

Title: Rescue tree monocultures! A phylogenetic ecology approach to guide the choice of seedlings for enrichment planting in tropical single-species plantations

Running head: Phylogenetics for enrichment planting

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Abstract

Monoculture tree plantations have been preferred by farmers and companies because they maximize the production of specific products and are easier to manage, while multi-species plantations can provide multiple ecosystems services but have still been adopted at very limited scales. One potential midway to enhance the ecological contribution of monoculture plantations is to introduce native tree species in the plantation understory. We conducted phylogenetically-explicit enrichment planting experiments beneath the monocultures of two tree species native to the Brazilian Atlantic Forest to assess if the evolutionary distance of each seedling species to the overstory tree explained the variations in seedlings performance measured. We planted in the understory of two replicates of plantations of *Esenbeckia leiocarpa* Engl. (Rutaceae; 38 and 25 years old) and *Zeyheria tuberculosa* (Vell) (Bignoniaceae; both replicates were 30 years old) six native tree species, ranging in their evolutionary distances to these overstory species. We assessed individual seedling survival and height at one, seven, and nineteen months after planting. We found a weak yet significant, positive correlation between seedling performance (growth and survival), and the phylogenetic distance of the planted seedling to the overstory species, which was driven by the poor performance of conspecifics. Seedlings of the same order and class as the overstory trees showed a significantly lower risk of death compared to conspecifics and to the furthest relative, *C. aschersoniana*. These findings highlight that very close relatives to the overstories should be avoided when planting beneath monoculture plantations, but that knowledge on species-specific requirements is still the most important for a successful planting.

Keywords: adaptive management; biodiversity conservation; evolutionary relations; Janzen Connell hypothesis; tropical forest restoration; seedling performance.

Implications for practice

- Enrichment planting can be employed to increase tree diversity in monoculture tree plantations.
- Conspecific seedlings to the overstory should be avoided in enrichment planting of monoculture plantations as they survive and grow poorly.
- We observed a trend of increasing performance of enrichment planted seedlings with phylogenetic distance that should be further corroborated with studies that include more species combinations and areas.
- Using phylogenetic ecology for planning enrichment plantings does not replace species specific performance information but can help guide species choice when specific information is lacking.

Introduction

Fifty-eight countries of the world have committed to the restoration of 170.4 million hectares of degraded lands, out of a target of 350 million hectares to be achieved by 2030 (<http://www.bonnchallenge.org/>, Accessed February 2019). Although the restoration of other ecosystem types is equally important, most of the commitments center on the restoration of forests to achieve multiple goals such as climate change mitigation, improved human well-being and ecosystem services provisioning. Meeting these ambitious commitments require increasing the scale of forest restoration, from the site to the landscape. As landscapes include a variety of land uses, productive and protective, landscape restoration interventions should use a breadth of forest cover approaches to recover degraded forest ecosystems, such as natural regeneration, agroforestry, ecological restoration, and commercial tree plantations in a multifunctional approach to forest and landscape restoration (Aronson et al. 2017).

The global area of commercial tree plantations is currently estimated in 264 million hectares, seven percent of the world's forest cover. Plantation areas have increased at an annual rate of 1.81%, and are expected to continue increasing, due the growing demand for wood, pulp, rubber, and other tree-based products (FAO 2015). Most of this area comprises monocultures of fast growing species that are exotic in many parts of the world (Kelty 2006). Commercial reforestation has traditionally relied on monoculture tree plantations that maximize the production of specific products demanded by markets and are easier to manage (Brancalion et al. 2017). However, several studies have demonstrated

the potential of monoculture tree plantations for large-scale forest restoration in different global regions (Ashton et al. 1997; Scarano 2002; Yirdaw & Luukkanen 2003; Lamb et al. 2005; Pryde et al. 2015), yet this potential was directly dependent upon favorable conditions for the spontaneous recolonization of plantation understory by native species (Puettmann et al. 2015). Large areas of monoculture tree plantations have, however, been established in unfavorable local and landscape conditions for natural regeneration, and the use of these plantations in a forest and landscape restoration context remains an important challenge (Lamb 2018).

