40 species and 394 individuals belonging to 11 families (A complete list of species is provided in the supplementary material Table S.4). In the original networks, we observed an average of  $7 \pm 2$  beetle individuals on big-leaf mahogany ( $\pm$  standard error) a value below the mean across all tree species ( $9 \pm 2$ ). Meanwhile, the observed mean value of relative importance of mahogany was  $0.34 \pm 0.05$ , also below the mean across tree species ( $0.43 \pm 0.02$ ). Big-leaf mahogany was not identified as a core tree species in any of the observed networks (Fig. 2, see Supplementary Material for a list of tree core species). Finally, the observed mean value of relative interaction weights of mahogany was  $1.17 \pm 0.23$  a value below the mean across all tree species ( $1.88 \pm 0.15$ ).

### The influence of tree species on the importance of big-leaf mahogany in the plant–herbivore network

The removal of both tree species with a similar beetle community and the core tree species from the networks significantly increased the abundance of beetle on mahogany (core tree,  $\delta_T = 1.5$ , 91, CI [0.52, 1.14],  $P \leq 0.001$ ; similar tree  $\delta_T = 1.02$ , 95% CI [0.44, 0.98],  $P \leq 0.001$ ; Fig. 3). In both simulations the changes in abundance were significantly higher than the simulation of random species removal (core tree:  $\delta_T = 1.2$ , 95% CI [0.37, 0.9],  $P \leq 0.001$ , similar tree:  $\delta_T = 0.8$ , 95% CI [0.3, 0.819],  $P = 0.0005$ ), suggesting that the effect of the similar tree and the core tree species on the abundance of beetle on mahogany is independent of the number of tree species in the network (Fig. 3). Finally, the abundance of beetles on mahogany in the observed network vs. the random tree species removal was not statistically different ( $\delta_T = 0.22$ , 95% CI [− 0.45, 0.15],  $P = 0.85$ ) suggesting that species richness per se has no effect on the abundance of beetle on mahogany.

When we compared the relative importance of mahogany between the tree species simulations and the observed network, we found that tree species removal significantly affects relative importance of the species (Fig. 3). The removal of the tree species with a similar beetle community increased the relative importance of mahogany by 40% ( $\delta_T = 0.68$ , 95% CI [0.07, 0.2],  $P \leq 0.001$ ), meanwhile the removal of the core tree species increased the relative importance of mahogany by 50% ( $\delta_T = 1.98$ , 95% CI [0.17, 0.32],  $P \leq 0.001$ ). Finally, the removal of a tree randomly selected increased the

**Fig. 2** Network of the interacting species for each removal simulation considering all interactions recorded across the studied networks. In each network the high level in the network corresponds to beetle species and the low level to the tree species. Big-leaf mahogany is highlighted in light grey. The width of the boxes is proportional to the frequency of interaction of the species which indirectly shows the importance of a species in the network



relative importance of mahogany by 32% ( $\delta_T=0.5$ , 95% CI [0.04, 0.17],  $P \leq 0.001$ ).

However, we observed opposite results when comparing the simulations of the similar tree and core tree removal with the simulation of random tree species removal (Fig. 3). The effect of the removal of the core tree species on the relative importance of mahogany was significantly higher than the removal of tree selected randomly ( $\delta_T=0.88$ , 95% CI [0.06, 0.21],  $P=0.006$ ). In contrast, the effect of removing the similar tree was not significantly different to the random tree removal ( $\delta_T=0.14$ , 95% CI [-0.04, 0.1],  $P=0.92$ ). These results suggest that although tree species richness significantly affects the relative importance of mahogany, core species have a particular effect on the relative importance of mahogany which is independent of the number of tree species in the network.

