



Diversity Patterns of Tropical Epigeal Beetle Assemblages Associated with Monoculture and Polyculture Plantations with Big-Leaf Mahogany

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Abstract

Although commercial forest plantations have experienced a major growth in the tropics over the past decades, little attention has been paid to their role in the conservation of epigeal arthropod communities. We studied diversity patterns of the epigeal beetle community in monoculture and polyculture forest plantations with big-leaf mahogany (*Swietenia macrophylla*). Likewise, we explored the existence of indicator species of each plantation type. Our findings highlight that each plantation type promotes multiple impacts on diversity patterns. We found that monocultures positively influenced overall beetle species richness and ecological diversity. When broken down by guild, both predator and decomposer species richness were similar between monoculture and polyculture, whereas for beetle diversity we found contrasting responses by guild: decomposer diversity was greater in monoculture whereas predator diversity was higher in polyculture. In addition, species composition differed between monoculture and polyculture, except for the predator guild. Species turnover was the main component explaining beta diversity patterns at all levels, indicating that each plantation type promotes biologically distinct epigeal assemblages. Few superabundant heliophile species dominated the beetle community structure; moreover, monocultures had a composition skewed towards heliophile species whereas polyculture favored umbrophile species. These patterns could be attributed to differences in habitat complexity between plot types, namely differences in tree cover. Additionally, indicator species only were identified in polycultures, reflecting their higher spatial complexity. Monoculture and polyculture plantations with big-leaf mahogany are complementary agroecosystems for preserving diverse epigeal beetle communities and should be considered valuable tools for conservation purposes in the tropics.

Keywords Coleoptera · trophic guilds · tropical forest plantations · *Swietenia macrophylla* · indicator species

Introduction

Epigeal fauna feed on dead or dying vegetal or animal material, fungi or other organisms living in the understory during

part of their life cycle, with their activity promoting the transformation of such resources into simpler and more easily assimilable nutrients for plants, hence playing a key role in decomposition processes and the stability of food webs (Lavelle

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et al. 1994; Warren and Zou 2002; Nichols et al. 2008). Among epigeal organisms, invertebrates depict the most relevant group in tropical ecosystems in terms of biomass and species diversity, with Coleoptera being the most diverse taxa (Lavelle et al. 1994; Brown et al. 2001).

Studies assessing diversity patterns of epigeal beetle assemblages in tropical forest plantations and other managed tropical agroecosystems often use habitat indicators. Dung beetles (Scarabaeidae) have been one of the most widely used groups for that purpose, because of its standardized sampling, high species richness, and well-known taxonomy and ecological requirements (Favila and Halffter 1997; Halffter and Arellano 2002; Nichols et al. 2007; Maleque et al. 2009; Arellano et al. 2013; De Farias et al. 2015). However, different taxa or trophic guilds respond differently to land use intensification (landscape matrix where plantations are embedded), plantation management (tree and understory practices), or plantation design (plant density or individual tree traits) (Reyes-Novelo et al. 2007; Maleque et al. 2009; Price et al. 2011; Plath et al. 2012; Beiroz et al. 2014; De Farias et al. 2015; Salomão et al. 2018). Therefore, the study of various taxonomic groups, trophic guilds, or even the whole epigeal beetle community may provide more accurate conclusions about the drivers of diversity patterns in forest plantations.

Although several studies have suggested that tropical forest plantations have low potential to harbor species-rich epigeal beetle assemblages (Gormley et al. 2007; Plath et al. 2012), many others have highlighted its resemblance to natural or secondary forests in terms of species diversity (Estrada and Coates-Estrada 2002; Grimbacher et al. 2007; Nichols et al. 2007; Fagundes et al. 2011; Beiroz et al. 2014). For instance, *Brosimum alicastrum* (Moraceae) plantations housed higher richness of Scarabaeidae than secondary forests (Reyes-Novelo et al. 2007), whereas in *Guazuma ulmifolia* (Malvaceae) plantations their richness was higher than in pastures and tree fallows of tropical dry forest with livestock (De Farias et al. 2015). Tree composition and the structural complexity of forest plantations are key determinants of alpha diversity patterns of beetle communities and trophic guilds (Kanowski et al. 2003; Reyes-Novelo et al. 2007; Fagundes et al. 2011). Positive effects of mixed plantations on the diversity of arboreal beetle trophic guilds have been previously reported (Plath et al. 2012; Campos-Navarrete et al. 2015). Furthermore, the vegetation structure and environmental characteristics of many kind of tropical forest plantations benefit the diversity of decomposer (Reyes-Novelo et al. 2007; Arellano et al. 2013; Beiroz et al. 2014; De Farias et al. 2015) and predator beetles occurring in the understory (Vanbergen et al. 2005; Maleque et al. 2009). On the other hand, differences in tree composition and structure of plantations determine great dissimilarity in epigeal communities (Warren and Zou 2002; Gormley et al. 2007; Beiroz et al. 2014), and tropical anthropized landscapes with high

heterogeneity of tree cover forms promote high biotic heterogeneity of dung beetle communities, with species turnover being the main component explaining beta diversity patterns (Da Silva 2018; Bitencourt et al. 2019; Ramirez-Ponce et al. 2019). In spite of this, little is known about how forest plantation types, i.e., monospecific vs. mixed plantations, influence on diversity patterns of epigeal communities.

