



## Effects of Tree Genotypic Diversity and Species Diversity on the Arthropod Community Associated with Big-leaf Mahogany

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### ABSTRACT

Despite potential interactive effects of plant species and genotypic diversity (SD and GD, respectively) on consumers, studies have usually examined these effects separately. We evaluated the individual and combined effects of tree SD and mahogany (*Swietenia macrophylla*) GD on the arthropod community associated with mahogany. We conducted this study within the context of a tree diversity experiment consisting of 74 plots with 64 saplings/plot. We sampled 24 of these plots, classified as monocultures of mahogany or polycultures of four species (including mahogany). Within each plot type, mahogany was represented by either one or four maternal families. We surveyed arthropods on mahogany and estimated total arthropod abundance and species richness, as well as abundance and richness separately for herbivorous and predatory arthropods. Overall tree SD and mahogany GD had positive effects on total arthropod species richness and abundance on mahogany, and also exerted interactive effects on total species richness (but not abundance). Analyses conducted by trophic level group showed contrasting patterns; SD positively influenced herbivore species richness but not abundance, and did not affect either predator richness or abundance. GD influenced predator species richness but not abundance, and did not influence herbivore abundance or richness. There were interactive effects of GD and SD only for predator species richness. These results provide evidence that intra- and inter-specific plant diversity exert interactive controls on associated consumer communities, and that the relative importance of SD and GD may vary among higher trophic levels, presumably due to differences in the underlying mechanisms or consumer traits.

Abstract in Spanish is available with online material.

*Key words:* genotypic diversity; herbivores; predators; species diversity; species richness.

THERE IS MOUNTING EVIDENCE THAT PLANT SPECIES DIVERSITY (SD) AFFECTS PRIMARY PRODUCTIVITY (e.g., Koricheva *et al.* 2000, Crutsinger *et al.* 2006, Cook-Patton *et al.* 2011, McArt & Thaler 2013) as well as arthropod species richness and abundance (Koricheva *et al.* 2000, Haddad *et al.* 2009). Recent work has shown parallel and qualitatively similar effects of plant genotypic diversity (GD; *i.e.*, within plant species) on ecosystem function and consumer communities (Agrawal *et al.* 2006, Castagnyrol *et al.* 2012, Hambäck *et al.* 2014). The bottom-up effects of both sources of plant diversity on consumers may result in altered consumer top-down control, which may in turn influence ecosystem function (Carnus *et al.* 2003, Haddad *et al.* 2009, Moreira *et al.* 2012). For example, enhanced predator top-down control of herbivores may mediate positive effects of plant diversity on primary productivity (Carnus *et al.* 2003, Haddad *et al.* 2009, Moreira *et al.* 2012).

Plant diversity could affect community structure at higher trophic levels via different mechanisms. For example, the Resource Specialization Hypothesis (Root 1973, Keddy 1984) poses that greater plant diversity increases the availability of resources or niches that can then accommodate more specialized consumer species. Alternatively, the More Individuals Hypothesis postulates that greater plant diversity increases the availability of resources (e.g., through increased productivity) and, consequently, the abundance of consumers, increases the probability of having more consumer species in the community (Hutchinson 1959, Srivastava & Lawton 1998).

While the mechanisms by which plant diversity affects higher trophic levels have been relatively well studied, the influence of plant trait variation related to such diversity is less understood. For instance, the phenotypic variation among plant species is usually greater than the genotypic variation within each component species in a community; thus, SD would be expected to have stronger effects on consumers than would GD. However, recent work has shown that plant GD may have equally strong (Cook-Patton *et al.*

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2011) or stronger (Crawford & Rudgers 2013) effects on arthropod communities. Furthermore, plant GD and SD may interactively influence higher trophic levels (Crawford & Rudgers 2013), but most studies have evaluated these effects separately. Accordingly, the relative importance and potential for interactive effects between plant intra- and inter-specific diversity are not clear.

In addition, the effects of plant GD and SD on higher trophic levels vary among consumer functional groups or trophic levels (Vehviläinen *et al.* 2007, 2008). For example, differences in mobility may influence the ability of herbivores or predators to disperse and thus respond to resource heterogeneity (Koricheva *et al.* 2000, Bommarco & Banks 2003). These findings highlight the need to compare the effects of different sources of plant diversity across higher trophic levels (or guilds within trophic levels) that vary in traits predicting consumer responses to resource heterogeneity (Johnson *et al.* 2006).

Here, we evaluated the individual and interactive effects of GD within the tropical tree *Swietenia macrophylla* King (big-leaf mahogany) and overall SD of tropical trees on the arthropod community in southern México. To uncover potential differences in effects across trophic levels, we tested for plant diversity effects on total arthropod abundance and species richness, as well as separately for herbivorous and predatory arthropods. By sampling only mahogany plants, our test of SD addresses the influence of tree species neighborhood on arthropods recruiting to one component tree species in the system. The same rationale extends to interpreting the interactive effects between sources of diversity. We also sampled all mahogany genotypes at both low and high GD, which enabled us to test for an effect of GD on arthropods.

We addressed the following questions: (1) what is the relative importance of mahogany GD and tree species neighborhood diversity effects on the arthropod community associated with mahogany? (2) Do these sources of diversity exert interactive effects? (3) Do the individual and interactive effects of intra- and inter-specific diversity on the arthropod fauna associated with mahogany vary across arthropod trophic levels (herbivores vs. predators)?

## METHODS

**FOCAL SPECIES.**—The focal tree species, big-leaf mahogany (*S. macrophylla*, Meliaceae), is a self-compatible, long-lived perennial tree distributed from southern México to Bolivia (Pennington & Sarukhán 2005). Individuals are monoecious and produce unisexual flowers (Styles & Khosla 1976); fruits are woody capsules containing wind-dispersed seeds (Loveless & Gullison 2003). In tropical forests of the Yucatán Peninsula where this study was conducted, big-leaf mahogany co-occurs with five other tree species that are also the subject of this experiment: *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 are long-lived, deciduous and distributed from central México to Central and South America (Pennington & Sarukhán 2005).