Enrichment planting has been proposed as a strategy for making use of existing monoculture plantations in the restoration of tropical forests by introducing native tree species in the understory of monoculture plantations (Puettmann et al. 2015). Enrichment planting would allow to combine the ecological benefits of higher diversity tree stands (Bertacchi et al. 2016; Amazonas et al. 2018), with the establishment of commercial densities of high value timber trees for further exploitation, if desired (Montagnini et al. 1997, Griscom & Ashton 2011). Enrichment planting is done either by sowing seeds or by planting nursery-grown seedlings in a plantation understory. Planting seedlings is more costly, but usually guarantees better survival (Cole et al. 2011). The drivers of enrichment planted seedlings performance are, however, poorly understood (Paquette et al. 2006), and can include several factors as the ecophysiology of planted species, microsite conditions (i.e. Bertacchi et al. 2016), disturbances, and overstory composition (Schweizer et al. 2013). The latter factor, in particular, can play a major role in determining seedlings'

performance in enrichment plantings because it affects the light environment, nutrient availability, and biotic interactions in the understory.

Little research has been conducted, however, on understanding the role that overstory species identity and its phylogenetic history to the enrichment planted seedlings can play in the success of enrichment planting interventions. Previous research by authors of this paper found that seedling performance improved with phylogenetic distance to overstory tree species in monoculture tree plantations in Panamá (Schweizer et al. 2013), but was not affected by it in high-diversity restoration plantations in Brazil (Schweizer & Brancalion 2018). The former finding corroborate expectations of negative interactions among close relatives due to, for example, shared deleterious symbionts (Gilbert and Webb 2007, Parker et al. 2015). The latter finding suggests that the benefits of phylogenetic distance to overstory tree species may be limited to plantations dominated by one or few species that can exert a stronger influence on the planted seedlings.

The potential advantages of far-related species in enrichment plantings suggests that phylogenetic information could guide the selection of species to be planted so as to maximize performance and, in turn, introduce phylogenetic, functional trait and taxonomic diversity to monoculture tree plantations. However, the benefits of using phylogenetic information when choosing species for enrichment planting is still unclear and requires further experimental testing. Here, we conducted an enrichment planting experiment beneath monoculture tree plantations of native tree species in an Atlantic Forest region in

Brazil. We selected seedling species based on their phylogenetic distance to the overstory trees, and expected that seedling height and survival would be predicted by its phylogenetic distance to the overstory. Our premise is that monoculture tree plantations negatively affect close relatives growing in their understory due to the sharing of phylogenetically conserved deleterious symbionts and competition for resources. If models of performance based on phylogenetic information are successful, this tool can avoid the costly and time-consuming need of gathering species and site-specific information, since overstories affect sites in ways that would be captured in the model (i.e. Laughlin & Clarkson 2018).

Methods

Study site

We conducted the study in the Anhembi Experimental Station of Forest Sciences, University of São Paulo, located in Anhembi-SP, southeastern Brazil (22°40' south and 48°10' west, 455 msl.). The climate of the region is mesothermal Cwa (Köppen) with wet, hot summers and dry, cool winters (Alvares et al. 2013). The mean annual temperature is 19°C with an annual precipitation of 1,170 mm. The soil is sandy (5% silt, 13% clay, and 82% sand) with low nutrient content, characterized as Yellow Distrophic Latossols (Embrapa 2006). The study region was originally covered by Seasonal Semideciduous Forest, one of the most threatened vegetation types of the Brazilian Atlantic Forest Biome, with only 7% forest cover remaining (Ribeiro et al. 2009).

Monoculture tree plantations

We selected two replicate monoculture plantations from two native Brazilian Atlantic Forest species: *Esenbeckia leiocarpa* Engl. (Rutaceae) and *Zeyheria tuberculosa* (Vell) (Bignoniaceae). The species have contrasting leaf phenology. *E. leiocarpa* is evergreen and creates a densely shaded and litter-covered understory, whereas *Z. tuberculosa* is deciduous with an open understory usually colonized by exotic, fodder grasses. The two stands of *Z. tuberculosa* were planted between 1984 and 1985, and those of *E. leiocarpa* were established in 1976 and 1989. Trees were planted at 2.0×3.0 m spacing.

Enrichment planting

We selected the seedling species from a pool of available species in a local nursery based on their phylogenetic distance to *E. leiocarpa* and *Z. tuberculosa*, respectively (Table 1). We constructed the tree of phylogenetic relations among all the species using the most recent angiosperm phylogeny at the time of the experiment (R20120829). To estimate the ages of the interior nodes and evenly space the nodes we employed the *Bladj* algorithm from Phylocom (Webb et al. 2008b) and evolutionary ages published by Wikstrom et al. (2001). Before aging the file we checked for internal node inconsistencies as recommended by Gastauer & Meira-Neto (2013). We estimated the distance (in millions of years) that separated each pair of species since they split from their common ancestor using the Phylomatic software, implemented in Phylocom (Webb et al. 2008a). We selected six species to be planted that ranged in their evolutionary distances to the two overstory species (Table 1).

