RESEARCH ARTICLE

Indicators of restoration success in riparian tropical forests using multiple reference ecosystems

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Forest restoration by planting trees often accelerates succession, but the trajectories toward reference ecosystems have rarely been evaluated. Using a chronosequence (4–53 years) of 26 riparian forest undergoing restoration in the Brazilian Atlantic Forest, we modeled how the variables representing forest structure, tree species richness and composition, and the proportion of plant functional guilds change through time. We also estimated the time required for these variables to reach different types of reference ecosystems: old-growth forest (OGF), degraded forest, and secondary forest. Among the attributes which follow a predictable trajectory over time are: the basal area, canopy cover, density and tree species richness, as well as proportions of shade tolerant and slow growing species or individuals. Most of the variation in density of pteridophytes, lianas, shrubs and phorophythes, proportion of animal-dispersed individuals, rarefied richness and floristic similarity with reference ecosystems remain unexplained. Estimated time to reach the reference ecosystems is, in general, shorter for structural attributes than for species composition or proportion of functional guilds. The length of this time varies among the three types of reference ecosystems for most attributes. For instance, tree species richness and proportion of shade tolerant or slow growing individuals become similar to secondary forests in about 40 years, but is estimated to take 70 years or more to reach the OGF. Of all the variables considered, canopy cover, basal area, density, and richness of the understory—by their ecological relevance and predictability—are recommended as ecological indicators for monitoring tropical forest restoration success.

Key words: assembly rules, chronosequence, ecological indicators, forest structure, functional guilds, linear models, monitoring, semideciduous tropical forest

Implications for practice

- The expected values of most plant community attributes for each age of forest restoration plantings can be predicted by modeling on the basis of a chronosequence, facilitating monitoring of intermediate goals.
- The best indicators for monitoring forest communities being restored are: canopy cover, basal area, density of saplings, and richness of the understory.
- Reference ecosystems for setting final goals of restoration projects should represent the entire range of histories and regimes of disturbance within a same ecological region.
- Within the same ecological region, forest restoration by planting trees result in a standard trajectory, predictable for most attributes of structure, richness, and functional guilds, which should guide the establishment of targets for restoration. Floristic composition, however, is not predictable.

Introduction

Interventions aiming to restore tropical forests generally accelerate the recovery of plant communities in areas degraded by human occupation. The intentional planting of trees (restoration plantings) allows the forest structure to quickly recover and thereby provides a suitable habitat for colonization by late successional species (Chapman & Chapman 1996; Aide et al. 2000;

Souza & Batista 2004; Chazdon 2008; Holl & Aide 2011). Even in highly degraded environments, like most pasture areas (Florentine & Westbrooke 2004; Sansevero et al. 2011) or mining areas (Parrotta et al. 1997; Parrotta & Knowles 1999), the planting of tree species facilitates the process of recolonization by native species, which originate from the regional species pool (Lugo 1992; Parrotta et al. 1997; Ruiz-Jaen & Aide 2005b). However, both the understanding and prediction of successional trajectories of forest restoration through planting is understudied (Souza & Batista 2004; McClain et al. 2011; Sansevero et al. 2011; Suganuma et al. 2014).

In forest restoration there are different theories about the outcome of succession from a disturbed state to the final state of the ecosystem. From the different theories, one can expect

that forest restoration (1) will lead the ecosystem being restored to a state similar to natural ecosystems attributes (White & Walker 1997; Society for Ecological Restoration International Science and Policy Working Group [SER] 2004) or (2) will lead to successions of alternative stable states which are different from the natural ecosystems in their functional and structural aspects (Hobbs et al. 2009), or even, (3) will lead to ecosystems that are different in species composition, although functionally similar to the original forest (Hobbs & Norton 2004; Hobbs et al. 2006; Lugo 2010). Studies on secondary tropical forests undergoing succession point to the third alternative (Liebsch et al. 2008; Dent & Wright 2009), but there is no evidence that this is also true for forests being recovered by active restoration intervention.

In addition to there being no consensus on the final result of the restoration, there are also different theories about the pathways that can lead to this final state. To be able to recognize when an ecosystem requires restoration interventions depends on the ability to predict the effect of interventions and non-interventions on the successional trajectories (Suding and Hobbs 2009; Holl & Aide 2011), to ensure that there will be no unnecessary waste of labor, time and money (Ruiz-Jaen & Aide 2005a; Florentine 2008). Three possible trajectories for ecosystem restoration were proposed by Suding and Hobbs (2009): (1) the gradual continuous model, where changes in the environment and the successional trajectory of the community gradually drift, becoming similar to the ecosystem before the disturbance; (2) the stochastic model, where there is an imbalance between changes in the ecosystem and changes in the environment without any predictable trajectory; and (3) the threshold model, in which small changes in environmental conditions lead to abrupt changes in the ecosystem from one stable state to another.

Data obtained from chronosequences have been used to build predictive models of community changes over time, using the gradual continuous model pattern in attributes such as forest structure, sapling density, richness and biomass (Chazdon 2003; Chazdon et al. 2007; Letcher & Chazdon 2009; Maza-Villalobos et al. 2011). The majority of these studies were performed to model the successional trajectory of secondary forests (SFs) (Chazdon 2003; Chazdon et al. 2007; Liebsch et al. 2007, 2008; Letcher & Chazdon 2009; Lebrija-Trejos et al. 2010; Maza-Villalobos et al. 2011). In the case of restoration planting, only a few studies on succession exist (Reay & Norton 1999; Souza & Batista 2004; Ruiz-Jaen & Aide 2005b; McClain et al. 2011; Suganuma et al. 2014) and they are insufficient to assess either the effectiveness of this technique in triggering successional processes or in predicting whether the restoration goals can be achieved.

Monitoring the evolution of communities requires good ecological indicators, which remains a challenge in evaluating the results of restoration interventions (Ruiz-Jaen & Aide 2005a; Suding 2011). Specifically, this requires the selection of a maneuverable set of ecological indicators that together meet the following criteria: (i) the variables are easily measured, (ii) sensitive to stresses on the system, (iii) have predictable and known responses to disturbances or anthropogenic stresses, (iv)

are anticipatory and can predict changes that can be prevented by management actions, and (v) are integrative (Dale & Beyeler 2001). A large set of variables have been used as ecological indicators for tropical forests undergoing restoration, such as stem density, basal area, aerial biomass, plant species richness and relative abundance of plant life forms other than trees, woody plants in natural regeneration, soil properties, and even richness and abundance of faunal groups (Aide et al. 2000; Ruiz-Jaen & Aide 2005a; Letcher & Chazdon 2009). Little evidence exists, however, of the predictive power of these variables as indicators of ecosystem recovery over time.

For the Brazilian Atlantic Forest, especially in riparian areas, restoration through planting of seedlings has increased in recent decades (Rodrigues et al. 2009), providing an unusual opportunity to study successional trajectories. We constructed a chronosequence using these existing forest restorations and compared with a set of natural forest ecosystems as references to reply the following questions: (1) Do the attributes of the forests being restored follow predictable trajectories over time? (2) How long will it take for each attribute to reach the reference level? This allowed us to: (1) build predictive models that represent changes in each attribute of the plant community over time in this ecological region and select good indicators for monitoring progress toward restoration; and (2) estimate, by using the most robust models, the time required for the attributes of a forest under restoration to reach the same values as that of reference ecosystems. Based on the premise that native forests with distinct histories of disturbances differ in their attributes (Hobbs & Norton 1996; Choi 2004), and that using as reference a broad spectrum of natural ecosystems has been recommended (Brinson & Rheinhardt 1996), we used three different categories of reference forests for this estimation.

Methods

Study region

All 35 study areas are located in an extensive region previously covered by Semideciduous Tropical Forest—STF, one of the subtypes of the Brazilian Atlantic Forest, which is characterized by climate seasonality. These areas are in the state of São Paulo, Paraná and Mato Grosso do Sul, spanning an area of approximately 80,000 km² (Fig. 1). The average annual temperature in this region ranges between 21°C and 24°C, with average minimum temperatures around 10°C and average maximum of 30°C. The average annual rainfall varies between 1,150 and 1,630 mm, and may be less than 40 mm in the driest months which occurs in the winter (Sentelhas et al. 2003).

