**Early successional understory communities show idiosyncratic phylogenetic patterns in
early in Neotropical silvicultural plantations.**

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Abstract

One approach in forest restoration is to plant trees that will establish an initial canopy to promote forest recovery through the colonization of other species. The identity of the planted tree affects which species are able to recruit in its understory. Here we evaluate the phylogenetic structure of young understory plant communities recruiting beneath eleven different species planted in single species stands and relate those structures with processes affecting community assembly. We expected the presence of negative biotic interactions between closely related overstory and understory species, as well as among related understory species, to lead to phylogenetic overdispersion. However, we did not find consistent phylogenetic patterns maybe due to the young age of the understory communities at the time of sampling. Most overstories showed a higher than expected presence of close relatives due to the recruitment of conspecifics, whereas, the higher recruitment of the ancient clade of Piperaceae beneath Fabaceae trees led to overdispersion. The presence of various Asteraceae species in understories that had been invaded by the grass, *Saccharum spontaneum*, led to significant clustering suggesting the conservatism of traits that allow overcoming the strong competition imposed by the grass. Phylogenetic patterns among the recruiting species showed that dispersal and competition are playing a role in shaping the communities but this changed among overstories. Our results highlight the importance of choosing an adequate set of species to plant in a restoration project since they dictate the subsequent regeneration of a forest community.

Keywords: tropical forest regeneration, restoration, forestry plantations, community assembly

1. Introduction

One method that is often employed to restore tropical forests consists of planting tree species to establish canopies that will shade invasive grasses and create suitable conditions for the establishment of other forest species (Parrota *et al.*, 1997; Holl *et al.*, 2000; Carnevale and Montagnini, 2002; Butler *et al.*, 2008). Careful selection of which species to plant is important since some tree species induce greater recruitment and establishment (Kuusipalo *et al.*, 1995; Parrota, 1995; Haggard *et al.*, 1997; Celentano *et al.*, 2011). However, testing plantation species one-by-one to evaluate subsequent recruitment is slow and resource intensive (e.g. Guariguata *et al.*, 1995; Powers *et al.*, 1997; Carnevale and Montagnini, 2002; Jones *et al.*, 2004). In this study we evaluate whether tools and interpretations from phylogenetic ecology can provide insights regarding processes of community assembly beneath single-species tree plantations.

The acknowledgment that species are linked to each other by their shared evolutionary history gives community ecologists an additional perspective to understand processes involved in community assembly and species interactions (Vamosi *et al.*, 2009). An assumption of most phylogenetic ecology research is that close relatives share ecologically important traits and thus interact with their environment in similar ways (Webb, 2000; Gomez *et al.*, 2010; Burns and Strauss, 2011). This similarity among close relatives is called “phylogenetic signal”, which is common among species for a wide range of morphological, physiological, behavioral, ecological and life history traits (Prinzing *et al.*, 2001; Blomberg *et al.*, 2003; Chazdon *et al.*, 2003; Gilbert and Webb, 2007; Gossner *et al.*, 2009; Cavender-Bares and Reich, 2012; Savage and Cavender-Bares, 2012). A recent article showed that traits related to the ability of tree species to colonize former agricultural areas are

evolutionarily conserved; a finding that directly shows the application of phylogenetic ecology to understand community assembly in restored forests (Baeten *et al.*, 2015).

The key question in phylogenetic ecology is whether species present in a community are a non random subset from the pool of species that could colonize the site (Webb *et al.*, 2002).

Assuming the conservatism of ecologically important functional traits, communities can show two distinctive phylogenetic patterns. If coexisting species are closer together in the evolutionary tree than expected at random they show “phylogenetic clustering”. On the other hand, if species in a community are less related than expected by chance the pattern is called “phylogenetic overdispersion” (Webb, 2000). In its simplest interpretation, conservation of traits important in habitat use among close relatives (e.g., drought tolerance) should lead to phylogenetic clustering (e.g. Tilman, 1994; Weiher *et al.*, 1998; Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006; Merwin *et al.*, 2012). In contrast, phylogenetic overdispersion can result from negative biotic interactions among close relatives such as competitive exclusion (e.g. Lovette and Hochachka, 2006; Helmus *et al.*, 2007; Wilson and Stubbs, 2012) and the sharing of pests and pathogens (Webb *et al.*, 2006). Negative interactions among conspecific seedlings, mainly mediated by shared species-specific pests and pathogens, led to the Janzen-Connell hypothesis of seedlings density-dependent mortality at high densities and in close proximity to a parent tree (Janzen, 1970; Connell, 1971).