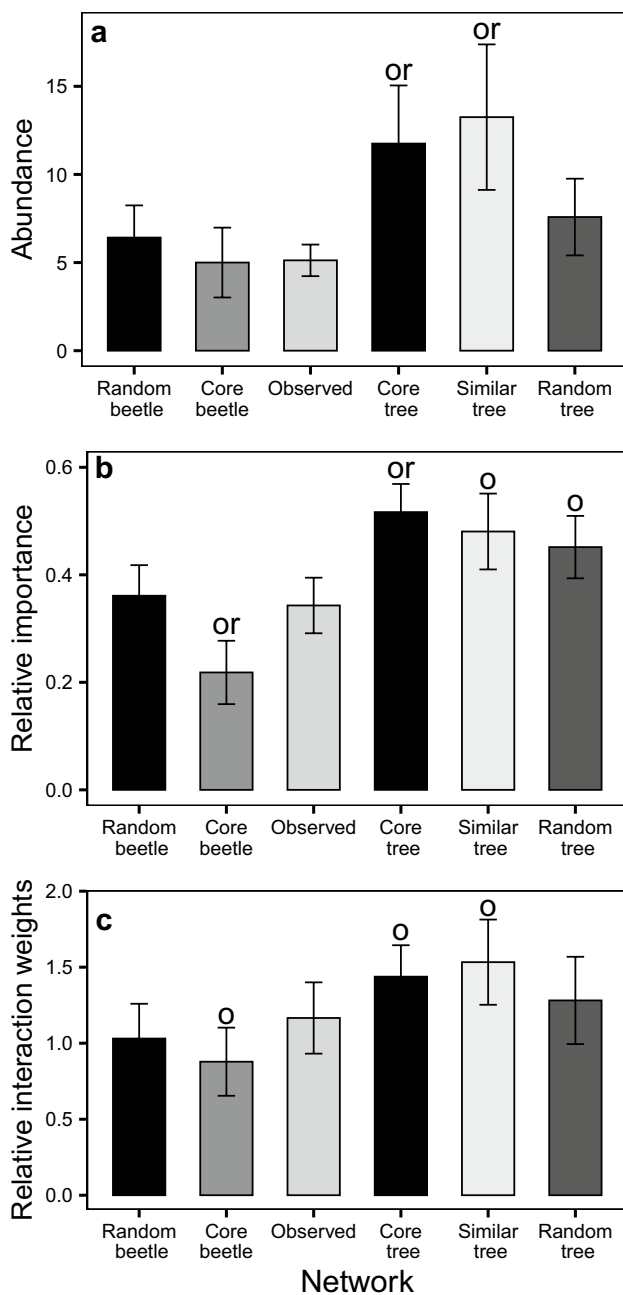
Finally, we observed that the removal of the tree species with a similar beetle community (similar tree) increased the relative interaction weights of mahogany by 31% ( $\delta_T=0.42$ , 95% CI [0.18, 0.55],  $P=0.008$ ) while the removal of the core tree species increased relative interaction weights of mahogany by 28% ( $\delta_T=-0.40$ , 95% CI [0.14, 0.5],  $P=0.01$ ). Meantime, the removal of a tree randomly selected had no significant effect on the relative interaction weights of mahogany ( $\delta_T=0.13$ , 95% CI [-0.07, 0.3],  $P=0.8$ ). Similarly, we observed no significant differences between the simulation of random tree species removal and the similar tree species removal ( $\delta_T=0.29$ , 95% CI [0.07, 0.43],  $P=0.09$ ) and between the random species removal and the simulation of the core tree species removal ( $\delta_T=-0.33$ , 95% CI [0.08, 0.44],  $P=0.07$ ). These results suggest an

interactive effect of species richness, core species and similar species on the relative interaction weights of mahogany.

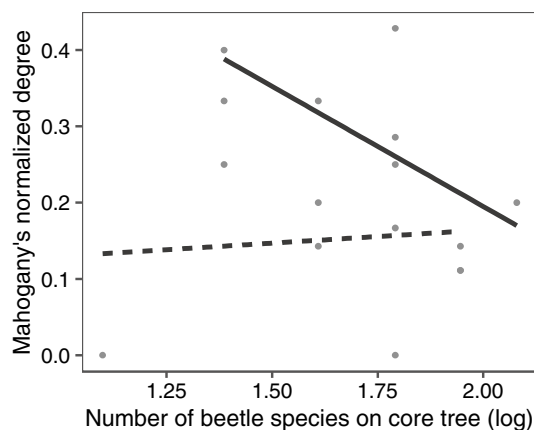
### The influence of beetle species on the importance of big-leaf mahogany in the plant–herbivore network

The abundance of beetles on mahogany in the simulation of core beetle removal was not significantly different from the observed network's abundance ( $\delta_T=-0.42$ , 95% CI [-0.65, 0.03],  $P=0.41$ ), or to the abundance in the simulation of the random beetle species removal ( $\delta_T=0.41$ , 95% CI [-0.04, 0.64],  $P=0.46$ ). Similarly, the abundance of beetles on mahogany in the simulation where a beetle species was randomly removed was not different to the abundance in the observed networks ( $\delta_T=-0.02$ , 95% CI [-0.33, 0.3],  $P=0.9$ ; Fig. 3).