**SEED SOURCES AND COLLECTION.**—From January 2011 to March 2011, we collected seeds of all species from adult trees located in southern Quintana Roo (México) (18°35'44"N, 88°21'45"W), and germinated them at the Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias (INIFAP) campus in Mocochoá, Yucatán (México) (21°6'40"N, 89°26'35"W). For all species, we collected seeds from six mother trees (distance among trees ranged from 0.5 to 50 km, depending on species). For *S. macrophylla*, the distance among mother trees spanned from 3 to 50 km, which falls within the range used by previous studies to define distinct populations of this species (Gillies *et al.* 1999, Loveless & Gullison 2003). In a previous study, we found significant variation among *S. macrophylla* maternal families (progeny of each family composed of mixture of full- and half-siblings) in growth-related traits (*e.g.*, canopy size: 2.5-fold), herbivore resistance (*e.g.*, stem borer attack: 3.8-fold) (Table S1), and chemical defenses (polyphenolics: five-fold variation 10.44 mg/g to 50.39 mg/g;  $F_{5,50} = 6.30$ ,  $P < 0.0001$ ; data from Moreira *et al.* 2014, see also Abdala-Roberts *et al.* 2014).

**STUDY SITE AND EXPERIMENTAL DESIGN.**—We established the experimental plots in December 2011 by planting 4-mo-old seedlings at a 7.2-ha site owned by the INIFAP, located near the town of Muna (20°24'44"N, 89°45'13"W). We fertilized the plants once in January 2012 with N, P, and K (20:30:10), and irrigated them with 2 L water three times per week from January 2012 until June 2012. The design consisted of 74 plots of 21 m by 21 m, with 64 plants within each plot and 3-m spacing among plants ( $N = 4780$  plants); distance between plots was 6 m. Plots were established on a recently cleared site where vegetation consisted mostly of grasses and shrubs, and which was surrounded by a matrix of secondary tropical forest. Mahogany was planted in 59 of these plots, which were classified into four types depending on the diversity treatment: (1) *S. macrophylla* monocultures of one maternal family (M-1; 12 plots, two replicate plots/family), (2) *S. macrophylla* monocultures of four maternal families (M-4; 20 plots), (3) species polycultures within which all *S. macrophylla* saplings planted were of one maternal family (P-1; 12 plots, two plots/family), and (4) species polycultures within which mahogany plants were represented by four maternal families (P-4; 15 plots) (see Fig. S1). Treatments for both neighborhood tree SD and mahogany GD included equal numbers of individuals of four species and four *S. macrophylla* maternal families drawn randomly from pools of six species and six maternal families, respectively. All non-mahogany species were equally represented across polycultures (each species present in six polyculture plots) (See Fig. S1). Likewise, *S. macrophylla* maternal families were represented in a similar number of *S. macrophylla* monocultures of four maternal families (8–9 plots per family), and also in a similar number of species polycultures where *S. macrophylla* plants were of four maternal families (9–10 plots per family). We interspersed plots of each treatment throughout the experimental landscape. For the present study, we restricted arthropod sampling to a subset of these 59 plots with mahogany, spanning all treatments. Because we sampled only mahogany plants, our test of SD effects evaluates inter-specific neighborhood effects on the arthropod community

associated exclusively with mahogany. Contrastingly, by sampling all maternal families at low and high GD, we were able to evaluate the overall effects mahogany GD on arthropods associated with this focal tree species.

**ARTHROPOD SAMPLING.**—We sampled six plots for each of the four diversity treatments (M-1, M-4, P-1, P-4). We conducted arthropod surveys in June 2012, September 2012, and January 2013. During each survey, we randomly selected two plots for each diversity treatment ( $N = 8$ ), and within each plot we randomly selected 30 mahogany plants in mahogany monocultures (M-1 and M-4), and 5–16 mahogany plants in polycultures (P-1, P4), depending on plant availability (see Table S2). In total, we sampled 467 mahogany plants across surveys. We used a sampling scheme with replacement, in which we censused different plots and plants during each survey.

During each survey, we sampled all arthropods on each plant from 0800 to 1200 h when arthropod activity was highest. We visually examined the entire canopy and main stem of each plant and collected all arthropods present; mahogany saplings had an average height  $76.2 \pm 0.55$  cm at the time of insect sampling, which permitted a thorough examination of each plant in search of arthropod specimens. Specimens were preserved in 70 percent ethanol and subsequently identified to the lowest possible taxonomic level. Specimens for which the species was not identified were treated as morphospecies. Specimens were classified into herbivores and predators based on anatomical features such as mouthparts, as well as natural history information and direct observations in the field (Borrow & White 1970, Triplehorn & Johnson 2005). Parasitoids and pollinators were not included in the analysis due to their small size (which complicated detection and sampling), high mobility, and very low abundances. While we also surveyed ants, this functional group was not analyzed as these species could act both as omnivores and predators, and because they were the subject of another study.

**DATA ANALYSES.**—Prior to evaluating diversity effects, we conducted a rarefaction analysis to calculate the total arthropod species richness for each sampled individual. We used the Vegan module in R v. 3.01 (R Core Team 2013) with the function ‘specaccum’ and the method ‘rarefaction’ with 100 iterations (Oksanen *et al.* 2013). We used generalized linear mixed models (GLMM) to test for effects of SD [two levels: monoculture (M) vs. polyculture (P)], genotypic diversity GD [two levels: one

maternal family (G1) vs. four maternal families (G4)], and their interaction on rarefied total arthropod species richness, total abundance, and richness and abundance by trophic level (herbivores and predators). We treated diversity levels (GD and SD) and interactions as fixed effects. To account for non-independence of plants sampled within each plot, we incorporated a random effect using Poisson error distribution with log link function. Results from the above models remained qualitatively unchanged after including the effect of survey date (Table S3). In addition, we performed analyses excluding the two most abundant arthropod species (the leafhopper *Oncometopia* sp. and an unidentified Salticidae spider ‘sp1’ see Table S4) to determine if diversity effects were driven by the dominant species in the system.

