



Changes in plant species composition and functional traits along the successional trajectory of a restored patch of Atlantic Forest

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Abstract: Studies on the dynamics of ecosystems undergoing restoration are needed to verify whether they are following the expected trajectory, developing in unexpected ways, or becoming stabilized in a non desirable intermediate stage of blocked succession. In order to elucidate the successional trajectory of the plant community in a 20 ha patch of riparian Atlantic Forest (southeastern Brazil) undergoing restoration, we assessed native tree and shrub species regenerating at 18, 28 and 38 years after planting. We analyzed changes in floristic composition and proportions of functional traits, by comparison with the set of 166 species originally planted most of which were non-native, and with the plant assemblages of two reference riparian ecosystems – a primary-type and a secondary forest, in the same eco-region. Despite isolation from extant forests, immigrating native species have enriched and dominated the community undergoing restoration. Thus, the floristic composition and the proportions of species among functional guilds is becoming more distinct through time from the set of species planted and more similar to the nearest secondary forest (1.6 km), but is still dramatically different from that of a primary forest 50 km away. The proportions of functional guilds among individuals regenerating have shown stability over time but differ in general from the primary forest, particularly for the higher proportion of zoochorous plants in the forest undergoing restoration. The proportion of non-native species as well as of individuals of these species in the community have decreased over time, even though they were the majority of the species planted, refuting the hypothesis of priority effect driving the community assembly.

Abbreviation: SSF–Seasonally Semideciduous Forests.

Introduction

Old restoration and rehabilitation projects provide multiple opportunities for ecological studies on community structure and ecosystem processes to inform and improve modern restoration practices (Valauri et al. 2002, Del Moral et al. 2007, Hobbs 2007, McClain et al. 2011, Lennox et al. 2011). Such long-term ecological studies can help elucidate whether communities undergoing intervention are following a predictable trajectory resembling – both floristically and functionally – the presumed native ecosystems, or they are stagnant in an intermediate, undesirable stage or following a distinct trajectory, without perspectives of reaching the attributes and the resilience of native forests (Vallauri et al. 2002).

Research and observations on the successional trajectories of ecosystems undergoing restoration in different regions of the world suggest a pattern of increasing species diversity over time (Vallauri et al. 2002, in the southern French Alps, Ruiz-Jaen and Aide 2005 in Puerto Rico, Rayfield et al. 2005 in Canada, Letcher and Chazdon 2009 in Costa Rica, McClain et al. 2011 in the USA, and Sansevero et al. 2011 in Brazil). Even though the expected richness would primarily be comprised of native species (SER 2004), restoration projects often include non-natives, particularly old projects such

as the site studied here. If we focus on the fate of non-native species in the communities undergoing restoration, no single tendency has been found. The dominance of the community by those first arrived – the priority effect – has been observed in some studies related to exotics in communities undergoing restoration (e.g., Grman and Suding 2010, in grasslands of California). In a chronosequence of agricultural areas abandoned for up to 52 years in the region of shrub steppe in the US (Kulmatiski 2006), resistant exotic species changed the local flora and continue to prevent colonization by native species in the region, resulting in a relatively stable alternative state. Rayfield et al. (2005), analyzing the role of planted trees and non-native species in boreal forests restored by using different techniques, did not find clear tendencies. These authors found an increasing number of natives over time, but the non-natives were still dominating the restored communities after 25 years. In contrast, a chronosequence survey of abandoned tropical pasture in tropical forest regions, in Puerto Rico, showed that the exotic species *Spathodea campanulata* has provided a favorable environment for the recruitment of various native species and has been replaced by them over time (Aide et al. 2000). Apparently, tropical forests differ from other ecosystem types as for the role of non-natives included in restoration projects. Studies on the role of exotics used in

restoration are very rare and thus do not permit generalizations. Rodrigues et al. (2009) highlight the need for studies to determine whether the understory of restored patches of Atlantic Forest has been colonized by the regional pool of species or if alien species planted are dominating and modifying the functional attributes of the communities in the forests undergoing restoration.

In addition to the geographical range of species planted, their functional traits have also been investigated as factors driving the successional trajectory of restored communities. Sansevero et al. (2011) observed that the proportion of zoochorous species introduced and the continuous supply of resources for dispersers have positively influenced the number of immigrating species colonizing the understory of restored Atlantic Forest, beyond those planted. Other studies have shown, however, that species regenerating spontaneously are mostly different from the set of species planted (Vallauri et al. 2002, in the southern French Alps, Anand et al. 2005 in boreal forests of Canada; Sansevero et al. 2011 in the Atlantic Forest; McClain et al. 2011, in the floodplain of Sacramento River, US). It is hard to know whether the community assembly of restored ecosystems follows patterns related to ecological regions, resilience of the landscapes, or if the patterns are independent of climate or vegetation types. Studies worldwide do not as yet permit generalizations about the trajectory of restored ecosystems. Tropical forests are naturally diverse ecosystems and planting high diversity forests has been widely recommended in Brazil with the argument that there are no seed sources and effective processes of propagules dissemination that could enrich naturally the restored areas (Rodrigues et al. 2009, Brancalion et al. 2010). However, the absence of long-term studies of restored forests with high diversity precludes practical recommendations based on these assumptions (Durigan et al. 2010).

