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Atlantic rain forest recovery: successional drivers of floristic and structural patterns of secondary forest in Southern Brazil

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Keywords
Causal models; Chronosequences; Environmental and spatial variables; Regeneration patterns; subtropics

Abreviations
S1 stage 1; S2 stage 2; S3 stage 3
S4 stage 4

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Abstract

Questions: The growing importance of secondary forests has stimulated research on the patterns of structure, biomass, species diversity and species composition of successional tropical forests. Despite current knowledge, the future of tropical forests and their ability to recover from human impacts are still a challenge for researchers. The Atlantic Forest is one of the most endangered ecosystems on Earth, yet has been reduced in size and distribution due to human disturbance such that most of the remaining fragments are secondary forest at different successional stages. How do these forests recover structure and species composition during succession? What are the main drivers of community assembly during succession?

Location: Subtropical Atlantic rain forest, South Brazil (29°42′S, 50°11′W).

Method: Using four replicate chronosequences, we described floristic and structural successional patterns of subtropical Atlantic Forest in Brazil, and investigated causal relationships with environmental, spatial and temporal variables in structuring tree species composition. The chronosequences were described by four successional stages, according to floristic (species composition and richness) and structural (density, basal cover and height of trees) characteristics, tested using ANOVA with randomization tests. Time since abandonment and environmental conditions of topsoil, relief and spatial components were considered as possible successional drivers. Hypotheses about causal relationships in the successional process were tested using path analysis, considering the influence of those variables on the successional forest communities.

Results: We found that forest stands of 26–45 yr old displayed structural characteristics similar to those of old-growth stands, but that species composition of successional forest was somewhat different from reference areas (old-growth forests). In our study, time since abandonment overcame the influence of environmental and spatial variables on forest assembly patterns in the chronosequences.

Conclusions: Our study is the first one describing floristic and structural successional patterns of the Atlantic rain forest in a subtropical context and proposing causal relationships between recovery age, environment and community composition of secondary successional forests. We conclude that the dynamic of forest succession is autogenic and not entirely predictable from local environmental conditions of soil, space and relief.

Introduction

Approximately 60% of the world's remaining tropical forests are secondary (ITTO 2002; FAO 2005), a figure predicted to increase due to industrialization and urbanization (Guariguata & Ostertag 2001). Large tracts of agricultural land have been abandoned, while many reasonably preserved forests have been converted to agriculture (van der

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Maarel 1988; Myers et al. 2000; FAO 2005, 2007). Facing this scenario of loss of primary forests and the expanse of secondary forests in the context of biodiversity conservation (Brown & Lugo 1990; Finegan 1996; Gardner et al. 2009), we ask: how are the secondary forests structured; and how do forest structure and species composition recover along succession?

The growing importance of secondary forests has stimulated research on their patterns of species diversity, biomass, structure and species composition in the tropics (Aide et al. 2000; Blanc et al. 2000; Scudeller et al. 2001; Kennard 2002; DeWalt 2003; van Breugel et al. 2007; Klanderud et al. 2009; Letcher & Chazdon 2009; Piotto et al. 2009). Despite the breadth of knowledge on successional dynamics, the future of tropical forests and their capacity to recover considering the extent of human impact are still uncertain (Gardner et al. 2009; Fridley 2013). In the context of forest succession, factors such as proximity to seed source, intensity and type of land use prior to abandonment, presence and movement patterns of animal dispersers, as well as plant life-history traits increase the complexity of succession. Furthermore, the monitoring of forest dynamics over time requires long-term projects and sometimes multiple generations of researchers. The space-for-time substitution (Pickett 1989), known as the chronosequence approach, is often the only viable alternative for investigating temporal change in forest regeneration (Wildi 2002). However, this approach rests on the assumption that environmental conditions at different sites are similar, which is often unrealistic (Chazdon 2008). Thus, the selection of forest stands of different ages for chronosequence studies should be based on objective criteria, such as similarity in land-use history and soil type (Chazdon et al. 2007; Chazdon 2008).