To test for enhanced top-down effects of predators on herbivore diversity, we estimated the individual and interactive effects of SD and GD on the ratio of predator abundance to herbivore abundance and on the ratio of predator species richness to herbivore richness using a binomial error distribution with logit link function. We fitted all models using the Penalized Quasi-Likelihood method (Crawley 2002, 2007). Whenever an interaction was significant, we used *a posteriori* contrasts to test for differences among pairs of means for a given factor within each level of the other factor (Crawley 2007). We conducted GLMM analyses using the R statistical package v. 3.01. (R Core Team 2013), with the MASS module and the glmmPQL function (Venables & Ripley 2002).

## RESULTS

**TOTAL ARTHROPOD ABUNDANCE AND SPECIES RICHNESS.**—We collected a total of 360 arthropod specimens on mahogany saplings representing the orders Coleoptera, Hemiptera, Lepidoptera, Orthoptera, Dermaptera, Mantodea, Thysanoptera, and Araneae, and totaling 34 families, 25 identified species, and 61 morphospecies. The families with the highest abundance were Cicadellidae (98 individuals) and Salticidae (40). Species and morphospecies identifications, functional group assignments, and abundances are provided in Table S4.

*Tree diversity effects on arthropod species richness.*—Species diversity had a significant positive effect on rarefied total arthropod species richness associated with mahogany (Table 1), where P exhibited a 14 percent greater mean value relative to M (Fig. 1A). We also

TABLE 1. Results from generalized linear mixed models testing for the effects of mahogany (*Swietenia macrophylla*) genotypic diversity (GD) and tree species diversity (SD) on arthropod community structure associated with mahogany. Significant effects ( $P < 0.05$ ) are in bold; for all models we included plot (treated as a random effect).

Source	Total arthropods		Herbivores		Predators	
	Richness	Abundance	Richness	Abundance	Richness	Abundance
SD	<b><math>F_{1,20} = 4.97</math> (0.02)</b>	<b><math>F_{1,20} = 4.50</math> (0.03)</b>	<b><math>F_{1,20} = 3.58</math> (0.05)</b>	$F_{1,20} = 0.91$ (0.33)	$F_{1,20} = 2.98$ (0.08)	$F_{1,20} = 0.08$ (0.83)
GD	<b><math>F_{1,20} = 6.64</math> (0.01)</b>	<b><math>F_{1,20} = 5.12</math> (0.02)</b>	$F_{1,20} = 0.77$ (0.38)	$F_{1,20} = 0.84$ (0.35)	<b><math>F_{1,20} = 5.93</math> (0.01)</b>	$F_{1,20} = 0.76$ (0.33)
SD × GD	<b><math>F_{1,20} = 16.43</math> (&lt;0.0001)</b>	$F_{1,20} = 0.02$ (0.88)	$F_{1,20} = 2.08$ (0.14)	$F_{1,20} = 2.45$ (0.11)	<b><math>F_{1,20} = 4.84</math> (0.02)</b>	$F_{1,20} = 0.28$ (0.49)

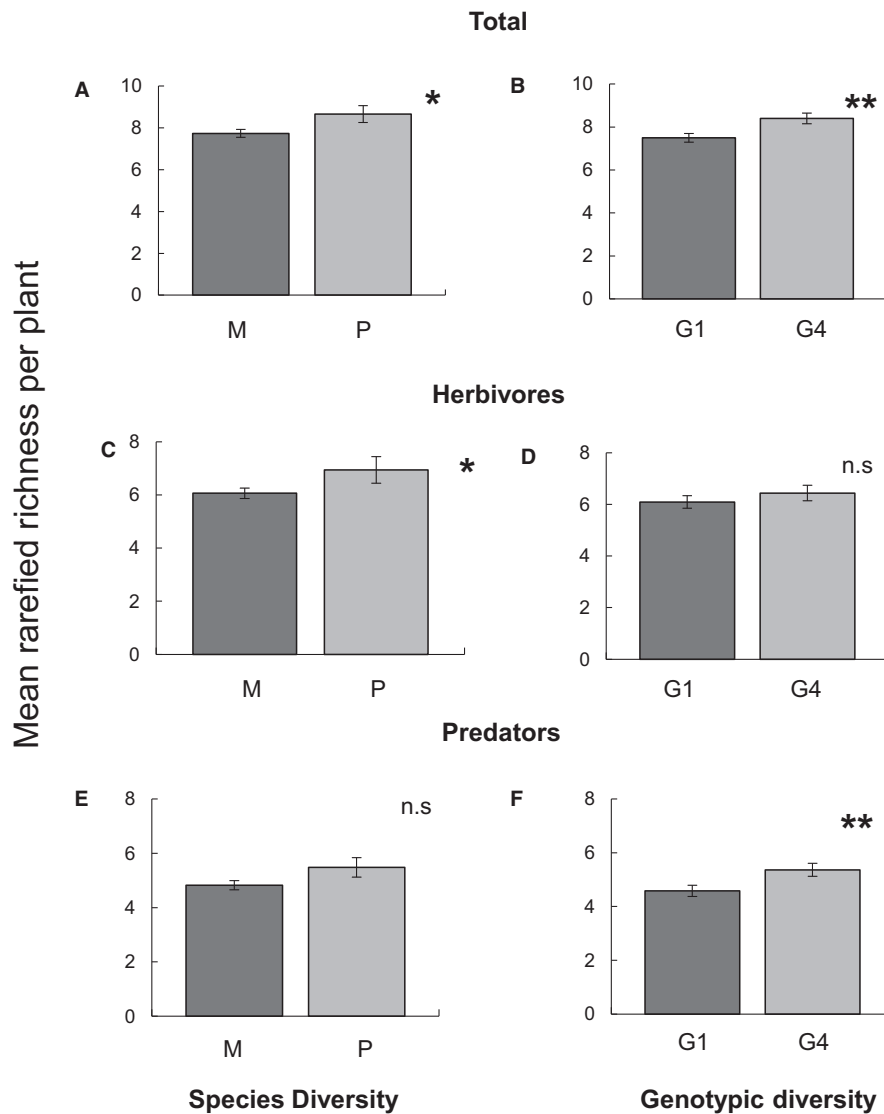


FIGURE 1. Effects of tree species diversity and mahogany (*Swietenia macrophylla*) genotypic diversity on total arthropod species richness (A, B), herbivore species richness (C, D) and predator species richness (E, F) on mahogany plants. Bars are means  $\pm$  SE, and species richness is based upon rarefied data. \* $P < 0.05$ , \*\* $P < 0.01$ , n.s. = not significant. M = Monoculture, P = Polyculture, G1 = plots with one mahogany maternal family, G4 = plots with four mahogany families.

