



Effects of tree species diversity on a community of weaver spiders in a tropical forest plantation

Luis Esquivel-Gómez¹, Luis Abdala-Roberts¹, Miguel Pinkus-Rendón², and Víctor Parra-Tabla^{1,3}

¹ Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Apartado Postal 4-116, Itzimmá, Merida, 97000 Yucatan, Mexico

² Centro Peninsular en Humanidades y Ciencias Sociales, Universidad Nacional Autónoma de México, Merida, 97150 Yucatan, Mexico

ABSTRACT

The effects of producer diversity on predators have received little attention in arboreal plant communities, particularly in the tropics. This is particularly true in the case of tree diversity effects on web-building spiders, one of the most important groups of invertebrate predators in terrestrial plant communities. We evaluated the effects of tree species diversity on the community of weaver spiders associated with big-leaf mahogany (*Swietenia macrophylla*) in 19, 21 × 21-m plots (64 plants/plot) of a tropical forest plantation which were either mahogany monocultures (12 plots) or polycultures (seven plots) that included mahogany and three other tree species. We conducted two surveys of weaver spiders on mahogany trees to evaluate the effects of tree diversity on spider abundance, species richness, diversity, and species composition associated with mahogany. Our results indicated that tree species mixtures exhibited significantly greater spider abundance, species richness, and diversity, as well as differences in spider species composition relative to monocultures. These results could be due to species polycultures providing a broader range of microhabitat conditions favoring spider species with different habitat requirements, a greater availability of web-building sites, or due to increased diversity or abundance of prey. Accordingly, these results emphasize the importance of mixed forest plantations for boosting predator abundance and diversity and potentially enhancing herbivore pest suppression. Future work is necessary to determine the specific mechanisms underlying these patterns as well as the top-down effects of increased spider abundance and species richness on herbivore abundance and damage.

Abstract in Spanish is available with online material.

Key words: enemies hypothesis; mahogany; plant diversity; predator; species richness; weaver spider.

THE EFFECTS OF PLANT DIVERSITY ON HIGHER TROPHIC LEVELS HAVE RECEIVED INCREASING ATTENTION OVER THE LAST TWO DECADES (Haddad *et al.* 2009, Scherber *et al.* 2010). Such effects have typically been assessed by manipulating the number of plant species (*i.e.*, plant species richness, hereafter referred to as plant species diversity) in patches or stands and recording changes in associated faunas (Moreira *et al.* 2016). Overall, studies have found strong positive effects of plant species diversity on associated faunas, especially so in the case of arthropod species richness and abundance (*e.g.*, Siemann *et al.* 1998, Koricheva *et al.* 2000, Haddad *et al.* 2009, Scherber *et al.* 2010). In particular, the effects of plant diversity on arthropods species at the third trophic level (predators & parasitoids) have been attributed to habitat features such as increased physical complexity and number of refuges from enemies, as well as due to increased abundance or diversity of resources or prey (Root 1973, Langelloto & Denno 2004, Denno *et al.* 2005). Higher predator abundance and diversity with increasing plant diversity is expected to in turn lead to stronger top-down control over herbivore populations (Andow 1991, Barbosa *et al.* 2009, Abdala-Roberts *et al.* 2015).

Traditionally, most work testing for effects of plant diversity on arthropod predators and parasitoids has been conducted in agroecosystems (reviewed by Russell 1989, Andow 1991) and is strongly biased toward temperate regions (*e.g.*, Haddad *et al.* 2009, Scherber *et al.* 2010, Crawford & Rudgers 2013). In contrast, much less work has tested for plant diversity effects in arboreal plant communities (Jactel & Brockerhoff 2007), particularly in tropical regions where predator and parasitoid diversity are highest and top-down control of herbivore populations is expected to be strongest (Schemske *et al.* 2009). Knowledge gained on the effects of tree diversity on predators is also important from an applied perspective as increased predator abundance and diversity may lead to enhanced pest control in managed systems such as forest plantations (Muiruri *et al.* 2015).

Spiders are one of the most important groups of invertebrate predators in terrestrial ecosystems as they exert dramatic effects on the abundance and diversity of species at lower trophic levels (Turnbull 1973, Culin & Yeorgan 1983). Although prey preferences, hunting modes, and behavior vary among spider guilds or species, the characteristics exhibited by co-existing species of spiders are frequently complementary which favors increased suppression of herbivore populations (Riechert 1999). In particular, the guild of weaver spiders comprises more than

Received 30 November 2015; revision accepted 18 April 2016.

