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# No Effect of Variations in Overstory Diversity and Phylogenetic Distance on Early Performance of Enrichment Planted Seedlings in Restoration Plantations

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## Abstract

Enrichment planting is a strategy to increase tree diversity and reintroduce desirable species in restored forests, mainly in fragmented landscapes. However, the conditions that improve the performance of enrichment planted seedlings are not yet fully known. Here, we evaluate the role that overstory taxonomic diversity and mean overstory to seedling phylogenetic distance have as predictors of early performance of native tree seedlings planted beneath mixed-species restoration plantations in the Brazilian Atlantic Forest. By applying a phylogenetic approach, our study responds to recent calls for testing the application of such tools in restoration. We planted 12 mid- to late-successional species beneath a mixed-species restoration plantation with three nested tree diversity levels of 19, 58, and 107 species and estimated the mean phylogenetic distance between each seedling species and the overstory community. Seedling performance was not significantly affected by overstory diversity or mean phylogenetic distance. Overall good performance of the seedlings shows that enrichment planting beneath a mixed-species overstory can be successful even under variations in overstory species number and phylogenetic distance. However, significant species-specific differences in performance highlight the importance of an informed selection of which species to enrich plant.

## Keywords

enrichment planting, forest restoration, seedling performance, phylogenetic ecology, mixed-species plantings

## Introduction

Forest restoration projects have been mostly established in human-modified landscapes, where historical conversion and degradation of natural ecosystems have compromised biodiversity conservation and ecosystem services provisioning (Chazdon et al., 2017; Holl, 2017; Suding et al., 2015). As a consequence of reduced and fragmented forest cover and an intense soil use, natural regeneration potential tends to be limited in agricultural lands (Arroyo-Rodríguez et al., 2017; Crouzeilles et al., 2016; Zermeno-Hernandez, Mendez-Toribio, Siebe, Benitez-Malvido, & Martinez-Ramos, 2015). Under such conditions, mixed species restoration plantations have been promoted to conserve biodiversity and enhance ecosystem functionality (Hulvey et al., 2013; Lamb, 2018; Sapijanskas, Paquette, Potvin, Kunert, & Loreau, 2014).

High-diversity plantations have been particularly recommended for the restoration of certain areas of

the Brazilian Atlantic Forest (Brancalion et al., 2010; Rodrigues et al., 2011), where long-term, continuous deforestation left 12% of its original extent as isolated fragments embedded within agricultural landscapes (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Evidence shows that planting a high number of species leads to self-sustainable forests (Rodrigues, Lima, Gandolfi, & Nave, 2019), partially due to the mixing of early and late-successional guilds. When

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only pioneer species are planted, their early mortality of pioneers can arrest forest succession by allowing invasion of aggressive grasses (Maluf de Souza & Ferreira Batista, 2004).

Despite the planting of a diverse overstory, in some areas, prevailing fragmentation and loss of seed dispersers limits the colonization of restored forests by late successional tree species (Silva & Tabarelli, 2000; Tabarelli, Aguiar, Ribeiro, & Metzger, 2012). In those cases, the understory remains scarcely populated by native tree seedlings (Maluf de Souza & Ferreira Batista, 2004; Rodrigues et al., 2009), showing lower biological complexity, resilience and biomass than native forest remnants (Costa, Melo, Santos, & Tabarelli, 2012; Solar et al., 2015). Poor recruitment in the understory of restoration areas can be overcome by enrichment planting (Bertacchi et al., 2016; Cole, Holl, Keene, & Zahawi, 2011; Lamb, Erskine, & Parrotta, 2005). Enrichment planting consists of the active reintroduction of tree species in the understory of a regenerated or planted forest in a shaded environment created by overstory species (Paquette, Hawryshyn, Senikas, & Potvin, 2009). This technique is useful to introduce species of ecological or economic importance that are not recruiting at the site (Bertacchi et al., 2016; Griscom & Ashton, 2011). But the ecological factors driving the success of enrichment plantings are not yet fully understood.

Overstory composition affects the light environment, the soil nutrients, water availability and determine biotic interactions in the understory, thus playing a major role in determining seedlings' performance in enrichment plantings (Bertacchi et al., 2016; Parrotta, 1995; Schweizer, Machado, Durigan, & Brancalion, 2015). The effects of the overstory on the planted seedlings may be explained not only by its taxonomic composition but also by its phylogenetic relations to the seedling species. Close relatives have been shown to share diseases and herbivores and compete for similar resources due to the conservatism of traits regarding resource use and defense (Gilbert & Webb, 2007; Novotny, Basset, Miller, Drozd, & Cizek, 2002; Parker et al., 2015; Wiens et al., 2010), whereas facilitation among far relatives can aid in their coexistence (Verdu, Gomez-Aparicio, & Valiente-Banuet, 2012). Therefore, seedlings performance is expected to be negatively affected by the presence of close relatives in the canopy (Schweizer, Gilbert, & Holl, 2013).