The aim of this study was to assess diversity patterns of epigeal beetle assemblages in an experimental forest plantation consisting of big-leaf mahogany monocultures and mixed plots containing big-leaf mahogany in southeast Mexico. We compared overall beetle richness and ecological diversity as well as by trophic level (namely, decomposers and predators) associated with mahogany in monocultures and polycultures with this species, and further compared patterns of beetle species composition. Specifically, we sought to answer the following: (1) does plantation type affect beetle species richness and ecological diversity, and do these patterns vary by trophic guild? We expected to find higher taxonomic and ecological diversity in mixed plantations (alpha diversity), owing to greater habitat complexity and resource diversity for decomposers and hence also for predators. (2) Does plantation type affect beetle species composition and turnover (beta diversity patterns) across plots? In this case, we were also especially interested in whether plantation type promoted the presence of beetle indicator species. For beta diversity, we predicted high beetle heterogeneity between plantation types due to differences in tree cover and structural complexity. Moreover, each plantation type will exhibit different habitat indicator species and that polycultures will harbor indicator species more closely associated with natural forested habitats.

Materials and methods

Study site and sampling design

The study was carried out at the UADY Tree Diversity Experiment (<http://www.treedivnet.ugent.be/ExpUADY.html>) 8 months after the establishment of this mixed forest plantation (in December 2011). This system is located within the premises of the Sitio Experimental Uxmal (20°24'44"N, 89°45'13"W), Yucatan (Mexico), owned by the National Institute of Forestry, Crop and Livestock Research (INIFAP). The site is 20 m a.s.l., and the climate is warm and sub-humid, with average temperature of 25°C and annual rainfall of 1200 mm. The predominant soil is Luvisol, a type of soil typical of forested areas and very rich in nutrients, and suitable for agriculture and forestry (Uribe-Valle and Dzib-Echeverría 2006). Plots were established on a recently cleared area where previous vegetation consisted mostly of grasses, shrubs, and early successional forest species, and is

surrounded by tropical secondary dry forests and agricultural areas.

The plantation consists of 74 plots classified as either monocultures or polycultures (random combinations of four species from a pool of six) (Abdala-Roberts et al. 2015). Each plot was 21 m × 21 m, with separation distance of 6 m and contained 64 plants, with planting distance of 3 by 3 m. The species planted were native tree species that naturally co-occur with big-leaf mahogany *Swietenia macrophylla* (Meliaceae) in tropical forests of the Yucatan Peninsula: *Ceiba pentandra* (Bombacaceae), *Cordia dodecandra* (Boraginaceae), *Enterolobium cyclocarpum* (Fabaceae), *Piscidia piscipula* (Fabaceae), and *Tabebuia rosea* (Bignoniaceae). These species may increase ecological complementarity because they exhibit substantial differences in attributes such as growth rate and leafing phenology (Abdala-Roberts et al. 2015). For the present study, we selected 32 monoculture plots of big-leaf mahogany and 22 polyculture plots with mahogany (Online Resource 1). Saplings were 4 months old when planted. Understory management was based on weeding, occasional application of herbicide, and irrigation three times per week during the dry season (March to May).

The beetle community was sampled in the middle-wet season, from August 1 to August 15 of 2012 (a single sampling of 2 weeks). We used non-baited pitfall traps, which is a suitable passive method to survey epigeal arthropod communities, particularly ground-dwelling species (Bouget 2009; Siewers et al. 2014). Three pitfall traps with soapy water were equidistantly placed at the center of each plot, 6 m apart from each other and from the plot edge (subsamples). We used the accumulated richness and abundance per plot for diversity analysis (replicates). This method of beetle collection has been proven efficient to assess diversity patterns of edaphic beetle communities in other study systems (Costa et al. 2017; Ramírez-Ponce et al. 2019). Sampling was carried out during the wet season as this is when the epigeal fauna is more active in tropical dry forests in Mexico (Brown et al. 2001; Jiménez-Sánchez et al. 2009). The average tree height ranged from 1.5 to 2.5 m when the sampling was conducted (Moreira et al. 2014), with mahogany polycultures constituting more shady and complex environments (Campos-Navarrete et al. 2015). Specimens were identified to family level in the laboratory (Ferret-Bouin 1995). We were assisted by external taxonomists for genus and species identification of many families (see “Acknowledgements”). Collected species were assigned to different trophic guilds, namely decomposers (detritivores and fungivores) and predators following Lassau et al. (2005), taking into account aspects as their mouthparts, natural history information, direct observations in the field, and the advice of taxonomists. The examined material was deposited in the “Colección Entomológica del Departamento de Ecología Tropical de la UADY”, Yucatan, Mexico.