Specifically, we were interested in the restoration technique of planting nursery-raised tree seedlings. We selected 26 sites in which the restoration technique was applied between 4 and 53 years ago. The sites varied in the size of the restored area (0.5–135.3 ha), composition and number of species planted (1 to more than 100), proportion of native species (45–100%), density of seedlings (625–2,667 seedlings per ha), soil fertilization, after-care (1 to more than 3 years), distance from seed sources (0–5,700 m), previous land use (pasture or agriculture). Importantly, these selected sites represented different climate and soil
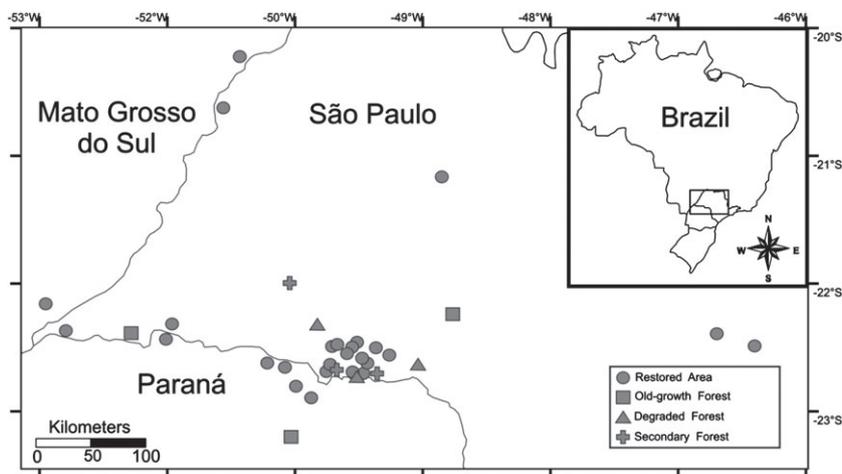
Figure 1. Location of the 35 study sites in the states of São Paulo, Paraná and MatoGrosso do Sul, Brazil.

conditions, landscapes and the wide spectrum of techniques used for forest restoration by seedling planting in the Atlantic Forest region. (Detailed information about the 26 restoration sites are presented as Table S1, Supporting Information.)

For the different reference ecosystems, we selected nine riparian forests in patches of different sizes, different soil types and climates within the STF. These sites were categorized according to their ecological integrity as: (1) Old-growth Forest—OGF: three primary forests within large areas (376–34,000 ha), without any evidence of disturbance; (2) Degraded Forest—DF: three small fragments (3–20 ha) of primary forests experiencing edge effects, the presence of cattle or selective wood harvesting until the 1970s; (3) SF: three forests in the process of natural regeneration (3–10 ha) with an estimated time of abandonment between 35 and 60 years, in areas previously used as pastures (Fig. 1). (Detailed information on the nine reference ecosystems can be found in Table S2.)

Plant community sampling

For each of the 35 sites, we sampled a total area of 1,000 m². In order to capture variability throughout the forest, this area was subdivided into 10 plots of 20 × 5 m, parallel to the border of the water. Plots were randomly distributed between 0 and 50 m away from the water body, and above the flooding level, stretching at least 200 m and no more than 700 m.

In every plot, all individuals of tree species of height (h) equal or greater than 0.5 m were counted and identified. The sampled individuals were categorized according to their diameter at breast height (measured at 1.3 m) into three size classes: (1) understory with dbh <1 cm; (2) understory with 1 cm ≤ dbh <5 cm; and (3) dbh ≥5 cm for the overstory. All individuals were categorized as either planted or regenerating naturally (out of the planting row alignment and/or not in the list of species planted). Total height and dbh of overstory trees were also measured.

To estimate the abundance of non-tree species, in each plot we recorded pteridophytes (terrestrial ferns), lianas (if taller

than 0.5 m and with the main root inside the plot), shrubs (h ≥0.5 m) and epiphytes. Considering the difficult in quantifying epiphytes, we used the density of phorophytes (trees with epiphytes) as the variable in the analyses.

To measure crown cover, a periscope-like densitometer (Forestry Suppliers, Inc.—GRS Densitometer) was positioned 1.50 m above the ground and 20 measurements were taken (one measurement per meter), systematically distributed along the center line of each plot, recording categorical coverage data (i.e. presence or absence of foliage). The measurement was then converted to a percentage value for each plot (i.e. where 100% represents total coverage and 0% represents no coverage at all).

Functional guilds

We chose functional traits that were relatable to the relevant assembly mechanisms in recovering forests, as recommended by Götzenberger et al. (2011). If there are dispersal filters influencing the trajectories of the communities, the abundance and proportion of animal-dispersed species should indicate the presence of these barriers. We expected a trend similar to secondary succession, in which the proportions of animal-dispersed species tend to increase and wind-dispersed species decrease over time (Frankie et al. 1974). If soil water is a limiting factor, the richness and abundance of slow growing species, which consume less water (Brix 1962; Gholz et al. 1990), should increase over time, as competition increases. Considering that light competition should be relevant, we also quantified the abundance and the proportion of shade tolerant species (Walters et al. 1993; Reich et al. 1998). Based on these assumptions, each tree species was categorized by dispersion mode as either animal-dispersed or non-animal–dispersed (Van der Pijl 1972; Yamamoto et al. 2007; Almeida-Neto et al. 2008). The growth rate was categorized as slow, moderate, or fast and shade tolerance was categorized as tolerant or intolerant, based upon an extensive review on dendrology, ecology, and silvicultural performance of Brazilian trees (Carvalho 2003) and a functional

categorization based on field data from 83 sites in the study region (Durigan et al. 2004). Analyses were done on the following guilds expected to increase along the succession processes: animal-dispersed (Tabarelli & Peres 2002; Liebsch et al. 2008), shade tolerant, and slow growing species (Liebsch et al. 2008).

Data analysis

Linear regressions were applied to the data to fit linear models to the trajectory of the community after the planting of the trees (age of the community undergoing restoration). For each response variable, we selected the best fit model obtained from the 26 sites (i.e. the highest r^2 value; Zar 1999; Liebsch et al. 2008). Each model was subjected to an *F-test* using $p < 0.05$ as the significance level. In the second step, the selected models were used to estimate the required time for each community attribute to reach the mean values of the reference ecosystems (i.e. OGF, DF, or SF). The mean values for the different reference types were compared through a one-way analysis of variance (ANOVA), followed by a Tukey post-hoc test to determine differences among ecosystem types. All analyses were performed in R (version 3.1.0.).

The following variables were used in the models: basal area of the overstory (dbh $\geq$5 cm), canopy cover, density of pteridophytes, lianas, shrubs and phorophytes, density and richness of tree species, and floristic similarity with the reference ecosystems. Species richness in this study is defined as a count of the number of tree species in each study site (1,000 m^2), following the definition by Magurran (2004). Considering that predictability for density of individuals and species richness should vary when including plants of different size classes, we performed the analyses using different data sets. For density of trees we analyzed: total density (all individuals sampled), density of the understory (height from 0.5 m and dbh <5 cm), and density of saplings (1 cm $\leq$ dbh $\leq$5 cm). To represent the number of tree species in each site we analyzed total richness (all individuals sampled), overstory richness (dbh $\geq$5 cm), richness of the understory (height from 0.5 m and dbh <5 cm), and richness of saplings (1 cm $\leq$ dbh $\leq$5 cm). In addition, we calculated the rarefied richness (Magurran 2004) for 100 individuals, in different layers. By incorporating evenness, this variable provides a good surrogate for plant diversity in tropical forests (Durigan 2009). Floristic similarity was calculated by Jaccard coefficient (Müeller-Dombois & Ellenberg 1974), using presence/absence data. We compared the whole community (planted and regenerating of all sets) among the tree reference ecosystems, and for the regression analyses each restoration site was compared with the regional species pool (using the data of all reference sites) and separately for each of the three reference types. All analyses were performed in R (version 3.1.0.), with package "vegan": Community Ecology Package (version 2.0).

Results

In the 26 sites undergoing restoration, we recorded 16,475 individuals, across 313 tree species. In the nine reference sites we recorded 9,321 individuals, across 185 tree species. Among the forests under restoration, only the 53-year-old community was more species rich (95), than the richest among the reference ecosystems (90). The largest basal area was recorded in the 38-year-old community (60.7 m^2/ha^{-1}), followed by the area that was 17-year-old (52.1 m^2/ha^{-1}). Among the 26 restoration sites, seven exceeded the maximum basal area observed among the nine reference ecosystems (41 m^2/ha^{-1}), and 16 exceeded the mean basal area of all reference ecosystems (25.7 m^2/ha^{-1}).

Trajectory of the attributes of the restored forest over time

Most variables representing the structure, richness, and proportion of functional guilds were significantly positively related to the time elapsed since planting (Figs. 2–4), with logarithmic models showing the best fit. For the two attributes where the value of r^2 was slightly higher in the rectilinear model than in the logarithmic model – total richness ($r^2 = 0.44$ and $r^2 = 0.43$, respectively) and richness of saplings ($r^2 = 0.59$ and $r^2 = 0.56$, respectively), we chose the logarithmic model for forecasting, because the rectilinear model does not make long-term ecological sense, as in reality all ecosystems are expected to stabilize at some future time.