Seedlings were planted in June 2014 when they ranged between 120 and 180 days old, which is the age when they are usually planted in Atlantic Forest restoration interventions. We randomly placed two 6×13 m subplots beneath each of the two monoculture replicate stands. The subplots were placed two meters inward from the plot border to avoid immediate edge effects and with 4-m separation between them. We only placed two replicate subplots beneath the stands due to their size and the need to place a fence around them to avoid cattle grazing. We mowed the areas colonized by the grass *U. decumbens* within *Z. tuberculosa* stands and sprayed glyphosate on the resprouting stumps before enrichment planting. We re-sprayed glyphosate yearly during the study.

We planted the tree seedlings along six 13-m planting lines separated at 1 m from each other in each subplot. We planted 240 individuals total in the *Z. tuberculosa* stands (120 per plot), and 284 in the stands of *E. leiocarpa* (142 per plot). We did not fertilize or irrigate the seedlings to better capture the influence of overstory species in seedling performance. We controlled leaf-cutter ants (*Atta* spp.) in all sites two times after planting. We believe that controlling these ants did not affect the responses of the seedlings to the experiment because this ant species is a generalist (Leal et al. 2014), whereas not controlling them would have had enormous deleterious effects on seedlings performance.

Enrichment planting performance

We assessed individual seedling survival and height at one, seven, and nineteen months after planting. We measured canopy openness in each of the subplots in order to control for differences in resources availability mediated by the overstory, as this variable relates

to temperature, irradiance, and humidity in the understory (Gilbert et al. 2007). We measured canopy openness using a fish-eye lens mounted on a digital camera (Fuji S 5000) at 1 m over the seedlings. We took two photos per subplot and used the average value for each subplot (Figure S1). We took photos during the rainy and the dry seasons, but employed a mean of the two seasons in the analysis as we were not interested in seasonality effects (Fig S1). The photos were analyzed using the program Hemisfer 1.5.3 (Schleppi et al. 2007). We have also classified the seedling species according to their shade tolerance, using information from (Poorter & Kitajima, 2007; Their & Wesenberg 2010), in order to complement the assessment of canopy openness and further disentangle the effects of phylogenetics from the light environment. We did not considered other potential confounding variables, such as soil variables, and used monoculture tree identity as a proxy for them under the assumption that the overstory species modifies the plantation environment and consequently affects seedlings performance in a way that could be predicted by the phylogenetic distance to the seedlings planted, which was the objective of our experiment. Furthermore, previous experience and research has also shown that soil conditions tend not to explain seedling performance in enrichment plantings (Schweizer et al. 2016) or are considered homogeneous in the sites and are thus not included in the models (Dumais et al. 2019).

Data Analyses

We used the number of days an individual seedling survived in a Cox proportional survival analysis. This analysis is semiparametric and does not assume a specific

distribution of the survival function (Cox 1972). We transformed growth to the natural logarithm to reduce differences in height among species. We used height through time in a repeated measures linear mixed effects model. In both, the survival analysis and the mixed effects model we checked the effect of the following independent variables: phylogenetic distance, percent canopy openness and shade tolerance as model predictors. We ranked species from 1 to 3 based on their shade tolerance as either: 1= shade tolerant, 2= medium shade tolerant, 3= light demanding (Table 1). We used a Gaussian distribution in the GLM model and checked model assumptions by visual inspection of the residual plots. We used plot by treatment, subplot, individual ID, and species identity as random factors. We used species identity as a random factor as we were interested in the effect of phylogenetic distance irrespective of the species taxonomic identity. We conducted all analyses in R 3.1.1 packages (R Core Team 2013): “lme4” (Bates et al. 2014) and “survival” (Therneau & Lumley 2009).