We assessed the regenerating plant community under a riparian forest undergoing restoration in southern Brazil, at three different stages of its trajectory, incorporating abundance and trait data to improve the analyses of the community assembly (Götzenberger et al. 2012). We sought to determine if the forest composition is changing towards the set of species planted (priority effect or initial floristic composition – IFC model, McClain et al. 2011) or it is becoming similar to the regional species pool, an approach related to the Field of Dreams myth (“if you build it, they will come”: a passive relay floristic approach – RF, McClain et al. 2011), where the species from the vicinity will enrich the restored area (Palmer et al. 1997, Hildebrand et al. 2005).

Material and methods

Study area

The riparian forest studied is located at Cananéia Farm, Cândido Mota municipality, state of São Paulo, Brazil (22°47'27" S / 50°28'04" W, at 430 m a.s.l.). Pre-existing vegetation is Seasonally Semideciduous Forest – SSF, one of the Atlantic Forest subtypes, with only 1.6% remaining

in the municipality (Kronka et al. 2005). The regional climate is classified as seasonal tropical (Cwa, according to the Köppen's classification), with the rainy season occurring over the summer and four to six dry months occurring in the winter. Average annual precipitation is about 1,550 mm and the region is subject to sporadic severe frosts. High fertility and clayish texture characterize the local soil, classified as Eutrudox (Pulitano et al. 2004).

Deforestation of the restored area occurred at the beginning of the 20th century for coffee plantation followed by some decades of cattle grazing. After a severe dry season when water sources were depleted and the cattle died, the land use was changed to agriculture and a broad program of soil and water conservation was initiated. The restoration of the riparian forest was part of that program. The restoration project started in 1972, protecting the margins of a reservoir (study area, Fig. 1), extending over a total area of 20 ha. A total of 166 tree species were randomly planted in the whole area, by using nursery-raised seedlings at an average density of 890 trees per hectare. Native and non-native species were planted, as enhancing forest diversity was the goal, and since at that time no recommendation of using only native species existed. Trees were intercropped with agriculture (beans and cassava) up to three years before cultivation was hampered by shade (Pulitano et al. 2004). Chemical fertilizers were not applied, since the natural fertility of the soils was very high. Weeds were manually controlled until canopy closure and the chemical control of leaf cutting ants decreased with time, but never ceased. After 28 years, the density of trees above 5 cm dbh was 1,117 trees ha⁻¹ and the basal area was 51.3 m² ha⁻¹ (Pulitano et al. 2004). After 38 years (Suganuma 2013), density was 1,360 trees ha⁻¹ and basal area 60.7 m² ha⁻¹.

We used two sites as references for the native vegetation in the region: 1) a 9 ha fragment of primary riparian Atlantic Forest, with no obvious evidence of human disturbance, located in similar environmental conditions (soil and climate), in the same watershed, 50 km distant (22°49'02"S/49°59'12"W, at 425 m a.s.l.); and 2) a secondary riparian



Figure 1. Top: Study area in 1974 (Cananéia Farm, Cândido Mota, São Paulo State, Brazil. Photograph: M. A. Souza Dias); Bottom: Study area in 2011 (Photograph: M. S. Suganuma).

forest covering 20 ha, 1.6 km distant from the restored area (22°46'51"S/ 50°28'54"W, at 414 m a.s.l.), used as pasture and abandoned for at least 30 years (only floristic survey).

Data collection

Floristic and functional changes in the plant community were analysed on the basis of relative density of arboreal species populations regenerating in the area undergoing restoration, at three different stages after planting: 18, 28 and 38 years (data collected in 1990, 2000 and 2010, respectively). At 18 years, natural regeneration was surveyed in 40 plots, 5 m² each, randomly distributed through the planted forest. All woody plants ranging from 5 to 200 cm in height were identified and counted (secondary data, obtained from Durigan and Dias 1990). At 28 and 38 years after planting, as well as in the primary forest, ten plots, 100 m² each, were randomly selected, and all woody plants with a minimum height of 50 cm and diameter at breast height from 5 cm were counted and identified. At 38 years after planting, individuals were separated in three size classes – dbh < 1 cm, 1 cm ≤ dbh < 5 cm and dbh ≥ 5 cm. Despite the distinct inclusion criteria, we considered that data obtained at age 18 would bring an important contribution to the understanding of community dynamics. To avoid misinterpretation due to differences in inclusion criteria, data analysis was based on the relative density of species and functional groups regenerating at each stage instead of absolute density.