Data analysis

We considered two levels of analysis, the overall community and disentangling trophic guilds: decomposers and predators. First, we evaluated the inventory completeness of each plot type by using sample coverage estimator (\hat{C}_m) which is a less biased estimator of sample completeness (Chao and Jost 2012). Sample coverage values range from 0 (minimal completeness) to 100% (maximum completeness). Next, we compared beetle diversity between plot types using the Hill numbers qD (Jost 2006) of orders 0D and 1D . The former represents species richness, whereas the latter 1D (ecological diversity) uses the inverse of the exponential of Shannon’s entropy to estimate the effective species number, which weights each species by its frequency in the sample without favoring either common or rare species (Jost 2006). We obtained diversity values for each plot and compared observed qD values between plots using confidence intervals (CI) at 95% for plantation types. All the diversity analyses were conducted in iNEXT package v. 2 (Hsieh et al. 2019) in R program (R Core Team 2016). In addition, to evaluate plot type differences in assemblage structure, we constructed species-rank abundance distribution curves.

Venn diagrams were used to compare the dissimilarities in species composition between plantation types at both community and guild levels, using the ‘VennDiagram’ package (Chen and Boutros 2011) in R program (R Core Team 2016). Differences in species composition at community and guild levels were analyzed using Morisita-Horn index calculating by plots with a permutational multivariate analysis of variance after 999 permutations of residuals under reduced model (PERMANOVA). After permutation, a pairwise test was applied to assess differences between plot types. We used a multidimensional scaling (MDS) to graph the relative position of the plots according to their similarity in species composition using bootstrap procedure. We created 100 bootstrap randomizations of the original multivariate data to obtain the bootstrap replications of the Morisita-Horn matrix, with this information; we plotted the 95% confidence ellipse for each point in the multidimensional scaling (MDS). PERMANOVA and MDS analyses were conducted using PRIMER v7 (Clarke and Gorley 2015). In addition, we partitioned β -diversity following Baselga (2010), where the total dissimilarity (β_{cc}) is 1 minus the similarity coefficient of Jaccard index. β_{cc} was partitioned into two additive components: species replacement or dissimilarity due to turnover (β_{-3}) and dissimilarity due to species richness differences (β_{rich}), with the equation $\beta_{cc} = \beta_{-3} + \beta_{rich}$. Plot type comparisons were conducted by using the script of Carvalho et al. (2012) in R (R Core Team 2016).

In order to assess habitat preferences, the indicator value (*IndVal*) of Dufrêne and Legendre (1997) was calculated for the overall epigeal community, using the ‘indicpecies’ package (De Cáceres and Legendre 2009) in R program (R Core

Team 2016). This indicator relates the habitat specificity of a species in a particular habitat type (relative abundance) to the species fidelity to that particular habitat (relative frequency) (Dufrene and Legendre 1997). The *IndVal* is especially useful for elucidating patterns of habitat affinity among taxa for which scarce ecological information is available (Pohl et al. 2007). Its value is higher when all the individuals of a species are found under a single habitat type or when that species occurs in all samples of that group (García-López et al. 2016). The statistical significance was analyzed using a permutation test between pairs of species and for plot type using the *multipatt* function in R (De Cáceres et al. 2010, 2012).

Results

Alpha diversity patterns in big-leaf mahogany plantations

We recorded 73 species and 17,274 individuals belonging to 23 Coleoptera families (Appendix). Of this total, 37 species were decomposers (15,506 individuals) and 35 were predators (1767 individuals) (Table 1 and Online Resource 2). Only one species could not be classified into these guilds, *Taphroscelidia linearis* (LeConte) (Passandridae); so, it was not considered for analyses at guild level.