³Corresponding author; e-mail: victor.parratabla@gmail.com

11,500 species representing about 30 percent of all spider species (Ubick *et al.* 2005), and includes several of the most abundant spider families (*e.g.*, Araneidae, Linyphiidae, Theridiidae, Tetragnathidae). Weaver spiders are highly abundant in both managed and natural ecosystems and are easily detected in surveys because of their conspicuous webs; accordingly, this predator group has been proposed as a suitable model in biodiversity studies (Blanco *et al.* 2003). Although numerous studies have documented the diversity of weaver spiders in both natural and agricultural ecosystems (Robinson & Robinson 1974, Pinkus-Rendón *et al.* 2006, de la Cruz *et al.* 2009, Ferreira-Ojeda *et al.* 2009, Bhat *et al.* 2013), very few have evaluated the effects of plant species diversity on this group (Lubin 1978), and this is true for spiders in general (but see Koricheva *et al.* 2000, Haddad *et al.* 2009, Scherber *et al.* 2010). Furthermore, most studies have been conducted in herbaceous plant communities in temperate regions, whereas very little work has looked at the effects of plant diversity on spiders in tropical tree communities. Plant diversity may directly influence the abundance and species composition of spiders through effects on habitat features such as structural complexity which determines site-choosing preferences for web building in the case of weaver spiders (Langelloto & Denno 2004, Tews *et al.* 2004, Jiménez-Valverde & Lobo 2007), as well as through effects on the abundance of refuges from other predators, availability of sites for reproduction, as well as prey availability (Samu *et al.* 1999, de la Cruz *et al.* 2009). One of the few available studies found a greater diversity of web-building spiders with increasing tree diversity, although such effects were contingent upon the presence of ants which may directly or indirectly interact with spiders (Schuldt & Staab 2015). The effects of tree diversity on predators, particularly web-building spiders are of high relevance for forestry, as increased predator abundance and diversity generally result in enhanced predator suppression of herbivores (Griffin *et al.* 2013, Long & Finke 2014, Gontijo *et al.* 2015) and potentially higher tree growth (Moreira *et al.* 2012). Research investigating such effects is sorely needed to assess the trade-offs between greater management/harvesting costs and ecosystem services (higher productivity, pest control) of mixed forest plantations.

In this work, we report on the results of a study conducted within the context of a large-scale (7.2-ha, 4780 plants), recently established (2.5 yr old at the time this study was conducted) tropical forest plantation in southern Mexico (Yucatan), testing for the effects of tree species diversity on arthropod communities. Here, we report on findings from surveys of abundance and species richness of weaver spiders using a subset of plots within this experiment for which we exclusively sampled big-leaf mahogany (*Swietenia macrophylla* King), one of the component tree species in this system. Specifically, we asked whether there was an effect of tree species diversity on weaver spider species composition, abundance, and species richness, and predicted that weaver spider abundance and richness on mahogany would be greater in tree species mixtures relative to mahogany monocultures. This study provides a unique test of the effects of tree species diversity on an important (but often overlooked) predator functional group in

a tropical agroecosystem. Results from this study have important implications for the understanding of ecological dynamics in mixed forest plantations and argue in favor of using tree species mixtures to maximize the ecosystem services derived from enhanced top-down control of herbivore populations by predators in tropical forest plantations.

METHODS

STUDY SPECIES AND EXPERIMENTAL DESIGN.—This study was conducted within the context of a broader experiment evaluating the effects of tree species diversity on plant growth and arthropods (see Moreira *et al.* 2014, Abdala-Roberts *et al.* 2015, Campos-Navarrete *et al.* 2015), and was based on a subset of plots within this system.

Tree species and seed collection.—The experiment included the following tropical tree species: *S. macrophylla* King (Meliaceae), *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 and adult trees reach from 20 m (*e.g.*, *P. piscipula*) to 40 m (*e.g.*, *C. pentandra*) in height (Pennington & Sarukhán 2005) depending on the species. All six species naturally co-occur in tropical forests of the Yucatan Peninsula.

From January 2011 to March 2011, seeds of all species were collected from adult trees located in southern Quintana Roo (México), and germinated at the INIFAP (Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias) in Mococho, Yucatan, Mexico (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 the species), hereafter referred to broadly as genotypes. Previous work in this system has shown that mahogany genotypes vary substantially in growth-related traits, herbivore resistance, and chemical defenses (Moreira *et al.* 2014, Abdala-Roberts *et al.* 2015). In December 2011, we established the experiment by planting 4-mo-old seedlings at a site owned by INIFAP near Muna, Yucatan (100 km southwest of Mococho; 20°24'44" N, 89°45'13" W). Saplings were fertilized once in January 2012 with N, P, and K (20:30:10), and drip irrigated with 2 L of water three times per week from January 2012 until June 2012.

Overall design.—The experimental design consisted of 74 plots of 21 × 21 m each at a planting density of 64 plants per plot, 3-m spacing among trees, for a total of 4780 plants. Plot size was chosen based on previous work showing that plot sizes of 20 by 20 m or greater are appropriate for realistically assessing the effects of diversity on competitive dynamics of plants and associated fauna (Potvin & Gotelli 2008, Bruelheide *et al.* 2014). Aisles between plots were 6-m wide and the experiment covered a total area of 7.2 ha. *Swietenia macrophylla* (big-leaf mahogany) was the most abundant species in the system ($N = 2480$ plants; other species ranged from 432 to 480 plants), and was present in 59 of

the 74 plots. Overall, plots were of two types: species monocultures (two plots per species, except for mahogany for which a larger number of monocultures were established to test for genotypic diversity effects (see below)) and polycultures (composed of random mixtures of four of the six species). In addition, the 59 plots where mahogany was planted were classified into four types: (1) mahogany monocultures of one genotype (12 plots, two replicate plots/genotype); (2) mahogany monocultures of four genotypes (20 plots); (3) species polycultures within which all mahogany trees planted were of one genotype (12 plots, two plots/genotype); and (4) species polycultures within which mahogany trees were represented by four genotypes (15 plots). Plots for each diversity treatment combination were randomly interspersed throughout the experimental site. The effects of tree diversity assessed in this study correspond to dynamics occurring relatively early in the establishment of a forest plantation (<3 yrs after establishment), and thus any effects of tree diversity on spiders should be interpreted within the context of an early stage of development of a forest plantation. In addition, we note that tree diversity in adjacent forests patches of similar size as our experimental plots is typically higher than in polycultures of our study. Therefore, results from this system are also of value for understanding ecological dynamics to the extent that it is viewed as a test of tree diversity effects at the lower end of the diversity gradient in natural forests and under biologically more simplified conditions.

