



Restoration over time: is it possible to restore trees and non-trees in high-diversity forests?

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Keywords

Ecological restoration; Forest chronosequence; High-diversity forest systems; Long-term restoration; Native species plantations; Restoration ecology; Tropical forest

Nomenclature

Lista de Espécies da Flora do Brasil (<http://floradobrasil.jbrj.gov.br>) and The Plant List (www.theplantlist.org/; revised Jun 2016), accessible at speciesLink network (<http://www.splink.org.br/>)

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Introduction

Restoration programmes provide an excellent opportunity to elucidate successional principles, and to test whether

Abstract

Questions: Do different growth forms have distinct temporal patterns of recovery of their structure, diversity, and composition in restored Atlantic Rain forest? Are tree and non-tree assemblages structured by the same factors?

Location: Atlantic Rain Forest, restored by planting an assemblage of high-diversity tree species, Brazil.

Methods: We measured plant colonization of restoration sites of different ages to evaluate restoration success in terms of species diversity, colonization by non-tree species and structure measures among stands. We used Procrustes analysis to test whether the same conditions that influence tree composition influence non-tree composition (congruence between non-trees and trees present on the same sites).

Results: Many structural aspects of recovering forests, e.g. tree basal area, canopy cover, height, tree richness, and non-tree floristic composition resembled a mature forest within five decades. Although tree species diversity increased according to restoration age of sites, planted sites did not recover the richness of all growth forms even after five decades of restoration, and particularly lacked climbers and epiphytes. We detected significant similarity between corresponding points (tree and non-tree composition) from separate ordinations only in the reference forest. Therefore, naturally assembled communities are more concordant than those originating from active restoration.

Conclusion: Non-tree assemblages respond to different factors than the tree assemblages in restoration sites. Hence, non-tree recovery may not result as a natural consequence of tree recovery, and specific restoration strategies for non-tree species must be applied. Tree richness recovered after two decades. Only half of the non-tree species richness was recovered in old restoration sites, but their composition similarity reached expected levels of reference values. Further studies will investigate if low richness of non-tree species is a consequence of low input of allochthonous propagules (landscape filter) or whether they are arriving but not establishing (environmental filter). Enrichment planting of non-tree species may be required if the problem is propagule input. We recommend enrichment planting should be implemented within 10 yrs after initial restoration planting because of the need for trees as supporting structures. However, if propagules are arriving but not establishing, the solution is to detect which environmental filters are important and to manipulate them through forest management.

reversing the degradation process is possible (Hobbs 2007; Walker & Moral 2009). An important question for forest restoration practice is whether it is possible to restore trees and non-tree species in high-diversity forests. This

question is crucial for successful restoration of the overall forest plant community, but has not been well addressed in tropical forests because of a lack of long-term restoration age gradients for study. Old restored areas can be examined to recognize problems that can prevent successful restoration. Through studying such areas we can obtain clues about how these problems can be solved, avoiding the waste of resources and project failures. Studying a restoration age gradient is an excellent opportunity to assess these questions.

Only a limited number of studies have investigated the influence of planted trees on the subsequent development of forest restoration in high-diversity tropical forest systems. The combinations of planted tree species chosen during restoration can influence natural regeneration (Parrotta 1995; Powers et al. 1997; Senbeta & Teketay 2001; Cusack & Montagnini 2004). Restoration success also depends on planting and maintenance strategies, as well as on characteristics of the surrounding landscape (Rodrigues et al. 2009; Crouzeilles & Curran 2016). Major known barriers to species colonization for replanted forests include lack of seed sources, poor germination, lack of faunal colonization, weed infestation, soil degradation (compaction, absence of seed banks, unsuitable soil microclimates, depletion of soil nutrients), landscape constraints and long and continued histories of anthropogenic disturbance (e.g. fire, fuelwood collection, non-timber forest products, land clearance, etc.) (Wunderle 1997; Holl 1999; Holl et al. 2000; Florentine & Westbrooke 2004; Lamb et al. 2005; Viani et al. 2010; Griscom & Ashton 2011). Some combination of such factors may explain why past restoration projects have not produced high-diversity self-perpetuating forests in the Brazilian Atlantic Forest (Barbosa et al. 2003; Souza & Batista 2004).