Sample coverage was > 98% for the overall epigeal community and for both trophic guilds, indicating suitable sampling effort. At the community level (overall), differences between plantation types were found both for species richness (${}^0D_{monoculture} = 62$ and ${}^0D_{polyculture} = 50$) and ecological diversity (${}^1D_{monoculture} = 4.34$ and ${}^1D_{polyculture} = 3.73$), being higher in monoculture than in polyculture based on the 95% CI (Fig. 1). Analyses by guild indicated no difference between plot types in decomposer species richness (${}^0D_{monoculture} = 32$ and ${}^0D_{polyculture} = 31$), but a significant difference for ecological diversity was found, being higher in monocultures (${}^1D_{monoculture} = 3$ and ${}^1D_{polyculture} = 2.50$). Predator species richness presented similar communities for species richness parameter (${}^0D_{monoculture} = 22$ and ${}^0D_{polyculture} = 22$), but ecological diversity was higher in polycultures (${}^1D_{monoculture} = 3.87$ and ${}^1D_{polyculture} = 4.80$) (Fig. 1).

Table 1 Differences in species richness and abundance between plantation types for the overall beetle assemblage and disentangling by trophic guilds

	Monocultures		Polycultures	
	Richness	Abundance	Richness	Abundance
Overall community	62	7936	50	9138
Decomposer guild	32	7000	25	8506
Predator guild	29	935	25	832

The overall epigeal community was dominated by *Pseudocanthon perplexus* (LeConte) in both plot types, followed by *Canthon leechi* (Martínez, Halffter & Halffter) and *Onthophagus landolti* Harold (all of them Scarabaeidae), though the species dominance profile differed between plantation types (Online Resource 3). A similar pattern was observed for the decomposer guild, where *P. perplexus*, *C. leechi*, and *O. landolti* accounted for nearly 90% of individuals in both plot types. *Canthon cyanellus* LeConte (Scarabaeidae) was the fourth species in order of importance, accounting for around 2% of the individuals in polycultures. For predatory species, Aleocharinae sp.1 (Staphylinidae) dominated in both plot types, followed by Aleocharinae sp.2, and *Galerita ruficollis* Dejean (Carabidae) (Online Resource 3).

Species composition between plantation types

We found significant differences in species composition between plot types. The Venn diagrams revealed that 53–55% of species were shared between plot types at both the community and guild level, whereas the number of unique species was nearly double in monocultures in all cases (Fig. 2). PERMANOVA analysis showed significant differences in species composition between plot types for the overall community and the decomposer guild ($F_{pseudo} = 3.34$, $df = 1$, $P = 0.04$; $F_{pseudo} = 4.01$, $df = 1$, $P = 0.02$, respectively) (Fig. 3). Conversely, the species composition of predators did not differ between plantation types ($F_{pseudo} = 0.51$, $df = 1$, $P = 0.7$). Significant results are shown in Fig. 3.

Results comparing beta diversity patterns between monocultures and polycultures indicated an overall value of (β_{cc}) 0.46, and partitioned between its components, we found for β_{-3} a value of 0.30 and for β_{rich} a value of 0.16. In other words, the change in species composition is less likely the result of the differences in species richness (β_{rich}), indicating that replacement (β_{-3}) is the most important component of the total average beta (β_{cc}). With regard to comparison of dissimilarity values for decomposer guild between monoculture and polyculture, we obtained the same pattern ($\beta_{cc} = 0.45$, $\beta_{-3} = 0.27$, and $\beta_{rich} = 0.18$), and also was found for predator guild ($\beta_{cc} = 0.45$, $\beta_{-3} = 0.34$, and $\beta_{rich} = 0.11$). So, this pattern was consistent among overall epigeal species and disentangling their trophic guilds.

Habitat indicator response of epigeal beetle species

Monoculture plots did not exhibit any indicator species. In contrast, for polyculture plots, we found that the decomposers *Conotelus* sp. (Nitidulidae) (*IndVal* = 0.28, $p = 0.04$), *C. cyanellus* (*IndVal* = 0.35, $p = 0.04$), and *O. landolti* (Scarabaeidae) (*IndVal* = 0.39, $p = 0.03$), and the predators *Belonuchus rufipennis* (Fabricius) (*IndVal* = 0.36, $p = 0.03$),