Most phylogenetic ecology studies have evaluated phylogenetic patterns in old growth forests, with a few recent studies looking at secondary forests under succession (Letcher, 2010; Letcher *et al.*, 2012; Norden *et al.*, 2012; Whitfield *et al.*, 2012; Li *et al.*, 2015).

However, the tools of phylogenetic ecology have proved useful for shedding light into processes of community assembly and the successional trajectory of restoration forests

(Chang *et al.*, 2015; Shooner *et al.*, 2015; Schweizer *et al.*, 2015). In this study, we assessed the phylogenetic patterns of species recruiting beneath single-species tropical tree stands. We asked the following question: Does negative biotic interactions drive the species composition of an early successional understory community? Based on a trait conservatism assumption, by which close relatives are expected to share similar functional traits, we hypothesized that negative interactions among closely related species were going to lead to phylogenetic overdispersion. We analyzed the data at two levels: between the overstory tree species and the understory community and among the understory community.

2. Materials and methods

2.1 Research site

This study was conducted in a plantation site of the PRORENA project (The Native Species Reforestation Project, <http://research.yale.edu/prorena/>), led by the Smithsonian Tropical Research Institute and the Yale School of Forestry and Environmental Studies. It is located in the Soberania National Park, in the watershed of the Panama Canal, Republic of Panama (Figure 1). The area receives a mean annual rainfall of 2226 mm and 4.1 dry months annually (defined as months with <100 mm rainfall) (Wishnie *et al.*, 2007). The soils are tropical ultisols, derived from the weathering of primary materials, that are predominantly clay or silty clays (Park *et al.*, 2010).

Figure 1. Map with the location of all three PRORENA sites including the study site (Map modified from Wishnie *et al.*, 2007; original map source ANAM, 1992).

Most of Soberania National Park is covered by secondary tropical rain forest. The study site, however, had been deforested before the 1960s and then farmed for several decades but it lies next to a large secondary forest tract. In 2003, when the PRORENA project began, the site had not been farmed for at least 10 years, and was invaded by the exotic grass *Saccharum spontaneum* L. subsp. *spontaneum* (Wishnie *et al.*, 2007). This grass has invaded extensive deforested areas along the Panama Canal and significantly arrests natural forest recovery (Hooper *et al.*, 2002; Hooper, 2008).

2.2 Recruiting species census

The PRORENA project planted 22 native and two exotic tree species in 9×12 -m single-species plots, with three replicate plots per species. The plots were placed next to each other in the planting area, however, the species were randomly assigned to each plot (see detailed description in Schweizer *et al.*, 2013). Plots were established in 2003 and thinned in 2005 to a density of 10 trees each, at 6-m spacing (Wishnie *et al.*, 2007). We selected 11 species that performed well, meaning the majority of the planted species had survived and they had grown enough so as to close the canopy (over 80% canopy cover) at least during the rainy season (Please refer to Wishnie *et al.*, 2007 for mean performance values of the species

planted across all three *Prorena* sites). We selected species that performed well since good overstory cover tends to minimize *Saccharum* reinvasion and allow us to study the effect of the overstory on the understory community. Nevertheless, our species selection was limited by the poor growth of some overstory species, therefore, we included two non-native species, *Acacia mangium* and *Tectona grandis*, in our dataset (Table 1). We acknowledge that non-native species interact differently with the native plant, insect and fungal communities, which may affect phylogenetic patterns. However, our study is conducted in the context of forestry management, and both species are often employed in timber plantations in the tropics, which may become important areas of forest regeneration if abandoned (Lamb *et al.*, 2005).

We evaluated canopy openness as a proxy for light reaching the understory in the dry and the rainy seasons. Canopy openness changes with seasonality mainly for some canopy species that are deciduous. We took three hemispherical canopy photos per plot during the wet and dry season using a fish-eye lens mounted on a leveled digital camera (Nikon Coolpix, model 995). Pictures were taken at dusk and always facing north. We took pictures with the camera placed on a tripod 1 m above the ground. The program Gap Light Analyzer v.2 (Frazer *et al.*, 1999) was used to calculate the percent canopy openness from the photos; estimates were averaged for each of the three photos taken at a given camera height.