The Atlantic Forest is one of the most biodiverse ecosystems in Brazil, and is recognized as one of the 34 hotspots (priority areas) for biodiversity conservation worldwide (Mittermeier et al. 2005). The Atlantic Forest has more than 13 000 angiosperm species, of which half are endemic to the ecosystem (Werneck et al. 2011). Its evolutionary history and biogeography has resulted in a very particular floristic composition (Metzger 2009). Nonetheless, its location along the Atlantic coast of Brazil has facilitated a long history of human occupation and degradation (Dean 1997; Tabarelli et al. 2010), reducing the forest to approximately 12% of its original extent (Ribeiro et al. 2009). The remaining forest fragments are predominately small patches subject to degradation processes largely due to edge effects (Santos et al. 2008, 2010; Tabarelli et al. 2008; Lopes et al. 2009). Alternatively, some deforested areas have since been abandoned to natural recovery, potentially leading to states similar to those of old-growth forests. Despite the importance of these secondary forests for ecosystem services and species diversity, it is often assumed that most of the endangered and/or sensitive species that characterize pristine forests cannot survive in secondary forests (Teixeira et al. 2009).

The current status and the dynamics of recovery of the Atlantic Forest is poorly understood at its southernmost limit, where tropical forest species thrive in a subtropical climate and many species occur at the limit of their distribution (Waechter 2002). The literature on tropical forests indicates relatively fast recovery of species richness and forest structure after disturbance (Kennard 2002; Vieira 2003; Liebsch et al. 2008; Piotto et al. 2009), but it is questionable whether these patterns are applicable to subtropical forests. If so, we expect that secondary forests 30–50 yr after abandonment would display structure (e.g. tree density, cover, biomass and height) and species richness similar to those found for old-growth forests. Furthermore, if environmental variables prevail as drivers of species assembly during succession (e.g. Martinez-Duro et al. 2010), we should find a strong correlation between community patterns and environmental variables and only some influence of plot age – i.e. the time of forest recovery.

We studied successional forest recovery from a slash-and-burn agricultural system in the southern limit of the Brazilian Atlantic rain forest, using a chronosequence approach. We aim to assess floristic and structural patterns during the process of succession, as well as causal effects of spatial components, local environmental factors (topsoil and relief variables) and time since abandonment on species composition of Atlantic Forest recovery in subtropical climate conditions.

Methods

Study area

The subtropical climate conditions of southern Brazil (ca. 29°S) constrain the southward distribution of the Atlantic Forest (*stricto sensu*) (Rambo 1956; Teixeira et al. 1986; Oliveira-Filho 2009). At this latitude, the Atlantic rain forest is restricted to a width of ca. 30 km between the basaltic plateau (about 900 m a.s.l.) and the coast. Watercourses originating from the sharp edges of the plateau shape the Maquiné River Basin (29°42′S, 50°11′W) in the northeast of Rio Grande do Sul State in Brazil (Fig. 1). The climate is humid subtropical, type Cfa according to Köppen's classification, with mean annual temperature above 18 °C, the absence of a dry period, and an annual mean rainfall of 1400–1800 mm (Hasenack & Ferraro 1989; Nimer 1990). The natural vegetation consists of subtropical moist broadleaved forest, which displays its broad physiognomic variation along an altitudinal gradient within this region