Functional attributes and native range of the species

Species were classified according to their dispersal strategy (zoochory, anemochory or autochory) and shade tolerance (tolerant or intolerant), which are functionally relevant to the assembly mechanisms addressed, as recommended by Götzenberger et al. (2012). On the basis of the supplementary material of Almeida-Neto et al. (2008), who classified 2,292 arboreal species of the Atlantic Forest biome as a whole, we categorized the species by dispersal strategy. Shade tolerance as well as the native range (native or non-native as occurring or not in the Seasonally Semideciduous Forest) were obtained from Durigan et al. (2004). These authors categorized 501 species of the native flora in the region of this study by functional traits, based on 83 previous floristic or phytosociological studies. For exotic species, dispersal strategy was obtained from Pulitano et al. (2004) and shade tolerance has been observed at the restored area, being categorized as tolerant, by definition, those species surviving or establishing in shaded environments.

Data analysis

Relative density of each species (number of individuals of a species per total number of individuals sampled, expressed in percentage) was calculated at 18, 28, and 38 years after planting, and for the primary forest. Subsequently, for each data set (three ages and primary forest), the following data were obtained: 1) species richness, rarefied at 900 indi-

viduals on the basis of the smaller data set (Magurran 2004), and 2) frequency of functional attributes (for either species or individuals sampled), frequency of species and individuals by geographical range (if native or not from the SSF). For the secondary forest we analyzed only the frequency of attributes among species and not among individuals, since no quantitative data were available.

Jaccard's dissimilarity index (JDI) was calculated among the data sets of the community regenerating at different ages, and also comparing these data sets with the two reference sites (the primary and the secondary forest) and the pool of planted species, in order to verify if the planted species drive the floristic composition of the restored community or if it is evolving towards the native forests. The clustering method was the complete linkage algorithm.

We applied chi-square tests to the frequencies of functional attributes and alien species in the community at different ages, to verify: 1) the null hypothesis that the community does not change with time. In this case, the same frequencies obtained at 18 years would be expected at 28 and 38 years after planting; and 2) the alternative hypothesis that the community undergoing restoration is getting similar to the native forests in terms of frequency of functional attributes. In this case, the expected frequency is that of the reference ecosystem and the observed frequencies were those obtained at 18, 28 and 38 years. Considering that we have a primary and a secondary forest as references, we tested both separately. This approach (observed x expected variance in guild proportions) is recommended by Götzenberger et al. (2012) to analyze guild proportionality in plant community assembly.

Results

A total of 115 arboreal species were sampled in this study: 2,813 individuals (140,650 indiv. ha⁻¹) recorded at 18 years, 2,246 individuals (22,460 indiv. ha⁻¹) at 28 years, 947 individuals (9,470 indiv. ha⁻¹) at 38 years, and 1,222 individuals (12,220 indiv. ha⁻¹) sampled in the native forest. The high absolute density of individuals at 18 years is not comparable, since the criterion of inclusion at this age was different from the other data sets.

Richness and floristic similarity

The richness of the community in regeneration is composed by planted species (31%) in addition to immigrant species from the rare seed sources in the vicinity (69%). The rarefied richness for 900 individuals increased from 30 species at 18 years, to 34 species at 28 years and 46 species at 38 years after planting, still not reaching the 51 species in the understory of the primary forest (Fig. 2). Over the whole period, 72 species were recorded in the sample plots of the forest undergoing restoration, of which 36 were not planted. The proportion of immigrant species (not planted) increased from 39% at 18 years to 48% at 38 years.

The plant community in regeneration had 25 species in common with the set of planted species at 18 years and 24

Table 1. The ten most abundant species in natural regeneration at 18, 28 and 38 years since the beginning of a riparian Atlantic Forest restoration project, southeastern Brazil. RD: relative density. Non-native species are in bold.

18 years		28 years		38 years	
Species	RD (%)	Species	RD (%)	Species	RD (%)
<i>Nectandra megapotamica</i>	63.8	<i>Nectandra megapotamica</i>	64.7	<i>Nectandra megapotamica</i>	23.5
<i>Eriobotrya japonica</i>	13.6	<i>Rollinia rugulosa</i>	6.2	<i>Eugenia uniflora</i>	14.2
<i>Rollinia rugulosa</i>	7.2	<i>Eugenia uniflora</i>	5.4	<i>Eugenia involucrata</i>	13.8
<i>Tabernaemontana catharinensis</i>	2.8	<i>Eriobotrya japonica</i>	4.9	<i>Chrysophyllum gonocarpum</i>	10.1
<i>Ocotea puberula</i>	1.7	<i>Chrysophyllum gonocarpum</i>	3.9	<i>Rollinia rugulosa</i>	8.3
<i>Leucaena leucocephala</i>	1.7	<i>Syzygium cumini</i>	3.5	<i>Cestrum sendtnerianum</i>	4.2
<i>Eugenia uniflora</i>	1.5	<i>Plinia cauliflora</i>	1.3	<i>Psychotria carthagenensis</i>	3.3
<i>Syzygium cumini</i>	1.5	<i>Piper glabratum</i>	1.3	<i>Eriobotrya japonica</i>	2.5
<i>Chrysophyllum gonocarpum</i>	0.9	<i>Lonchocarpus muehlbergianus</i>	1.1	<i>Matayba elaeagnoides</i>	2.5
<i>Tetrapanax papyriferum</i>	0.7	<i>Ocotea puberula</i>	0.8	<i>Rollinia sylvatica</i>	2.1