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142 Table 1. Overstory species employed in the study. Shown is the mean of three measurements of canopy
 143 openness conducted in each of the three replicate plots per species $\pm$ SD. Foliar periodicity was determined
 144 from the ratio of dry:wet season canopy openness, where: evergreen ≤ 1.5 ; semideciduous 1.51 to 3; deciduous
 145 >3.0 . Wet season measurements were taken in August 2009 and dry season measurements in March 2010.

Canopy Cover %			
Overstory species	Wet season	Dry season	Foliar periodicity
<i>Acacia mangium</i> Willd.	12.72 $\pm$ 1.55	19.15 $\pm$ 0.22	Evergreen
<i>Colubrina glandulosa</i> Perkins	17.98 $\pm$ 5.18	33.31 $\pm$ 0.21	Semi-deciduous
<i>Dyphisa robinoides</i> (Mill.) M. Sousa	13.44 $\pm$ 1.78	18.14 $\pm$ 3.94	Evergreen
<i>Gliricidia sepium</i> Kunth ex Steud.	11.44 $\pm$ 3.55	16.73 $\pm$ 5.79	Evergreen
<i>Inga punctata</i> Willd.	11.48 $\pm$ 0.57	20.74 $\pm$ 3.55	Semi-deciduous
<i>Luehea seemannii</i> Triana & Planch.	17.97 $\pm$ 9.45	18.83 $\pm$ 0.14	Evergreen
<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	18.71 $\pm$ 3.96	30.77 $\pm$ 5.19	Semi-deciduous
<i>Pachira quinata</i> (Jacq.) W.S. Alverson	12.77 $\pm$ 3.18	38.17 $\pm$ 5.33	Deciduous
<i>Spondias mombin</i> L.	24.60 $\pm$ 2.34	32.28 $\pm$ 3.50	Evergreen
<i>Tectona grandis</i> L. f.	6.79 $\pm$ 0.92	44.65 $\pm$ 4.43	Deciduous
<i>Terminalia amazonica</i> (J.F. Gmel.)	12.40 $\pm$ 3.52	20.31 $\pm$ 0.70	Semi-deciduous

146 * Non native species

147 For two years following planting, the understory was cleared of competing vegetation
 148 with machetes whenever competing vegetation was taller than 1m (Wishnie *et al.*, 2007) and
 149 the trees were sprayed with insecticide as needed. The application of insecticides to the
 150 planted trees until three years prior to the start of the study may have had some legacy
 151 impacts on the herbivore community (Endlweber *et al.*, 2006; Meire *et al.*, 2012). However,
 152 such treatments were uniformly applied across species and form part of the established
 153 timber management system. Once again we examined phylogenetic responses of the
 154 recruitment community in the context of forestry management.

155 During July and August 2008, three years after understory clearing ceased and the
 156 overstory trees were thinned, we ran one 15-m long transect diagonally across each plot and

at every meter counted and identified all the understory species that touched a 1.5-m tall stick, held vertically, at that meter. Species were identified in the field. Unknown species were collected for later identification and vouchers deposited in the National Herbarium of the University of Panama.

2.3 Community phylogenetic structure

Phylogenetic relationships among the understory and overstory species were estimated using the Phylomatic tool implemented in the Phylocom program, version 4.2 (Webb and Donoghue, 2005; Webb et al. 2009). Phylomatic maps the input community onto a resolved phylogenetic “supertree” of the angiosperms, which is a tree assembled by merging smaller phylogenies together. We created the observed species phylogenetic tree from the most recent resolved angiosperm supertree, R20120829.new, which is based on APG3 phylogenies and is available online at www.phylodiversity.net. We made sure that our observed taxa names matched the names in the APG3 phylogeny. We limited the species list to angiosperms to avoid biases from inclusion of species far too distant in the evolutionary tree.

We estimated the ages of the interior nodes of the phylogeny using the BLADJ algorithm from Phylocom and evolutionary ages published by Wikstrom *et al.*, (2001). We used the Wikstrom *et al.*, (2001) ages file after correcting name-change discrepancies between this file and the R20120829 Newick file as recommended in Gastauer and Meira-Neto, . To reduce polytomies in our community phylogenetic tree, we used published phylogenies of all the families with polytomies and manually grafted the evolutionary relationships of tribes within those families to the original newick file (Appendix A). Following the construction of the tree, we calculated the phylogenetic distance matrix, meaning the million years separating each pair of taxa, using Phylocom.