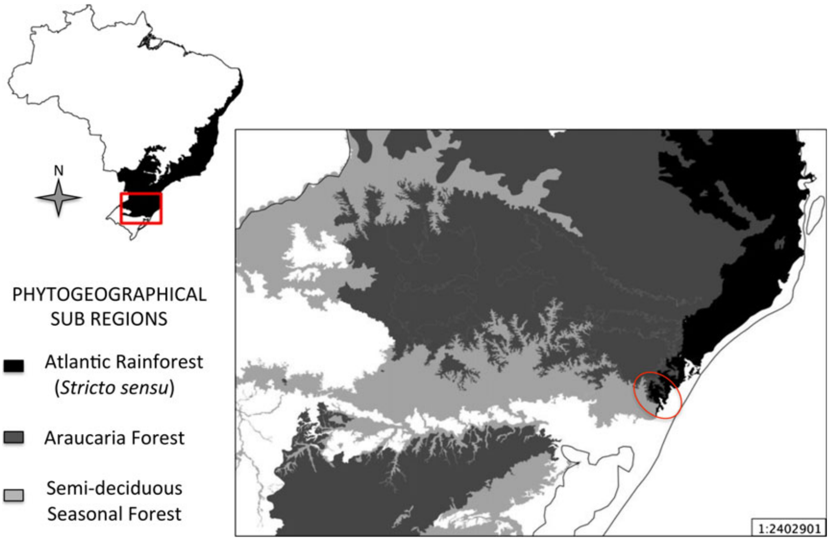

Fig. 1. The distribution of the Brazilian Atlantic Forest (small picture) and a detail of the phytogeographic sub-regions (Atlantic Rain forest *stricto sensu*, Araucaria Forest and Seasonal Forest) at the southern limit. The Maquiné River Basin is circled and the study area was restricted to the Atlantic Rain forest *stricto sensu*.

(Rambo 1956; Teixeira et al. 1986; Bergamin et al. 2012). This study was conducted in the lower-montane forest (Teixeira et al. 1986; Oliveira-Filho 2009) in plots that ranged from 259 to 456 m a.s.l., minimizing floristic variation related to altitude and soil type. The soils of the region are derived from basalt, and are considered fertile and classified as shallow lithic leptsols with occasional rocky outcrops and luvic phaeozem (Streck et al. 2008).

In the study region, slash-and-burn small subsistence agriculture has replaced the original vegetation in many places, but difficulties of access to the mountainous terrain and legal restrictions against forest removal have led to the abandonment of cleared lands, resulting in a mosaic of forest patches at different stages of recovery. Unlike other regions of Brazil where the Atlantic Forest has been reduced to isolated patches within an anthropogenic matrix (Ranta et al. 1998), the study region maintains a mosaic of agriculture, pastures or forestry, forests at different stages of succession (22% initial, 35% intermediate and 20% late-successional stages) and protected areas (conservation units) in a relatively limited space (Becker et al. 2004).

Sampling design and data collection

Four chronosequences (replicates) were sampled in three valleys of the Maquiné River Basin, each one containing a set of plots differing in time since abandonment, ranging between 6 and45 yr old, and old-growth stands considered as reference areas. Although old-growth forests in this region have not suffered clear-cutting, they were likely affected by selective logging for local use and trade in the past century. Plots were selected based on information gathered through semi-structured interviews with local informants, gauging land-use history and time elapsed since abandonment. Aerial photographs from 1964 and satellite images from Landsat 5 TM and 7ETM (base year: 2002) were used to cross-check information from informants. Each plot had an area of 0.25 ha, a common size for slash-and-burn fields in the region, within which vegetation and soil data were sampled in three circular subplots of 100 m^2 at random locations. A total of 28 plots comprised the four chronosequences, corresponding to an area of 0.84 ha.

To describe community structure, we measured trees with a DBH $\geq$ 10 cm. For individuals with multiple basal stems, up to ten stems per individual were measured, given that at least one stem was $\geq$10 cm DBH and all stems were included in basal area calculations. We measured DBH and visually estimated height to the nearest 1 m. Trees were identified to species and grouped into families following APG III (2009).

Four environmental variables were measured: relief (terrain slope and aspect), topsoil nutrient concentrations (see below), topsoil texture (percentage organic matter and clay fraction) and space (geographic coordinates), as well as time since abandonment estimated for each plot. Time since abandonment was considered as years since the last planting cycle indicated by local informants. For old-growth forests, we assigned an arbitrary value of 150 yr old, considering the limitations for age estimation by local people. Recovery time was log-scaled for analysis, considering that changes in forest structure occur more rapidly at the onset of succession.