When aiming to draw practical application guidelines regarding the use of seedlings for enrichment plantings, taxonomic identity becomes a limited variable to employ (Faith, 1992). Understanding the influence of the canopy species on the performance of enrichment planted seedlings using a phylogenetic ecology approach can provide easily applicable, general rules for forest restoration that are especially important in high-diversity tropical

forests, where species-specific planting performance information is generally lacking for most species (Brancalion & Holl, 2016). Phylogeny integrates the evolutionary history of traits that drive the ecological dynamics of communities (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009) and can be a useful predictor of restoration success that has not yet been fully embraced in restoration ecology (Hipp et al., 2015; Verdu et al., 2012).

In this study, we evaluated the early performance (i.e., survival and growth) of nursery-grown seedlings of mid to late-successional tree species planted beneath the canopy of restoration plantations with three levels of species diversity. We tested the hypothesis that seedling performance will increase with overstory diversity and mean phylogenetic distance (MPD) of the planted seedlings to the overstory trees. Our premise is that a higher overstory taxonomic and phylogenetic distance reduces the ecological pressure of negative biotic interactions and competition for resources on the seedlings.

## Methods

### Site Description

The study was conducted in the Anhembi Experimental Station of Forestry, University of São Paulo, located in Anhembi-SP, southeastern Brazil (22°40' S and 48°10' W, 455 masl). The climate of the region is mesothermal Cwa (Köppen) with wet, hot summers and dry, cool winters (Alvares, Stape, Sentelhas, Moraes Goncalves, & Sparovek, 2013). The mean temperature is 19°C and the annual precipitation is 1,170 mm. The soils are sandy (5% silt, 13% clay, and 82% sand) with low nutrient content, characterized as Yellow Dystrophic Latossols (Embrapa, 2006). The study region was originally covered by seasonal semideciduous Atlantic Forest.

### Enrichment Planting

The experiment made use of a previously established restoration plantation conducted in 2008 on a former pasture area covered by the exotic grass *Urochloa decumbens* (Stapf) R.D.Webster (Poaceae). Trees were planted in lines on 45-m × 48-m plots with a spacing of 3.0 m × 1.5 m between individual trees (480 individuals per plot). Selected tree species were planted as seedlings in three, nested, species richness levels: 19, 58, and 107 species per plot, four replicates per treatment (Table 1S), hereafter referred as low-, medium-, and high-diversity treatments. Each diversity treatment contained a subset of the species from the previous level, keeping the same proportion between fast- and slow-growing species. All

treatments had the same number of individuals; therefore, as the number of species decreased, the number of individuals per species increased. These species were randomly planted along the planting lines.

We selected 12 mid- to late-successional native tree species from a list of available species at two local nurseries to do the enrichment planting. The species selected represent a sample of species commonly employed in restoration plantations in the study region (Table 1). Of the 12 species selected, 5 also occurred as overstory trees. Seedlings were planted in February 2014, when they were between 120 and 180 days old. We randomly placed four 6 m × 13 m subplots beneath three replicate plots in each of the three diversity levels. The subplots were placed 2 m inward from the plot border to avoid immediate edge effects and were separated by 10 m from each other.

We planted a total of 2,160 seedlings along six 13-m long planting lines separated at 1 m from each other in each subplot. We did not add fertilizer or irrigate the seedlings to simulate natural regenerating conditions. We controlled leaf-cutter ants in all sites once after planting by distributing insecticide, sulflurami baits. We assumed that ants would not affect the responses of the experiment because the species controlled (*Atta* spp.) is generalist thus with a wide spatial foraging (Leal, Wirth, & Tabarelli, 2014). We monitored seedling apical growth and survival at 1, 5, 12, 16, and 31 months after planting.