2.4 Overstory-to- understory species phylogenetic structure

We took a Monte Carlo resampling approach to evaluate whether recruiting species were more likely to be closely related (clustered) or distantly related (overdispersed) to the overstory species. For this analysis we employed seven (7×3 replicates per species) of the eleven overstories given that *S. spontaneum* reinvaded the understories of four species (*Ochroma pyramidale*, *Spondias mombin*, *Luehea seemannii*, and *Colubrina glandulosa*), which confounds the desired effects of the overstory species on the identity of the understory recruits.

Observed phylogenetic distance distributions, per overstory species, were compared to those drawn at random from among the pool of all recruiting species sampled. This means that the null community was restricted to those species that were able to disperse to the study plots and grow under the general environmental conditions of the site. Choosing species known to be able to establish in a site improves the power of phylogenetic tests for detecting phylogenetic structure (Swenson, 2009; Kraft and Ackerly, 2010).

We chose to use the set of species that were able to disperse into the study plots for two additional reasons. First, dispersal limitation of many animal-dispersed species would likely produce an ecological filter for which species arrive to the plots, limiting which species even had the opportunity to interact with the overstory trees. It is also more conservative, because comparisons to larger species pools are more likely to show phylogenetic clustering than are comparisons to more local pools (Swenson *et al.*, 2007). Second, a rigorous comparison to a regional species pool would have required extensive vegetation inventories without a clearly defined appropriate spatial scale, coupled with quantification of relative propagule

production over several years. Such work would be useful, but is far beyond the scope of the present study.

We compared the observed phylogenetic distances (in million years of independent evolution) from the overstory species to the recruiting species with those of a null community created by random sampling 1000 times from the species pool. For each resampling, we drew the same number of individuals that had been originally observed in the plot with the probability of selection weighted by the overall abundance of that species. This approach examines differences across the full distribution of phylogenetic distances among the species, which are themselves not normally distributed. Random communities were created using the R program (R-Development-Core-Team, 2013).

For both observed and random samples, we plotted quantiles of the cumulative distribution of phylogenetic distances from understory species to the overstory tree species. To plot these quantile graphs we organized all individual observations (from the observed and the null communities) in order of increasing phylogenetic distance to the overstory tree (million of years that separate the understory species from the overstory) beneath which they were found and determined the 1,5,10, 20, 25, 50, 75, 90, and 95% quantiles. Then we plotted the phylogenetic distance found at each quantile. We used 95% confidence intervals of the null distribution to evaluate whether close relatives to the overstory species were observed more or less frequently than expected by chance.

2.5 Phylogenetic structure among recruiting species

We evaluated the phylogenetic structure among understory species under each overstory tree species using two metrics: the net relatedness index (NRI) and the nearest taxon index (NTI), which are the observed Mean Phylogenetic Distance (MPD) and the Mean Nearest

Taxon Distance (MNTD) standardized to those measures estimated from 1000 random communities (Eqs. 1 and 2). MPD is the average distance between all pairs of taxa in the phylogenetic tree and is a measure of phylogenetic structure for the community as a whole. MNTD estimates the distance between each taxa and its closest neighbor on the tree; therefore, it is a metric of the relatedness at the tips of the phylogeny (Webb, 2000). The MNTD value is sensitive to tree topology (Letcher, 2010); therefore, interpretations of this index must pay attention to polytomies occurring within families. However, it has greater power to pick up phylogenetic structure than MPD if traits are conserved (Kraft *et al.*, 2007).

$$NRI: -[(MPD_{observedPD} - Mean MPD_{nullPD}) / sd_{MPDnullPD}] \quad (Eq.1)$$

$$NTI: -[(MNTD_{observedPD} - Mean MNTD_{nullPD}) / sd_{MNTDnullPD}] \quad (Eq.2)$$

The random communities were generated using the same species pool as described above, keeping observed plot abundance of recruiting species and species selection weighted by overall abundance. We estimated these indexes using the Picante package version 0.7.2 (R-Development-Core-Team, 2013; Kembel *et al.*, 2010). A positive index value indicates phylogenetic clustering and a negative value indicates phylogenetic overdispersion (Webb 2000).

3. Results

We encountered 59 plant species (548 stems) from 26 different families recruiting in the understories of the selected overstory tree species (Appendix B and C). The most commonly encountered families were Fabaceae (8 species) and Asteraceae (8 species). Woody species able to grow over 10-m tall were the most common growth form (34% of all species). Zoochory was the most common dispersal syndrome (57% of all species). The only species

dispersed by both birds and bats were restricted to the genus *Piper* (4 *Piper* species and 20% of all individuals).