Although literature on tropical forest restoration ecology is growing, little attention has been paid to non-tree plant assemblage development (Garcia et al. 2014, 2015). Understorey vegetation is influenced by colonization rates, as well as by canopy composition and structure, via changes in resource availability (light, water, and soil nutrients; Barbier et al. 2008). While the influence of tree composition may not be immediately apparent, trees will likely influence microsite conditions below their crown over time, thus acting as a filter that may be permeable to some species and impermeable to others (Gandolfi et al. 2007). In restoration sites most trees are planted, and the resulting canopy composition may influence non-tree establishment and survival. Hence, we investigated the concordance among naturally established assemblages (non-tree species) and planted trees through time, and in comparison with a reference forest, where all strata were naturally established. Hence, we examined whether trees and non-tree assemblages are structured by the same factors, in

which case creating conditions for tree re-establishment would also help the recovery of other growth forms. If there is no concordance, recovery of non-tree species will need to be manipulated independently from tree recovery. Moreover, by predicting changes in community patterns throughout time, which is an important issue for restoration practitioners, we evaluated how quickly structure, diversity and species composition of different growth forms in restoration sites resembled that of old-growth forest.

Methods

Study area

We surveyed four riparian forest sites, three of which are restoration sites and one is a reference forest, in the Piracicaba, Capivari and Jundiá (PCJ) watershed in São Paulo state, Brazil. Sites are located with 27–65 km of each other (Appendix S1), in a matrix composed of pastures, sugarcane plantations, and urban areas. The restoration sites were chosen for restoration actions because they are situated on the margin of rivers that are water sources for urban areas. Very few studies (among 12%) have compared restored sites in riparian vegetation with reference sites to evaluate restoration success (González et al. 2015). In this study, we compared these sites (12, 23 and 55 yrs) to a reference forest that is the second largest natural remnant (244.9 ha, in size) of forest that was formerly continuous in the municipality of Campinas (Santos et al. 2009). The four sites contain seasonal semi-deciduous forest within the Atlantic Forest biome, have similar climates (mean annual rainfall of 1000–1700 mm (Vasconcellos et al. 2013), mean annual temperature of 21.5 °C (Amazonas et al. 2011), and are all at similar elevations (554–711 m a.s.l.). The hydrology is similar in all sites as they are all riparian forests not subjected to seasonal flooding, and there are no additional streams inside sampling areas. All sites are topographically similar and mostly flat, with only a few small topographic features in the oldest (55-yr-old) restoration site. The restoration sites, all formerly cultivated for sugarcane, were plantations of different ages (12, 23 and 55 yrs). The site sizes are: 30 ha (12-yr site); 50 ha (23-yr site) and 30 ha (55-yr site). The soils have similar pH and physical structure, and details on physical and chemical attributes of soil are available from earlier studies from Amazonas et al. (2011) and Vasconcellos et al. (2013).

The initial restoration was conducted with a combination of pioneer and non-pioneer species in 12- and 23-yr sites and random heterogeneous planting (i.e. without consideration of combining ecological successional groups, planting lines and spacing) in the 55-yr site. These sites were restored via planting of a high diversity of tree species (>70 species), chosen according to availability of seedlings

from commercial sources, as well as from seeds collected in the surrounding landscapes, using mostly native species, but also some exotic species (planted species list available in: Nogueira 1977; Rodrigues et al. 1992; Siqueira 2002; Vieira & Gandolfi 2006). Restoration project goals for these sites were to use native species as much as possible, and to reach maximum possible species numbers. The sites are located in a highly fragmented landscape, isolated from natural forest remnants and with few connections with young secondary natural riparian forests; hence they were unlikely to recover effectively without intervention (Rodrigues et al. 2010; Bertacchi et al. 2016).

Sampling methods

At each site, we randomly selected a 2.5-ha stand, following the sampling design of Cielo-Filho et al. (2007), who established the plots at the reference site. To reduce environmental variation among plots, they were located randomly in forest areas without signs of recent anthropogenic disturbances (e.g. charcoal on the ground, soot on trunks, presence of stumps or coppiced trees). Stands were located near watercourses, but in areas that do not undergo cyclic flooding. Within stands, we then randomly established 30 (10 m × 10 m) plots in the restoration sites following the same design established in the reference forest (Cielo-Filho et al. 2007).

Within these plots, all trees with DBH ≥ 4.8 cm (1.3 m above ground) were identified and measured for DBH and height. Measurements in the reference forest were made by Cielo-Filho et al. (2007) and re-measured in 2010 (Zulqamain et al. 2016); trees in the 23- and 55-yr sites were measured by Amazonas et al. (2011); we measured the trees in the 12-yr site in 2010.