Subset of diversity experiment used in this study.—We selected 19 of the 59 plots where mahogany was planted (see above), namely: 12 mahogany monocultures of a single genotype of this species and seven polycultures within which *C. pentandra* (L.) Gaertn and *C. dodecandra* A. DC were also present (plus a fourth species for which the identity varied depending on the plot). Within these polyculture plots, three plots contained mahogany trees represented by one genotype and four plots had mahogany represented by four genotypes (see Fig. S1—Online Supplementary Material). From this point on, we refer to methods, analyses, and results that pertain exclusively to sampling for these 19 plots.

SAMPLING.—We recorded weaver spiders associated exclusively with mahogany ($N = 19$ plots), and conducted two surveys, one in late May 2013 and another in late September 2013, approximately 2.5 yrs after the establishment of the experiment. During each survey we sampled the same 19 plots, but selected a different set of mahogany trees within each plot because collection of spider specimens during the first survey could influence spider abundance or species composition during the second survey had the same plants been re-sampled. For monocultures, we originally sampled a total of 20 plants per plot across both surveys (10 plants per plot, per survey), whereas for the polycultures we sampled on average six plants per plot across surveys (mean of 2.4 ± 0.36 plants per plot for survey 1, and 3.5 ± 0.28 plants per plot for survey 2). To avoid edge effects on spider abundance, species richness, and species composition, we did not sample mahogany plants located on the outer rows of each plot.

Across plots and surveys, a total of 283 mahogany plants were sampled.

Surveys were conducted in the morning (700–1300 h), following the exhaustive search method proposed by Coddington *et al.* (1991). This technique consists of two stages: ‘looking down’, for which the plant is inspected from ground level up to a height of 0.5 m, and the ‘looking up’ for which the search is continued up to 2 m of height. The inspection of each plant lasted 6 min on average and we searched for weaver spiders by locating the web using a water sprinkler. Thus, we ended up collecting only resident spiders on mahogany that had a fully established web or were in the process of building it. At the time of sampling, mahogany plants were on average 368 ± 4 cm tall. All specimens were collected (adults and juveniles), preserved in 70 percent ethanol, and transported to the Laboratory of Ecology of the Campus de Ciencias Biológicas y Agropecuarias of the UADY as well as to the Centro Peninsular de Humanidades y Ciencias Sociales of the Universidad Nacional Autónoma de México for species identification using specialized literature (Levi 1955, 1968, 1970, 1975, 1978, 1991, Ubick *et al.* 2005). Scientific names were updated as required using the World Spider Catalog of Norman I. Platnick (<http://research.amnh.org/iz/spiders/catalog/>, 25 January 2014). Unidentified individuals were classified as morphospecies.

STATISTICAL ANALYSES.—To evaluate the effects of tree diversity on weaver spider species composition and relative abundances, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2001) with 1000 random permutations based on a dissimilarity distance matrix using species abundances, calculated with the Bray-Curtis index (Chao *et al.* 2006, Anderson & Walsh 2013). This analysis was performed with the VEGAN package of R v.3.0.2 (R Core Team 2013). In addition, to further describe differences in relative abundance and species composition of weaver spiders between levels of diversity, we constructed rank-abundance curves separately for monocultures and polycultures. Because both the PERMANOVA test and the rank-abundance curves are necessarily influenced by having sampled more plants per plot and more plots in monoculture than in polyculture (*i.e.*, unbalanced design, see above), we conducted both analyses by randomly selecting seven monoculture plots and six plants per monoculture, resulting in a balanced design (*i.e.*, seven plots and six plants per plot for both levels of diversity). We repeated this analysis using alternative (random) subsamples of 7 of the 12 monoculture plots and results were consistent in eight of ten cases suggesting this analysis was not strongly influenced by the specific subsample used (see Results).

We tested the effects of tree diversity on weaver spider abundance, species richness, and species diversity using general linear models performed with PROC GLM in SAS v.9.2 (SAS Institute 2009, Cary, North Carolina, U.S.A.). These models assume a normal distribution for the errors and this assumption was confirmed by inspection of diagnostic plots of the residuals and Shapiro-Wilk tests (≤ 0.93 , $P \geq 0.22$). We used Shannon-Wiener Index to describe spider diversity because it is highly

sensitive to rare species (Magurran 1988) and a substantial portion (47%) of the spider species recorded were singletons (represented by only one individual) (see Results). We report diversity values in terms of effective species number, which is biologically easier to interpret (Jost 2006). As for the PERMANOVA and rank-abundance curves, for these general linear models we used the same subsample of randomly selected six plants per monoculture to achieve an equal number of plants sampled per plot across both treatment levels. However, in contrast to the analyses of community composition, these models used all of the 19 plots originally sampled because richness and abundance data were analyzed at the plot level (cumulative values across plants within each plot) rather than at the plant level (as the PERMANOVA and rank-abundance curves) and were thus not influenced by a difference in the total number of plants sampled between treatments from having sampled more plots in monoculture than polyculture. In addition to these three general linear models, we performed a subsidiary model which assessed whether tree diversity effects on spider species richness were driven by an increase in abundance in mixtures relative to monocultures. We did this by running the spider species richness model again including spider abundance as a covariate, as well as the squared term for spider abundance to account for non-linearity in the relationship between abundance and richness. If diversity effects on spider species richness are mediated by effects on spider abundance, then a significant effect on richness in the initial model should turn non-significant once abundance is accounted for.