We did not find a significant correlation between the compositional similarity of understory species and physical distance (estimated as the distance from the center of one plot to the next) among the selected overstory species (Mantel test, $Z = 1629.7$, $P = 0.1657$). Therefore, we evaluated the composition of understory species for all the overstory species as a function of phylogenetic distance and not physical proximity. We found a low density of understory species beneath most plots (as low as 6 individuals beneath some *Tectona grandis* replicate plots) and since the overstory species was the unit of interest for analysis, we combined the data from the three replicate plots per overstory species prior to conducting the phylogenetic ecology analyses.

We found no consistent evidence of phylogenetic overdispersion among the understory recruiting species and the overstory tree species that would imply negative biotic interactions as a plausible mechanism of community assembly (Figure 2). Three overstories showed a higher than random presence of close relatives, two of them, *Terminalia Amazonia* and *Tectona grandis*, had conspecifics recruiting in their understories and *Pachira quinata* had a close relative, *Helicteres guazumifolia*. Most Fabaceae overstories showed a greater than random presence of distant relatives (observed in the quantile graphs as phylogenetic distances around 300 My for the 80% percentile), driven by species the ancestral clade: Piperaceae (Figure 2). Understory composition beneath the non-native *Acacia mangium* was more similar to other legumes than of the non-legumes ($F_{1,10} = 2.1$, $P = 0.0040$) and a similar phylogenetic structure to the other native close relatives in the Fabaceae.

Figure 2. Quantiles of phylogenetic distance for each overstory tree species, obtained from plotting the observed vs. the random cumulative distribution of phylogenetic distances. Continuous line represents observed data, dashed line represents the median quantiles expected if the natural recruits were a random selection of species from the species pool; thin fragmented lines are the 95% confidence intervals.

The phylogenetic structure among the recruiting species showed two distinctive patterns.

Beneath legumes, the enhanced recruitment of species belonging to clades are evolutionarily distant from each other, such as Piperaceae and Asteraceae, plus the recruitment of species from close clades, like Fabaceae and Malvaceae, led to random phylogenetic structures in the NTI (Figure 3A) and to a trend toward clustering in the NRI due to the presence of several species within one clade, for example Pipers (Figure 3B). In contrast, understory recruits showed tendencies toward phylogenetically clustering under most of the non-legume overstory species for both phylogenetic structure metrics (Figure 3A & 3B). Clustering under the non-legumes was a result of the dominance of one clade: the Asteraceae.

Figure 3. Phylogenetic indices of the community of recruiting species per overstory tree species. A: Measure of phylogenetic structure of the natural recruitment community as a whole (NRI), B: Measure of phylogenetic structure at the tips of the phylogeny (NTI). A positive index indicates a higher than expected presence of close relatives, whereas a negative value indicates a higher than expected presence of far relatives. Asterisk indicates p values less than 0.05 for clustering and greater than 0.95 for overdispersion.

4. Discussion

We observed the expected presence of far relatives beneath most legume overstory species due to the presence of the ancient *Piper* clade, however, this phylogenetic pattern was not maintained for the other overstory species. Most of the other species showed phylogenetic clustering due to the presence of conspecific recruits to the overstories or to a higher than random recruitment of *Asteraceae* species.

In a study conducted at the same site, we observed that enrichment planted tree seedlings performed better the further related they were to the overstory (Schweizer *et al.*, 2013). A

result led by the poor survival of conspecifics over the good performance of extra ordinal species. Studies in old-growth tropical and subtropical forests have observed predominantly negative density dependence among close relatives (e.g. Webb *et al.*, 2006; Gonzalez *et al.*, 2010; Metz *et al.*, 2010; Liu *et al.*, 2012; Paine *et al.*, 2012). Therefore, the lack of a consistent overdispersion pattern in the phylogenetic distances between species observed in the present study was somewhat surprising. However, we must consider the young age of the understory communities, the low number of stems sampled, and the presence of *S. spontaneum* in some understories all affecting the results.

A limitation of the present study was the young age of the understory communities since the understory of the plantations had been cleared three years prior to the conduction of the study. As a result, some overstory species had very bare understories. In addition, in the early stages of succession, dispersal and abiotic conditions, not biotic interactions, may be stronger determinants of community composition. Biotic interactions become more important during the later stages of succession (Guariguata and Ostertag, 2001; Chazdon, 2008b). We may see stronger phylogenetic patterns in older understory communities.