In the restoration sites, most trees were planted and non-tree species were mainly naturally established, and hence we separate these growth forms into two categories: trees and non-trees ('non-trees' as sub-shrubs, shrubs, herbs, epiphytes, hemi-parasites and climbers). We sampled all angiosperm plants except graminoids monthly for 2 yrs (May 2008 to Apr 2010), searching for all reproductive individuals present in all plots (i.e. which presented flowers and/or fruits) at all sites. The same person (LCG) verified all reproductive individuals present in plots through visual observation during the above period, by scanning the plot with binoculars, and by using a portable aluminium clipper to collect epiphytes or climbers in trees. In addition, we also included trees with DBH ≥ 4.8 cm that were not in reproduction during the above period to compare vegetation structure (basal area, density, average height of trees) among studied sites. We identified species with reference to specimens in the UNICAMP herbarium (UEC), consultation in the literature, and consultation

with taxonomists and researchers to confirm identifications. The botanical material collected was deposited in the herbarium collection at the Universidade Estadual de Campinas (UEC) and at the Escola Superior de Agricultura 'Luiz de Queiroz,' Universidade Estadual de São Paulo (ESA). Nomenclature (Appendix S2) follows *Lista de Espécies da Flora do Brasil* (<http://floradobrasil.jbrj.gov.br>) and The Plant List (www.theplantlist.org/) and are digitally accessible at speciesLink network (<http://www.splink.org.br/>).

Within each larger plot (10 m × 10 m; 100 m²), we established smaller subplots to estimate species density for two very abundant species: the shrub *Pombalia atropurpureus* (A.St.-Hil.) Paula-Souza (Violaceae) and the herb *Lepidaploa remotiflora* (DC.) Baker in Mart. (Asteraceae) (25 m² for *P. atropurpureus* and 4 m² for *L. remotiflora*, in view of the high abundance of the latter). To examine details of spatial distribution between the two species, we compared variances of numbers of individuals among subplots (25 m² or 4 m²). As we found similar variances for the two species (evaluation of homogeneity of variances via Levene test: 0.302; $P = 0.302$), we could use the same adjustment. We counted the number of individuals from five of the larger plots (100 m²) and then estimated it from subplots. As a result, we found that, on average, small plots overestimated the value of larger plots for *L. remotiflora* five-fold and that for *P. atropurpureus* four-fold; thus we used those correction factors to estimate the abundance of these species in the entire plot (100 m²). Lastly, we used these values (four and five, respectively, for each species) as an adjustment measure in the final calculation of the estimated density of larger plots for these two species.

To estimate canopy cover, we used a spherical concave densitometer (Lemmon 1957), considered an efficient method for characterizing forest light environments or canopy cover (Englund et al. 2000; Suganuma et al. 2008). As highlighted in Englund et al. (2000), consistency of measurement when using a densitometer is increased by user practice; hence measures of this study were performed by the same person, who had experience with the method. We took one measurement at the centre of each plot, at a height of 1 m. To compensate for peak readings caused by sunflecks, readings were taken facing the four cardinal directions from each point; the average of the four readings was taken as the canopy cover for the plot (Barbosa et al. 2009). We took measurements during the dry season (August), the period with greatest canopy openness, and which is most likely to affect germination and establishment (Vieira & Scariot 2006).

Because of spatial and time constraints and lack of long-term restoration age gradients for study, we considered random sampled plots within each site as replicates of plantation age in our experimental design. Treating sample

plots as independent observations allows for the comparison of different plantations (Sansevero et al. 2011). Such chronosequences provide a cost-effective and quick method for investigating forest change over time (Letcher & Chazdon 2009) and are generally used in restoration project comparisons where no replication across the landscape is possible since replicate sites might not exist (Hurlbert 1984; Michener 1997; Block et al. 2001; Guiliam 2002). More practically, finding other sites with similar environmental conditions or restoration models for comparison is very difficult in the study area, and the approach used is the only way to gain insight into long-term trends. Several studies have been published recently with similar sample designs using the same sites as those studied here (Amazonas et al. 2011; Bonfim et al. 2013; Vasconcellos et al. 2013; Garcia et al. 2014, 2015; Sant'Anna et al. 2014; Silvia et al. 2015). In addition, the performance of old projects is poorly assessed compared with recent projects, and much restoration literature reports on assessment for only 6 yrs after restoration (González et al. 2015); hence any information that can be gleaned from long-term restoration projects is a valuable addition.

Data analysis

Canopy cover, richness, and abundance of tree and non-tree species, average basal area and height of trees, and densities of trees and shrubs were calculated for all plots and sites. Differences among sites were tested with non-parametric ANOVA (Kruskal–Wallis test), with Dunn *post-hoc* multiple comparison tests. We arcsin square root-transformed canopy cover percentage before analysis. We also calculated numbers of individuals per diameter class with intervals between classes based on Spiegel's formula, which considers the range between the lowest and the highest value found for basal area, and numbers of individuals sampled (Spiegel 1976; Felfili 1997). We tested for differences in frequency diameter distribution among sites via chi-square tests. All statistical analyses were carried out using the BioEstat package (<http://www.mamiraua.org.br/pt-br/downloads/programas/bioestat-versao-53/>).