found a significant effect of GD on arthropod species richness (Table 1), where plots G4 exhibited 10 percent greater mean species richness than plots G1 (Fig. 1B). Furthermore, there were interactive effects of GD and SD on arthropod species richness (Table 1), where the effect of GD was positive at low SD (30% increase) but negative at high SD (Fig. 2); at the same time, SD had positive effects on richness at low GD but no effect at high GD (Fig. 2). Subsequent analyses indicated no effect of SD on arthropod species richness after excluding the top two most abundant species (Table S5), suggesting that this diversity effect was driven by the dominant arthropod species on mahogany.

*Tree diversity effects on arthropod abundance.*—We also found significant effects of SD and GD on total arthropod abundance

associated with mahogany (Table 1), with P and plots G4 exhibiting a 35 percent greater mean value than M and plots G1, respectively (Fig. 3A). However, there was no evidence of interactive effects between SD and GD on arthropod abundance (Table 1). We found no effect of SD or GD on arthropod abundance after excluding the most abundant species (Table S5), again showing that diversity effects were driven by the dominant arthropod species on mahogany.

**TREE DIVERSITY EFFECTS ON HERBIVORE ABUNDANCE AND SPECIES RICHNESS.**—Herbivores represented 69 percent (249 individuals) of the specimens sampled (Table S4). Within this group, the leafhopper *Oncometopia* sp. (Cicadellidae) was the most abundant species. SD had a significant positive effect on rarefied herbivore



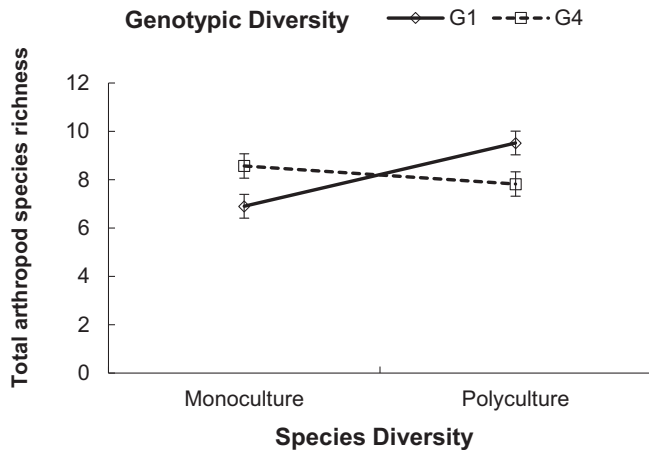


FIGURE 2. Effects of tree species diversity (SD; monoculture, polyculture) and mahogany genotypic diversity (GD; G1 = one mahogany maternal family, G4 = four families) on rarefied arthropod species richness associated with big-leaf mahogany (*Swietenia macrophylla*). Values are means  $\pm$  SE. GD had a positive effect on arthropod species richness at low SD ( $F_{1,20} = 24.0$ ,  $P = 0.0001$ ), whereas at high SD this effect was negative ( $F_{1,20} = 6.51$ ,  $P = 0.01$ ). In addition, we found a positive effect of SD at low GD ( $F_{1,20} = 24.4$ ,  $P < 0.0001$ ), whereas at high GD the effect of SD was not significant ( $F_{1,20} = 1.64$ ,  $P = 0.20$ ).

species richness (Table 1), with P having a 15 percent greater mean value relative to M (Fig. 1C). By contrast, the effect of GD was not significant (Table 1; Fig. 1D), and there was no evidence of interactive effects between SD and GD (Table 1). We found no effects on herbivore abundance of SD (Fig. 3C), GD (Fig. 3D), or their interaction (Table 1). Subsequent analyses indicated no effect of SD on herbivore species richness after excluding the most abundant herbivore species (Table S5).

**TREE DIVERSITY EFFECTS ON PREDATOR ABUNDANCE AND SPECIES RICHNESS.**—Predators represented 31 percent (111) of the specimens sampled, with an unidentified salticid spider being the most abundant species (Table S4). In contrast to herbivore species richness, there was no effect of SD on rarefied predator species richness (Table 1; Fig. 1E), while GD had significant positive effect (Table 1); plots G4 exhibited 18 percent greater mean predator species richness relative to plots G1 (Fig. 1F). In addition, we found interactive effects between SD and GD on predator species richness (Table 1; Fig. 4), where the effect of GD was significant (positive) at low SD but non-significant at high SD. Conversely, SD had a positive effect on predator species richness at low GD, but no effect at high GD (Fig. 4). Finally, there were no effects of SD (Fig. 3E), GD (Fig. 3F), or their interaction on predator abundance (Table 1). Subsequent analyses excluding the top two most abundant predator species remained qualitatively unchanged (Table S5).

**DIVERSITY EFFECTS ON THE RATIO OF PREDATOR TO HERBIVORE ABUNDANCE AND SPECIES RICHNESS.**—Genotypic diversity had a sig-

nificant effect on the ratio of predator species richness to herbivore richness, which was greater in plots G4 relative to those plots G1 (Table S6). In addition, there was a significant GD  $\times$  SD interaction (Table S6) where the effects of GD on the predator to herbivore richness ratio were positive at low SD, but negative at high SD. There was no effect of SD on the ratio of predator to herbivore species richness (Table S6). In addition, there were no individual or interactive effects of GD or SD on the ratio of predator abundance to herbivore abundance (Table S6).