after 38 years. The number of species in common with the primary forest decreased from 10 at 18 to 9 at 38 years, and with the secondary forests increased from 23 at 18 to 28 at 38 years after restoration planting (Fig. 3a). The huge number of species planted which do not regenerate and the high number of species from the reference forests which never arrived to the forest undergoing restoration make Jaccard's dissimilarity index (Fig 3b) very high. The forest being restored more closely resembled the nearest secondary forest than the set of species planted or the primary forest.

In addition to changes in floristic composition, the relative density of the species has changed through time. From the ten more abundant species in the community at 18 years, only four were among the ten first 20 years later (Table 1).

Native range

From the 166 species planted, 57% are non-natives of the SSF. Among the most abundant species in the community re-

generating, the exotics were four at 18 years and decreased to one at 38 years (Table 1). The only exotic species remaining among the most abundant (*Eriobotrya japonica*) was lowered from the second position (13.6% of the individuals regenerating) to the eighth position (2.5%) in the same pe-

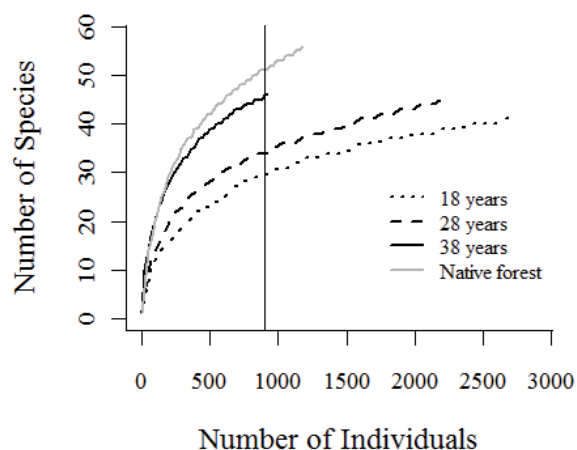


Figure 2. Rarefaction curves at 18, 28 and 38 years from the beginning of the restoration project and in the primary forest reference. The vertical continuous line indicates where the curves are intercepted for 900 individuals (Cândido Mota, Brazil).

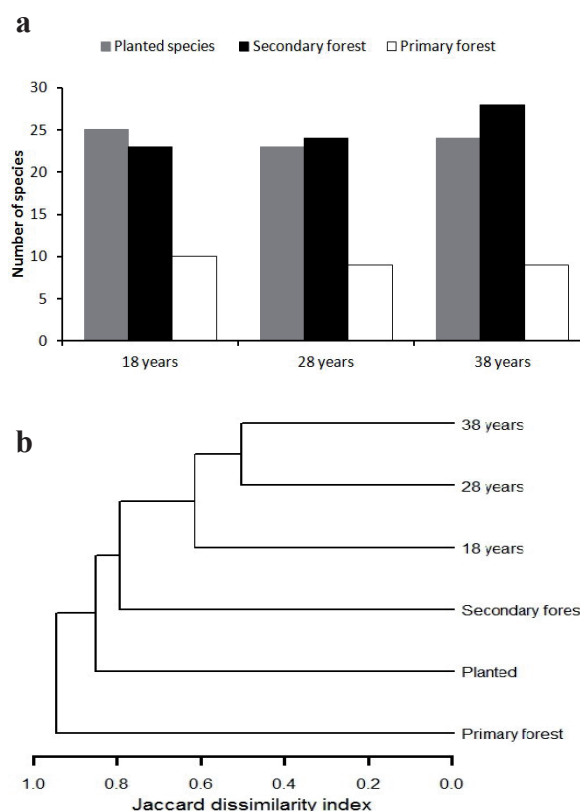


Figure 3. (a) Number of species regenerating at 18, 28 and 38 years after the initiation of restoration efforts, which are common to the set of species planted, the secondary forest and the primary forest; (b): Complete linkage dendrogram with Jaccard's dissimilarity index among the community undergoing restoration at 18, 28 and 38 years, the set of species planted, and the primary and the secondary forests selected as references.

Table 2. Chi-square analyses of the observed frequency of dispersal syndrome, shade tolerance and origin (native range) among species regenerating at different ages of a forest community undergoing restoration, and the set of planted species, the species pool of a secondary forest and the species pool of a primary forest used as references.