### Mean Phylogenetic Distance

We constructed the tree of phylogenetic relations among all the species planted, both in the overstory and as

**Table 1.** Seedling Species Planted in the Understory of the Restoration Plantations.

Family	Species	Species code
Anacardiaceae	<i>Astronium graveolens</i> Jacq.*	<i>Astrgr</i>
Lecythidaceae	<i>Cariniana estrellensis</i> (Raddi) Kuntze*	<i>Caries</i>
Meliaceae	<i>Cedrela odorata</i> L.*	<i>Cedrod</i>
Boraginaceae	<i>Cordia glabrata</i> (Mart.) A. DC.	<i>Cordgl</i>
Lauraceae	<i>Cryptocarya aschersoniana</i> Mez	<i>Crypas</i>
Fabaceae	<i>Erythrina verna</i> Vell.	<i>Erytve</i>
Rutaceae	<i>Esenbeckia febrifuga</i> (A.St.-Hil.) A. Juss. ex Mart.	<i>Esenfe</i>
Bignoniaceae	<i>Handroanthus chrysotrichus</i> (Mart. ex DC.) Mattos*	<i>Handch</i>
Bignoniaceae	<i>Jacaranda puberula</i> Cham.	<i>Jacapu</i>
Lythraceae	<i>Lafoensia pacari</i> A. St.-Hil.*	<i>Lafopa</i>
Rubiaceae	<i>Simira sampaioana</i> (Standl.) Steyererm	<i>Simisa</i>
Lamiaceae	<i>Vitex montevidensis</i> Cham.	<i>Vitemo</i>

Note. Asterisk next to the species name denotes their presence also as overstory trees in the restoration plantations (Table S1).

enrichment planted seedlings using the angiosperm phylogeny: R20120829 (available at: [github.com/camwebb/](https://github.com/camwebb/)). We employed the Bladj algorithm from Phylocom (Webb, Ackerly, & Kembel, 2008) and evolutionary ages published by Wikstrom, Savolainen, and Chase (2001) to estimate the ages of interior nodes and evenly space the nodes between them. Before aging the file, we checked for internal node inconsistencies as recommended by Gastauer and Meira-Neto (2013). An internal node represents a hypothetical common ancestral population and is a point of species diversification (Faith, 1992). We built the phylogenetic distance matrix, which gives the million years that separate each pair of species, among all species pairs using the Phylomatic software implemented in Phylocom. The phylogenetic distances ranged from 26.8 million years (my) for congeners up to 324 my for extraordinary species.

Using the distance matrices, we estimated the MPD of each enrichment planting seedling species to the overstory trees at the plot and subplot scales. However, as results did not differ between the two scales, we report results at the plot scale only. MPD evaluates the average branch length that separates each enrichment planted seedling species to all trees planted in the overstory (Webb, 2000). Branch length is the distance between two nodes in a cladogram in millions of years. The higher the MPD, the further related the overstory species are to that specific seedling species.

There are different phylogenetic metrics that can be employed when linking phylogenetics and community ecology. We chose MPD as it is less susceptible to problems of tree resolution at the tips of the tree than the Mean Nearest Taxon Distance (MNTD) and correlates less with taxonomic diversity than phylogenetic diversity (PD) (Tucker et al., 2017). MPD was significantly different among overstory diversity treatments (Kruskal–Wallis test  $X^2 = 84.894$ ,  $p < .0001$ ) but did not correlate with taxonomic diversity (Figure 1S), thus adding valuable information of the potential effect of evolutionary relatedness between seedlings and overstory species on seedlings performance.

### Light Interception by the Canopy

To control for differences in resources availability mediated by overstory diversity differences, we employed data on intercepted photosynthetic active radiation (iPAR) from the work of Melo Duarte (2018). iPAR is the difference between the PAR that reaches the canopy and the amount that passes through the canopy (Nouvellon et al., 2000), thus encompassing the portion of radiation intercepted by the canopy leaves. The higher the intercepting radiation, the less light reaches the

seedlings planted in the understory, which could affect their performance.

The iPAR was estimated in each one of the treatment replicate plots in 98 different points established by a 3 m × 6 m grid. In the center of each point the iPAR was measured using a leveled Decagon AccuPAR LP-80 ceptometer held 1-m high. In addition, an identical ceptometer was placed outside the plantations to estimate the PAR that reached the canopy. We employed an average of those points that were closer to the enrichment planted seedlings for an estimate of the light environment directly affecting the planted seedlings. Measurements were taken at the peak of the dry season (August 2015), when iPAR should be lowest due to the deciduousness of many of the overstory tree species, and again at the end of the rainy season (March 2016), when iPAR should be highest. Measurements were taken under clear sky conditions.

### Data Analysis

We modeled seedlings performance through time as a function of overstory taxonomic diversity and MPD but checked for the effect of two additional explanatory variables: enrich-planted seedlings identity and light. We modeled survival using the Cox proportional hazards model that allows relating survival of the seedlings through time as a function one of more predictor variables. The Cox model is semiparametric as it does not require a specific distribution of the survival function but does assume that the effect of the predictor variable is constant over time and that they are additive in one scale (Cox, 1972).