## DISCUSSION

Our results demonstrate that the relative importance of mahogany GD and tree species neighborhood diversity effects (SD) varied across higher trophic levels. While both GD and SD positively influenced total arthropod species richness and abundance associated with mahogany, the relative importance of each varied between herbivorous and predatory arthropods: neighborhood SD influenced herbivore species richness, whereas GD influenced predator species richness. In addition, our results suggest that responses of the most abundant arthropods on mahogany drive these effects.

Aside from their individual effects, we also found that GD and SD exerted interactive controls on total arthropod species richness (but not abundance), as well as predator species richness. GD effects became weaker at high neighborhood SD; on other hand, GD effects are higher on low SD. Only two studies have directly compared the relative strength of plant intra- and inter-specific diversity on higher trophic levels (Cook-Patton *et al.* 2011, Crawford & Rudgers 2013), and of these, only one tested for (and found) interactive effects (Crawford & Rudgers 2013). Our findings therefore emphasize the importance of considering the linkages between different sources of plant diversity in predicting the bottom-up effects of resource heterogeneity on higher trophic levels.

**TOTAL ARTHROPOD SPECIES RICHNESS AND ABUNDANCE.**—We found that both SD and GD positively influenced arthropod species richness and abundance associated with big-leaf mahogany, thereby corroborating previous studies in other systems (Koricheva *et al.* 2000, Crutsinger *et al.* 2006, Haddad *et al.* 2009, Scherber *et al.* 2010). Because arthropod species richness analyses were based upon rarefied data, (*i.e.*, accounting for abundance), our findings suggest that the observed effects of SD and GD on arthropod species richness were not predominantly driven by increased consumer abundance as proposed by the More Individuals Hypothesis (Srivastava & Lawton 1998). Otherwise, the effects of SD on rarefied arthropod species richness (*vs.* non-rarefied data) would have likely been non-significant (Crutsinger *et al.* 2006).

Instead, our results support the Resource Specialization Hypothesis (Hutchinson 1959, Srivastava & Lawton 1998), which proposes that greater resource availability and diversity at high plant diversity promotes the recruitment of specialized consumer

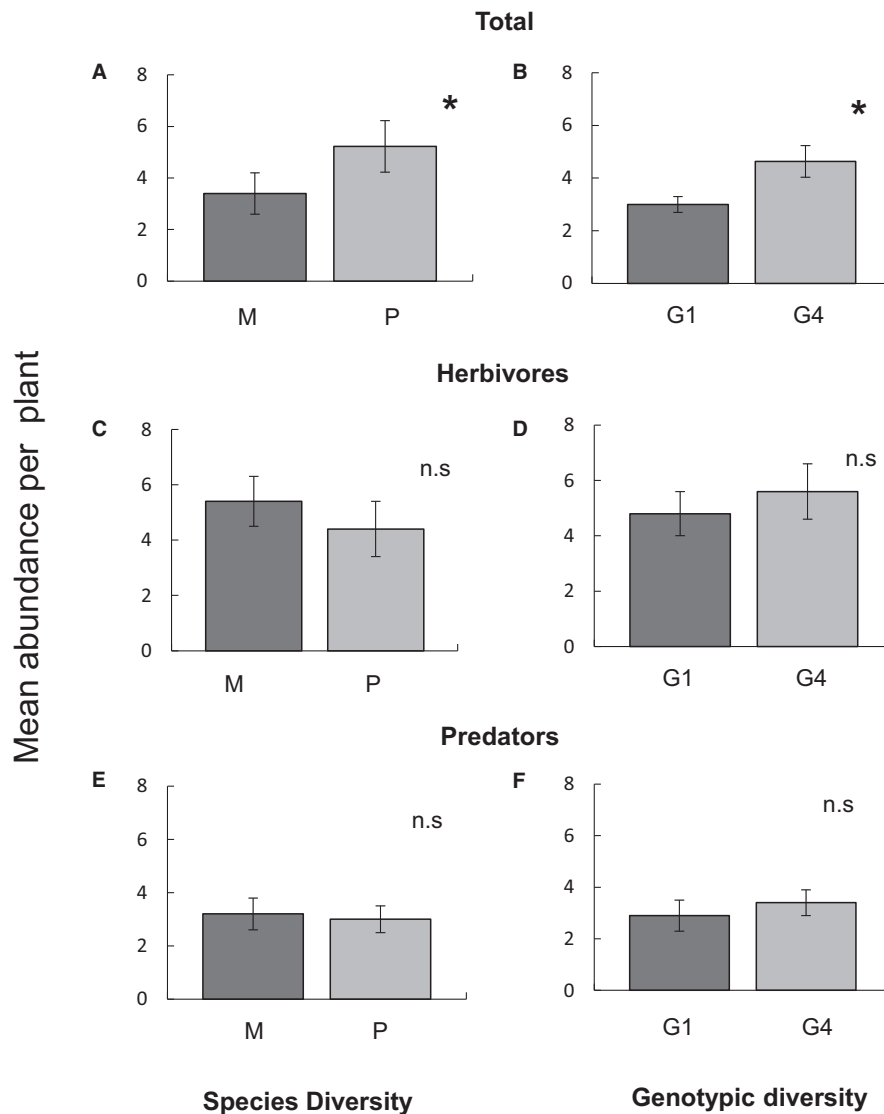


FIGURE 3. Effects of tree species diversity and mahogany (*Swietenia macrophylla*) genotypic diversity on total arthropod species richness (A, B), herbivore species richness (C, D) and predator species richness (E, F) on mahogany plants. Bars are means  $\pm$  SE. \* $P < 0.05$ , n.s. = not significant. M = Monoculture, P = Polyculture, G1 = plots with one mahogany maternal family, G4 = plots with four mahogany families.

species, which then drives an overall increase in consumer species richness. Taken together, our findings suggest that effects of both sources of diversity on total arthropod species richness and abundance were similar in magnitude and that effects on richness were driven by similar mechanisms (but see Discussion below on effects by trophic level). In contrast to our results, Cook-Patton *et al.* (2011) found that GD and SD effects on arthropod species richness were determined by different mechanisms: GD effects were abundance driven, whereas SD effects were due to accumulation of specialized consumers. We suggest that, to gain a predictive understanding of these dynamics, future work should address the prevalence and relative importance of the mechanisms by which different sources of plant diversity influence higher trophic levels.