Whenever the diversity effect on spider species richness or abundance was significant in a general linear model, we determined if such effect was additive or non-additive. The former occurs due to sampling effects, *i.e.*, a higher chance in mixtures of including a mahogany genotype or tree species to which spiders recruit more strongly, whereas non-additive effects arise from emergent properties of tree species mixtures (*e.g.*, spider spill-over among tree species, increased habitat complexity, etc.), which cannot be explained by sampling effects alone. Following Johnson *et al.* (2006), we calculated mahogany genotype means for richness and abundance at low diversity (*i.e.*, expected values) and compared these values to the mean of each genotype at high diversity (observed values) using one-way general linear models using the MIXED procedure in SAS v.9.2. These models also included the effects of plot and genotype nested within plot which made them analogous to a paired test (Johnson *et al.* 2006). A significant difference between observed and expected values is necessarily due to non-additivity as sampling effects are accounted for by including genotype-specific expected values.

RESULTS

Across both surveys and based on all 19 plots and plants originally sampled (20 plants per monoculture and six per polyculture) we found a total of 460 spider specimens on mahogany, representing four families, 20 genera, and 23 species (Table S1). An additional seven specimens were not identified and classified as six different morphospecies. Family Araneidae had the highest

richness with 12 species, followed by Theriididae with 10 species. Families Uloboridae and Tetragnathidae were each represented by only one species. The most common species was *Leucauge venusta* with 273 individuals (59.3% of the total), followed by *Araneus pegnia* with 57 specimens (12.3%) (Table S1).

EFFECTS OF TREE DIVERSITY ON SPIDER ABUNDANCE AND SPECIES RICHNESS.—The general linear model indicated a significant effect of tree diversity on the abundance of weaver spiders associated with mahogany ($F_{1,17} = 5.16$, $P = 0.036$), where polycultures exhibited a 52 percent greater mean value (14.5 ± 1.77 spiders per plot) relative to monocultures (9.5 ± 1.35 spiders per plot). Similarly, we also found a significant effect of tree diversity on spider species richness ($F_{1,17} = 13.88$, $P = 0.001$) with polycultures showing a 46 percent greater mean value (5.5 ± 0.38 species per plot) relative to monocultures (3.75 ± 0.29 species per plot). Subsidiary analyses indicated that effects of tree diversity on spider abundance and species richness were non-additive (*i.e.*, observed vs. expected values; abundance: $F_{1,16} = 8.32$, $P = 0.010$; richness: $F_{1,17} = 28.44$, $P = 0.001$). In addition, after accounting for spider abundance, the effect of tree diversity on spider species richness remained significant (diversity effect: $F_{3,15} = 6.21$, $P = 0.024$), suggesting that positive effects of diversity on spider richness were not mediated by an increase in spider abundance in tree species mixtures. Finally, similar to species richness and abundance, we also found a significant effect of tree diversity on the diversity of weaver spiders measured as the effective species number ($F_{1,17} = 4.82$, $P = 0.042$), with polycultures having a 25 percent greater effective spp. number (4.38 ± 0.32) than monocultures (3.49 ± 0.24).

EFFECTS OF TREE DIVERSITY ON SPIDER SPECIES COMPOSITION.—The rank-abundance curves showed a clear dominance of *L. venusta* across both levels of tree diversity (Fig. 1). However, the species relative abundances declined more steeply in monocultures than polycultures; for example, *A. pegnia* was the second most abundant species in monoculture and was substantially more abundant than the following most abundant species, whereas in polyculture the second most abundant was *Eriophora ravilla* and was followed closely by five to six other species (Fig. 1). In addition, we also found a greater number of ‘rare species’ (singletons, *i.e.*, represented by one individual) in polyculture (eight species) than in monoculture (four species). Despite these differences, the PERMANOVA analyses did not suggest statistical differences in spider community composition between monocultures and polycultures ($F_{1,12} = 1.42$, $P = 0.22$), and this finding remained consistent in most cases regardless of which subset of the data were analyzed (non-significant diversity effect in eight of ten cases using alternative random subsamples of seven monoculture plots, $F < 2.3$, $P > 0.07$; significant cases: $F > 2.85$ $P < 0.02$).

DISCUSSION

Our results demonstrate that increasing tree species diversity leads to substantially higher abundance, species richness, and

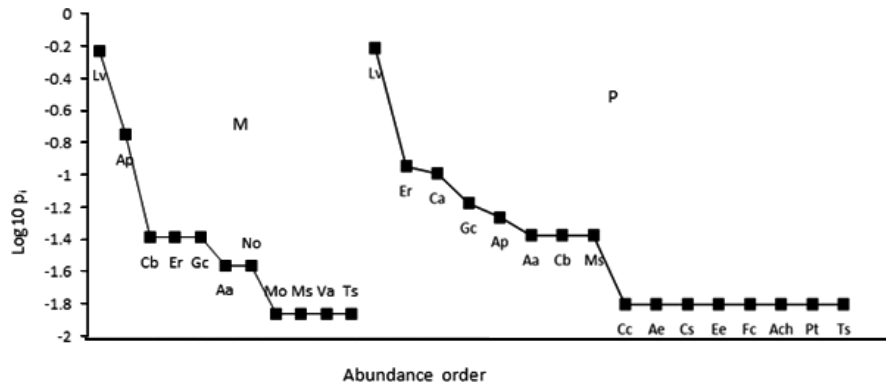


FIGURE 1. Rank-abundance curves for species of weaver spiders sampled on mahogany (*Swietenia macrophylla*) trees planted in mahogany monocultures and tree species polycultures (mahogany plus a random mixture of three other tree species). The X-axis shows the species rank (ordered from highest to lowest) based on relative abundance values (π_i), whereas the Y-axis shows the relative abundance of each species in a logarithmic scale ($\log_{10} \pi_i$). Each species is represented by the first letter of the genus and species names (for the full name of each species, see Table S1). $N = 7$ plots for monocultures and polycultures.