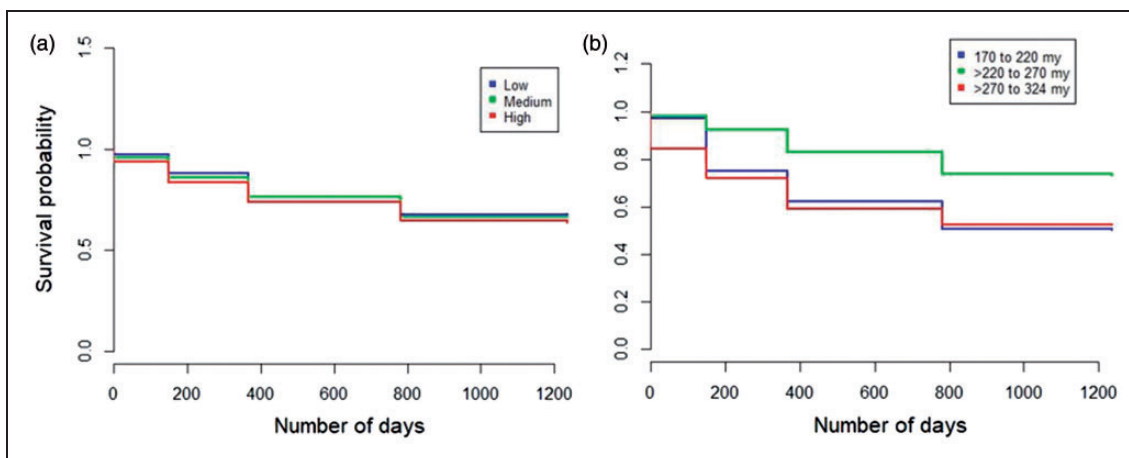
We modeled growth through time using linear mixed effect models. We employed the natural logarithm of growth to reduce variance heterogeneity. Plot by treatment, subplot within each treatment, and individual seedling number were used as random factors. We ran

models using seedling taxonomic identity as a random factor to extract the effect of taxonomic diversity and MPD. We checked model assumptions by visual inspection of residual plots.  $p$  values were obtained by likelihood ratio tests comparing the model derived from each fixed factor, and its interaction with time, against the model without the factor. Analyses were performed in R 3.1.1 packages (R Core Team, 2013): “lme4” (Bates, Maechler, Bolker, & Walker, 2014) and “survival” (Therneau & Lumley, 2009).

### Results

Over 40% of the individuals planted survived through time. However, there were differences among the species. The species *Astronium graveolens* Jacq. had close to 100% survival probability, while the species *Erythrina verna* Vell. had less than 25% survival (Figure 2S). Neither overstory diversity (Cox coefficient = 0.075,  $p > .05$ , Figure 1(a)) nor MPD (Cox coefficient = -0.02,  $p > .05$ , Figure 1(b)) affected seedling survival. The potential significance of MPD on survival was affected by the very low survival (<25%) of two species at opposite extremes of phylogenetic distance: *E. verna* Vell. had an MPD of up to 205 million years to the surrounding overstory and *Cryptocaria aschersoniana* Mez. had an average MPD of 324 million years (Figure 3S). Species survival was best explained by species identity (Table 2S).

Seedlings grew on average 2.27 cm more with every unit of increase in in phylogenetic distance ( $t_{379} = 3.09$ ,  $p = .002$ ). However, overstory diversity or MPD were not significant predictors of seedlings growth in the model (Table 2). There was a significant, positive, effect of time on seedlings growth, and this effect was different across treatments and along MPD. Increased light in the dry season positively affected seedling growth



**Figure 1.** Survival curve of enrichment planted seedlings as a function of (a) overstory taxonomic diversity and (b) MPD.

**Table 2.** Model Analysis of Variance of Seedling Growth in Response to Overstory Taxonomic Diversity, MPD, Light, and Seedling Species Identity.

	df	F value	p
<b>Diversity treatment</b>			
Intercept	6798	15,882.5	<.0001
Time	6798	1,788.9	<.0001
Treatment	6	2.4	.17
Time:Treatment	6798	22.6	<.0001
<b>MPD</b>			
Intercept	6799	13,452.00	<.0001
Time	6799	1,802.20	<.0001
MPD	379	0.77	.38
Time:MPD	6799	101.50	<.0001
<b>Light</b>			
Intercept	6798	15,920.50	<.0001
Time	6798	1,790.50	<.0001
Light dry season	1649	4.58	.03
Light rainy season	1649	0.01	.93
Time:Light dry	6798	48.60	<.0001
Time:Light rain	6798	4.40	.03
<b>Species identity</b>			
Intercept	6779	12,918.29	<.0001
Time	6779	2,849.59	<.0001
Species	6779	417.31	<.0001
Time:Species	6779	170.051	<.0001

Note. MPD = mean phylogenetic distance.