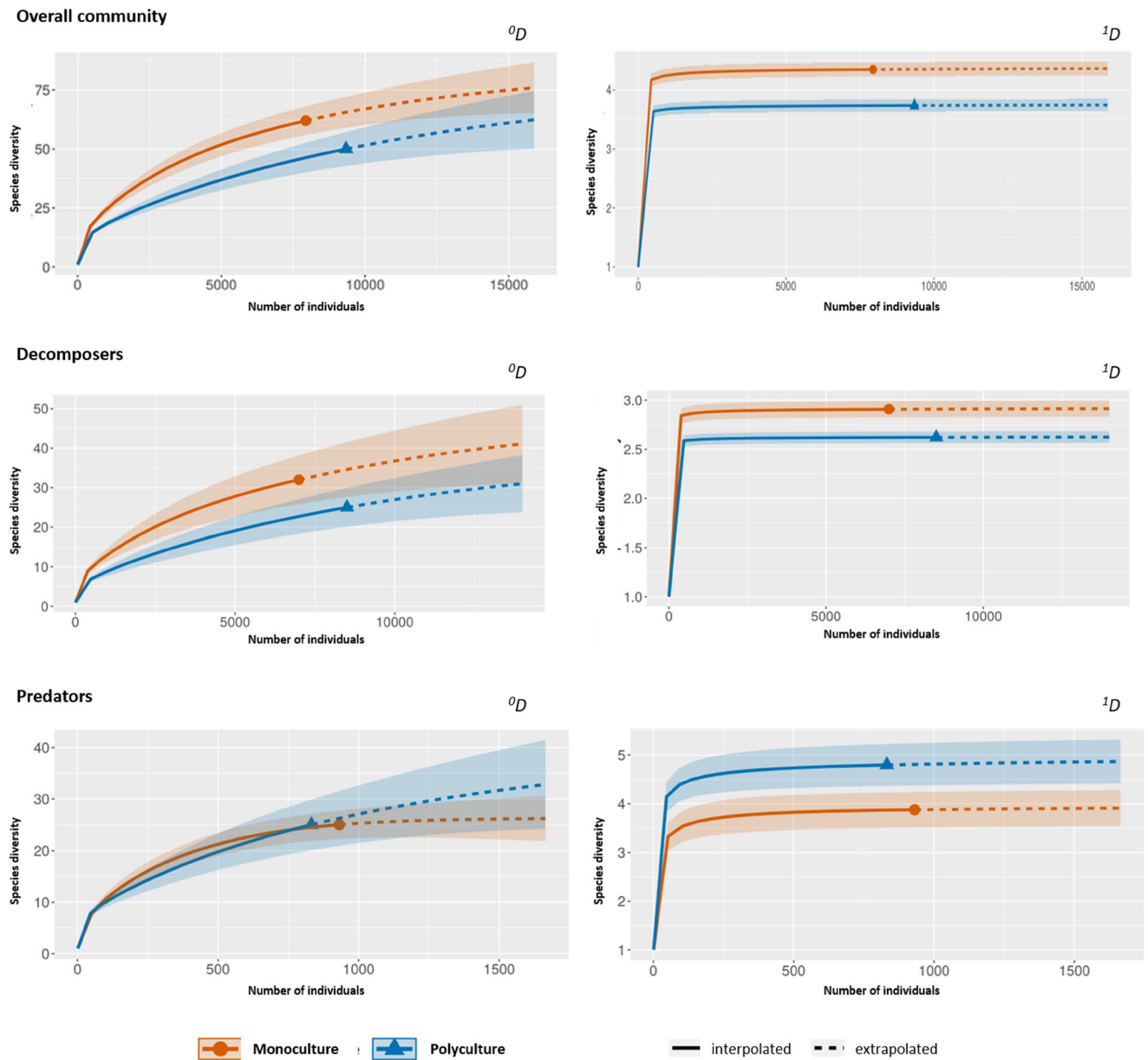


Fig. 1 Differences in species richness (0D) and ecological diversity (1D) of beetle assemblages between monocultures and polycultures

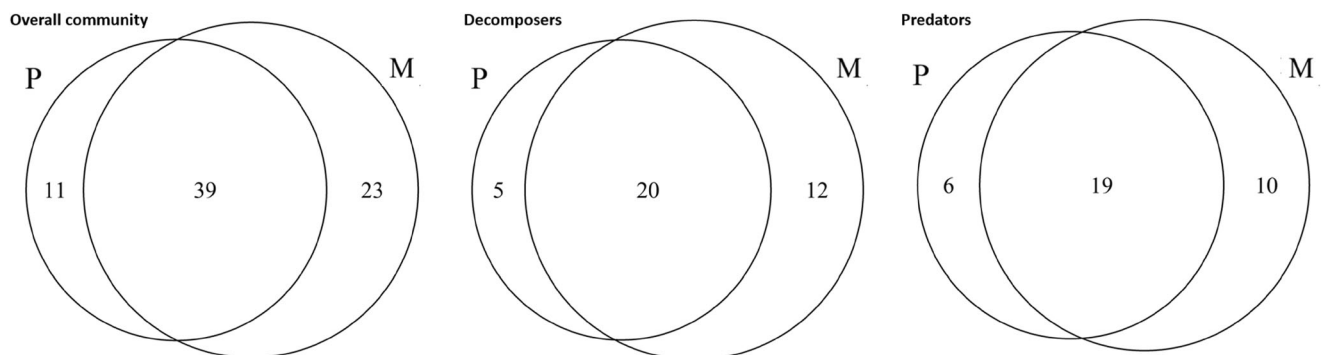


Fig. 2 Venn diagrams showing the main dissimilarities in species richness between plantation types for the overall community (left), for the decomposer guild (center), and for the predator guild (right). P, polyculture; M, monoculture