Four of the selected overstories (*Colubrina glandulosa*, *Luehea seemannii*, *Ochroma pyramidale*, and *Spondias mombim*) had been reinvaded by dense stands of *Saccharum spontaneum*, which strongly compete with other vegetation and creates conditions that strongly inhibit tree species recruitment and growth (Hooper *et al.*, 2004). The reinvasion of *Saccharum* beneath those species indicates they are poor species to use in restoration, because even though they survive and grow fast their canopies are not dense enough to inhibit grass reinvasion, and their litter lack allelopathic components to inhibit grass growth (Cummings *et al.*, 2012). However, it was interesting that the understories of those four

species were colonized by species in the diverse Asteraceae family leading to clustering at the tips of the phylogeny (NTI index). Many species from the Asteraceae family share traits that allow them to overcome strong habitat filters, such as invasive grass competition, present in highly disturbed sites (Lavorel *et al.*, 1999; Diaz *et al.*, 2004; Cole *et al.*, 2010). Filters to species colonization in disturbed areas lead to phylogenetic clustering among coexisting species (Verdu and Pausas, 2007; Dinnage, 2009; Yi *et al.*, 2012).

We must consider that phylogenetic patterns in restored communities, where humans dictate the original composition of the overstory, may show different phylogenetic patterns compared to natural succession forests (Schweizer *et al.*, 2015). A study conducted in tropical restored forests along the southern coast of China found random phylogenetic patterns early in succession and clustering later on (Chang *et al.*, 2015), whereas secondary tropical forests have shown a prevalence of closely related species early in succession moving toward overdispersion later on (Letcher *et al.*, 2012; Norden *et al.*, 2012). Future assessments of the understory community in our site will be interesting to evaluate whether the communities follow the pattern observed in restored forests or the pattern of natural succession sites in the Neotropics.

The use of pesticides on the overstory trees the first three years after planting could have affected the insect community and thus negative interactions between closely related plant species mediated by shared herbivores. We lack information of the specific pesticide employed in the plantations under study, however, the most commonly used pesticide in Panama is based on the active component Cipermetrina (Aizprua, pers. comm.), which once in contact with the soil begins to degrade. Therefore, we do not expect the insecticide to have had a strong effect in the results. In addition, our study lies in the context of forestry

management, which is important given that abandoned plantations serve as areas of potential forest regeneration (Lamb *et al.*, 2005; Chazdon, 2008a).

Our overstory species included two non-native trees: *Acacia mangium* and *Tectona grandis*. Non-native trees can differ in their interactions with pests and pathogens relative to native trees, so that they may escape the negative effects from some pests or pathogens that affect native species (Wolfe, 2002). However, the evidence is still equivocal in this regard (Keane and Crawley, 2002). Since we were limited in our selection of overstory species (see methods), we decided to include these non-natives in our dataset due to their good growth and low *Saccharum* reinvasion, besides we regarded this inclusion as appropriate due to the applied aspect of the research. *A. mangium* showed similar understory composition and phylogenetic structure to the native Fabaceae trees. *T. grandis* has been planted vastly in the tropics as a fast-growth and valuable timber species (Pandey and Brown, 2000). Therefore, it is relevant to evaluate the understory community beneath teak.

We did not test for mechanisms to explain the abundant presence of *Piper* species under Fabaceae trees. However, neotropical bats of the genus *Carollia*, which are *Piper* specialists, utilize human-modified agrarian landscapes where legumes are often employed as live fences or as shade for coffee and cacao (Estrada and Coates-Estrada, 2001; Estrada and Coates-Estrada, 2002). Bats use *Acacia* in Australia and Kenya as roosting sites (Law and Anderson, 2000; Webala *et al.*, 2004). We therefore cannot rule out that the overdispersion observed in the legumes, due to the enhanced presence of *Piper*, is the result of idiosyncratic use by seed dispersers and not the result of negative biotic interactions between the plant species.

Our results suggest that the assembly of early understory communities under monospecific tree stands is highly idiosyncratic. It became clear that forest management for

succession in reforestation and restoration should take into account the identity of the trees initially planted since they play an important role in the early configuration of the understory community mainly through their attraction of seed dispersers and their shading of invasive grasses.

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