Community structure. Among the structural attributes, significant models were obtained for basal area ($r^2 = 0.63$, $F_{1,24} = 40.5$, $p < 0.0001$; Fig. 2A), canopy cover ($r^2 = 0.44$, $F_{1,24} = 18.7$, $p < 0.001$; Fig. 2B), and density. Total density of the community ($r^2 = 0.31$, $F_{1,24} = 10.6$, $p = 0.0034$; Fig. 2C), and the density of the understory ($r^2 = 0.31$; $F_{1,24} = 10.8$, $p = 0.0031$; Fig. 2D) have similar paths and predictive power. Density of saplings proceeded more slowly and generated a better model fit ($r^2 = 0.62$, $F_{1,24} = 39.2$, $p < 0.0001$; Fig. 2E) than the total density and the density of the understory.

The densities of pteridophytes ($p = 0.24$, Fig. 3A), lianas ($p = 0.11$, Fig. 3B), phorophytes ($p = 0.61$, Fig. 3C), and shrubs ($p = 0.07$, Fig. 3D) showed no predictable trajectories over time and, with the exception of shrub density, are far from reach any of the reference ecosystems.

Tree species richness. Variables representing tree species richness generated significant models with the exception of rarefied richness; however, the quality of models depended on what size classes were included. The model based on total species richness ($r^2 = 0.43$, $F_{1,24} = 18.2$, $p < 0.001$; Fig. 4A) was less robust. For the understory, contrary to what was observed with density of trees, the model using the total understory ($r^2 = 0.59$, $F_{1,24} = 35.3$, $p < 0.0001$; Fig. 4B) resulted in a better fit than the model using only saplings ($r^2 = 0.56$, $F_{1,24} = 30.4$, $p < 0.0001$, Fig. 4C).

Rarefied richness for 100 individuals, which represents the diversity of the community, showed no predictable evolution with the age of the plantations when the whole community is analyzed, including planted trees (Fig. 4D). When the planted trees were excluded, there was a tendency of diversity increasing over time, even more than half of the variation among sites remain unexplained ($r^2 = 0.38$, $F_{1,24} = 16.5$, $p = 0.0005$; Fig. 4E).
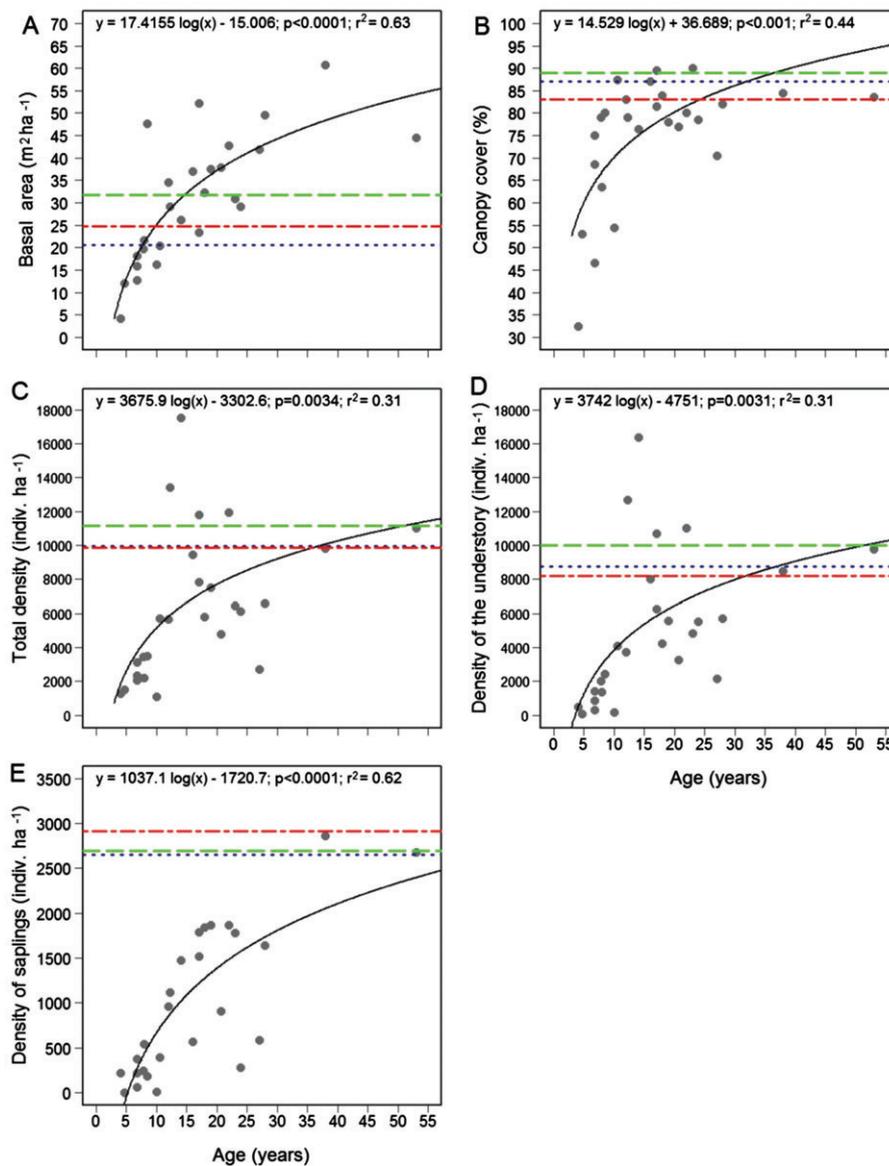
Figure 2. Structural change of the tree community in riparian forest restoration based on the age of the plantations: (A) basal area; (B) canopy cover; (C) total density (all individuals sampled); (D) density of the understory (height from 0.5 m and dbh < 5 cm); and (E) density of saplings (1 cm ≤ dbh <5 cm). The averages of the reference ecosystems for the region of study are represented by horizontal lines: Old-growth Forests = dash (− − −), Degraded Forests = dot (…); and Secondary Forests = dash and dot (−.−.).

Functional guilds. Trends observed in the functional guilds of tree species—shade tolerant, animal dispersed, and slow growing tree species—always showed higher predictability for proportions of species than proportions of individuals from different guilds. The proportion of animal-dispersed species increased in a predictable manner over time ($r^2 = 0.20$, $F_{1, 24} = 6.1$, $p = 0.021$; Fig. 5A), but their relative abundance was not predictable (Fig. 5B). The proportion of shade tolerant species increased over time in species richness ($r^2 = 0.68$, $F_{1, 24} = 51.9$, $p < 0.0001$; Fig. 5C) and abundance ($r^2 = 0.55$, $F_{1, 24} = 29.6$, $p < 0.0001$; Fig. 5D). Additionally, the proportion of slow growing species ($r^2 = 0.55$, $F_{1, 24} = 28.9$, $p < 0.0001$; Fig. 5E), as well as their relative abundance ($r^2 = 0.47$,

$F_{1, 24} = 21.1$, $p < 0.001$; Fig. 5F), increased over time in a predictable manner.