Results

Seedlings of the same order and class as the overstory trees showed a significantly lower risk of death compared to conspecifics and to the furthest relative, *C. aschersoniana*. In the case of *Z. tuberculosa*, seedlings in the same family showed a higher risk of dying but this was not the case for confamilials of *E. leiocarpa* (Figure 1). We found phylogenetic distance and shade tolerance, but not average canopy openness, to be significant in explaining risk of death in both monoculture species plantations. However, increased shade tolerance had opposite effects on seedlings survival in each of the two overstory

species plantation (Table S1). This result was driven by the poor survival of the conspecifics regardless of the species shade tolerance (Figure 1). *Z. tuberculosa* is a shade intolerant species whereas *E. leiocarpa* is a shade tolerant species but they both showed poor survival beneath its conspecific overstory.

We looked at various linear mixed effects models that could explain growth variations among the enrichment planted species (Table 2). The model with the lowest AIC value included all three independent variables evaluated: phylogenetic distance, shade tolerance and canopy openness. Yet, the best, more parsimonious model included weak positive correlations between growth and the explanatory variables of phylogenetic distance and shade tolerance (Table S2). The significant correlations found for both monoculture overstory species and phylogenetic distance were driven by the lower growth of conspecifics. Beyond the conspecifics, growth varied within and across species regardless of their phylogenetic distance to the overstory (Fig S2 and Fig S3). Time and its interactions with phylogenetic distance and shade tolerance were significant in the models for *E. leiocarpa* plantings but not in those for *Z. tuberculosa*. We did not find a significant effect of canopy openness on seedlings performance (Table S3).

Discussion

Our results show that enrichment planting interventions should avoid the use of conspecifics when planting beneath monoculture plantations. In addition, the trend of increased performance with phylogenetic distance indicates that enrichment planting

interventions that consider phylogenetic relations when choosing seedlings could improve the success of the planting. The increased influence of phylogenetic distance on seedling performance with time in one of the plantations, suggests that the impacts of phylogenetics in enrichment plantings may increase during seedling development. Research has shown an increase in the presence of far relatives, potentially as a result of increased negative interactions among close relatives, with succession in tropical forests (Letcher et al. 2012, Norden et al. 2012).

Shade tolerance correlated with survival, however, the direction of the correlation differed in each of the monoculture species. Both conspecifics, *E. leiocarpa* and *Z. tuberculosa* seedlings died significantly more than heterospecifics regardless of their shade tolerance, which agrees with expectations of the Janzen-Connell. Decreased performance of conspecifics is also consistent with a previous experiment conducted by one of the authors in Panama (Schweizer et al. 2013). Beyond conspecifics, survival and growth varied greatly depending on the taxonomic identity of the seedlings and thus irrespective of its phylogenetic relationship to the overstory. This may explain the weak effect of phylogenetic distance as predictor in our models and the relevance of other aspects of a species life history that lack a phylogenetic signal in explaining variations in performance. For example, the furthest relative, *C. aschersoniana*, although widely present in the Atlantic Forest biome and thus commonly used in Atlantic Forest restoration, prefers wetter conditions, such as those found in Mixed Ombrophilous Forests, than those drier conditions present at our study site (Moraes 2007).

We found a significant effect of shade tolerance in explaining seedlings performance but we did not find a significant effect of variations in canopy openness. Light may have a stronger effect on enrichment planting success when conducting direct seeding due to its effect on germination and increased incidence of soil borne pathogens on shaded understories (Bertacchi et al. 2016).

Verdu et al. (2012) argued that an understanding of species coexistence based on evolutionary history can be an important tool for ecological restoration. Our results partially corroborate this argument. We highlight our experiment should be taken as a pilot study on the use of phylogenetic tools to guide restoration efforts, as a wider diversity of species and ecosystems should be tested, and for a longer time. However, our results show the phylogenetic ecology approach described here can guide enrichment planting in monoculture tree plantations. One basic use of our results lies in the avoidance of conspecifics, and close relatives such as species within the same genus, when conducting enrichment planting in monoculture plantations. But this phylogenetic ecology approach cannot replace an understanding of the autoecology of each species as key for the successful performance of the planted species.