Species diversity (for trees and non-tree species) for each of four sites was calculated using the Fisher index with bootstrap procedure to calculate the confidence limits. This index is less affected by abundances of the most common species than the more frequently used Simpson and Shannon indices. Species richness among sites has been compared in a previous study of Garcia et al. (2015) using rarefaction curves.

To analyse differences in composition of plant communities associated with restoration age, we performed a non-metric multidimensional scaling (MDS) on the Bray-Curtis

similarity matrix, using two data sets: one for tree species and the other for non-tree species. Additionally we calculated abundance-based Chao-Jaccard and Chao-Sørensen indices of similarity (Chao et al. 2005) for trees and non-trees among study areas using the software SPADE (<http://chao.stat.nthu.edu.tw>).

We used Procrustes analysis to test congruence in species composition (presence and abundance of species) between non-tree and tree species present at the same sites. We conducted individual ordinations of trees and non-trees for each area. The Procrustes analyses were then conducted with each pair of ordinations (for trees and non-trees) from each area. The lower the test value, the greater the degree of association between the ordinations (i.e. the concordance between data sets). This method fits one configuration to another, minimizing the sum of squared distances between each point in the fitted configuration and corresponding points in the target solution (Ruokolainen & Salo 2006). The match between data sets provides an indication of processes determining association (Peres-Neto & Jackson 2001). This test is suitable for biotic data sets involving community-scale ecological comparisons (Paavola et al. 2006; Maccherini et al. 2013; Devoto et al. 2014). We used permutation tests (Protest, 1000 permutations) to assess the statistical significance of the Procrustes test, using the 'procrustes' and 'protest' functions of the vegan package in R (R Foundation for Statistical Computing, Vienna, AT).

Results

Canopy cover was related to restoration age and reference, and 55-yr sites had larger canopy cover than 23- and 12-yr sites ($H = 61.83$, $P < 0.0001$; Table 1, with similar canopy cover between 55- and 23-yr); the 55-yr site did not differ from the reference forest ($z = 1.08$, $P > 0.05$; Table 1). From the youngest (12-yr-old) to oldest (55-yr-old) restoration sites, the total number of species (trees and non-trees) ranged from 90 to 122, whereas 221 species were found in the reference forest (Table 1, Appendix S2). Tree richness and diversity showed slight, but progressive, increases with planting age, with both older sites resembling the reference site (Table 1).

Non-tree species diversity in the reference forest was significantly higher than in all restoration sites, and there were no significant differences among restoration sites of different ages (Table 1). Non-tree species richness was markedly lower in restored sites as compared to the reference forest (Fig. 1).

Density of trees was lower in restoration sites compared with the reference site ($H = 45.71$, $P < 0.0001$; Table 1), and diameter frequency distribution varied significantly among sites ($X^2 = 26.42$; $P < 0.0017$; Fig. 2). However,

Table 1. Comparison of vegetation characteristics of the three restoration sites [12-yr-old restored site (12-yr), 23-yr-old restored site (23-yr), 55-yr-old restored site (55-yr)] and the reference sites (RF).

	12-yr	23-yr	55-yr	RF
Canopy Cover (%)	68 ± 2.2 ^c	83 ± 2.2 ^b	91 ± 1.0 ^{ab}	93 ± 0.9 ^a
Species Richness (Tree and Non-Tree)	90	90	122	220
Trees Species	37	57	64	102
Non-Tree Species	53	33	58	118
Fisher a Diversity Index: Trees	11.2 ^c	21.9 ^b	25.5 ^b	38.2 ^a
Fisher a Diversity Index: Non-Trees	9.9 ^b	10.4 ^b	10.9 ^b	35.1 ^a
Density of Trees (ind.·ha ⁻¹)	987 ± 58 ^b	917 ± 55 ^b	963 ± 59 ^b	1713 ± 74 ^a
Basal Area of Trees (m ² ·ha ⁻¹)	26.9 ± 2.2 ^a	34.9 ± 3.3 ^a	36.4 ± 3.6 ^a	41.2 ± 5.4 ^a
Average Height of Trees (m)	6.9 ± 0.2 ^b	7.9 ± 0.3 ^b	10.0 ± 0.5 ^a	9.4 ± 0.3 ^a
Shrub Species	6	10	19	19
Density of Shrubs (ha ⁻¹)	413 ± 1 ^c	326 ± 1 ^c	5400 ± 9 ^a	1220 ± 1 ^b
Sub-Shrub Species	10	2	7	8
Herb Species	27	5	11	15
Epiphyte Species	2	0	5	15
Hemi-Parasitic Species	0	1	1	0
Climber Species	8	15	15	61