In contrast, when the core beetle was removed from the network, the relative importance of mahogany of big-leaf mahogany significantly decreased by 36% compared to the observed network ( $\delta_T=-0.61$ , 95% CI [-0.19, 0.06],  $P=0.004$ ; Fig. 2). Meanwhile, the relative importance of mahogany in the simulation of core beetle removal was significantly lower than the value observed in the simulation of the random beetle species removal ( $\delta_T=-0.69$ , 95% CI [-0.21, -0.07],  $P=0.001$ ) showing that the effect of beetle core species on the relative importance of mahogany is independent of the number of beetle species in the network. When we compared the relative importance of mahogany in the random beetle species removal simulation with the value of the observed networks, there were no differences between the two networks groups ( $\delta_T=0.01$ , 95% CI [-0.05, 0.08]



**Fig. 3** Differences in values of abundance of beetles (a) relative importance (b) and relative interaction weights (c) of big-leaf mahogany (*S. macrophylla*) between the observed networks and the networks of each species removal simulation. Core beetle: removal of the core or most generalist beetle species. Core tree: removal of the core or most generalist tree species. Observed: no species removal. Similar tree: removal of the tree species with a similar beetle species community than mahogany. Random beetle: removal of a randomly selected beetle species. Random tree: removal of a randomly selected tree species. Bars are mean  $\pm$  standard error. *o* significant difference compared to the observed network ( $P < 0.05$ ). *r* significant difference compared to the random species removal simulation ( $P < 0.05$ )



**Fig. 4** The relationship between the number of the beetle species observed on the core tree species and the relative importance of big-leaf mahogany. Solid line: Relationship in the observed networks ( $\beta = -0.32$ ,  $SE = 0.13$ ,  $R^2 = 0.46$ ,  $P = 0.02$ ). Dashed line: Relationship in the core beetle removal simulation networks ( $\beta = 0.03$ ,  $SE = 0.18$ ,  $R^2 = 0.005$ ,  $P = 0.8$ ). Number of species was log + 1 transform to meet the assumption of normality

$P = 0.98$ ), suggesting no effect of beetle species richness per se on the relative importance of mahogany.

Finally, the removal of the core beetle significantly decreased the relative interaction weights of mahogany by 25% ( $\delta_T = 0.4$ , 95% CI  $[-0.5, -0.11]$ ,  $P = 0.02$ ). However, there was no significant differences in the relative interaction weights of mahogany between the simulation of core beetle removal and the simulation of the random beetle species removal ( $\delta_T = 0.19$ , 95% CI  $[-0.3, 0.02]$ ,  $P = 0.6$ ). Similarly, when we compared the relative interaction weights observed in the simulation of random beetle species removal with the value of the observed networks, there were no differences between the two networks groups ( $\delta_T = -0.15$ , 95% CI  $[-0.3, 0.05]$ ,  $P = 0.7$ ). This suggests an interactive effect of beetle's roles and species richness on the relative interaction weights of mahogany.

### Mediating effect of core beetle species on the importance of big-leaf mahogany

Simulation analysis only showed a significant and species richness independent effects of both core tree and core beetle species on mahogany's relative importance (normalized degree; Supplementary information Fig. S1). Therefore, we tested for a possible mediating effect of core beetles on the influence of core trees on mahogany's importance in the network. We found that in the observed networks, the number of beetle species interacting with the core tree species was negatively related to the relative importance of mahogany ( $\beta = -0.32$ ,  $SE = 0.13$ ,  $R^2 = 0.46$ ,  $P = 0.018$ ; Fig. 4), i.e., the higher the number of beetles species interacting with the core tree species, the lower the importance of mahogany. In



contrast, in the network where the core beetle was removed, the number of beetle species interacting with the core tree species had no significant relationship with the relative importance of mahogany ( $\beta = 0.03$ ,  $SE = 0.18$ ,  $R^2 = 0.005$ ,  $P = 0.85$ ; Fig. 4 and Supplementary information Fig. S1); suggesting that the effect of core tree species on the relative importance of mahogany is mediated by core beetles in the network.