Attribute	Age (yrs)	28 years			38 years			Planted species			Secondary forest			Primary forest		
		χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p
Dispersal syndrome	18	0.62	2	ns	15.45	2	0.000	7.8	2	0.020	3.76	2	ns	6.15	2	0.045
	28	-	-	-	8.62	2	0.013	11.32	2	0.003	3.50	2	ns	7.39	2	0.020
	38	-	-	-	-	-	-	29.57	2	<0.001	10.16	2	0.006	18.58	2	<0.001
Shade tolerance	18	12.34	1	<0.001	1.63	1	ns	1.45	1	ns	3.86	1	0.049	80.08	1	<0.001
	28	-	-	-	3.66	1	ns	17.82	1	<0.001	1.71	1	ns	17.26	1	<0.001
	38	-	-	-	-	-	-	5.82	1	0.016	0.43	1	ns	49.44	1	<0.001
Origin	18	16.84	1	<0.001	12.36	1	<0.001	23.28	1	<0.001	-	-	-	-	-	-
	28	-	-	-	0.22	1	ns	69.47	1	<0.001	-	-	-	-	-	-
	38	-	-	-	-	-	-	62.75	1	<0.001	-	-	-	-	-	-

ns: non significant at the $p = 0.05$ level

Table 3. Chi-square analyses of the observed frequency of dispersal syndrome, shade tolerance and origin of the species among plants naturally regenerating in a forest community undergoing restoration at different ages (18, 28 and 38 years) and the set of planted species, the species pool of a secondary forest and the species pool of a primary forest used as references.

Attribute	Age (years)	28 years			38 years			Primary forest		
		χ^2	df	p	χ^2	df	p	χ^2	df	p
Dispersal syndrome	18	4.04	2	ns	4.04	2	ns	319.23	2	< 0.001
	28	-	-	-	0	2	ns	336.76	2	< 0.001
	38	-	-	-	-	-	-	336.76	2	< 0.001
Shade tolerance	18	1.37	1	ns	0	1	ns	16.16	1	< 0.001
	28	-	-	-	0.84	1	ns	4.04	1	0.045
	38	-	-	-	-	-	-	16.16	1	< 0.001
Origin	18	9.0	1	0.003	22.12	1	< 0.001	-	-	-
	28	-	-	-	1.38	1	ns	-	-	-
	38	-	-	-	-	-	-	-	-	-

ns: non significant at the $p = 0.05$ level

riod. *Leucaena leucocephala*, which corresponded to 1.7% of individuals at 18 years, was not sampled after 38 years.

The proportion of non-native species regenerating in the community undergoing restoration was lower than among the species planted since the first assessment, decreasing from 39% at 18 years to 24% at 38 years after planting (Table 2, Fig. 4a). The relative density of individuals by the origin of the species (Table 3, Fig. 4b) has continuously changed, with high predominance of natives in the whole period, increasing from 81% to 93% between 18 and 38 years after planting.

The relative density of exotics in the understory decreases from the upper to the lower size class at 38 years (Fig. 5), reinforcing the observation that the proportion of exotics in the community tends to decrease through time.

Dispersal syndromes and shade tolerance

The frequency of dispersal syndromes among species in the forest undergoing restoration was distinct compared either to the set of species planted or to the primary forest. These frequencies do not differ, however, from the secondary forest (Table 2). The frequency of zoochory, which was 59% among the planted species, has increased over time in

the community undergoing restoration (Fig. 4c). Zoochorous species regenerating in the area being restored increased from 71% at 18 years to 85% at 38 years. Wind dispersed species, which were 25% among those planted, decreased from 15% to 9% in the same period whereas autochorous species, which represented 16% of the planted and 15% of the understory at 18 years, decreased to 6% at 38 years. Analyzing the frequency of dispersal syndromes among individuals instead of regenerating species (Table 2), showed that the community undergoing restoration did not change with time, being constant the high dominance of zoochory (96% to 98%). This result is remarkably different from the primary forest, where autochory was predominant (72%) (Fig. 4d). This relative abundance of autochory in the primary forest was due to the high density of *Actinostemon conceptionis* (45%) and *A. concolor* (16%), both shade tolerant treelets dominating the understory.

The frequency of shade tolerant species (Fig. 4e) regenerating did not differ from the set of species planted (56%) at 18 years after planting (Table 2). At this time, the proportion of this attribute in the community undergoing restoration (60%) was distinct from both the primary (90%) and the secondary forest (75%). From 28 years on, the frequency of shade tolerant species in the community being restored became different