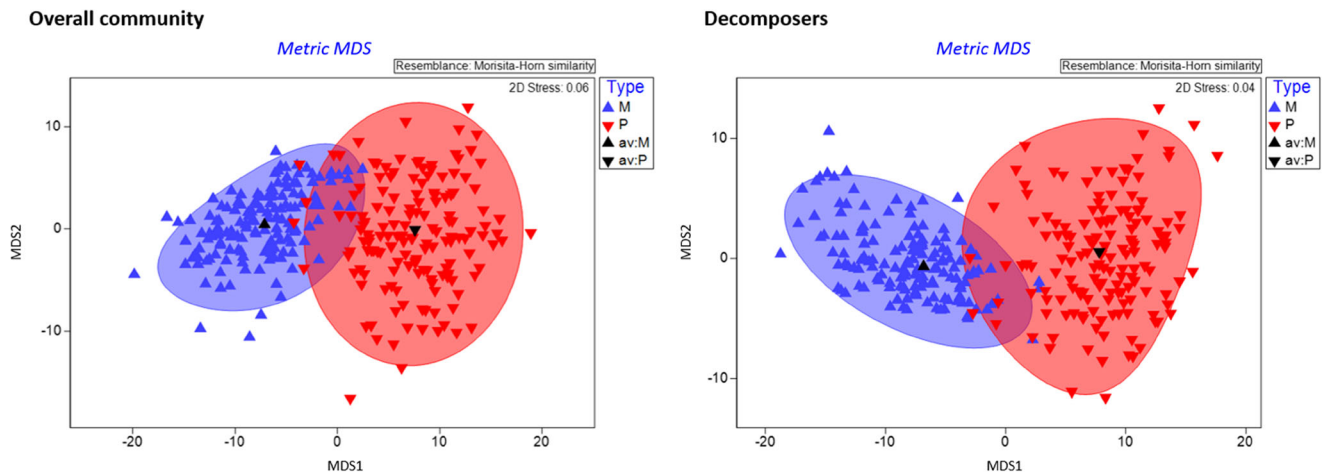


Fig. 3 Differences in species composition between monocultures and polycultures derived from bootstrap procedure (see “Materials and methods”) for the overall community (left) and for the decomposer guild

(right). M, monocultures; P, polycultures; av, average. Shaded areas are the 95% bootstrap confidence ellipses

and *Paederinae* sp.1 (Staphylinidae) ($IndVal = 0.38$, $p = 0.01$) were all found to be indicator species. The five indicator species had higher relative abundance in polycultures than in monocultures (habitat specificity), as well as high relative frequency throughout polyculture plots, being present in approximately 50% of the samples (habitat fidelity).

Discussion

This study represents the first comprehensive attempt to elucidate diversity patterns of epigeal beetle assemblages in monocultures and polycultures containing *S. macrophylla*. Our results were partially consistent with our predictions since we found contrasting responses on beetle diversity attributes. Importantly, we found that polyculture plantations did not necessarily promote more diverse beetle assemblages. In addition, a high species turnover was consistently found at community level and across trophic guilds, which supports our prediction that changes in habitat heterogeneity and trophic resources between plantation types may determine distinct epigeal beetle assemblages. Our results highlight that monoculture and polyculture containing *S. macrophylla* may contribute to preserve diverse epigeal beetle assemblages.

Alpha diversity patterns of epigeal beetle assemblages

Although the establishment of tropical forest plantations inherently implies considerable habitat transformation over time (i.e., site preparation, weeding during the early years, or thinning after crown closure) (Hartshorn and Whitmore 1999), such plantations are generally seen as favorable agroecosystems for the development of species-rich arthropod assemblages (Estrada and Coates-Estrada 2002; Warren and

Zou 2002; Reyes-Novelo et al. 2007; Fagundes et al. 2011; Beiroz et al. 2014; De Farias et al. 2015). Tropical plantations offer particular characteristics to epigeal assemblages which play a key role driving diversity patterns (Reddy and Venkataiah 1990; Warren and Zou 2002; Beiroz et al. 2014; De Farias et al. 2015; Salomão et al. 2018). In the studied experimental system, where tree species composition was the only differentiating factor between plantation types, we found different diversity patterns at the community level and by trophic guilds. This result is quite striking if we consider the short distance between plots as well as the intermixed spatial arrangement of the plots, suggesting that both plantation types can attract numerous but different ground-dwelling beetle species from surrounding habitats soon after planting (but see Campos-Navarrete et al. 2015). In terms of community ecology, both communities were constituted of a similar pool of dominant species, but polycultures exhibited lower equitability on the species abundance, which suggests that spatial heterogeneity influences abundance patterns and promotes dominant epigeal and decomposer species. Conversely, higher habitat heterogeneity promoted less dominant predator communities, as abundance patterns were equal in polycultures.