Floristic similarity with the reference ecosystems. The highest similarity found when comparing the floristic composition of each site undergoing restoration with the species pool of the three types of reference ecosystems was 31% (ISj =0.31). The absolute majority of sites did not reach 0.25 for the Jaccard coefficient, the limit above which two communities are considered similar (Müeller-Dombois & Ellenberg, 1974). Even at low values and low predictability, the floristic similarity tends to increase over time when compared to the OGF ($r^2 = 0.27$, $F_{1, 24} = 9.04$, $p = 0.006$; Fig. 6A),
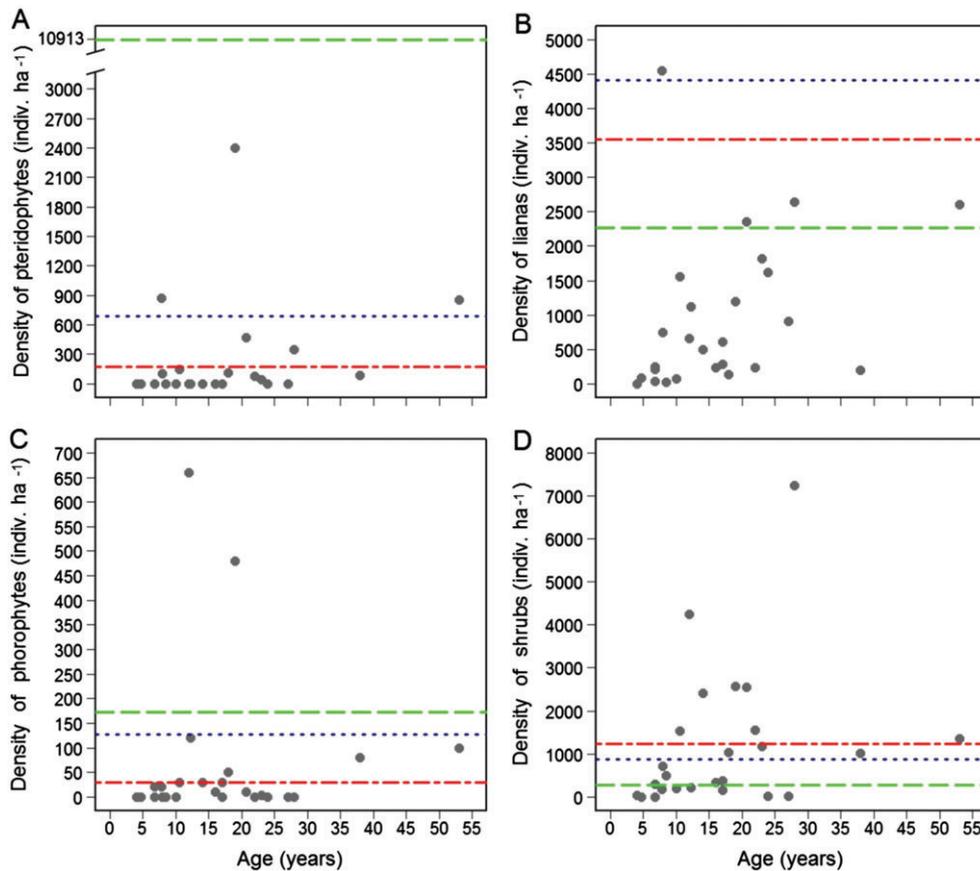
Figure 3. Density of individuals of non-woody life forms in riparian forests restoration based on the age of the plantations: (A) density of pteridophytes; (B) density of lianas; (C) density of phorophytes; (D) density of shrubs. The averages of the reference ecosystems for the region of study are represented by horizontal lines: Old-growth Forests = dash (---), Degraded Forests = dot (…); and Secondary Forests = dash and dot (-.-.).

the DF ($r^2 = 0.36$, $F_{1, 24} = 13.74$, $p = 0.001$; Fig. 6B), the SF ($r^2 = 0.40$, $F_{1, 24} = 15.88$, $p = 0.0005$; Fig. 6C), or to the regional species pool, represented by the nine sites of reference forests ($r^2 = 0.31$, $F_{1, 24} = 10.98$, $p = 0.003$; Fig. 6D).

Differences among the types of reference ecosystems. The three types of reference ecosystems did not differ for most attributes analyzed, including the proportions of functional guilds, tree species richness (except in the overstory), and most structural attributes (Table 1). Their floristic composition did not differ either, the Jaccard coefficients ranging from 0.40 between OGF and SF to 0.50 between SF and DF. For most attributes differing among ecosystem types, the OGF stood out above either one or both types of forests that suffered disruption. The DF and SF communities differ only in the density of phorophytes. The density of pteridophytes was higher in OGF when compared to either DF or SF ($F_{2, 6} = 53.7$, $p = 0.0002$). The density of phorophytes was lower in SF compared to either OGF or DF ($F_{2, 6} = 41.2$, $p = 0.0003$). The density of lianas was higher in DF than in OGF ($F_{2, 6} = 5.4$, $p = 0.046$). The only species richness attribute that differed among forest types was overstory richness, which was higher in OGF than in SF ($F_{2, 6} = 5.7$, $p = 0.042$).

Time to reach the different types of reference ecosystems

The estimated time for the forests being restored to equal the reference ecosystems was highly variable (Table 1). In general, structural attributes reach reference values sooner than the species richness values or functional attributes. Except for the density of saplings, all other reference values of the tree community structure (cover, basal area, and density) were reached within the time period covered by this study (53 years). However, there was substantial variation in the time it will take to equal the reference systems. For example, the model estimates that the basal area will take 15 years to equal the average of OGF but that the canopy cover will take 24 years to equal the average of the SF (Table 1).

For all the species richness indicators that developed over time in a predictable manner (Table 1), the time needed to reach the reference ecosystem increases from SF to OGF. Richness of OGF, in any of the size classes, is not expected to be reached within the time frame analyzed (53 years). The rarefied richness for 100 individuals naturally regenerating will take estimated 34 years to reach the average values of SF or DF and 39 years to equal the OGF (Table 1).

The proportions of species in the functional guilds (Table 1) recovered more quickly than the proportion of individuals,
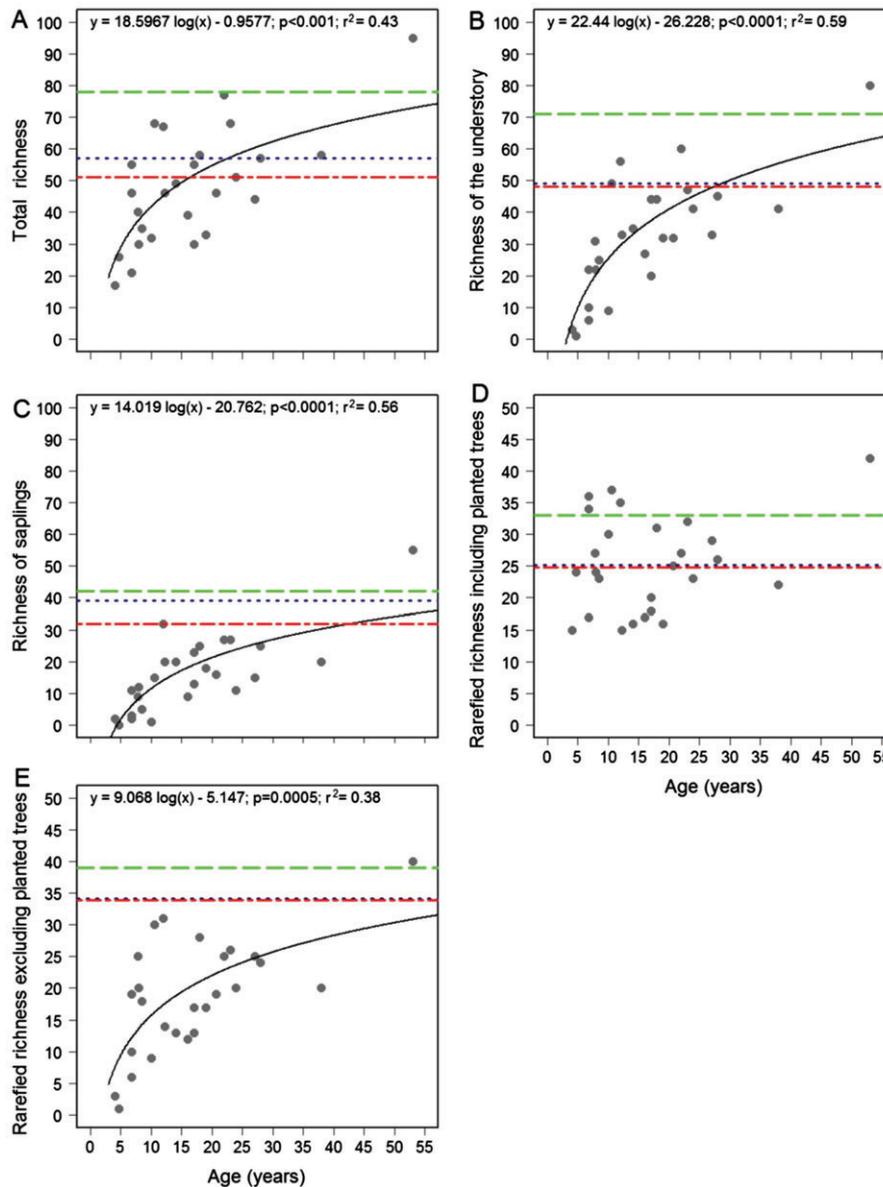
Figure 4. Tree richness (number of species in 1,000 m^2) in different size classes, related to the ages of riparian forest communities undergoing restoration. (A) Total richness (all individuals sampled); (B) richness of the understory (height from 0.5 m and dbh <5 cm); (C) richness of saplings (1 cm ≤ dbh < 5 cm); (D) rarefied richness for 100 individuals in the whole community; and (E) rarefied richness for 100 individuals naturally regenerating. The averages of the reference ecosystems for the region of study are represented by horizontal lines: Old-growth Forests = dash (---), Degraded Forests = dot (…); and Secondary Forests = dash and dot (-.-.).

except for the shade tolerant guild in SF. The time to recover the proportions of species is generally shorter in the slow growth guild, than the animal-dispersed and shade tolerant guilds. To recover the proportions between the guilds in abundance, the time required was the opposite: the proportion was higher for slow growth guilds than for shade tolerant guilds, but was unpredictable for animal-dispersed guilds. Analyzing the time required to reach the different types of reference ecosystems, SF values are reached faster in all functional attributes except for the proportion of animal-dispersed guilds, which reaches first the low proportion of the DF.