Superscripts indicate results of Dunn's *post-hoc* multiple comparison tests, except for Fisher a diversity index where differences were detected with bootstrap (95% confidence interval). Means ± SE.

basal area in restoration sites was similar to the reference forest ($H = 6.002$, $P = 0.111$; Table 1). Average tree height is related to restoration site age, and in the 55-yr site is similar to the reference forest ($H = 60.21$, $P < 0.0001$; Table 1). Density of shrubs was much higher in the 55-yr site than in other sites as a result of the high density (4340 stems·ha⁻¹) of the shrub *P. atropurpureus* (Violaceae), while young forests (12- and 23-yr sites) were similar in shrub density and less dense than the reference forest ($H = 77.31$, $P < 0.0001$; Table 1).

Plant communities of the four sites showed different composition ordinations, and the 23- and 55-yr-old sites were ordered in opposite directions on the second dimension when tree and non-tree species composition patterns are compared among sites, as simply a chance result of the ordination process (Fig. 3a, b). Stress levels for MDS plots

were high for the tree species matrix (0.26; Fig. 3a), but low for non-trees (0.16; Fig. 3b), indicating that sites were not well represented in two dimensions in the case of tree species. The similarity among sites according to tree distribution varied from 2.7% (reference forest vs 12-yr site) to 35% (23-yr vs 55-yr site) for Chao-Sørensen and from 1.4% (reference forest vs 12-yr site) to 21% (23-yr vs 55-yr site) for Chao-Jaccard (Table 2). Similar results were found for the similarity of non-tree species, which varied from 2.7% (reference forest vs 12-yr site) to 43% (23-yr vs 55-yr site) for Chao-Sørensen and from 1.4% (reference forest vs 12-yr site) to 27% (23-yr vs 55-yr site) for Chao-Jaccard (Table 2). We highlight a higher similarity between 55-yr site and reference forest for non-tree species compared with tree species (from 22% for trees and 38% for non-trees; Table 2).

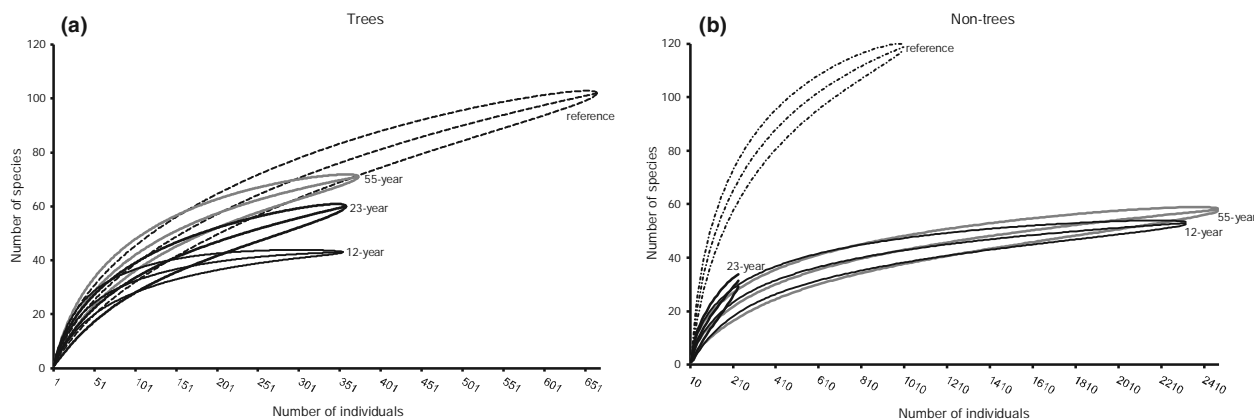


Fig. 1. Rarefaction curves (middle line) and 95% confidence intervals (upper and lower second lines) for total community species richness of tree and non-tree species in the three restoration sites (12, 23 and 55 yrs) and the reference forest (extracted from the original figure of Garcia et al. 2015).