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Tables

Table 1. Tree species planted in the understory of monoculture tree plantations and their phylogenetic relationship to the overstory species. *

Numbers for shade tolerance indicate: 1= shade tolerant; 2= partial shade tolerant; 3= low shade tolerance. 1: Information on shade tolerance from Poorter & Kitajima (2007); 2: Information on shade tolerance from Thier & Wesenberg (2010)

Tree monocultures				
Family	Seedling species planted in the understory	Shade tolerance*	<i>Zeyheria tuberculosa</i>	<i>Esenbeckia leiocarpa</i>
Apocynaceae	<i>Aspidosperma cylindrocarpon</i> Mull. Arg. ¹	2	Co-ordinal	not planted
Bignoniaceae	<i>Jacaranda puberula</i> Cham. ²	3	Confamilial	not planted
Bignoniaceae	<i>Zeyheria tuberculosa</i> (Vell.) ¹	3	Conspecific	not planted
Boraginaceae	<i>Cordia glabrata</i> (Mart.) A. DC. ^{1,2}	3	not planted	Different class
Fabaceae	<i>Anadenanthera colubrina</i> (Vell.) Brenan ¹	2	Different order	Different order
Lamiaceae	<i>Vitex montevidensis</i> Cham. ²	3	Co-ordinal	not planted
Lauraceae	<i>Cryptocarya aschersoniana</i> Mez ²	1	Different clade	Different clade
Meliaceae	<i>Cedrela odorata</i> L. ²	3	not planted	Co-ordinal

Myrtaceae	<i>Psidium myrtoides</i> O. Berg ²	3	not planted	Different order
Rutaceae	<i>Balfourodendron riedelianum</i> (Engl.) ²	1	not planted	Confamilial
Rutaceae	<i>Esenbeckia febrifuga</i> (A.St.-Hil.) A.Juss. ex Mart. ²	1	not planted	Conspecific

Table 2. AIC values of general linear mixed models of growth variations in the seedlings planted beneath *Z. tuberculosa* and *E. leiocarpa* as explained by the independent variables assessed: PD= Phylogenetic distance to the overstory; CO = Canopy openness, ST = Rank of shade tolerance. * Means the variable was significant in the model at $p < 0.05$.

AIC Values	Esenbeckia	Zeyheria
PD \times CO \times ST	-138.4714	-247.3651
PD \times CO	-223.2931	-342.8501
PD* \times ST*	-234.4871	-388.0541
CO \times ST	-256.7017	-349.9366
PD*	-269.6823	-415.1071
ST	-282.3803	-400.9892
CO	-290.3626	-362.6311

Figure captions

Fig 1. Seedling survival as a function of their phylogenetic distance measured in million years of independent evolution to the overstory species *Zeyeria tuberculosa* (A) and *Esenbeckia leiocarpa* (B).

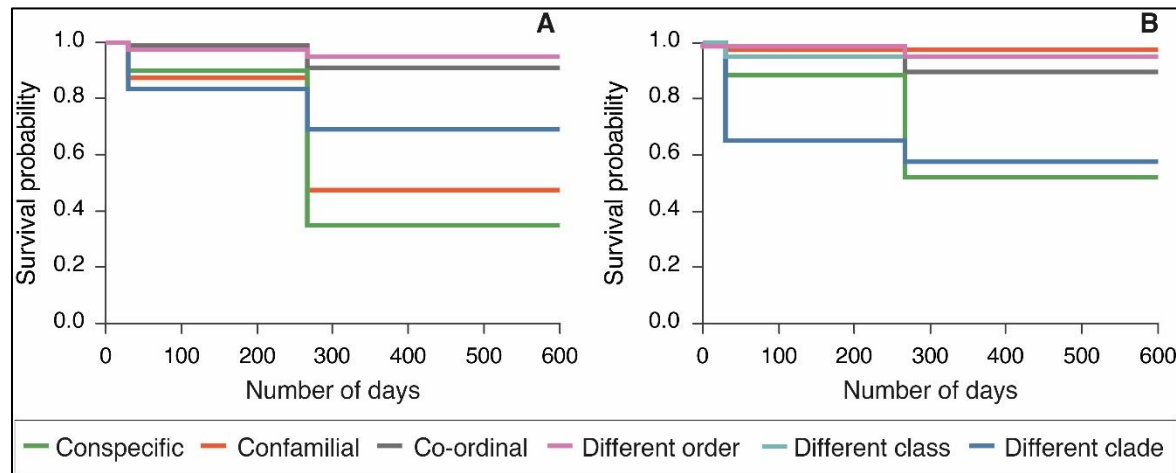


Fig2. Growth through time based on the phylogenetic distance of seedlings to the overstory species *Z. tuberculosa* (A) and *E. leiocarpa* (B). Regressions are significant to $p < 0.05$. The graph depicts the significant interaction of phylogenetic distance with time for the plantings beneath *Z. tuberculosa* (Table 2) showing the positive effect of phylogenetic distance on growth increased with time since planting. This interaction was not significant for the *E. leiocarpa* planting.