Discussion

Understanding the trajectories of ecosystems undergoing restoration is challenging because of the difficulty in obtaining robust data over an extensive period of time, and because recovery depends on complex interactions between many factors. In this study it was possible to analyze a wide range of data across a chronosequence of forest communities under restoration, in a large region occupied by the same type of vegetation-the STF. We were seeking for easily measurable attributes (1) representing relevant ecological processes, (2)
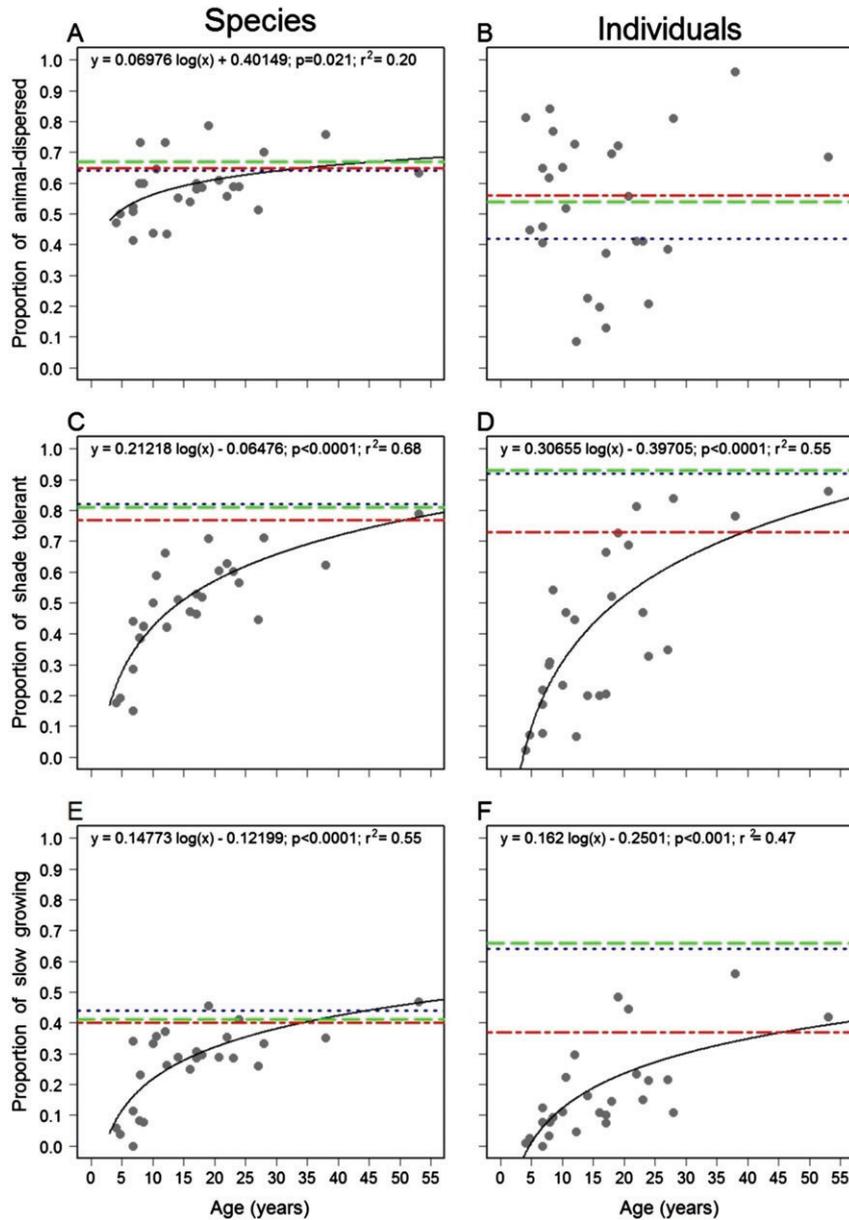
Figure 5. Changes in the proportion of richness and abundance of functional guilds in riparian forest restoration based on the age of the plantations: (A) proportion of animal-dispersed species; (B) proportion of animal-dispersed individuals; (C) proportion of shade tolerant species; (D) proportion of shade tolerant individuals; (E) proportion of slow growing species; and (F) proportion of slow growing individuals. The averages of the reference ecosystems for the region of study are represented by horizontal lines: Old-growth Forests = dash (---); Degraded Forests = dot (…); and Secondary Forests = dash and dot (-.-.).

whose trajectories since the intervention of restoration were predictable, to be used as indicators for monitoring ecological restoration projects in this extensive region, and (3) with a narrow variation range among reference ecosystems in spite of different degrees of disturbance, which could therefore help in setting long-term goals for future projects.

What is possible to predict about tropical forest restoration?

Although there is a measure of uncertainty in the models, due to factors other than age, the passage of time explained most of the variation in most of the attributes of tree communities in this study. The best models for the communities under restoration followed logarithmic trajectories, as observed in SF chronosequences (Liebsch et al. 2008, in Atlantic Forest; and Maza-Villalobos et al. 2011, in dry forest in Mexico). Among the theoretical models for successional trajectories proposed by Suding and Hobbs (2009) for ecosystems being restored, most of the attributes in this study fit better in the gradual continuous model. According to this model, changes in the environment and the successional trajectory of the community gradually drift, becoming similar to the ecosystem before the disturbance.
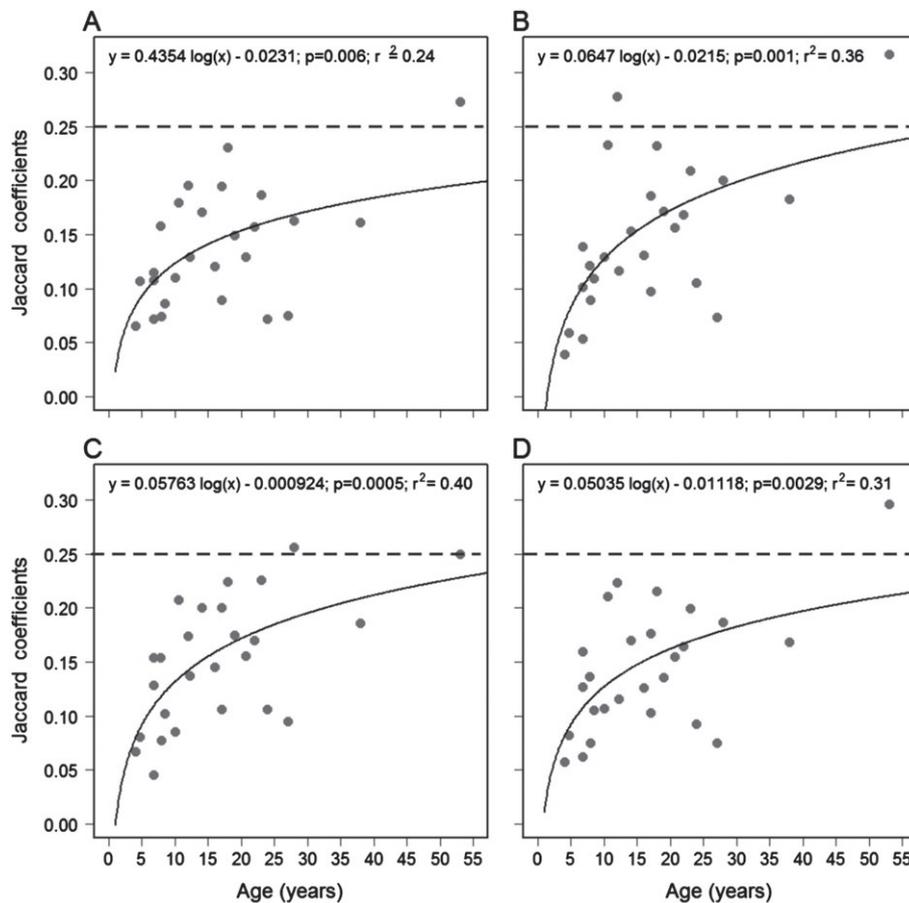
Figure 6. Changes over time in the floristic similarity (Jaccard coefficients) between riparian forests undergoing restoration and the floristic composition of (A) Old-growth Forests, (B) Degraded Forests, (C) Secondary Forests, and (D) the regional species pool (data from the nine reference sites altogether). The horizontal dash line (−−-) corresponds to the limit above which two communities are considered similar by Müeller-Dombois and Ellenberg (1974).