(Table 2), but differences in light interception across treatments (Figure 5S) did not make diversity treatment a significant predictor of performance. Seedling growth through time varied depending on the seedling species (Figure 4S). *A. graveolens* and *Esenbeckia febrifuga* (A.St.-Hil.) A.Juss. ex Mart. grew significantly more than the other species, irrespective of overstory diversity or MPD.

## Discussion

Overall, the enrichment planted seedlings survived well and overcame in 2014, the driest period of the last 80 years in the region. The seedlings did not suffer from the transplant shock reported for semideciduous tropical forest seedlings planted in unusually dry years (Barajas-Guzman, Campo, & Barradas, 2006). We expect, therefore, that a large portion of these seedlings will be able to recruit to larger size classes and play a relevant role in the future functioning of the restored ecosystem.

Seedling performance was not predicted by overstory taxonomic diversity or phylogenetic distance. We observed a weak positive relationship between MPD and seedling growth that indicates that, as expected, seedlings grew better when the overstory canopy was composed of further relatives. However, this result

may be taken with caution as our large dataset inflates the likelihood of a significant response. Relationships between taxonomic and phylogenetic distance and seedling performance is complex. A positive effect of MPD on performance agrees with studies that found that due to competition with close relatives, and the effect of shared enemies, plant species perform best when surrounded by further relatives (Burns & Strauss, 2012; Gilbert & Webb, 2007; Wilson & Stubbs, 2012). In contrast, competition irrespective of canopy species diversity or phylogenetic relatedness may be a stronger factor. A study conducted in a wet tropical forest found a stronger negative effect of overstory trees size than that of phylogenetic relatedness on seedlings first-year survival (Lebrija-Trejos, Wright, Hernandez, & Reich, 2014).

The use of a high number of tree species may have diluted the effect of each overstory species on the performance of the enrichment planted seedlings, thus reducing the importance of enrichment plantings' planning and design based on overstory species diversity or phylogenetic relations for mixed-species restoration plantings. In a previous study conducted in monoculture plantings, we found that enrichment planted seedling performance and foliar health significantly improved the further related seedlings were to the canopy species (Schweizer et al., 2013). The dry conditions of our study area may have reduced the effect of negative biotic interactions. A study by Inman-Narahari et al. (2016) found stronger negative density dependence among seedlings in wet, evergreen, forests than in dry forests. This effect mediated strongly by greater light availability in dry forests can reduce the likelihood of diseases.

Due to the deciduousness of the forest studied, light reaching the seedlings increased in the dry season and positively affected seedlings growth. Research has shown that deciduousness positively influences the seedling community of semideciduous forests (Souza, Gandolfi, & Rodrigues, 2014) as light is a highly influential factor of forest seedling dynamics (Dupuy & Chazdon, 2006). A previous study, conducted also in semideciduous Atlantic Forest restoration sites, found that decreased seedling survival in old restoration sites was driven by reductions in light reaching the understory (Bertacchi et al., 2016).

In temperate forests, canopies composed of a higher number of species have been found to be more complex and capture more light (Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011), thus reducing herb growth and diversity (Chamagne et al., 2016). However, significantly less light interception by the canopy species in the low-diversity treatment did not lead to better performance through time.

The lack of a significant response of seedling performance to changes in overstory diversity levels, MPD, or light interception may have been due to the nested setup

of the canopy species diversity treatments: The medium- and low-diversity treatments contained a subset of the species from the high-diversity treatment. Studies have found that a few dominant species can have very large impacts on ecosystem processes (Hooper et al., 2005). If a dominant species remained in all diversity treatments, there may not have been a significant change in the abiotic or biotic environment that affected the performance of the seedlings. For example, the species *Acacia polyphylla* was planted in all three overstory diversity treatments and was the single most dominant species naturally regenerating in the understory of the plots. This species is a pioneer dry forest species that dominates early successional logging gaps (Park, Justiniano, & Fredericksen, 2005).