## Discussion

The simulations of species removal show that tree species highly attractive to herbivores and generalist herbivore species (core species) significantly affect the importance of big-leaf mahogany in the plant–herbivore network in a mixed tree plantation. We also found that the negative effect of core tree species on the importance of mahogany's beetle assemblage is mainly through the sharing of core herbivore species. Other studies have reported that neighboring plants which are phylogenetically close or with similar antiherbivore defenses to focal plant species, make the species more vulnerable to herbivores attacks (i.e., Castagnéyrol et al. 2014; Endara et al. 2017). We observed that in polycultures with no related plant species, core tree species diminish both the abundance of herbivores and the importance of a focal species in the plant–herbivore network (normalized degree and species strength). In contrast, the presence of tree species hosting similar herbivores only affects herbivore abundance. Our results demonstrate that in addition to affecting the network's complexity at the community level (e.g., Maia et al. 2019; Nuwagaba et al. 2017) core species also affect the importance of other species in the network. These results are relevant for polyculture establishment, as identifying core tree species and introducing them together with a focal species could potentially decrease herbivory damage by attracting species away from the species of interest.

Several studies show that vegetation heterogeneity and characteristics of both neighboring plants and traits of the herbivore community (Barbosa et al. 2009; Grossman et al. 2019) rather than species richness per se affect the interactions between herbivores and a focal host plant (Yguel et al. 2011; Castagnéyrol et al. 2014; Schuldt et al. 2014). Here, we observed that “removing” tree species with a similar herbivore community to mahogany was not different in its effect on the relative importance and the relative interaction weights of mahogany than the random removal of tree species. Nevertheless, in both simulations, the importance of mahogany was higher than in the observed network. This result suggests that in terms of the relative importance of a focal species, tree species richness per se decreases the number of herbivore species interacting with a focal species regardless of the similarity in attractiveness to herbivores.

This supports the idea that species richness can reduce the impacts of herbivore attacks on plant species (Macfadyen et al. 2012). However, when we compared the abundance of herbivores, the random removal of tree species had no significant effect while both the removal of the tree species with a similar herbivore community to mahogany and the core tree species significantly increased the beetle's abundance on mahogany. The results suggest that these species have similar foliar attributes (e.g., low defenses, high water content, etc. (Barbosa et al. 2009) that attract generalist species individuals away from the focal species to suffer less attacks while species richness per se influence the number of beetle species that attack a focal tree species.

It could be argued that the observed increase in abundance of beetles in the simulations is a methodological artifact resulting from the re-allocation of interactions between species. However, our simulations are based on realized interactions and reallocations based on host preferences calculated from the frequency of interaction with no bias on reallocating interactions to any particular species (Morrison et al. 2020). In all the networks studied, big-leaf mahogany was not classified as a core species or as having the highest importance value, and only in one network did mahogany show the highest beetle abundance. Moreover, the low phylogenetic and taxonomic distance between species in our networks and previous report of lower attacks on mahogany by generalist herbivores in polycultures (Castagnéyrol et al. 2014; and see Abdala-Roberts et al. 2015) decreases the possibility that neighboring plants increase the presence of herbivores on mahogany (Barbosa et al. 2009; Bertheau et al. 2010; Gilbert et al. 2012). Nevertheless, we assumed that generalist species limit the interactions of other species. While there is evidence that supports this idea (Bird et al. 2019), experimental studies are needed to test to which extent this assumption describes the dynamics of mahogany's herbivore assemblages.

Although effects of tree diversity on mahogany's associated fauna have been shown to be stronger on specialist than generalists species (Abdala-Roberts et al. 2015). In general, the effect of tree diversity has been reported to be higher on generalist herbivores (Jactel and Brockerhoff 2007) since they are more likely to move away from a focal species according to the availability of hosts species (Heimonen et al. 2013). In this sense, the observed effect of core beetles on the relative importance of mahogany is not surprising. Previous studies on big-leaf mahogany in the UADY experiment, however, found different responses among generalist species—from no response, to responses mediated by other insect groups with differences between insect groups (Campos-Navarrete et al. 2015a, b; Abdala-Roberts et al. 2015). However, most of those studies, as with many others in the literature, studied only a single or few species from different taxonomic groups, ignoring possible

interspecific variation. Here, we study a beetle community of 40 species and observed the presence of beetle species that could be classified as generalist according to literature (feeding on species from different taxonomic families; Schoonhoven et al. 2006) but that were not identified as core species or observed on mahogany. This result shows the existence of interspecific variation within the same taxonomic group, and among generalists on both its role in the plant–herbivore network and its effect on a focal plant species. Variation such as this should be accounted for in future studies, particularly those which aim to compare responses between generalists and specialists.