The effects of SD and GD on total arthropod abundance, and of SD on total arthropod species richness and herbivore species richness, were non-significant after removing the two most abundant arthropod species. This suggests that these diversity effects were driven by the responses of the dominant arthropod species on mahogany.

Importantly, we also found that SD and GD exerted interactive controls on arthropod species richness. Specifically, the effect of GD reversed depending on the level of SD, whereas the effect of SD on mahogany became non-significant at high GD (Fig. 2). These findings suggest that SD and GD effects on arthropod abundance counteracted each other, possibly due to opposing mechanisms (Cook-Patton *et al.* 2011).

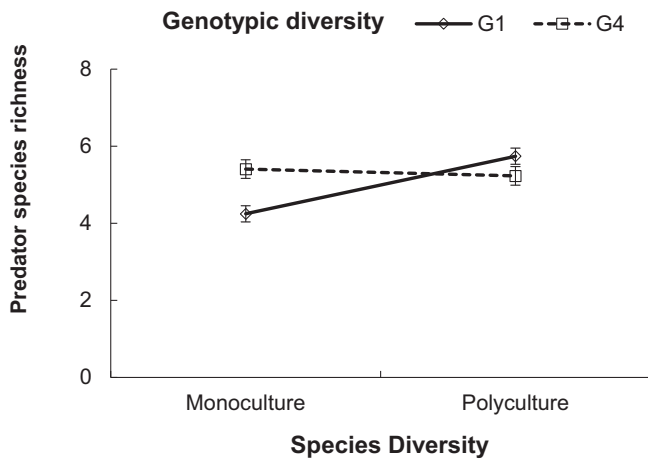


FIGURE 4. Effects of tree species diversity (SD; monoculture, polyculture) and mahogany genotypic diversity (GD; G1 = one mahogany maternal family, G4 = four families) on rarified species richness of predatory arthropods associated with big-leaf mahogany (*Swietenia macrophylla*). GD had a positive effect on arthropod species richness at low SD ( $F_{1,20} = 14.4$ ,  $P < 0.0001$ ), but no effect at high SD ( $F_{1,20} = 0.51$ ,  $P = 0.47$ ). In addition, we found a positive effect of SD at low GD ( $F_{1,20} = 10.59$ ,  $P < 0.001$ ), whereas at high GD the effect of SD was not significant ( $F_{1,20} = 0.15$ ,  $P = 0.69$ ).

HERBIVORE SPECIES RICHNESS AND ABUNDANCE.—Analyses conducted separately for herbivore and predator arthropods revealed differences in the SD and GD effects across trophic levels. We found that higher SD caused a 15 percent increase in herbivore species richness on mahogany, which is within the range of effect sizes observed in previous studies (Haddad *et al.* 2009, Cook-Patton *et al.* 2011, Crawford & Rudgers 2013). By contrast, we found no effect of GD on herbivore species richness, contradicting previous studies that showed substantial effects of GD on the abundance of herbivorous insects (reviewed by Hughes *et al.* 2008, Bailey *et al.* 2009). Interestingly, we found a higher ratio of predator to herbivore species richness at low GD, suggesting that responses of herbivores to high GD could have been counteracted by stronger top-down control by predators (Haddad *et al.* 2009). Alternatively, the lack of GD effects may have been due to low functional contrast among mahogany maternal families, which resulted in weak effects on herbivores (Castagneyrol *et al.* 2012).

We observed no effect of either SD or GD on herbivore abundance, which contrasts with previous studies that reported GD and SD effect sizes ranging from 20 to 40 percent (*e.g.*, Cook-Patton *et al.* 2011, Crawford & Rudgers 2013, McArt & Thaler 2013). This result is perhaps not surprising if we consider that effects of SD on arthropod abundance are frequently driven by increased biomass (*e.g.*, Koricheva *et al.* 2000, Crutsinger *et al.* 2006, Cook-Patton *et al.* 2011), and such effects were likely weak in our study. Other work in our study system has found no effect of either mahogany GD or SD on mahogany growth (Moreira *et al.* 2014, Abdala-Roberts *et al.* 2015), and overall effects of SD

and GD on plant growth across all tree species were possibly also weak due to limited interactions between widely spaced tree saplings early in the establishment of this experiment. Biomass-mediated effects of diversity on herbivore abundance in this system may emerge as plant-plant interactions become stronger.

Factors such as the spatial scale of the experiment in relation herbivore movement (Bommarco & Banks 2003) and variation in herbivore traits (Plath *et al.* 2012) could have influenced the detection of SD and GD effects. In particular, it is possible that herbivore responses observed in this study varied by functional group or species depending on traits such as mobility or diet breadth (Koricheva *et al.* 2000, Plath *et al.* 2012), and that analyzing responses by pooling all species could have obscured the detection of such dynamics. Work in this system using subsets of focal herbivore species has found that SD is contingent upon herbivore diet breadth (Abdala-Roberts *et al.* 2015), indicating that these effects deserve further attention. Our interpretation of effects of GD and SD on insect herbivores will likely depend on how many of these herbivore species are specialists to mahogany relative to generalist species that use the other tree species. We currently do not have this information for most of herbivores sampled on mahogany in the system, but plan to address this aspect in future work.

PREDATOR SPECIES RICHNESS AND ABUNDANCE.—We found that mahogany GD, but not SD, positively influenced species richness of predatory arthropods associated with mahogany, agreeing with expectations from the Enemies Hypothesis (Root 1973). This predicts that plant diversity favors greater predator diversity because of increased availability of refuges and resources expected to drive greater predation rates and thus reductions in herbivore abundance (Russell 1989). These findings are in contrast to those for herbivore species richness on which SD, but not GD, had a significant effect. More generally, our results disagree with previous work suggesting that plant genetic variation should have stronger effects on herbivores than on predators (Johnson & Agrawal 2005), and instead suggest that plant genetic effects do not always dampen across trophic levels as plant genetic variation may influence specific organisms or functional groups (regardless of trophic positioning) more than others (Bailey *et al.* 2009). In particular, our results agree with previous studies showing that the third trophic level can be highly responsive to plant intra-specific variation, particularly in the case of plant traits directly influencing predator recruitment (reviewed by Hare 2002, Mooney & Singer 2012). At the same time, our results for predator species richness do not provide support for the expectation that SD effects on consumers should be stronger due to greater underlying plant trait variation (see Cook-Patton *et al.* 2011), and suggest that the third trophic level can in some cases be more responsive to plant intra- than inter-specific diversity.