Time significantly affected the response of the seedlings to variations in overstory taxonomic diversity and phylogenetic distance. Therefore, we expect that with time seedlings in the high-diversity plantation may outperform those in the low-diversity planting as dominant pioneer overstory species leave the system, and biotic interactions become more important (Chazdon, 2014; Norden, Letcher, Boukili, Swenson, & Chazdon, 2012). Density-dependence effects and negative ecological interactions have long been described as key drivers of old-growth forest functioning and diversity (Paine et al., 2012; Terborgh, 2012; Wright, 2002) with phylogenetic distance among coexisting species increasing with succession (Letcher, 2010; Letcher et al., 2012).

In our experiment, seedling taxonomic identity better predicted variations in performance, highlighting the importance of field tests of species performance on a site by sites basis in forest restoration (González-Tokman et al., 2018). Some seedling species performed much better than others. The species *A. graveolens*, for example, had almost 100% survival until the last census, compared with others with less than 25% survival. Aspects of the species life history that lack a phylogenetic signal are important determinants of seedlings performance.

Recent research shows that seedling recruitment is greater below diverse forest canopies than below monocultures (Wills, Herbohn, Maranguit Moreno, Avela, & Firn, 2017). However, the effects of differential canopy diversity mixes may require long-term studies to better understand how the balance between environmental filters, competition, and other negative biotic interactions varies with time across different levels of canopy diversity during understory assembly. However, for the time we conducted our study, enrichment planting proved successful when conducted beneath mixed species plantations irrespective from the loss of certain species in the overstory but that it is important to adequately select seedling species when planning the enrichment planting as some grow faster and survive better than others.

## Implications for Conservation

The use of mixed species plantings in forest restoration is an important strategy for reintroducing high levels of taxonomic and phylogenetic tree diversity in fragmented landscapes with reduced natural regeneration potential. In addition, enrichment planting of the restored areas with additional taxa that will not disperse to the area can fill in missing species not naturally recruiting. We showed that tree seedlings planted beneath mixed species canopies had good survival overall and that any differences in performance were more due to species-specific traits and could not be predicted by differences in the overstory taxonomic diversity or phylogenetic distance. Therefore, our study highlights the importance of choosing adequate species to guarantee the success of enrichment planting, regardless of canopy diversity.

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## Declaration of Conflicting Interests

The author(s) declare no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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## References

- Alvares, C., Stape, J. L., Sentelhas, P. C., Moraes Gonçalves, J. L., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Metereologist Zeitschrift*, 22, 711–728.
- Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., . . . Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: New insights from forest