It is possible to predict that ecosystems that are formed by planting seedlings reach higher biomass, canopy cover and density similar to OGFs in the same region. It is also possible to predict that, although slowly, the number of species, the rarefied richness of species naturally regenerating, and proportions of functional guilds of tree species increase over time, even if the species composition does not seem to be predictable. The upward trend in the proportion of shade tolerant species poses the light availability as a relevant filter selecting the species which dominate the community long term. This trend was also found in the chronosequence of SFs in Atlantic Forest (Liebsch et al. 2008) and in riparian forest restoration in floodplains in the United States (McClain et al. 2011). Even the abundance of animal-dispersed species is not predictable, there is a tendency of the relative richness of this functional guild increasing over time, as observed by Chazdon (2003), when comparing trees of a SF with old-growth tropical forest in NE Costa Rica.

Although many attributes evolve in a predictable manner, there is a huge difference in the rate at which recovery occurs for each of them. The recovery of the structure is faster than biodiversity recovery and that has been repeatedly observed in studies of successional trajectories of tropical forests in

different parts of the world (Aide et al. 2000; Souza & Batista 2004; Ruiz-Jaen & Aide 2005b; Melo & Durigan 2006; Letcher & Chazdon 2009; Maza-Villalobos et al. 2011; Martin et al. 2013). The recovery of the structure is crucial, as these changes provide a more favorable environment for colonization by new species (Ruiz-Jaen & Aide 2005b; Engel & Parrotta 2008), and increase the availability of habitat for local seed dispersers (Tabarelli & Peres 2002; Kageyama et al. 2008). As the structure is recovered, increases also the fixation of atmospheric carbon in tree biomass (Melo & Durigan 2006), which is one of the expected ecosystem services from forest restoration. This and other studies of forest restoration in the Atlantic Forest region (Souza & Batista 2004; Melo & Durigan 2007) indicate that forests restored through the planting of seedlings tend to accumulate biomass far faster than natural ecosystems in the same region. At 20 years after planting, a restored forest is predicted to have more biomass than any kind of reference ecosystems, though the total number of species will still be similar to a SF or DF.

Richness and diversity are recovered at different rhythms among the community layers. The rarefied richness when the planted trees in the overstory are included in the analyses does

Table 1. Mean values for the attributes of riparian forest communities in three types of reference ecosystems (Old-growth Forest, Degraded Forest, Secondary Forest) in the region of Semideciduous Tropical Forest, Brazil, and estimated time (years) for communities undergoing restoration to reach those values on the basis of the models provided by the chronosequence. SE: standard error.

	Old-growth Forest (n =3)		*Degraded Forest* (n =3)		*Secondary Forest* (n =3)	
	Mean ± SE	*Time*	*Mean ± SE*	*Time*	*Mean ± SE*	*Time*
Forest structure						
Basal area (m^2 ha^{-1})	31.7 ± 4.6	15	20.5 ± 2.6	8	24.7 ± 1.6	10
Canopy cover (%)	89 ± 2	36	87 ± 2	32	83 ± 2	24
Total density of tree species (ind. ha^{-1})	11,180 ± 914	51	9,963 ± 1,646	37	9,927 ± 1,737	37
Density of the whole understory (ind. ha^{-1})	9,990 ± 805	51	8,743 ± 1,596	37	8,207 ± 1,781	32
Density of saplings (ind. ha^{-1})	2,693 ± 427	71	2,650 ± 187	68	2,913 ± 487	87
Density of pteridophytes (ind. ha^{-1})	10,913 ± 1,312[a]	—	690 ± 571[b]	—	170 ± 47[b]	—
Density of lianas (ind. ha^{-1})	2,273 ± 90 [b]	—	4,407 ± 720 [a]	—	3,547 ± 595[ab]	—
Density of phorophytes (ind. ha^{-1})	173 ± 19[a]	—	127 ± 3[a]	—	30 ± 6[b]	—
Density of shrubs (ind. ha^{-1})	273 ± 155	—	873 ± 559	—	1,237 ± 537	—
Richness (tree species in 1,000 m^2)						
Total richness	78 ± 7	70	57 ± 6	23	51 ± 10	16
Overstory richness	41 ± 3 [a]	—	30 ± 6[ab]	—	20 ± 4 [b]	—
Richness of the whole understory	71 ± 6	77	49 ± 3	29	48 ± 9	27
Richness of saplings	42 ± 11	86	39 ± 4	69	32 ± 9	43
Rarefied richness for 100 individuals naturally regenerating	33 ± 3	39	25 ± 2	34	25 ± 5	34
Functional guilds (tree species)						
Proportion of animal-dispersed species	0.67 ± 0.02	49	0.64 ± 0.01	29	0.65 ± 0.05	35
Proportion of animal-dispersed individuals	0.54 ± 0.11	—	0.42 ± 0.14	—	0.57 ± 0.13	—
Proportion of shade tolerant species	0.81 ± 0.04	61	0.82 ± 0.02	64	0.77 ± 0.05	51
Proportion of shade tolerant individuals	0.93 ± 0.01	75	0.92 ± 0.04	73	0.73 ± 0.12	40
Proportion of slow growing species	0.41 ± 0.04	36	0.45 ± 0.02	45	0.40 ± 0.05	34
Proportion of slow growing individuals	0.66 ± 0.08	270	0.64 ± 0.13	247	0.37 ± 0.06	46

Values followed by the same letter or not followed by letters in a line do not differ statistically by ANOVA followed by Tukey test ($p < 0.05$). For attributes where there are no time values, these values are omitted because they show no predictable trajectories over time.

not increase nor decrease predictably with the age of the plantations, turning around the average value of DF or SF (25 species per 100 individuals sampled). But it increases predictably when only trees in natural regeneration are considered. Density and richness of saplings, from which depend the replacement of dead canopy trees, will after 20 years have reached only about half of the average values of reference ecosystems in the same region. Apparently, the excess biomass in the overstory inhibits recruitment of saplings, since density of small individuals (below 1 cm dbh) is high, even exceeding the density of the natural forests in some sites. The light gap dynamic, which controls the seedlings establishment and saplings density (Hubbell et al. 1999), will likely take longer to reestablish. The proportions among functional guilds also take a long time to be recovered. After 20 years, the proportions of shade-tolerant or slow growth species will be about three quarters of the proportion observed in reference ecosystems. The relative abundance of these functional guilds is about half compared to OGFs and two-thirds compared to degraded or SFs.

Marked technical differences in restoration intervention methods among the study sites do not appear to exert significant influence on the successional trajectory of the tree communities, as models with good predictive power were obtained for most variables. Even if different techniques are applied in the number or combinations of species, density of seedlings or management practices, the tree communities that are restored through planting of trees seem to follow the same trajectory in terms of structure and functioning. This finding is highly relevant to the practice of restoration, as it makes it possible to reduce the cost of planting or maintenance. Recovering the forest structure seems to be enough to trigger the successional processes. This is the basis of the "framework species method," which has been used and recommended for restoring tropical forests in Australia (Goosem & Tucker 1995) and southeast Asia (Blakesley et al. 2002; Elliott et al. 2003; Wydhayagarn et al. 2009).

What cannot be predicted about succession in tropical forest restoration?

Not everything is predictable in the recovery of the tree community attributes over time after the intervention of restoration, at least in the period covered by this study and under the restrictions imposed by a chronosequence (Chazdon et al. 2007; Feldpausch et al. 2007). The floristic composition of the forests under restoration is far from the reference ecosystems, no matter the sort of disturbances they have suffered. While the reference forests, even submitted to a wide range of disturbances, are highly similar, sharing more than 40% of the species, the minimum level of 25% between forests under restoration and any of the reference types has not been reached. The OGF are a goal even more difficult to be reached, compared to DF or SF, as observed by Reay and Norton (1999) in New Zealand Temperate Forests. The models provided by the 26 sites for

floristic similarity with reference forests have low predictive power, particularly due to the high dispersion of data around an average level of 18% similarity after 15 years of planting age. In addition to the unpredictability of tree species composition, the expectation that non-arboreal life forms, like epiphytes, lianas, and ferns, naturally colonize all these forests (Siqueira-Filho & Tabarelli 2006; Brancalion et al. 2009; Martin et al. 2013), making them similar to the reference ecosystems, was not observed as a general tendency in this study. These components of the communities seem to depend on very specific conditions that provide for their colonization in one place but not in another, approximating a more stochastic model as proposed by Suding and Hobbs (2009). Apparently, the abundance of life forms other than trees, characteristic of intact forests, is lost due to the disturbance and does not recover with restoration actions.

Among the functional guilds analyzed, the proportion by dispersal syndromes has low predictive power, as the model explains only 20% of the variation in proportion of species and gives no prediction in relation to their abundance. The ecological filters that mediate colonization by shade tolerant or slow growing species, which are associated with competition for light and soil water, have been more effective than the animal seed dispersers in modulating the plant communities in restoration (Hubbell et al. 1999; Suganuma et al. 2014). The action of fauna depends on more complex factors such as distance from propagule sources in the landscape (Tambosi et al. 2013), which are highly variable between sites within the study area. The arguments of Hubbell et al. (1999) that biodiversity patterns of trees in forests are mostly explained by dispersal processes is not valid for the study region, where the abiotic barriers constraining seedlings establishment (e.g. water deficit in the dry season, and the decreasing light availability as biomass increases) seem to be more effective in driving the community assembly. As in most current studies designed to record biotic assembly rules (Götzenberger et al. 2011), this study revealed the importance of abiotic rules.