There is evidence that decomposer beetle communities are affected by habitat quality and complexity. Specifically, extensive tree cover, site heterogeneity, or soil physicochemical characteristics such as moisture, nutrient content, dry weight, or litter depth can benefit the richness, abundance, or diversity of decomposer beetle assemblages (Reyes-Novelo et al. 2007; De Farias et al. 2015; Salomão et al. 2019). For example, Grimbacher et al. (2007) compared different young monospecific and mixed tropical plantations of the same age and found rich but similar epigeal beetle richness, a parameter that was positively correlated with canopy tree cover and structural complexity. Furthermore, the predominant open structure of

young tree plantations, as in our system at the time the study was conducted, usually leads to increased abundance of heliophile or open site scarab species (Grimbacher et al. 2007; Nichols et al. 2007; Arellano et al. 2013). Accordingly, the ecological diversity of decomposers was higher in monocultures. Similar patterns of abundance have been observed in old mahogany monocultures, in which a profuse and continuous supply of leaf litter tends to create a homogenous litter layer allowing only those adapted species to become abundant (Sopsop and Lit Jr 2015). This suggests that young *S. macrophylla* monoculture plantations are homogeneous open habitats offering large amounts of a single type of leaf litter which may benefit both mahogany-like and open site decomposer beetle species.

Both mahogany plantation types were largely composed of generalist predator species (see Navarrete-Heredia et al. 2002; Jiménez-Sánchez et al. 2009), while the ecological diversity was higher in polycultures. Plantation heterogeneity may determine positive effects on generalist predator abundance, due to decreased temperature, and increased humidity and shade cover (Klein et al. 2002; Novais et al. 2017). This suggests that colonizing predator beetles may be favored under environmental conditions taking place in mixed plantations, such as higher availability of shaded environments, alternative preys or food resources (facultative feeding). Nevertheless, scarce attention has been paid to factors modeling diversity patterns of epigeal predators in forest plantations and further research is needed on this issue.

Effects of plantation types on beetle species composition

This is the first attempt to disentangling the beta components for epigeal beetle communities in tropical plantations. Species replacement was the most important component for total beta at community and guild levels, thus reflecting great variation in the species identity between plantation types. This consistency suggests that monoculture and polyculture forest plantations with big-leaf mahogany (*S. macrophylla*) support distinct epigeal beetle assemblages, which means they involve differentiating habitat characteristics mediating the species turnover. In a previous study in our experimental area, differences in the species richness and abundance of arboreal arthropods were attributed in part to microenvironmental differences between plot types (Campos-Navarrete et al. 2015). Inherent differences in the tree cover configuration between mahogany plantations may therefore be modeling beta diversity patterns, with monocultures constituting continuous and more open habitats offering one litter source and polycultures providing higher spatial heterogeneity and availability of shaded environments, litter variety, and additional ecological niches. Epigeal beetle assemblages exhibit high species turnover across successional stages in reforested habitats

(Grimbacher et al. 2007; Arellano et al. 2013) as well as across habitats with increasing tree cover (Goehring et al. 2002; Márquez 2003; Gormley et al. 2007; Beiroz et al. 2014; Neita and Escobar 2012; Filgueiras et al. 2016; Ramírez-Ponce et al. 2019). In addition, tree cover plays a major role in shaping dung beetle composition across multiple spatial scales in the Neotropical region (Sánchez-de-Jesús et al. 2016; Costa et al. 2017; Alvarado et al. 2018), and any type of forest conversion or severe tree cover loss involves local extinctions and rapid replacement towards open area species (Halffter and Arellano 2002; Nichols et al. 2013).

The beta diversity value found in our plantation landscape is similar to that found in dung beetle communities in some variegated tropical landscapes, where total beta explained around 60% of diversity, with turnover being the main component (80%) (Costa et al. 2017). Other studies pointed out high beta diversity and biotic heterogeneity (turnover) of dung beetles in areas with high habitat heterogeneity (Da Silva 2018; Bitencourt et al. 2019). On the contrary, epigeal predator assemblages in agricultural, suburban, and urban areas exhibited low total beta diversity (34.7%) in spite of the high spatial heterogeneity, and turnover and richness contributed equally to the variation in species composition between sites (Jiménez-Sánchez et al. 2019). In our mixed plots, the high turnover from monoculture to polyculture plots pointed out that the habitat heterogeneity in plots with more tree species is a factor that can promote edaphic beetle species replacement. In addition, although the contribution of beta richness to total beta diversity was low, it may be a subset of the original regional species pool.