- succession, forest fragmentation and landscape ecology research. *Biological Reviews*, 92, 326–340.
- Barajas-Guzman, M. G., Campo, J., & Barradas, V. L. (2006). Soil water, nutrient availability and sapling survival under organic and polyethylene mulch in a seasonally dry tropical forest. *Plant Soil*, 287, 347–357.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and s4*. (R package version 1, pp. 1–7). Retrieved from <http://CRAN.R-project.org/package=lme4>
- Bertacchi, M. I. F., Amazonas, N. T., Brancalion, P. H. S., Brondani, G. E., Oliveira, A. C. S., De Pascoa, M. A. R., & Rodrigues, R. R. (2016). Establishment of tree seedlings in the understory of restoration plantations: Natural regeneration and enrichment plantings. *Restoration Ecology*, 24, 100–108.
- Brancalion, P. H. S., & Holl, K. D. (2016). Functional composition trajectory: A resolution to the debate between Suganuma, Durigan, and Reid. *Restoration Ecology*, 24, 1–3.
- Brancalion, P. H. S., Rodrigues, R. R., Gandolfi, S., Kageyama, P. Y., Nave, A. G., Gandara, F. B., . . . Tabarelli, M. (2010). Instrumentos legais podem contribuir para a restauração de florestas tropicais biodiversas. *Revista Árvore*, 34, 455–470.
- Burns, J. H., & Strauss, S. Y. (2012). Effects of competition on phylogenetic signal and phenotypic plasticity in plant functional traits. *Ecology*, 93, S126–S137.
- Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *Plos One*, 4, e5695.
- Chamagne, J., Paine, C. E. T., Schoolmaster, D. R., Stejskal, R., Volarřík, D., Šebesta, J., . . . Matula, R. (2016). Do the rich get richer? Varying effects of tree species identity and diversity on the richness of understory taxa. *Ecology*, 97, 2364–2373.
- Chazdon, R. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation* (472 pp). Chicago, IL: University of Chicago Press.
- Chazdon, R., Brancalion, P. H. S., Lamb, D., Laestadius, L., Calmon, M., & Kumar, C. (2017). A policy-driven knowledge agenda for global forest and landscape restoration. *Conservation Letters*, 10, 125–132.
- Cole, R. J., Holl, K. D., Keene, C. L., & Zahawi, R. A. (2011). Direct seeding of late-successional trees to restore tropical montane forest. *Forest Ecology and Management*, 261, 1590–1597.
- Costa, J. B. P., Melo, F. P. L., Santos, B. A., & Tabarelli, M. (2012). Reduced availability of large seeds constrains Atlantic forest regeneration. *Acta Oecologica*, 39, 61–66.
- Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, 34, 187–220.
- Crouzeilles, R., Curran, M., Ferreira, M. S., Lindenmayer, D. B., Grelle, C. E. V., & Benayas, J. M. R. (2016). A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, 7, 11666.
- Dupuy, J. M., & Chazdon, R. L. (2006). Effects of vegetation cover on seedling and sapling dynamics in secondary tropical wet forests in Costa Rica. *Journal of Tropical Ecology*, 22, 65–76.
- Embrapa. (2006). Brazilian system of soil classification (2 ed.). D. F. Brasilia 286 pp. Legal instruments can contribute to the restoration of biodiverse tropical forests.
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.
- Gastauer, M., & Meira-Neto, J. A. A. (2013). Avoiding inaccuracies in tree calibration and phylogenetic community analysis using Phylocom 4.2. *Ecological Informatics*, 15, 85–90.
- Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 4979–4983.
- González-Tokman, D. M., Barradas, V. L., Boege, K., Domínguez, C. A., del-Val, E., Saucedo, E., & Martínez-Garza, C. (2018). Performance of 11 tree species under different management treatments in restoration plantings in a tropical dry forest. *Restoration Ecology*, 26, 642–649.
- Griscom, H. P., & Ashton, M. S. (2011). Restoration of dry tropical forests in Central America: A review of pattern and process. *Forest Ecology and Management*, 261, 1564–1579.
- Hipp, A. L., Larkin, D. J., Barak, R. S., Bowles, M. L., Cadotte, M. W., Jacobi, S. K., . . . Weiher, E. (2015). Phylogeny in the Service of Ecological Restoration. *American Journal of Botany*, 102, 647–648.
- Holl, K. D. (2017). Restoring tropical forests from the bottom up. *Science*, 355, 455–456.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., . . . Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35.
- Hulvey, K. B., Hobbs, R. J., Standish, R. J., Lindenmayer, D. B., Lach, L., & Perring, M. P. (2013). Benefits of tree mixes in carbon plantings. *Nature Climate Change*, 3, 869–874.
- Inman-Narahari, F., Ostertag, R., Hubbell, S. P., Giardina, C. P., Cordell, S., & Sack, L. (2016). Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. *Journal of Conservation Ecology*, 104, 773–780.
- Lamb, D. (2018). Undertaking large-scale forest restoration to generate ecosystem services. *Restoration Ecology*, 26, 657–666.
- Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science*, 310, 1628–1632.
- Leal, I., Wirth, R., & Tabarelli, M. (2014). The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. *Biotropica*, 46, 516–528.
- Lebrija-Trejos, E., Wright, J., Hernandez, A., & Reich, P. B. (2014). Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. *Ecology*, 95, 940–951.
- Letcher, S. G. (2010). Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B-Biological Sciences*, 277, 97–104.
- Letcher, S. G., Chazdon, R., Andrade, A., Bongers, F., van Breugel, M., Finegan, B., . . . Williamson, B. (2012).