Considering that we searched for predictable trajectories under the limitations of a chronosequence, we cannot disregard the hypothesis that the variables not following a predictable trajectory for the entire region can increase over time in a particular site. The unexplained variation of the valid models, as well as the broad variation found in non-arboreal life forms or relative abundance of animal-dispersed species, suggests that other processes are driving the community assembly in each site. Among these factors are landscape configuration, disturbance history, biotic interactions, and dispersal limitation (Lebrija-Trejos et al. 2010).

Are the attributes uniform across the different reference ecosystems?

The reality emerging from this and other recent studies (Choi 2004; Hobbs et al. 2009; Rey-Benayas et al. 2009; Suding 2011; Maron et al. 2012) is that part of the components and properties of historical ecosystems cannot be restored within an acceptable time frame for a restoration project. This conclusion leads to the need of rethinking the goals of restoration, which should not

include such components or properties. The differences between types of reference ecosystems, especially in their non-tree components, highlight the lack of a single regional pattern that can be extracted from historical ecosystems. The reference ecosystems that have suffered disturbances in the past (degraded or SFs) have not suffered human intervention in the last decades. Even though, they are still different in part of their attributes. Whether or not these ecosystems will recover their lost attributes depends on analyzing their dynamics based on long-term data. The ultimate goals of restoration should not be narrower than the amplitude of the attributes among different types of natural ecosystems remaining in a particular ecological region (Choi 2004), since all are, ultimately, possible ecosystems at the end of the succession.

On the other hand, the present study shows attributes whose variation among natural ecosystems, with different histories of disturbance, is very narrow within the study region, allowing them to be used in the establishment of the final restoration goal. Among these attributes, density and richness of saplings stand out. The attributes of native forests (SF and DF) that have suffered disturbances in the past can generally be reached at shorter intervals than the OGF. Even though, the time required to match the reference systems may be too long for these to be used as restoration goals. Intermediate targets should be set for different ages after planting, which can be verified and drive adaptive management. The predictive models obtained in this study, based upon a chronosequence of a broad range of restoration plantings, make it possible to set realistic restoration goals that are valid for an entire ecological region for each stage of the process.

The choice of indicators for monitoring tropical forest restoration

The restoration goals should be established based on attributes of ecosystems that can be assessed by means of good indicators (Ruiz-Jaen & Aide 2005a). Dale and Beyeler (2001) consider that a single ecological indicator cannot possibly represent everything we want to evaluate. For these authors, the ideal is to select a small set of indicators that are easily measured, change over time, are sensitive to stress factors, are surrogates for other attributes of the ecosystem and ecological processes, and respond to disturbances in a predictable manner, enabling the prediction of undesirable changes that may be averted by management actions. In terms of restoration, indicators to be used for monitoring shall be also good surrogates for ecosystem services, such as the protection of water resources and carbon sequestration.

This study points to several attributes that follow a predictable trajectory and therefore could be used as indicators in monitoring forest restoration. These attributes are: basal area, canopy cover, density and richness of tree species in different strata, proportion of species and individuals of shade tolerant and slow growth guilds. However, not all of these attributes may be good indicators. The proportions of functional guilds (shade tolerance and slow growth), although ecologically relevant, rely on the extensive labor of botanical identification and does not respond

to restoration and management interventions, being determined by abiotic factors. On the other hand, the species richness can be assessed in terms of morphospecies, not depending on taxonomic identification. Therefore, variables based in this attribute are good indicators of biodiversity recovery, an outcome often expected from restoration plantings. Among them, richness of saplings in natural regeneration (1 cm $\leq$ dbh <5 cm) stands out by its predictability and ecological meaning. This layer comprises species that overcame the barriers or filters of reproduction, dispersal, and establishment, clearly representing the self-sustainability of the ecosystem. Smaller plants that are not yet established or planted species that do not regenerate should not be counted.

From the whole set of attributes analyzed in this study, we consider the following as the best indicators for monitoring tropical forests undergoing restoration:

1 Canopy cover: it has a direct relation to the recovery of biomass, shelter for wildlife and relevant ecosystem services, such as the recovery of microclimate, nutrient cycling, erosion control, and regulation of water resources. It is a good indicator for the first 10 years after restoration intervention, when it changes clearly with age. Canopy cover can be assessed by different methods (hemispherical photos, densitometers, line interception, etc.), each of which generate distinct values. Therefore, for comparison, methods must be standardized.
2 Basal area: this is a classic indicator of biomass, representing the recovery of forest structure and carbon sequestration service. Basal area can be also a surrogate for most of the ecosystem services related to canopy cover. As only trees above 5 cm DBH are usually measured, this is not an indicator to be applied in the first years after planting, when basal area is highly influenced by the density of seedlings planted.
3 Understory density: the density of tree individuals naturally regenerating is the most direct indicator of resilience recovery. Among the size classes examined, saplings provided a more predictable response than smaller plants, which are subject to stochastic factors causing mortality or over-dominance. These variables cannot be assessed, however, in the early years (about five) after the restoration intervention.
4 Understory richness: the number of tree species in natural regeneration in the area undergoing restoration is the best indicator of the effective recovery of diversity and persistence of species in the ecosystem. As observed for understory density, it is not a good indicator to be applied in the first years of restoration.

Modeling the trajectories of ecosystems undergoing restoration on the basis of a robust set of ecological indicators help to improve the measurability of restoration outcomes and to estimate the probability of offset success (Maron et al. 2012). More realistic goals can be established when the limitations of restoration are predictable, as shown by this study in the Atlantic Forest, and other studies elsewhere (Rey-Benayas et al. 2009, Suding 2011). This is particularly important when restoration is used to deliver biodiversity offsets. In these cases restoration shall be accepted if the impacted biodiversity and ecosystem values can be explicitly defined and measured and evidence exist that restoration of these values is feasible (Maron et al. 2012).

Our study shows a high probability of success in restoring STF structure and related ecosystem services by planting nursery-raised seedlings, with a low influence of restoration techniques. The probability to recover the historical species composition and other life forms than trees, however, is very low and that cannot be disregarded when setting goals or accepting biodiversity offsets.

Acknowledgments

LITERATURE CITED

Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano-Vega H (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology 8:328–338

Almeida-Neto M, Campassi F, Galetti M, Jordano P, Oliveira-Filho A (2008) Vertebrate dispersal syndromes along the Atlantic Forest: broad-scale patterns and macroecological correlates. Global Ecology and Biogeography 17:503–513

Blakesley D, Elliot S, Kuarak C, Navakitibumrung P, Zangkum S, Anusarnsunthorn V (2002) Propagating framework tree species to restore seasonally dry tropical forest: implications of seasonal seed dispersal and dormancy. Forest Ecology and Management 164:31–38

Brancalion PHS, Gabriel VA, Gómez JM (2009) Do terrestrial tank bromeliads in Brazil create safe sites for pal establishment or act as natural traps for its dispersed seeds? Biotropica 41:3–6

Brinson MM, Rheinhardt R (1996) The role of reference wetlands in functional assessment and mitigation. Ecological Applications 6:69–76

Brix H (1962) The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiologia Plantarum 15:10–20

Carvalho PER (2003) Espécies arbóreas brasileiras. Vol 1. Embrapa Informação Tecnológica, Brasília, Brazil Embrapa Florestas, Colombo, PR

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives Plant Ecology, Evolution and Systematics 6:51–71

Chazdon RL, Letcher SG, Van Breugel M, Martinez-Ramos M, Bongers F, Finegan B (2007) Rates of change in tree communities of secondary neotropical forests following major disturbances. Philosophical Transactions of the Royal Society 326:273–289

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460

Chapman CA, Chapman LJ (1996) Exotic tree plantation and the regeneration of natural forest in Kibale National Park, Uganda. Biological Conservation 76:1301–1311

Choi YD (2004) Theories for ecological restoration in changing environment: toward "futuristic" restoration. Ecological Research 19:75–81

Dale VH, Beyeler SC (2001) Challenges in the development and use of ecological indicators. Ecological Indicators 1:3–10

Dent DH, Wright SJ (2009) The future of tropical species in secondary forests: a quantitative review. Biological Conservation 142:2833–2843