diversity (measured as effective species number) of weaver spiders associated with mahogany, which is in agreement with theoretical expectations of positive effects of plant diversity on species at the third trophic level due to increased habitat complexity, availability of refuges, and/or prey availability (*i.e.*, the Enemies Hypothesis; Root 1973, Russell 1989, Barbosa *et al.* 2009). These results provide evidence for the effects of tropical tree species diversity on a largely overlooked guild of important predatory arthropods, and as such emphasize the potential benefits of establishing mixed forest plantations, provided that increased predator diversity (and abundance) leads to enhanced suppression of herbivorous pests as suggested by a recent meta-analysis (Griffin *et al.* 2013). Interestingly, the fact that tree diversity effects were observed early in the establishment of the experiment indicates that strong effects of tree diversity on predator communities may arise early in young forest plantations potentially leading to strong top-down suppression of herbivore populations during critical stages of plant establishment and early development.

EFFECTS OF TREE DIVERSITY ON SPIDER SPECIES COMPOSITION.—The species composition, relative abundances, and identity of families of weaver spiders recorded in our study are consistent with findings from previous studies showing that Theridiidae and Araneidae are the best represented spider families (in terms of both species number and abundance) in both agricultural fields (Ibarra-Núñez 1990, Ibarra-Núñez & García-Ballinas 1998) and natural ecosystems (Llinas & Jiménez 2004, Maya-Morales *et al.* 2011, Gómez-Rodríguez & Salazar 2012). In addition, the most abundant spider species in our experimental plantation, *L. venusta*, has been reported, along with other species of the same genus (*Leucauge mariana* and *Leucauge argyra*), as the most abundant weaver spider in cacao (de la Cruz *et al.* 2009) and coffee plantations (Ibarra-Núñez & García-Ballinas 1998, Pinkus-Rendón *et al.* 2006) in southern Mexico. Species of the genus *Leucauge* are characterized by building horizontal webs with a high number of radius and spirals (Dondale 2003), which are structural features

that increase mechanical resistance against abiotic factors (*e.g.*, winds, branch movement) relative to vertical webs and thus likely contribute to the colonization success of these species.

The rank-abundance curves indicated differences in the relative abundance and species identity of weaver spiders associated with mahogany in tree species polycultures relative to monocultures. Considering that several of the spider species recorded have relatively specific habitat physical requirements (Uetz 1991, Galle & Schweger 2014), the observed differences in spider species composition between monocultures and mixtures could have been at least partly due to environmental differences between these two treatment levels. For example, differences in humidity, light availability, or habitat physical complexity have been shown to influence species composition of spider assemblages (Tews *et al.* 2004). Surprisingly, however, the PERMANOVA analysis did not reveal significant differences in spider community structure between monocultures and mixtures. We speculate that this negative result could have been due to low statistical power as we reduced the number of plots and plants sampled per plot in monoculture to achieve a balanced design at both levels of diversity (seven plots and six plants per plot in each case). Accordingly, previous work provides evidence that the reliability of PERMANOVA is highly contingent upon sample size, and it is unlikely to obtain results with an adequate statistical power with less than ten measures per group (Anderson & Walsh 2013, Kelly *et al.* 2015). Therefore, despite the lack of statistical support from the PERMANOVA analyses, the patterns observed in the rank-abundance curves suggest that better replicated studies may find greater support for differences in spider community composition between monocultures and polycultures.

EFFECTS OF TREE DIVERSITY ON SPIDER SPECIES RICHNESS, ABUNDANCE, AND DIVERSITY.—Our findings indicate that tree diversity drove an increase in the abundance, species richness, and diversity of weaver spiders associated with mahogany. These findings are in agreement with the Enemies Hypothesis which predicts that increasing plant species diversity leads to an increase

in the number of physical refuges or resource types available to organisms at higher trophic levels, which in turn preferentially recruit to high-diversity patches (Langelloto & Denno 2004). In this sense, previous work provides evidence that spider abundance and diversity are positively correlated with the diversity or abundance of prey (Rypstra 1986, Denno *et al.* 2005) and with the availability of web-building sites or shelters against other predators (Rypstra 1986, Langelloto & Denno 2004). The former could have mediated the observed tree diversity effects on spiders, as previous work in this plantation reported that mahogany plants in polycultures have higher species richness of insect herbivores relative to mahogany monocultures (Campos-Navarrete *et al.* 2015). Future work is necessary to determine the influence of prey availability relative to other abiotic factors (*e.g.*, canopy openness and temperature; Gunnarsson 2007, Wise 1993) and habitat complexity (Uetz 1991) affecting spider recruitment to tree stands.

Interestingly, the effect of tree diversity on spider species richness remained significant after accounting for spider abundance which suggests that diversity effects on spider richness were mediated by some mechanism other than an increase in abundance. This result runs counter to the More Individuals Hypothesis (Hutchinson 1959, Srivastava & Lawton 1998), which poses that higher producer biomass with increasing diversity leads to greater herbivore abundance, and this in turn leads to an abundance-driven accumulation of consumer species at higher trophic levels. Instead, tree diversity could have favored an increase in the number of habitat or prey-specialist spider species in mixtures (*i.e.*, The Resource Specialization Hypothesis; Root 1973, Keddy 1984). Accordingly, we found that polycultures had a greater number of rare species (singletons), suggesting that increased recruitment of rare, potentially specialized species contributed to the observed diversity effect. This argument, however, remains speculative and further work on the feeding habits and abiotic requirements of the spider species associated with this system is needed to test this hypothesis.