Relief variables for each plot included the terrain slope (measured as a percentage) and aspect (hillside orientation, from 0º to 360º). GIS methods were used to calculate relief variables using the tools of the 3D Analyst module available in ArcGIS 9.2. A 30-m resolution digital elevation model (DEM) was generated by TIN (triangulated irregular network) interpolation of hypsometric contour lines, and elevations were available from the 1:50 000 digital cartographic database of Rio Grande do Sul (Hasenack & Weber 2010). Aspect degree values were converted to radians and then transformed to sine aspect (eastness) and cosine aspect (northness) (Valeriano 2007). A cosine close to 1 indicates northward relief orientation, whereas values close to -1 indicate southward orientation; values close to 0 are either east or west. Sine values were interpreted similarly, but values close to 1 represent east-facing slopes.

Topsoil was collected to 5-cm depth with rectangular metal samplers (5 × 10 cm) at three locations within each 100-m^2 subplot. Samples within subplots were combined and homogenized in the field and analysed at the soil laboratory of the Agronomy Faculty of the University of Rio Grande do Sul, according to methods described in Tedesco et al. (1995). We considered the following soil variables: organic matter content (humid digestion method), clay fraction (%), total N content (Kjeldahl method), available P and K (Mehlich I method of extraction), exchangeable Al, Ca and Mg (extracted using KCl 1 $mol{\cdot}l^{-1}$), pH, potential acidity (Al+H), cation exchange capacity (CEC), Al saturation (% of CEC), base saturation (% of CEC), and the ratios of Ca/Mg, Ca/K and Mg/K. For analysis of soil variables we used the average subplot values.

Space was considered in the form of third-degree polynomials of geographic coordinates in the analysis, which permitted the representation of geographic variation in species composition by a cubic trend-surface of the latitude and longitude, capturing non-linear spatial relationships. The geographic coordinates in UTM (x, y) from each plot were first centralized and then derived in third-degree polynomials (xy, x^2, y^2, x^2y, xy^2, x^3 and y^3), resulting in nine variables for the analysis of spatial relationships (Legendre & Legendre 1998; Borcard et al. 2011).

Data analysis

Species composition of the plant communities along chronosequences was analysed using a data matrix of plot x species based on basal area data (matrix **C**), which was correlated to the environmental data matrices: plots x plot age (matrix **A**), plots x relief (matrix **R**), plots x topsoil texture (matrix **T**), plots x topsoil nutrients (matrix **N**), and plots x space (matrix **S**).

For analyses and the purpose of interpretation (e.g. visualization of plots in ordination space), we categorized plots into four successional stages according to age. We followed the age classes proposed by Chazdon (2008) for tropical successional forests. Stage 1 (S1) comprised plots between 6–10 yr of recovery (n = 4); stage 2 (S2) included those between 11–25 yr (n = 7); stage 3 (S3) was plots between 26–45 yr (n = 8); and we added a fourth category for reference areas (old-growth forest plots), considered as stage 4 (S4; n = 9). Each chronosequence was composed of a set of plots at these stages.

We used multivariate analysis of variance (MANOVA) with permutation testing (Pillar & Orlóci 1996) to compare species composition across successional stages (matrix **C**). The MANOVA was based on Bray–Curtis dissimilarity between plots, using square root-transformed data. Permutations were restricted within chronosequences so that differences between chronosequences were controlled, similar to a block design. Non-metric multidimensional scaling (NMDS) was also used to explore general trends in species composition in ordination space ('metaMDS' package in R, R Foundation for Statistical Computing, Vienna, AT). In order to identify the species characterizing each successional stage, we summarized species performance at each successional stage using relative density (RD), dominance (RC; basal area) and frequency (RF) (Mueller-Dombois & Ellenberg 1974) to define the importance value (VI = (RD + RC + RF)/3) for each species.