We observed that the effect of core tree species on mahogany's importance in the plant–herbivore network was primarily driven by the sharing of highly generalist beetle species (core species). Core beetle species made up most of the individuals observed on mahogany and significantly influenced the relative importance of mahogany, regardless of beetle species richness. No wonder the relationship between the number of species interacting with the core tree species and the relative importance of mahogany was lost when removing the core beetle species. In our networks, core tree species may serve as attractant or decoy species (Tahvanainen and Root 1972) drawing herbivores species away from mahogany, particularly the most generalist herbivore species. This result suggests that the influence of core tree species is limited by the herbivore community (Barbosa et al. 2009).

Interestingly, our results are not density-dependent since all the tree species are present with the same abundance (see “Material and methods”). Abundance has been commonly regarded as the main feature defining both the role of species in the network (where the most abundant species are usually the core or generalist species; see Fort et al. 2016; Vázquez et al. 2007) and the effect of neighboring plants on focal species (higher frequency of the host plant can increase the insect attacks and higher frequency of neighboring plants can diminish insect attacks; Kim and Underwood 2015). Nevertheless, we detected the presence of core plants species and influence of other tree species on mahogany's associated beetles. These results highlight that species' traits other than abundance are also determinants of the species role in the network and its effect on focal species (e.g., González-Castro et al. 2012; Hackett et al. 2019). We also observed that core beetle species increased the importance of mahogany in the plant–herbivore network and affected other tree species' effect on big-leaf mahogany. Similarly to pollination networks, our results demonstrate that species' roles also depend on the traits of their interacting species (Junker et al. 2010; Coux et al. 2016). The stability of these patterns through time remains to be tested, particularly regarding the temporal changes in species roles (Miele et al. 2020).

Effects of diversity depend not only on species richness per se but also on different species traits (Barbosa et al. 2009). However, measuring various traits might be complicated for stakeholders due to resource limitations. Here, we demonstrate that relatively simple data (abundance and co-occurrence) allows the detection of tree species with a strong influence on the herbivore assemblages of a focal species. Nevertheless, species undergo morphological (i.e., height) and physiological changes that alter their herbivore defenses, microclimate, etc., ultimately affecting plant–herbivores relationships (Boege et al. 2011). Future research is needed to see how neighboring species' influence changes as tree species achieve a mature state and how ecological network analysis could help detect such species. A final consideration is the spatial scale of the ecological network as this can affect the observed effect. In the UADY experiment, when the whole network for the field site is analyzed (all plots together), mahogany appears as one of the hub species in the network (Quinto et al. 2022). However, when we studied the networks at plot level, mahogany was never the most interconnected (core) species. Associational effects among species are higher as the distance between neighbors decreases (Grossman et al. 2019). So, we recommend building small-scale networks within the field site to better estimate associational effects.

Species within the network of interacting species not only contribute to the structure of the network, but also affect the importance of the species within it. Plant species richness decreases the importance of a focal plant species in the plant–herbivore network mainly through the presence of species that are highly attractive to the herbivore community (core species), species that host a similar herbivore community and species richness per se. However, the effects of the core tree species are mediated by the core beetle species in the network. This relationship shows that species' role in the plant–herbivore network are not only influenced by other plant species in the network, but also by the generalist core herbivore species. Future research is needed to understand how representative these results are for all plant species in the network and the magnitude of benefit of plant diversity for those plant species identified as core species. Likewise, different taxonomic groups beyond Coleoptera should be accounted for as diversity affects functional taxonomic groups of arthropods differently (Campos-Navarrete et al. 2005). Similarly, there is considerable evidence for the importance of maintaining the network's complexity to preserve ecosystem services at the community level (Delmas et al. 2019). However, there's still insufficient evidence on the effects at the species level. Understanding the associational effects of diversity on herbivores assemblages would help establish mixed tree plantations that rely less on pesticides and have less undesirable collateral effects.

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**Author contributions** EVG formulated the idea and analyzed the data. LA-R and VP-T conceived and designed the experimental site. JQ and MJC-N designed and conducted fieldwork. EVG wrote the manuscript with input from LA-R and VP-T; other authors provided editorial advice.

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**Availability of data and material** All data produced from this study are provided in this manuscript as supplementary material.

**Code availability** Code can be consulted on the supplementary material.

## Declarations

**Conflicts of interest** The authors declare that there is no conflict of interest.

**Ethical approval** “All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.”

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