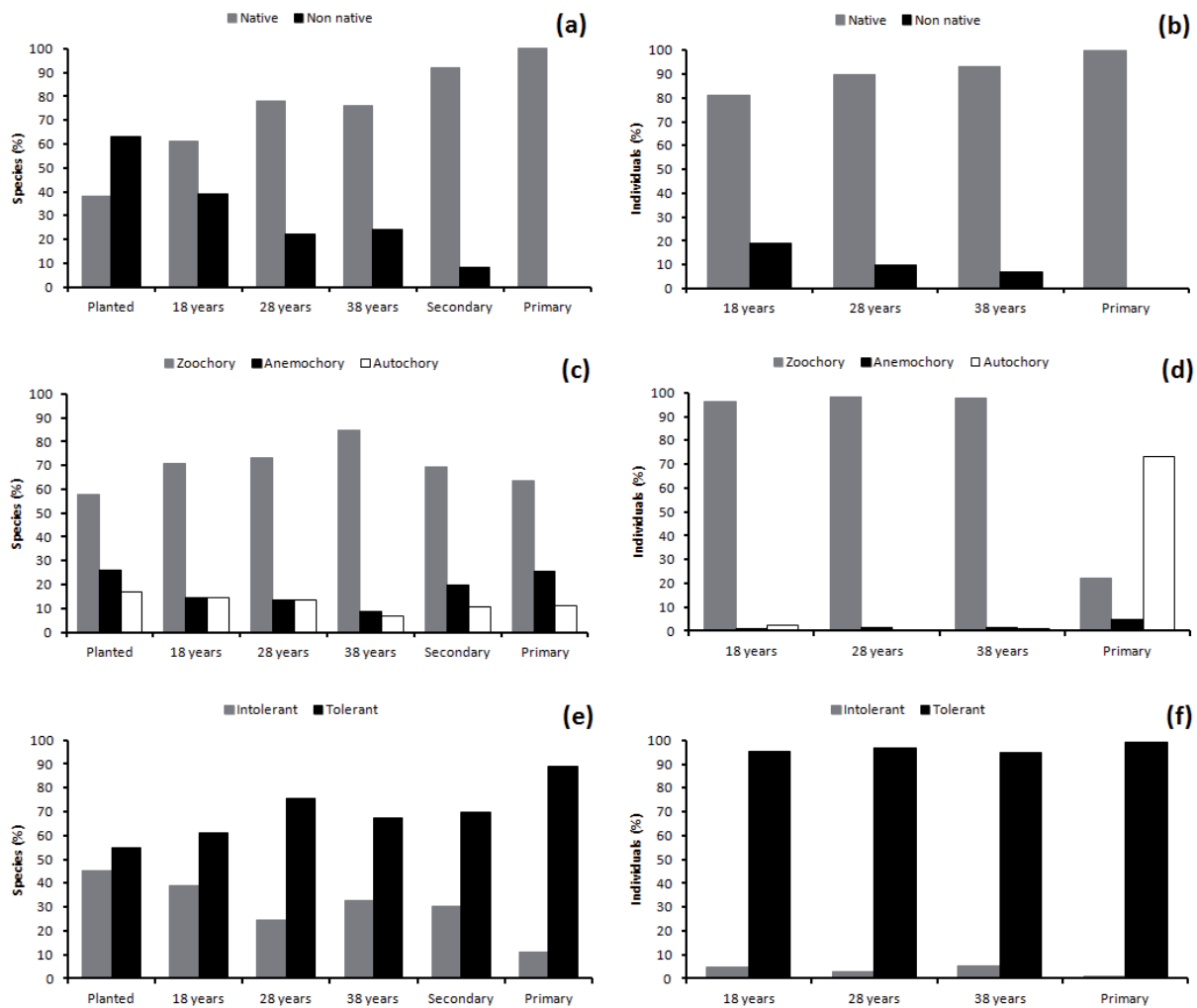


Figure 4. Proportion of species (left) and individuals (right) classified according to functional traits and native range in the planted stand, the regenerating community at different ages (18, 28 and 38 years), the secondary and the primary forest (Cândido Mota, Brazil). Native range of species (a), and native range of individuals (b); dispersal syndromes of species (c), dispersal syndromes of individuals (d), shade tolerance of species (e), shade tolerance of individuals (f).

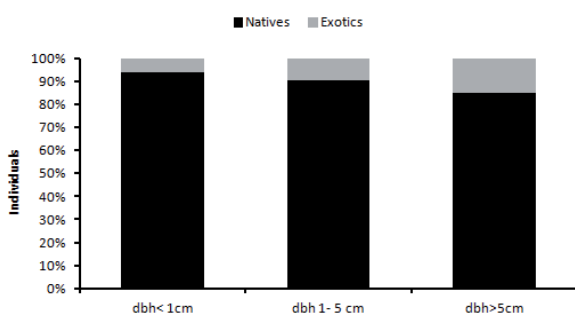


Figure 5. Proportion of native and non-native species regenerating in three size classes, in a riparian forest at 38 years after the initiation of restoration efforts (Cândido Mota, Brazil).

from the set of planted species and similar to the secondary forest (Table 2). The relative abundance of shade tolerance (Table 3) did not change in a predictable manner along the successional trajectory in the community undergoing restoration. Shade tolerance among individuals was high since the first assessment (95-97%) and did not differ from the primary forest at 18 and 38 years (Fig. 4f).

Discussion

Planted trees or regional species pool? Who is colonizing the restored forest?