Species composition was influenced by abundance patterns for the whole community and the decomposer guild. As in other young tropical plantations (Grimbacher et al. 2007; Neita and Escobar 2012; Arellano et al. 2013), the community structure was dominated by small-size generalist heliophile scarab species, reflecting the open site configuration of both plantation types. However, several heliophile species were favored in monocultures (i.e., *C. leechi*, *Canthidium pseudopuncticolle* Solís & Köhlmann, or *Canthon indigaceus* LeConte), while both heliophile (i.e., *P. perplexus* or *O. landolti*) and umbrophile species (i.e., *C. cyanellus*, *B. rufipennis* or Paederinae) were enhanced under polyculture conditions. More importantly, a constant high proportion of rare species was found across levels of analysis, many of which could correspond to species with low dispersal ability (early colonization) or tourist species that eventually take advantage of the plantation resources. Therefore, differential tree cover characteristics of plantation systems have direct effects on the composition of epigeal and decomposer assemblages. Otherwise, the predator composition did not have differences between plantations (so abundance did not affect compositional patterns), a fact that may be attributed to the closeness between plots and to the ability for movement and

foraging behavior typical of predatory beetles. Given the rapid spatial variation done in young tropical forest plantations (Piotto et al. 2004; Healy et al. 2008; Paul et al. 2011), high species replacement is expectable across successional stages (as seen in Grimbacher et al. 2007, Arellano et al. 2013); consequently, long-term studies assessing how epigeal beetle assemblages evolve as the spatial complexity of tropical forest plantations increases are required.

Species associated with forest plantations

Indicator values between 45 and 70% are required for Scarabaeidae, Carabidae, or Staphylinidae representatives to be considered indicator species of a given habitat (Pohl et al. 2007; Verdú et al. 2011; Arellano et al. 2013; Beiroz et al. 2014). However, this indicator value and the number of indicator species decrease with increasing disturbance (Caballero and León-Cortés 2012; Bitencourt et al. 2019). For example, indicator values lower than 30% were reported by Mazón et al. (2018) for beetle families in mixed plantations of cacao and native trees (including *S. macrophylla*), in which Staphylinidae were associated with *T. rosea*. In our case, higher values were found (27–40%) but indicator species were only identified in polycultures. Among them, *C. cyanellus* and *B. rufipennis* are forest-associated species, preferentially distributed in less disturbed and moister habitats, whereas *O. landolti* and Paederinae are open site species (Halffter 2003; Márquez 2003; Reyes-Novelo et al. 2007). Such indicators may be reflecting the combined effect of open site, but spatially heterogeneous characteristics done in young mixed plantations. This is a first approach towards identifying representative epigeal beetle species of big-leaf mahogany plantations, although further research should be done to evaluate how the composition of indicator species evolve over time.

Implications for conservation

Tropical anthropogenic landscapes providing different forms of tree cover promote the conservation of epigeal beetle assemblages, due to high species replacement between habitats led to increased diversity at the landscape scale (Halffter and Arellano 2002; Nichols et al. 2007; Filgueiras et al. 2016; Costa et al. 2017; Alvarado et al. 2018; Ramírez-Ponce et al. 2019). The permanent tree cover of forestry and agroforestry systems help to increase the structural complexity of the landscape matrix by providing trophic resources, refuge, or increasing the habitat connectivity (Bhagwat et al. 2008; Neita and Escobar 2012), which benefits the diversity of epigeal communities as well as the whole animal biodiversity (Harvey et al. 2006; Bhagwat et al. 2008).

Our results emphasize that monoculture and polyculture forest plantations with big-leaf mahogany (*S. macrophylla*) are favorable for the establishment of epigeal beetle assemblages but encourage different diversity attributes. In addition, a conspicuous colonization of beetle species took place in spite of the short time elapsed after planting, indicating that ecological services can be recovered in the short-term, such as the improvement of the soil fertility carried out by decomposers or the biological pest control carried out by predators (Giraldo et al. 2011). The implementation of management and conservation strategies in the tropics should take into consideration that different plantation conditions enhance different trophic guilds and ecosystem functions. Furthermore, the identity of species varied between plantation types across all levels, which means they harbor biologically distinct epigeal communities. Therefore, monospecific and mixed forest plantations with big-leaf mahogany are complementary agroecosystems and should be seen as valuable tools for conservation purposes.

Conservation strategies for epigeal communities in the Neotropical region should be directed towards preserving not only natural forest areas or forest remnants within the landscape matrix but also consider entire heterogeneous landscapes covering habitats with distinctive tree cover, emphasizing the important contribution that forest plantations can make for biodiversity conservation.

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Declarations

Conflict of interest The authors declare no competing interests.

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