In closing, it is interesting to note that, in contrast to this study, previous work in this experimental system has found no effect of tree diversity on salticid spiders (Salticidae) associated with mahogany (Abdala-Roberts *et al.* 2015). This could be explained by differences in mobility or hunting mode between these two guilds; salticid species are cursorial spiders that do not build webs and therefore may be less influenced by habitat requirements for web-building relative to weaver spiders (Tews *et al.* 2004). An important goal for future research in this system will be to achieve a better understanding of how spider traits determine the effects of diversity on this ecologically important group of predators.

CONCLUSIONS

The observed positive effects of tree diversity on spider abundance, species richness, and diversity are noteworthy as these predators, despite being present at low abundances, can exert strong impacts on arthropod communities and regulate herbivore

populations (Maloney *et al.* 2003). Accordingly, this study suggests that establishing mixed forest plantations may represent a strategy to conserve biodiversity and promote the ecosystem services provided by predatory arthropods (control of herbivorous insects) (Verheyen *et al.* 2016). More broadly, these results emphasize the role of tree species diversity in structuring communities at higher trophic levels and argue in favor of conserving tree diversity to maintain diversity at higher trophic levels (Castagneyrol & Jactel 2012).

ACKNOWLEDGMENTS

This research was supported by a CONACyT grant awarded to VP-T (128856). INIFAP provided logistic accommodations and infrastructure for the establishment of the experiment, subsequent sampling and maintenance. LE-G thanks CONACyT for financial support through a scholarship. LAR was supported by a CONACyT repatriation grant (250934).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Subset of the forest diversity experiment used to test for effects of tree species diversity on the abundance, species richness, and diversity of weaver spiders associated with big-leaf mahogany (*Swietenia macrophylla*).

TABLE S1. List of species of weaver spiders sampled on mahogany (*Swietenia macrophylla*) in a forest diversity experiment in southern Mexico (Yucatan).

LITERATURE CITED

- ABDALA-ROBERTS, L., K. A. MOONEY, T. QUIJANO-MEDINA, M. J. CAMPOS-NAVARRETE, A. GONZÁLEZ-MORENO, AND V. PARRA-TABLA. 2015. Comparison of tree genotypic diversity and species diversity effects on different guilds of insect herbivores. *Oikos* 124: 1527–1535.
- ANDERSON, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26: 32–46.
- ANDERSON, M. J., AND D. C. I. WALSH. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecol. Monogr.* 83: 557–574.
- ANDOW, D. A. 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* 36: 561–586.
- BARBOSA, P., J. HINES, I. KAPLAN, H. MARTINSON, A. SZCZEPANIEC, AND Z. SZENDREI. 2009. Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annu. Rev. Ecol. Evol. Syst.* 40: 1–20.
- BHAT, P., K. SRIKUMAR, AND T. RAVIPRASAD. 2013. Seasonal diversity and status of spiders (Arachnida: Araneae) in cashew ecosystem. *World Appl. Sci. J.* 22: 763–770.
- BLANCO, E., G. AMAT, AND E. FLÓREZ. 2003. Araneofauna orbicular (Araneae: Orbiculariae) de los Andes de Colombia: Comunidades en habitats bajo regeneración. *Rev. Iberoam. Aracnol.* 7: 189–203.
- BRUELHEIDE, H., K. NADROWSKI, T. ASSMANN, J. BAUHUS, S. BOTH, F. BUSCOT, X.-Y. CHEN, B. DING, W. DURKA, A. ERFMEIER, J. L. M. GUTKNECHT, D. GUO, L.-D. GUO, W. HÄRDITL, J.-S. HE, A.-M. KLEIN, P. KÜHN, Y. LIANG, X. LIU, S. MICHALSKI, P. A. NIKLAUS, K. PEI, M. SCHERER-