Of the 166 species planted in the whole area, more than 80% were not found in the samples aimed to monitor autogenic regeneration. Most of the species planted that were not

found to be regenerating were non-natives to this ecological region, never reproducing or establishing in the community undergoing restoration (e.g. *Adansonia digitata*, *Tipuana tipu*, *Juglans regia*, *Artocarpus heterophyllus*, *Pinus strobus*). Native trees not able to establish in the area being restored as yet, consisted of another portion. Our research showed that most species in regeneration under the planted trees are arriving from seed sources in the vicinity. Changes in the forest structure and in ecological processes through succession likely provide high diversity of niches, attracting seed dispersers and, as a consequence, facilitating colonization by new plant species (McClanahan and Wolfe 1993, Ruiz-Jaén and Aide 2005, Jules et al. 2008).

The distance of propagule sources to study area has been mentioned as a strong factor constraining the development and sustainability of restored ecosystems (Zimmerman et al. 2000, Guariguata and Ostertag 2001, Souza and Batista 2004, Hobbs and Norton 2004, Battaglia et al. 2008, Wright et al. 2009). The high and increasing proportion of immigrant native species in the community being restored, however, means that dispersal agents are bringing seeds of native species from the neighborhood. Thus, we can consider that 1.6 km does not impose a threshold of distance for seed sources in this ecological region, a much larger distance than the 100 m mentioned by Rodrigues et al. (2009). The distance after which a native remnant cannot contribute to richness increase in a community undergoing restoration is still to be demonstrated and should be distinct among ecological regions. We cannot expect, however, that the primary forest analyzed, at a 50 km distance, even while serving as a good functional reference model, can be a seed source for the area being restored. The few species in common between this fragment and the forest undergoing restoration are widespread species which occur in the whole SSF.

In addition to species richness, the relative abundance of planted species regenerating, even native, was low since the first assessment, and has decreased with time in the community being restored, while the abundance of immigrating species increased continuously. These results refute the priority effect, when the first species to arrive decrease the success of later species (Facelli and Facelli 1993, Grman and Suding 2010). The priority effect has been often demonstrated for herbaceous communities in the short term, but has not been demonstrated for forests or even for other ecosystem types in the long term.

Clearly, the arboreal species planted in the studied area, even in extremely high diversity, are not the ones driving the community assembly, and that undermines the argument that high diversity of species planted is the key for restoration success (Rodrigues et al. 2011; Brancalion et al. 2010). As observed by Johnston (2011) in restored riparian ecosystems at Sacramento river, USA, by Florentine (2008), in restored tropical forests in Queensland, Australia, Parrotta et al. (1997) in the Amazon, Souza and Batista (2004) and Barbosa et al. (2007) in the Atlantic Forest, the combination of species which can provide favorable conditions to foster successional processes is more important than planting a large number of species which will not persist long term.

Natives vs. alien species? Who wins the battle of the community assembly?

In spite of the huge number of non-native species planted in the study site, the decreasing proportion of these species and their relative abundance over time point to an unexpected capacity of the ecosystem to spontaneously eliminate them, discarding the risk of dominance by exotics. The dominance of natives over exotics has also been observed along the successional processes of old fields towards canopy closed forests (Meiners et al. 2002). However, the dominance of exotics has been recorded in other biomes, such as the transitional forest zone between Boreal coniferous forest and Carolinian deciduous forest in Canada (Rayfield et al. 2005), as well as grasslands in California (Grman and Suding 2010). The dominance of exotics can also vary among the species considered and their attributes (Aide et al. 2000). The distinct role of exotics among different ecosystems undergoing restoration can be analyzed from the point of view of biological invasions. Davis et al. (2000) consider that community's susceptibility to invasion is directly related to the availability of resources such as light, nutrients and water. Fine (2002), trying to explain the low occurrence of exotics in undisturbed tropical forests, did not find a clear relationship with high diversity of species or functional types, concluding that it is most likely due to the requirement of shade tolerance, which is a rare attribute among exotics transported to tropical countries. The competition for those resources, light in particular, increases considerably with time in tropical forest communities undergoing restoration, with natives tending to win the battle whenever exotics are not shade tolerant.

The use of non-native species in ecological restoration is discouraged (SER, 2004). There are, however, many situations where the biotic and abiotic thresholds of degradation were surpassed and most natives cannot readily establish themselves, but exotics can assist the recovery of ecological structure and slowly trigger the desired successional processes. Such species can provide shading, inhibiting the entrance of undesirable species, such as invasive grasses (Modna et al. 2010), and facilitating the establishment of desirable species of more advanced successional stages (Aide et al. 2000, Zavaleta et al. 2001, Ewel and Putz 2004, Wright et al. 2009). Two reviews on the regeneration of native species under purely commercial plantations with exotic species in Brazil (Viani et al. 2010) and elsewhere (Brockerhoff et al. 2008) reinforce the observation that native species tend to dominate the understory of planted forest stands.