Durigan G, Siqueira MF, Franco GADC, Contieri WA (2004) A flora arbusto-arbustiva do Médio Paranapanema: base para a restauração de ecossistemas naturais. Pages 199–239. In: Vilas-Bôas O, Durigan G (eds) Pesquisas em conservação e recuperação ambiental no Oeste Paulista: resultados da cooperação Brasil/Japão. Páginas e Letras, São Paulo, Brazil

Durigan G (2009) Estrutura e diversidade de Comunidades florestais. Pages 185–215. In: Martins VS (ed) Ecologia de florestas tropicais do Brasil. Editora UFV, Viçosa, Minas Gerais, Brazil

Elliott S, Navakitibumrung P, Kuarak C, Zangkum S, Anusarnsunthorn V, Blakesley D (2003) Selecting framework tree species for restoring seasonally dry tropical forests in northern Thailand based on field performance. Forest Ecology and Management 184:177–191

Engel VL, Parrotta JA (2008) Definindo a restauração ecológica: tendências e perspectivas mundiais. Pages 1–26. In: Kageyama PY, Oliveira RE, Moraes LFD, Engel VL, Gandara FB (eds) Restauração ecológica de ecossistemas naturais. FEPAF, Botucatu, Brasil

Feldpausch TR, Prates-Clark CD, Fernandes ECM, Riha SJ (2007) Secondary forest growth deviation from chronosequence predictions in central Amazonia. Global Change Biology 13:967–979

Florentine SK, Westbrooke ME (2004) Restoration on abandoned tropical pasturelands—do we know enough? Journal for Nature Conservation 12:85–94

Florentine SK (2008) Species persistence and natural recruitment after 14 years in a restoration planting on ex-rainforest land in north-east Queensland. Ecological Management & Restoration 9:217–221

Frankie GW, Baker HB, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881–919

Gholz HL, Ewewl KC, Teskey RO (1990) Water and forest productivity. Forest Ecology and Management 30:1–18

Goosem SP, Tucker NIJ (1995) Repairing the rainforest—theory and practices of rainforest re-establishment in North Queensland's Wet Tropics Management Authority. Cairns, Australia

Götzenberger L, Bello F, Brathen KA, Davison J, Dubis A, Guisan A, et al. (2011) Ecological assembly rules in plant communities–approaches, patterns and prospects. Biological Reviews 87:111–127

Hobbs RJ, Norton DA (1996) Toward a conceptual frame-work for restoration ecology. Restoration Ecology 4:93–110

Hobbs RJ, Norton DA (2004) Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. Pages 72–95. In: Temperton VM, Hobbs RJ, Nuttle T, Halle S (eds) Assembly rules and restoration ecology. Island Press, Washington, D.C.

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, et al. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24:599–605

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? Forest Ecology and Management 261:1558–1563

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, Loo de Lao S (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557

Kageyama PY, Gandara FB, Oliveira RE (2008) Biodiversidade e a restauração da floresta tropical. Pages 27–48. In: Kageyama PY, Oliveira RE, Moraes LFD, Engel VL, Gandara FB (eds) Restauração ecológica de ecossistemas naturais. FEPAF, Botucatu, Brasil

Lebrija-Trejos E, Perez-Garcia A, Meave JA, Bongers FE, Poorter L (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91:386–398

Letcher SG, Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chonosequence in northeastern Costa Rica. Biotropica 41:608–617

Liebsch D, Goldenberg R, Marques MCC (2007) Florística e estrutura de comunidades vegetais em uma cronoseqüência de Floresta Atlântica no estado do Paraná, Brasil. Acta Botânica Brasílica 21:983–992

Liebsch D, Marques MCC, Goldenberg R (2008) How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. Biological Conservation 141:1717–1725

Lugo AE (1992) Comparison of tropical tree plantations with secondary forest of similar age. Ecological Monographs 62:1–41

Lugo AE (2010) Let's not forget the biodiversity of the cities. Biotropica 42:576–577

Magurran AE (2004) Measuring biological diversity. Blackwell Science Ltd, Oxford, United Kingdom

Martin PA, Newton AC, Bullock JM (2013) Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proceedings of the Royal Society B: Biological Sciences 280:1–8

Maron M, Hobbs RJ, Moilanen JW, Christie K, Gardner TA, Keith DA, Lindenmayer DB, McAlpine CA (2012) Faustian bargains? Restoration realities in the context of biodiversity offset policies. Biological Conservation 155:141–148

Maza-Villalobos S, Balvanera P, Martínez-Ramos M (2011) Early regeneration of tropical dry forest from abandoned pastures: contrasting chronosequence and dynamic approaches. Biotropica 43:666–675

McClain CD, Holl KD, Wood DM (2011) Successional models as guides for restoration of riparian forest understory. Restoration Ecology 19:280–289

Melo ACG, Durigan G (2006) Fixação de carbono em reflorestamentos de matas ciliares no Vale do Paranapanema, SP, Brasil. Scientia Forestalis 71:149–154

Melo ACG, Durigan G (2007) Evolução estrutural de reflorestamentos de restauração de matas ciliares no Médio Vale do Paranapanema. Scientia Forestalis 7:101–111

Müeller-Dombois D, Ellenberg E (1974) Aims and methods of vegetation ecology. Wiley, New York

Parrotta JA, Knowles OH, Wunderle JJM (1997) Development of floristic diversity in 10 year-old restoration forests on a bauxite mined site in Amazonia. Forest Ecology and Management 99:21–42

Parrotta JA, Knowles OH (1999) Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restoration Ecology 7:103–116

Reay SD, Norton DA (1999) Assessing the success of restoration plantings in a temperate New Zealand Forest. Restoration Ecology 7:298–308

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C (1998) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Functional Ecology 12:395–405

Rey-Benayas JM, Newton AC, Diaz A, Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1124

Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. Biological Conservation 142:1242–1251

Ruiz-Jaen MC, Aide TM (2005a) Restoration success: how is it being measured? Restoration Ecology 13:569–577

Ruiz-Jaen MC, Aide TM (2005b) Vegetation structure, species diversity and ecosystem processes as measures of restoration success. Forest Ecology and Management 218:159–173

Sansevero JBB, Prieto PV, de Moraes LFD, Rodrigues JFP (2011) Natural regeneration in plantations of native trees in lowland Brazilian Atlantic forest: community structure, diversity, and dispersal syndromes. Restoration Ecology 19:379–389

Sentelhas PC, Marin FR, Ferreira AS, Sá EJA (2003) Banco de Dados Climáticos do Brasil. Embrapa Monitoramento por Satélite, Campinas, São Paulo,

Brazil (available from http://www.bdclima.cnpm.embrapa.br) (accessed 10 Jan 2014)

Society for Ecological Restoration International Science and Policy Working Group (SER) (2010) Primer on ecological restoration (available from http://www.ser.org/content/adoption.asp (accessed 20 Dec 2011)

Siqueira-Filho JA, Tabarelli M (2006) Bromeliad species from the Atlantic forest of north-east Brazil: losses of critical populations of endemic species. Oryx: Journal of Fauna and Flora International 40:218–224

Souza FM, Batista JLF (2004) Restoration of seasonal semideciduous forests in Brazil: influence of age and restoration design on forest structure. Forest Ecology and Management 191:185–200

Suding KN, Hobbs RJ (2009) Models of ecosystem dynamics as frameworks for restoration ecology. Pages 3–21. In: Hobbs RJ, Suding KN (eds) New models for ecosystem dynamics and restoration. Island Press, Washington, D.C.

Suding KN (2011) Toward an era of restoration in ecology: successes, failures and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42:465–487

Suganuma MS, de Assis GB, Durigan G (2014) Changes in plant species composition and functional traits along the successional trajectory of a restored patch of Atlantic Forest. Community Ecology 15:27–36

Tabarelli M, Peres CA (2002) Abiotic and vertebrate seed dispersal in the Brazilian Atlantic Forest: implications for forest regeneration. Biological Conservation 106:165–176

Tambosi LR, Martensen A, Ribeiro MC, Metzger JP (2013) A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. Restoration Ecology 22:169–177

Van Der Pijl L (1972) Principles of dispersal in higher plants. Spring-Verlag, New York

Walters MB, Kruger FL, Reich PB (1993) Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia 94:7–16

White PS, Walker JL (1997) Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5:338–349

Wydhayagarn C, Elliott S, Wangpakapattanawong P (2009) Bird communities and seedling recruitment in restoring seasonally dry forest using the framework species method in Northern Thailand. New Forests 38:81–97

Yamamoto LF, Kinoshita LS, Martins FR (2007) Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. Acta Botânica Brasílica 21:553–573

Zar JH (1999) Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey

Supporting Information

The following information may be found in the online version of this article:

Table S1. Detailed information on the 26 sites of riparian forests undergoing restoration, concerning to their age, size, previous land use, landscape, environment and restoration techniques.

Table S2. Detailed information on the history, environment and total area covered by forest in each site sampled as reference ecosystem.