- LORENZEN, T. SCHOLTEN, A. SCHULDT, G. SEIDLER, S. TROGISCHE, G. VON OHEIMB, E. WELK, C. WIRTH, T. WUBET, X. YANG, M. YU, S. ZHANG, H. ZHOU, M. FISCHER, K. MA, AND B. SCHMID. 2014. Designing forest biodiversity experiments: General considerations illustrated by a new large experiment in subtropical China. *Methods Ecol. Evol.* 5: 74–89.
- CAMPOS-NAVARRETE, M. J., M. A. MUNGUÍA-ROSAS, L. A. ABDALA-ROBERTS, J. QUINTO, AND V. PARRA-TABLA. 2015. Effects of tree genotypic diversity and species diversity on the arthropod community associated with big-leaf mahogany. *Biotropica* 47: 579–587.
- CASTAGNEYROL, B., AND H. JACTEL. 2012. Unravelling plant-animal diversity relationships: A meta-regression analysis. *Ecology* 93: 2115–2124.
- CHAO, A., R. CHAZDON, R. COLWELL, AND T. SHEN. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62: 361–371.
- CODDINGTON, J. A., C. GRISWOLD, D. DÁVILA, E. PEÑARANDA, AND S. LARCHER. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In E. Dudley (Ed.), *The Unity of evolutionary biology: Proceedings of the fourth international congress of systematic and evolutionary biology*, pp. 44–60. Dioscorides Press, Portland, Oregon.
- CRAWFORD, K., AND J. A. RUDGERS. 2013. Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* 94: 1025–1035.
- de la CRUZ, A., S. SÁNCHEZ, C. ORTIZ, AND Y. M. PÉREZ-DE LA CRUZ. 2009. Diversidad y distribución de arañas tejedoras diurnas (Arachnida, Araneae), en los microhábitats del agroecosistemas de cacao en Tabasco, México. *Bol. Mus. Entomol. Univ. Valle* 10: 1–9.
- CULIN, J., AND K. YEARGAN. 1983. The effects of selected insecticides on spiders in alfalfa. *J. Kansas Entomol. Soc.* 56: 151–158.
- DENNO, R. F., D. L. FINKE, AND G. A. LANGELLOTTO. 2005. Direct and indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. In P. Barbosa, and I. Castellanos (Eds.), *Ecology of predator-prey interactions*, pp. 211–239. Oxford University Press, New York City, New York.
- DONDALE, C. 2003. The orb-weaving spiders of Canada and Alaska: Araneae: Uloboridae, Tetragnathidae, Araneidae, Theridiosomatidae, pp. 51–52. NRC Research Press, Ontario, Canada.
- FERREIRA-OJEDA, L., E. FLÓREZ, AND A. SABOGAL-GONZÁLEZ. 2009. Arañas orbitales de un bosque húmedo subtropical de la Sierra Nevada de Santa Marta (Magdalena, Colombia). *Caldasia* 31: 381–391.
- GALLE, R., AND S. SCHWEGER. 2014. Habitat and landscape attributes influencing spider assemblages at lowland forest river valley (Hungary). *N. West. J. Zool.* 10: 36–41.
- GÓMEZ-RODRÍGUEZ, J., AND C. SALAZAR. 2012. Arañas de la región montañosa de Miquihuana, Tamaulipas: Listado faunístico y registros nuevos. *Dugesiana* 19: 1–7.
- GONTIJO, L. M., E. H. BEERS, AND W. E. SNYDER. 2015. Complementary suppression of aphids by predators and parasitoids. *Biol. Control* 90: 83–91.
- GRIFFIN, J. N., J. E. K. BYRNES, AND B. J. CARDINALE. 2013. Effects of predator richness on prey suppression: A meta-analysis. *Ecology* 94: 2180–2187.
- GUNNARSSON, B. 2007. Predation on spiders: Ecological mechanisms and evolutionary consequences. *J. Arachnol.* 35: 509–529.
- HADDAD, N., G. CRUTSINGER, K. GROSS, J. HAARSTAD, J. KNOPS, AND D. TILMAN. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol. Lett.* 12: 1029–1039.
- HUTCHINSON, G. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93: 145–159.
- IBARRA-NÚÑEZ, G. 1990. Los artrópodos asociados a cafetos en un cafetal mixto del Soconusco, Chiapas, México. *Variabilidad y abundancia*. *Folia Entomol. Mex.* 79: 207–231.
- IBARRA-NÚÑEZ, G., AND J. GARCÍA-BALLINAS. 1998. Diversidad de tres familias de arañas tejedoras (Araneae: Araneidae, Tetragnathidae, Theridiidae) en cafetales del Soconusco, Chiapas, México. *Folia Entomol. Mex.* 102: 11–20.
- JACTEL, H., AND E. G. BROCKERHOFF. 2007. Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* 10: 835–848.
- JIMÉNEZ-VALVERDE, A., AND J. LOBO. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: Climate and altitude vs. habitat structure. *Ecol. Entomol.* 32: 113–122.
- JOHNSON, M. J. T., M. J. LAJUENESSE, AND A. A. AGRAWAL. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* 9: 23–34.
- JOST, L. 2006. Entropy and diversity. *Oikos* 113: 363–374.
- KEDDY, P. A. 1984. Plant zonation on Lakeshores in Nova Scotia: A test for Resource Specialization Hypothesis. *J. Ecol.* 72: 797–808.
- KELLY, B. J., R. GROSS, K. BITTINGER, S. SHERRILL-MIX, J. D. LEWIS, R. G. COLLMAN, F. D. BUSHMAN, AND H. LI. 2015. Power and sample-size estimation for microbiome studies using pairwise distances and PERMANOVA. *Bioinformatics* 31: 2461–2468.
- KORICHEVA, J., C. 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.
- LANGELLOTTO, G., AND R. DENNO. 2004. Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia* 139: 1–10.
- LEVI, H. 1955. The spider genera *Chryso* and *Tidarren* in America (Araneae: Theridiidae). *J. New York Entomol. Soc.* 63: 59–81.
- LEVI, H. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* 136: 319–352.
- LEVI, H. 1970. The Ravilla group of the orbweaver genus *Eriophora* in North America (Araneae: Araneidae). *Psyche* 77: 280–302.
- LEVI, H. 1975. The American Orb-weaver genera *Larinia*, *Cercidia* and *Mangora* from North of Mexico (Araneae, Araneidae). *Bull. Mus. Comp. Zool.* 147: 101–135.