We observed interactive effects of SD and mahogany GD on predator species richness (but not abundance) associated with big-leaf mahogany, where GD effects changed depending on the

level of SD. In particular, we found that GD caused a significant increase in predator species richness at low SD (*i.e.*, in mahogany monocultures), but had no effect at high SD. This pattern suggests that GD effects were overcome by increased habitat or resource heterogeneity in species polycultures (Cook-Patton *et al.* 2011, Crawford & Rudgers 2013), and this dynamic could have driven the interactive effects of SD and GD on total species richness. In addition, SD effects on mahogany predator species richness were contingent upon mahogany GD, with a positive effect of SD present at low GD but no effect at high GD (Fig. 4). Thus, despite being underlain by a lower magnitude of trait variation, mahogany GD effects nonetheless influence tree SD effects on arthropods. Further work is necessary to determine the mechanisms producing this pattern; perhaps the characteristics of the dominant species (*e.g.*, architecture, chemical defenses) that depend on GD have an effect on the consumer community.

## CONCLUSIONS

Our study emphasizes the importance of simultaneously testing the effects of multiple forms of plant diversity, as these may act concurrently and lead to non-additive effects on higher trophic levels. Furthermore, we show that independent and interactive effects of plant intra- and inter-specific diversity may vary among consumer functional groups or trophic levels. Future work should focus on understanding how different sources of plant diversity and consumer trait variation interact in shaping community structure across trophic levels.

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## AUTHOR CONTRIBUTIONS

MJC-N, VP-T, and LA-R designed the experiment, MJC-N, LA-R, and JQ collected data, MJC-N and JQ identified the specimens, MAM-R and MJC-N analyzed data, MJC-N, VP-T, LA-R, MAM-R, and JQ wrote the manuscript.

## SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Design of the forest diversity experiment.

TABLE S1. *General linear models testing for big-leaf mahogany.*

TABLE S2. *Sample sizes for mahogany saplings per plot.*

TABLE S3. *Arthropod fauna associated with big-leaf mahogany in a tree diversity experiment.*

TABLE S4–S6. *Results from generalized linear mixed models testing.*

## LITERATURE CITED

- ABDALA-ROBERTS, L., K. MOONEY, T. QUIJANO-MEDINA, M. J. CAMPOS-NAVARRETE, A. GONZÁLEZ-MORENO, AND V. PARRA-TABLA. 2015. Comparisons of tree genotypic diversity and species diversity on different guilds of insect herbivores. *Oikos* doi:10.1111/oik.02033.
- ABDALA-ROBERTS, L., X. MOREIRA, J. C. CERVERA, AND V. PARRA-TABLA. 2014. Light availability influences growth-defense trade-offs in big-leaf mahogany (*Swietenia macrophylla* King). *Biotropica* 46: 591–597.
- AGRAWAL, A. A., J. A. LAU, AND P. A. HAMBÄCK. 2006. Community heterogeneity and the evolution of interactions between plants and insect herbivore. *Q. Rev. Biol.* 81: 349–376.
- BAILEY, J., J. A. SCHWEITZER, F. ÜBEDA, J. KORICHEVA, C. J. LEROY, M. D. MADRITCH, B. J. REHILL, R. K. BANGERT, D. G. FISCHER, G. J. ALLAN, AND T. G. WHITHAM. 2009. From genes to ecosystems: A synthesis of the effects of plant genetic factors across levels of organization. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364: 1607–1616.
- BOMMARCO, R., AND J. E. BANKS. 2003. Scale a modifier in vegetation diversity experimental: Effects on herbivores and predators. *Oikos* 2: 440–448.
- BORROW, D. J., AND R. E. WHITE. 1970. *Insects. Peterson field guides.* Houghton Mifflin, New York, New York.
- CARNUS, J., M. PARROTTA, J. BROCKERHOFF, M. ARBEZ, H. JACTEL, A. KREMER, D. LAMB, K. O. HARA, AND B. WALTERS. 2003. Planted forests and biodiversity. UNFF Intersessional Experts Meeting on the Role of Planted Forests in Sustainable Forest Management. 24–30 Marzo, Nueva Zelanda.
- CASTAGNEYROL, B., L. LAGACHE, B. BIFFARD, A. KREMER, AND H. JACTEL. 2012. Genetic diversity increases insect herbivory on oak saplings. *PLoS One* 7: e44247.
- COOK-PATTON, S. C., S. H. MACART, A. L. PARACHNOWITSH, J. S. THALER, AND A. A. AGRAWAL. 2011. A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology* 92: 915–923.
- CRAWFORD, K. M., AND J. A. RUDGERS. 2013. Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* 94: 1025–1035.
- CRAWLEY, M. J. 2002. *Statistical computing. An introduction on data analysis using S-Plus.* John Wiley & Sons Ltd., Chichester, UK.
- CRAWLEY, M. J. 2007. *The R book.* John Wiley & Sons Ltd, Chichester, UK.
- CRUTSINGER, G. M., M. D. COLLINS, J. A. FORDYCE, Z. GOMPERT, C. C. NICE, AND N. J. SANDERS. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313: 966–968.
- GILLIES, A. C. M., C. NAVARRO, A. J. LOWE, A. C. NEWTON, M. HERNÁNDEZ, J. WILSON, AND J. P. CORNELIUS. 1999. Genetic diversity in Mesoamerican populations of mahogany (*Swietenia macrophylla*), assessed using RAPDs. *Heredity* 83: 722–732.
- HADDAD, N., G. M. CRUTSINGER, K. GROSS, J. HAARSTAD, J. M. H. KNOPS, AND D. TILMAN. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol. Lett.* 12: 1029–1039.