- Phylogenetic community structure during succession: Evidence from three Neotropical forest sites. *Perspectives in Plant Ecology and Evolution Systems*, 14, 79–87.
- Maluf de Souza, F., & Ferreira Batista, J. L. (2004). Restoration of seasonal semideciduous forests in Brazil: Influence of age and restoration design on forest structure. *Forest Ecology and Management*, 191, 185–200.
- Melo Duarte, M. (2018). *How is forest restoration plantations' functioning affected by tree diversity?* (Doctorate Theses, p. 73) Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Brazil.
- Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14, 1211–1219.
- Norden, N., Letcher, S. G., Boukili, V., Swenson, N. G., & Chazdon, R. (2012). Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. *Ecology Supplement*, 93, S70–S82.
- Nouvellon, Y., Begue, A., Moran, M. S., Seen D. L., Rambal, S., Luquet, D., . . . Inoue, Y. (2000). PAR extinction in shortgrass ecosystems: Effects of clumping, sky conditions and soil albedo. *Agriculture and Forest Meteorology For Meteorol*, 105, 21–41.
- Novotny, V., Basset, Y., Miller, S. E., Drozd, P., & Cizek, L. (2002). Host specialization of leaf-chewing insects in a New Guinea rainforest. *Journal of Animal Ecology*, 71, 400–412.
- Paine, C. E. T., Norden, N., Chave, J., Forget, P. M., Fortunel, C., Dexter, K. G., & Baraloto, C. (2012). Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters*, 15, 34–41.
- Paquette, A., Hawryshyn, J., Senikas, A. V., & Potvin, C. (2009). Enrichment planting in secondary forests: A promising clean development mechanism to increase terrestrial carbon sinks. *Ecology and Society*, 14, 31–46.
- Park, A., Justiniano, M. J., & Fredericksen, T. S. (2005). Natural regeneration and environmental relationships of tree species in logging gaps in a Bolivian tropical forest. *Forest Ecology and Management*, 217, 147–157.
- Parker, I. M., Saunders, M., Bontrager, M., Weitz, A. P., Hendricks, R., Magarey, R., . . . Gilbert, G. S. (2015). Phylogenetic structure and host abundance drive disease pressure in communities. *Nature*, 520, 542–544.
- Parrotta, J. A. (1995). Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science*, 6, 627–636.
- R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: Author.
- Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 1141–1153.
- Rodrigues, R. R., Gandolfi, S., Nave, A. G., Aronson, J., Barreto, T. E., Vidal, C. Y., & Brancalion, P. H. S. (2011). Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management*, 261, 1605–1613.
- Rodrigues, R. R., Lima, R. A. F., Gandolfi, S., & Nave, A. G. (2009). On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation*, 142, 1242–1251.
- Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., & Loreau, M. (2014). Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, 95, 2479–2492.
- Schweizer, D., Gilbert, G. S., & Holl, K. D. (2013). Phylogenetic ecology applied to enrichment planting of tropical native tree species. *Forest Ecology and Management*, 297, 57–66.
- Schweizer, D., Machado, R., Durigan, G., & Brancalion, P. H. S. (2015). Phylogenetic patterns of Atlantic forest restoration communities are mainly driven by stochastic, dispersal related factors. *Forest Ecology and Management*, 354, 300–308.
- Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of north-east Brazil. *Nature*, 404, 72–74.
- Solar, R. R. C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., . . . Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecological Letters*, 18, 1108–1118.
- Souza, F. M., Gandolfi, S., & Rodrigues, R. R. (2014). Deciduousness influences the understory community in a semideciduous tropical forest. *Biotropica*, 46, 512–515.
- Suding, K. N., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., . . . Schwartz, K. Z. S. (2015). Committing to ecological restoration. *Science*, 348, 638–640.
- Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., & Metzger, J. P. (2012). The conversion of the Atlantic forest in anthropogenic landscapes: Lessons for the conservation of biological diversity of tropical forests. *Interiencia*, 37, 88–92.
- Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *American Naturalist*, 179, 303–314.
- Therneau, T. M., & Lumley, T. (2009). *Survival R package* (R version >2.13). Mayo Foundation for Medical Education and Research (Copyright 2000).
- Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., . . . Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, 92, 698–715.
- Verdu, M., Gomez-Aparicio, L., & Valiente-Banuet, A. (2012). Phylogenetic relatedness as a tool in restoration ecology: A meta-analysis. *Proceedings of the Royal Society Biological Sciences*, 279, 1761–1767.
- Webb, C. O. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *American Naturalist*, 156, 145–155.
- Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 24, 2098–2100.
- Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., . . . Stephens, P. R. (2010).

- Niche conservatism as an emerging principle in ecology and conservation biology. *Ecological Letters*, *13*, 1310–1324.
- Wikstrom, N., Savolainen, V., & Chase, M. W. (2001). Evolution of the angiosperms: Calibrating the family tree. *Proceedings of the Royal Society of London*, *268*, 2211–2220.
- Wills, J., Herbohn, J., Maranguit Moreno, M. O., Avela, M. S., & Firn, J. (2017). Next-generation tropical forests: Reforestation type affects recruitment of species and functional diversity in a human-dominated landscape. *Journal of Applied Ecology*, *54*, 772–783.
- Wilson, J. B., & Stubbs, W. J. (2012). Evidence for assembly rules: Limiting similarity within a saltmarsh. *Journal of Ecology*, *100*, 210–221.
- Wright, J. (2002). Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia*, *130*, 1–14.
- Zermeno-Hernandez, I., Mendez-Toribio, M., Siebe, C., Benitez-Malvido, J., & Martinez-Ramos, M. (2015). Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, *18*, 443–455.