- LEVI, H. 1978. The American orb-weaver genera *Colpbepeira*, *Micrathena*, and *Gasteracantha* North of Mexico (Araneae, Araneidae). *Bull. Mus. Comp. Zool.* 148: 417–442.
- LEVI, H. 1991. The neotropical and Mexican Species of the orb-weaver genera *Araneus*, *Dubepeira* and *Aculepeira* (Araneae, Araneidae). *Bull. Mus. Comp. Zool.* 152: 167–315.
- LLINAS, J., AND M. JIMÉNEZ. 2004. Arañas de humedales del sur de Baja California, México. *An. Inst. Biol. Univ. Nac. Auton. Mex. Ser. Zool.* 75: 283–302.
- LONG, E. Y., AND D. L. FINKE. 2014. Contribution of predator identity to the suppression of herbivores by a diverse predator assemblage. *Environ. Entomol.* 43: 569–576.
- LUBIN, Y. 1978. Seasonal abundance and diversity of web building spiders in relation to habitat structure on Barro Colorado I, Panama. *J. Arachnol.* 6: 31–51.
- MAGURRAN, A. 1988. *Ecological diversity and its measurement*, pp. 7–45. Princeton University Press, Princeton, New Jersey.
- MALONEY, D., F. DRUMMOND, AND R. ALFORD. 2003. Spider predation in agroecosystems: Can spiders effectively control pest populations? *Technical bulletin 190*, pp. 1–32. Maine Agricultural and Forest Experiment Station. The University of Maine, Orono, Maine.
- MAYA-MORALES, J., G. IBARRA-NÚÑEZ, J. L. LEÓN-CORTÉS, AND F. INFANTE. 2011. Understorey spider diversity in two remnants of tropical montane cloud forest in Chiapas, Mexico. *J. Insect Conserv.* 16: 25–38.
- MOREIRA, X., L. ABDALA-ROBERTS, V. PARRA-TABLA, AND K. A. MOONEY. 2014. Positive effects of plant genotypic and species diversity on anti-herbivore defences in a tropical tree species. *PLoS One* 9: e105438.
- MOREIRA, X., L. ABDALA-ROBERTS, S. RASMANN, B. CASTAGNEYROL, AND K. A. MOONEY. 2016. A. Plant diversity effects on insect herbivores and their natural enemies: Current thinking, recent findings, and future directions. *Curr. Opin. Insect Sci.* 14: 1–7.
- 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. R. Soc. Lond. B Biol. Sci.* 279: 4464–4472.
- MUIRURI, E. W., K. RAINIO, AND J. KORICHEVA. 2015. Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia* 180: 619–630.
- PENNINGTON, T., AND J. SARUKHÁN. 2005. *Árboles Tropicales de México* (3rd Edition). Fondo de Cultura Económica, México, DF.
- PINKUS-RENDÓN, M. A., G. IBARRA-NÚÑEZ, V. PARRA-TABLA, J. A. GARCÍA-BALLINAS, AND Y. HÉNAUT. 2006. Spider diversity in coffee plantations with different management in southeast Mexico. *J. Arachnol.* 34: 104–112.
- POTVIN, C., AND N. GOTELLI. 2008. Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecol. Lett.* 11: 217–223.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RIECHERT, S. 1999. The hows and whys of successful pest suppression by spiders: Insights from case studies. *J. Arachnol.* 27: 387–396.
- ROBINSON, M., AND B. ROBINSON. 1974. A census of web-building spider in a coffee plantation at Wau, New Guinea, and an assessment of their insecticidal effect. *J. Trop. Ecol.* 15: 95–107.
- 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.
- RYPSTRA, A. 1986. Web spiders in temperate and tropical forests: Relative abundance and environmental correlates. *Am. Midl. Nat.* 115: 42–51.
- SAMU, F., K. SUNDERLAND, AND C. SZINETAR. 1999. Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: A review. *J. Arachnol.* 27: 325–332.
- SAS. 2009. SAS, version 9.2. SAS Institute Inc., Cary, North Carolina.
- SCHEMSKE, D. W., G. G. MITTELBACH, H. V. CORNELL, J. M. SOBEL, AND K. ROY. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Syst.* 40: 245–269.
- 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.
- SCHULDT, A., AND M. STAAB. 2015. Tree species richness strengthens relationships between ants and the functional composition of spider assemblages in a highly diverse forest. *Biotropica* 47: 339–346.
- SIEMANN, E., D. TILMAN, J. HAARSTAD, AND M. RITCHIE. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* 152: 738–750.
- 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.
- TEWS, J., U. BROSE, V. GRIMM, K. TIELBÖLGER, M. WICHMANN, M. SCHWAGER, AND F. JELTSCH. 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *J. Biogeogr.* 31: 79–92.
- TURNBULL, A. 1973. Ecology of the true spiders (Araneomorphae). *Annu. Rev. Entomol.* 18: 305–348.
- UBICK, D., P. PAQUIN, P. CUSHING, AND V. ROTH. 2005. Spiders of North America: An identification manual, pp. 25–38, 68–74, 235–243. American Arachnological Society, Middletown OH.
- UETZ, G. 1991. Habitat structure and spider foraging. In: S. Bell, E. McCoy, and H. Mushinsky (Eds.). *Habitat structure. The physical arrangement of objects in space*, pp. 325–348. Chapman and Hall, London, U.K.
- VERHEYEN, K., M. VANHELLEMONT, H. AUGE, L. BAETEN, C. BARALOTO, N. BARSOUM, S. BILODEAU-GAUTHIER, H. BRUELHEIDE, B. CASTAGNEYROL, D. GODBOLD, J. HAASE, A. HECTOR, H. JACTEL, J. KORICHEVA, M. LORÉAU, S. MEREU, C. MESSIER, B. MUYS, P. NOLET, A. PAQUETTE, J. PARKER, M. PERRING, Q. PONETTE, C. POTVIN, P. REICH, A. SMITH, M. WEIH, AND M. SCHERER-LORENZEN. 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* 45: 29–41.
- WISE, D. 1993. Spiders in ecological webs, pp. 152–158. Cambridge University Press, Cambridge, U.K.