- HAMBÄCK, P. A., B. D. INOUE, P. ANDERSSON, AND N. UNDERWOOD. 2014. Effects of plant neighborhoods on plant-herbivore interactions: Resource dilution and associational effects. *Ecology* 95: 1370–1380.
- HARE, J. D. 2002. Plant genetic variation in tritrophic interactions. Multitrophic level interactions. In T. Tschamntke, and B. A. Hawkins (Eds.). *Multitrophic level interactions*, pp. 8–43. Cambridge University Press, Cambridge, UK.
- HUGHES, A. R., B. D. INOUE, M. T. JOHNSON, N. UNDERWOOD, AND M. VELLEND. 2008. Ecological consequences of genetic diversity. *Ecol. Lett.* 11: 609–623.
- HUTCHINSON, G. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93: 145–159.
- JOHNSON, M. T., AND A. A. AGRAWAL. 2005. Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology* 4: 874–885.
- JOHNSON, M. J. T., M. J. LAJUNESSE, AND A. A. AGRAWAL. 2006. Additive and interactive effects of plant genotypic diversity in arthropod communities and plant fitness. *Ecol. Lett.* 9: 24–34.
- KEDDY, P. A. 1984. Plant zonation on Lakeshores in Nova Scotia: A test for resource specialization hypothesis. *J. Ecol.* 72: 797–808.
- KORICHEVA, J., C. P. H. MULDER, B. SCHMID, J. JOSHI, AND K. HUSS-DANELL. 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125: 271–282.
- LOVELESS, M. D., AND R. E. GULLISON. 2003. Genetic variation in natural mahogany populations in Bolivia. In A. E. Lugo, J. C. Figueroa Colón, and M. Alayón (Eds.). *Big-leaf mahogany. Genetics, ecology and management*, pp. 9–28. Springer-Verlag, New York, New York.
- MCART, S. H., AND J. S. THALER. 2013. Plant genotypic diversity reduces the rate of consumer resource utilization. *Proc. R. Soc. B* 280: 20130639.
- MOONEY, K. A., AND M. S. SINGER. 2012. Plant effects on herbivore–enemy interactions in natural systems. In T. Ohgushi *et al.* (Eds.). *Trait-mediated indirect interactions: Ecological and evolutionary perspectives*, pp. 107–130. Cambridge University Press, Cambridge, UK.
- MOREIRA, X., L. A. ABDALA-ROBERTS, V. PARRA-TABLA, AND K. A. MOONEY. 2014. Positive effects of plant genotypic and species diversity on anti-herbivore defenses in a tropical tree species. *PLoS ONE*, 9: e105438.
- MOREIRA, X., K. A. MOONEY, R. ZAS, AND L. SAMPEDRO. 2012. Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. *Proc. Biol. Sci.* 279: 4464–4472.
- OKSANEN, J., F. GUILLAUME BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, M. HENRY, S. WAGNER, AND S. WAGNER. 2013. *Vegan: Community ecology package*. R package version 2.0-7. <http://CRAN.R-project.org/package=vegan>.
- PENNINGTON, T. D., AND J. SARUKHÁN. 2005. *Árboles tropicales de México. Manual para la identificación de las principales especies*. Texto Científico Universitario, D.F. México.
- PLATH, M., S. DORN, J. RIEDEL, H. BARRIOS, AND K. A. MODY. 2012. Associational resistance and associational susceptibility: Specialist herbivores show contrasting responses to tree stand diversification. *Oecologia* 169: 477–487.
- R CORE TEAM. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- ROOT, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43: 95–124.
- RUSSELL, E. P. 1989. Enemies hypothesis: A review of the effect of vegetational diversity on predatory insects and parasitoids. *Environ. Entomol.* 18: 590–599.
- SCHERBER, C., N. EISENHAEUER, W. W. WEISSER, B. SCHMID, W. VOIGT, M. FISCHER, E. D. SCHULZE, C. ROSCHER, A. WEIGELT, E. ALLAN, H. BEBLER, M. BONKOWSKI, N. BUCHMANN, F. BUSCOT, L. W. CLEMENT, A. EBELING, C. ENGELS, S. HALLE, I. KERTSCHER, A. M. KLEIN, R. KOLLER, S. KÖNIG, E. KOWALSKI, V. KUMMER, A. KUU, M. LANGE, D. LAUTERBACH, C. MIDDELHOFF, V. D. MIGUNOVA, A. MILCU, R. MÜLLER, S. PARTSCH, J. S. PETERMANN, C. RENKER, T. ROTTSTOCK, A. SABAI, S. SCHEU, J. SCHUMACHER, V. M. TEMPERTON, AND T. TSCHARNTKE. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553–556.
- SRIVASTAVA, D. S., AND J. H. LAWTON. 1998. Why more productive sites have more species: An experimental test of theory using tree-hole communities. *Am. Nat.* 152: 510–529.
- STYLES, B. T., AND P. K. KHOSLA. 1976. Cytology and reproductive biology of Meliaceae. In J. Burley, and B. T. Style (Eds.). *Tropical trees: Variation, breeding and conservation*, pp. 61–68. Linnean Society Symposium, Academic Press, London, UK.
- TRIPLEHORN, C. A., AND N. F. JOHNSON. 2005. *Borror & DeLong's introduction of the study of insects*, 7th edn. Belmont, California.
- VEHVILÄINEN, H., J. KORICHEVA, AND K. RUOHOMÄKI. 2007. Tree species diversity influences abundance and damage: Meta-analysis of long-term forest experiments. *Oecologia* 152: 287–298.
- VEHVILÄINEN, H., J. KORICHEVA, AND K. RUOHOMÄKI. 2008. Effects of stands tree species composition and diversity on abundance of predatory arthropods. *Oikos* 6: 935–943.
- VENABLES, W. N., AND B. D. RIPLEY. 2002. *Modern applied statistics with S*, 4th edn. Springer, New York, New York.