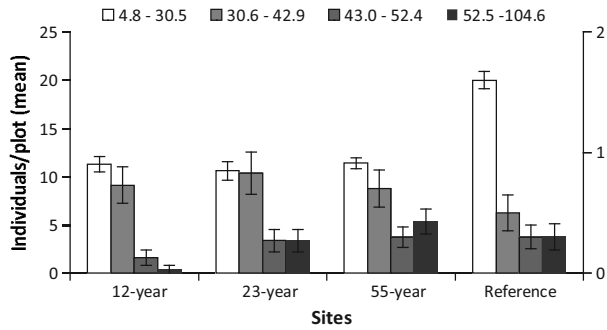


Fig. 2. Mean number \pm SE of tree individuals per diameter class (cm) per plot (100 m²) for three restoration sites of different ages (12-, 23- and 55-yr) and the reference forest. The left vertical axis is values of the first diameter class (4.8–30.5 cm – white bars) and the right vertical axis refers to the other three diameter classes (grey scale).

Comparisons of tree and non-tree species area matrices revealed discordant patterns in all restoration forests. However, concordance was highly significant only between the two matrices in the reference forest (Procrustes analyses; $m^2 = 0.5763$, $P = 0.001$).

Discussion

Findings on structure, diversity and floristic recovery

Our results demonstrated that aspects of vegetation structure, such as tree basal area, canopy cover, height and 40% of non-tree composition were indeed restored over a five-decade period in the restoration forests we studied. While restoration sites showed a progressive increase in tree species with restoration age, reaching reference site richness in 23- and 55-yr sites, colonization of non-trees appears to be a slower process.

Trees reached the same basal area in all restoration sites as in the reference forest, despite the lower tree density, indicating that recovery of this important structural component was possible. This result coincides with findings of many other studies, where restored basal area reached values comparable with older sites within 4–70 yrs of secondary succession (Aide et al. 2000; Denslow & Guzman 2000; Toniato & Oliveira-Filho 2004; Liebsch et al. 2008; Letcher & Chazdon 2009). It is interesting to note from our results that although the smallest tree diameter class (4.8–30.5 cm) was the most abundant class in all of the forests (Fig. 2a), we found higher numbers of individuals only in the reference forest. This size class can represent an intermediate layer between canopy and shrubs. Hence, this layer may reflect increased structural complexity of the natural forest. Although structural complexity may increase with age of planting (Munro et al. 2009), it is likely that this change may take much longer in restoration sites.

Our results suggest progressive increases in tree diversity and richness with age of restoration site. Restoration sites have recruited a considerable number of new tree species, and are on a trajectory toward vegetation structure recovery. We found fairly high levels of recovery in terms of trees, with tree species diversity and richness in the 55-yr site reaching 64% and 63% of the values in the reference forest, respectively. Conversely, non-tree species reached only 31% of reference diversity and less than 50% of reference richness. This contrast is likely a result of the difficulties of restoration in Atlantic Forest systems, a highly diverse ecosystem that is also highly degraded and extensively fragmented. In natural succession, the Atlantic Forest system requires 100–300 yrs to reach full understorey species richness of mature forests, and 1000–3000 yrs to reach mature forest endemism levels (Liebsch et al. 2008). Our data support this prediction at least in broad terms.

We detected significant successional trends of growth forms in restoration forests. Herbaceous and sub-shrub species were dominant during the first decade of restoration, but were replaced by shrubs in the course of five decades. For instance, the densities of the herb *L. remotiflora* of 4270 stems·ha⁻¹ in the 12-yr site are typical of early successional stages and are related to places where canopy openings allow more light input. In the case of the 55-yr site, the shrub *P. atropurpureus*, which is a typical shrub understorey species of seasonal semi-deciduous forests, is found as a dominant species and growth form of the understorey. Similar patterns of decreasing herbaceous species dominance and increasing tree species richness were described for seed banks in Sorreano (2002) in these same restoration sites (23- and 55-yr forests). Climbers are an important component of mature seasonal semi-deciduous forests, but were much scarcer in the restoration sites, as has also been reported in other studies (Salinas & Guirado 2002; Barbosa & Pizo 2006).

The ordinations of trees and non-trees show that the first axis separates reference from restored sites, while most of the difference between the restored sites is along the second axis. This difference can be better understood with reference to Table 2. The 23- and 55-yr sites are the most similar sites according to tree composition and the 12-yr and reference sites the least similar. This pattern emphasizes the large difference between the reference and 12-yr site shown in the ordinations (Fig. 3). Tree similarity among reference and 23-yr or 55-yr sites is broadly the same (~20%); while for non-trees, the 55-yr site is twice as similar to the reference site (~40%) than the 23-yr site (~20%). Mean similarity for climbers among natural forest sites of the same region is ~30% (Santos et al. 2009), and hence it may be concluded that non-tree composition was at least partially recovered in old restoration forests despite the lower richness. This pattern could also be explained by