The proportionality of trait attributes

When the ecosystem undergoing restoration was compared to native forests on the basis of functional traits of the plant community, we observed that those species which are shade tolerant and dispersed by animals were more successful in colonizing new habitats than others. As observed by Duarte et al. (2011), colonization success under tropical forests depends on the plant response to habitat conditions and also to the characteristics of the diaspores. Even the proportion of

shade tolerant species in the study site increased from the planted trees to the regenerating community, after 28 years it has shown stabilization at the level of the secondary forest. The stable proportion of shade tolerant plants since the age of 18, just a little under the proportion of the primary forest, is certainly a response to the rapid structural evolution of the restored riparian forests in this region, reaching the reference forests after 9 years in canopy cover and after 15 years in basal area (Melo and Durigan 2007). The light availability in the forest undergoing restoration has been, probably, very similar to that in the reference forests since the earlier successional stages.

If functionality in terms of shade tolerance was quickly recovered and stabilized, the same was not observed for dispersal strategies. The proportion of zoochory among species has increased through time and, counter intuitively for a fragmented landscape, was higher in the last survey of the community being restored than in either, the secondary or the primary forest. All observed proportions fit in the range of 45.5 to 90.7% of endozoochorous species in a single patch, found by Almeida-Neto et al. (2008) throughout the Atlantic Forest, but are lower than mentioned for patches of evergreen Atlantic Forest (Tabarelli and Peres 2002, Liebsch et al. 2008, Sansevero et al. 2011). As demonstrated by several previous studies (Willson et al. 1989, Tabarelli et al. 2003, Almeida-Neto et al. 2008, Duarte et al. 2009), the proportion of zoochory is inversely correlated to annual mean precipitation. Considering that the duration of the dry season is the main conditioning factor for species composition of the SSF (Oliveira-Filho and Fontes 2000), the proportions of species found correspond to what was expected.

When species abundance (proportion of individuals) was analyzed instead of presence alone, the predominance of zoochory in the community undergoing restoration was even more remarkable, reaching levels as high as that found in the evergreen forest (Liebsch et al. 2008). We consider that this can be less related to the success of biotic dispersal, than to the fail of abiotic dispersal within the community being restored. We cannot disregard either, abiotic filters instead of dispersal filters driving the community assembly in the study site, by constraining species establishment. Soil water availability in the riparian zone favors the production of fleshy fruits (Hampe 2003) and low light availability under the high biomass of the forest being restored is a limiting factor for light demanding arboreal species (Dupuy and Chazdon 2006) like the anemochorous overstory trees (Richards 1996). We believe that the riparian habitat within a seasonally dry region poses less restrictions to species establishment than randomly expected for the region. Thus, the abiotic assembly rules (Götzenberger et al. 2012) select for a proportion among guilds in the riparian zone of the seasonally dry forest which is more similar to evergreen forests.

Is the restored forest evolving towards one of the reference ecosystems?

The ecosystem undergoing restoration is becoming floristically and functionally more distinct over time from the set

of species planted and more similar to the nearest secondary forest (1.6 km), but is still different from a distant primary forest (50 km). The selection and use of pristine ecosystems as references to drive projects and to evaluate the success of restoration have been criticized as they would be a goal not possible to reach (Pickett and Parker 1994, Hobbs 2007, Choi 2007, Suding 2011). Our results indicate, indeed, that the primary forest analyzed is an unrealistic goal for most of its functional traits and floristic composition at least for the time frame of this study. The secondary forest, in this case, would be a more feasible goal, at least for some of its functional attributes. We consider that the goal of a restoration project should be broad, ranging from secondary to primary forests in the same eco-region, and exclusively for those attributes whose values along the successional trajectory are predictable.

Conclusions

The contribution of the planted species to the floristic composition of the community undergoing restoration was low and decreased with time. Across the succession in restored tropical forests, the first species to arrive – the set of species planted – will not necessarily dominate the community long term, refuting the priority effect. The importance of the identity and number of species to plant, therefore, must be reconsidered when designing restoration projects.

Even in the highly fragmented landscape studied, native immigrants are arriving and slowly dominating the restored community. The limitations for the arrival of new species beyond those planted are not clear, but the potential contribution of extant forest fragments to the colonization of forest communities undergoing restoration is certainly larger than it has been claimed, at least for the Atlantic Forest.

The alien tree species planted have gradually lost space in the community to the advantage of native species, and their presence, alone, does not appear to threaten the “naturalness” of the forest. Non-native species, therefore, should not automatically and indiscriminantly be extirpated from sites undergoing restoration. Monitoring is recommended to provide early detection of exotics which offer real threat of dominating the restored forests or, worse, of invading the natural ecosystems in the vicinity. These invaders should surely be removed.

The relative abundance of the dominant species in the community keeps changing with time, but the proportionality in terms of shade tolerance and dispersal strategy stabilizes early in the successional process, not necessarily equating to the primary forests of the same region. Apparently, the proportion of functional guilds is driven more by abiotic filters than by interspecific interactions in tropical forests.

The successional processes in a tropical forest undergoing restoration leads to increasing diversity with time, which depends considerably on the effective seed sources in the vicinity. Over time, the floristic composition of restored forests will be determined by the regional species pool, as opposed to the set of species planted. On the other hand, the proportions of functional attributes in the community depend on the abiotic filters constraining species establishment.

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