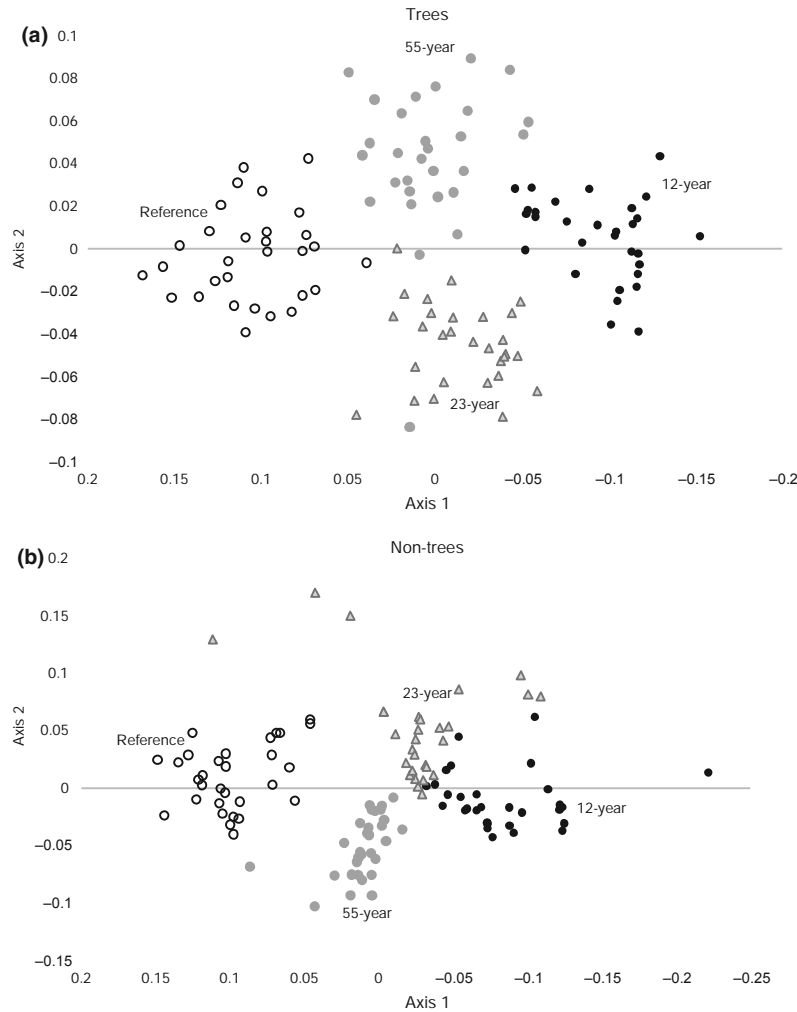


Fig. 3. Non-metric multidimensional scaling (MDS) with Bray-Curtis dissimilarities and 95% ellipsis for total community species richness for three restored sites (12, 23 and 55 yrs) and the reference forest **(a)** trees, and **(b)** non-trees compared to observed species richness in all sites (PERMANOVA: $P = 0.0001$ for trees; $P = 0.0001$ for non-trees).

the restoration history, given that tree species were planted in all three sites while non-tree species naturally colonized these sites from the regional pool of species. Based on natural differences among forest remnants, we would expect a similarity of 40–60% in the same region (Santos et al. 2007). Hence, a tree similarity of ~20% among 23-, 55-yr and reference sites is a substantial floristic recovery, since it is half of what would be expected if these fragments underwent natural regeneration. A bigger difference among tree composition compared to non-trees is also expected because of their increased longevity and slow temporal replacement, the influence of trees chosen in the initial planting on subsequent colonization and stochastic events affecting forest remnants. In conclusion, tree richness recovered in the 23-yr site but with low similarity to the reference site (Chao-Sørensen similarity index value of

~0.22). Whereas richness of non-tree species was not recovered in the 55-yr site, its non-tree community had considerable similarity with the reference forest (Chao-Sørensen similarity index value of 0.38).

Recovering floristic composition after deforestation is a difficult challenge, both in restoration and during secondary succession after disturbance. Some studies found that species composition may never return to that of intact forest, or that the time required may be exceedingly long, such that systems effectively might never naturally recover (Aide et al. 2000). In contrast, other authors have found species composition returning to pre-disturbance levels within 40 yrs after abandonment (Toniato & Oliveira-Filho 2004; Letcher & Chazdon 2009); this is likely a function of landscape configuration.

Table 2. Results of abundance-based Chao-Jaccard and Chao-Sørensen index of similarity for trees and non-trees among three restoration sites [12-yr-old restored site (12-yr), 23-yr-old restored site (23-yr) and 55-yr-old restored site] and the reference forest site (RF).

	Chao-Sørensen/Chao-Jaccard			
	12-yr	23-yr	55-yr	RF
Trees				
12-yr	–	0.171	0.158	0.014
23-yr	0.292	–	0.211	0.127
55-yr	0.274	0.349	–	0.125
RF	0.027	0.225	0.222	–
Non-trees				
12-yr	–	0.246	0.058	0.014
23-yr	0.395	–	0.274	0.114
55-yr	0.109	0.431	–	0.235
RF	0.027	0.204	0.381	–

Chao-Sørensen results are indicated in the lower left and Chao-Jaccard in the upper right.

Effects of planted tree species on composition of recovering forests

Only the reference forest showed concordance between tree and non-tree species area matrices, detected with Procrustes analysis. These findings imply that tree species in the reference site have been influenced by the same environmental conditions as non-tree species. However, we did not detect a significant relationship of tree and non-tree species in restoration sites. Tree and non-tree species have had a longer time to establish in the reference site and may therefore better reflect a climatic community, where all growth forms are responding to the same abiotic and biotic conditions.

Our results provide clues to the interpretation of correlations between tree and non-tree species. Climbers and epiphytes are the growth forms most directly related to trees in view of their direct physical contact with tree bark; hence, it is interesting to find significant concordance between these communities only in the reference forest. Not surprisingly, and corroborating these trends, climbers represented 28% of species in the reference forest, which holds 4.2-fold more species than the maximum number of climber species found in restoration sites and three-fold more epiphyte species. Therefore, the association of tree and non-tree species composition will perhaps be present only in sites with a rich community of climbers and epiphytes, but this needs further investigation.

Recommendations

As the results of Procrustes analyses showed, non-tree communities are responding to different factors than the tree community in restoration sites. Hence, non-tree

recovery cannot be expected as a natural consequence of tree recovery, and specific strategies must be applied to facilitate their restoration. Given that richness of non-tree species has not reached reference numbers, further studies will investigate if this is a consequence of low input of allochthonous propagules (landscape filter) or whether they are arriving but not establishing (environmental filter). If the propagules are arriving but not establishing, the solution is to determine the relevant environmental filters and try to overcome them through forest management. Light availability is a common environmental filter. Under-planting is a method of artificial regeneration in the tropics that favours survival in intermediate light levels, and can be useful for shade-tolerant species such as some epiphyte species that depend on light attenuation by the canopy (Parrotta & Knowles 1999; Callaway et al. 2002; Paquette et al. 2006). Considering the importance of resource provision (e.g. flowers and fruits; Garcia et al. 2014) and functional diversity (Garcia et al. 2015), enrichment planting of epiphytes and climbers after some years of restoration may be required if the problem is propagule input. In this case, it is important that diameter of branches is sufficiently thick to support liana growth (Madeira et al. 2009; Bourlegat et al. 2013; Duarte & Gandolfi 2013), which occurs usually after 10 yrs of restoration according to our observations. Hence, it is necessary to establish whether structural complexity has a significant influence on establishment of these growth forms. As lianas are generally detrimental to the trees that support them, and have significant competitive effects on tree performance (Putz 1984; Tobin et al. 2012) for seedling establishment success, it is better to avoid climbers in early planting stages. Despite the ecological importance of lianas, caution should be exercised in enrichment planting, since liana tangles can potentially lead to arrested succession by reducing non-pioneer tree growth and density (Schnitzer et al. 2000; Schnitzer & Bongers 2002). As epiphytes can take 25 yrs to reach tree branch saturation (Nieder et al. 2001), and larger orchids can have long life-spans of >50 yrs (Zotz 1995), it is also important not to establish them on phorophytes that are pioneer species that have short life spans.

Assessing the success of restoring complex ecosystems such as the Atlantic Forest is especially urgent because of the demand for restoration following changes in the current environmental law (Garcia et al. 2013; Brancalion et al. 2016). Fragments undergoing restoration can conserve not only actual species richness, but also, under proper management, preserve many more species that they retain today. Our study shows the need for continued management of restoration areas, to enhance their diversity conservation role, and at the same time, optimize ecological process. Interesting patterns found in this study provide insights that can be applicable to systems where

fragmentation and degradation influences are strong enough to hamper natural colonization, and where active restoration by total planting and enrichment would be the only option for improving flora recovery.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Black points indicate location of study sites in São Paulo state, Brazil.

Appendix S2. Occurrence of species in the sample plots and their growth forms among three restoration sites (12-

year old restored site (12-yr), 23-year old restored site (23-yr), and 55-year old restored site) and the reference forest site (RF).