Species richness was compared across successional stages using rarefaction curves, where the number of species was standardized by the number of sampled individuals (Gotelli & Colwell 2001) using the software PAST (Hammer et al. 2008). Rarefaction curves are indicated for species richness comparisons when there may be differences in the average number of individuals per sample (Gotelli & Colwell 2001). Such is the case of many succession studies, as a higher density of individuals at intermediate stages is generally expected (Aide et al. 2000; Kennard 2002; Piotto et al. 2009).

Forest structure was described in each plot by the variance, maximum, minimum and average of tree heights; and by the total basal area and total density of living and dead trees (standing dead trees). Successional stages were compared for these parameters using ANOVA with permutation tests.

Finally, we used path analysis to test postulated causal models of species composition (**C**) by different sets of environmental data – age (**A**), topsoil (**T** and **N**), relief (**R**) and space (**S**) (Shipley 2002). For this purpose, we first evaluated Mantel correlations between all matrix pairs (zero-order correlation matrices) and then those links with significance ($P > 0.05$) were included in the proposed models. Soil nutrient parameters were first subjected to forward selection using 'packfor' in R to reduce the number of variables to the most significant subset related to species composition, which resulted in a matrix **N** with only N, P and CEC. Matrices **N** and **T** were submitted to a principal components analysis (PCA) to explore differences in topsoil across forest successional stages. As a premise, age had the highest order in the hierarchy (because time since abandonment is not determined by any other studied variable) and space and relief were only predictors. Second, we assessed the validity of causal models using partial Mantel correlations and testing the independence of sets of variables that were not connected in the models (*d-separation*; Shipley 2003). Model validation was based on Fisher's C statistics ($P \geq 0.05$); the model with the highest *P*-value was considered the most plausible. Path coefficients of valid models were calculated by regression (Lichstein 2007), based on standardized data, such that path coefficients were comparable. The response and predictor variables of regression models were defined according to causal hierarchy indicated by the path models. Uni- and multivariate analysis of variance, as well as path analyses, was performed with the software MULTIV (v 2.6.8. beta, available at http://ecoqua.ecologia.ufrgs.br).

Results

Species richness and composition patterns

We sampled 672 trees belonging to 95 species and 41 families. Families with the largest number of species were: Euphorbiaceae, Lauraceae, Myrtaceae (seven species each); Fabaceae (6); Meliaceae (5); and Annonaceae, Moraceae, Primulaceae, Urticaceae and Sapindaceae (4). Successional stages 1, 2, 3 and 4 had 22, 32, 50 and 52 species, respectively. The rarefaction analysis estimated 22, 23.2, 25.8 and 31.4 species for the respective stages considering the standardization of 67 sampled individuals (Fig. 2). An increase in richness was evident between successional stages 2 and 4, but richness in stage 1 was indistinguishable from richness in stages 2 and 3, but different from stage 4.

The block design MANOVA applied to matrix **C** indicated significant differences in species composition ($P \leq 0.01$) between old-growth forests (S4) and all other successional stages. The earlier stages of forest succession (S1 and S2) did not differ from each other (Fig. 3), but S3 differed significantly from S2 ($P = 0.014$) and S1 ($P = 0.048$). The NMDS ordination (Fig. 3) clearly showed old-growth forest plots (S4) grouped together in the ordination space, whereas species composition overlapped more so for S1 and S2, confirming the results of the MANOVA. Differences in species composition between S2 and S3 were less evident within chronosequences in ordination space, but were observed for the performance of some species. Considering the importance values (IV) of each species by successional stage (Table 1), changes in species dominance show a clear pattern of substitution through succession. *Tibouchina sellowiana* and *Myrsine coriacea* characterize initial stages (S1, S2), but their presence declines abruptly in intermediate and advanced stages (S3 and S4). *Cabralea canjerana* is present at all stages but is most important at S2 and S3. As the canopy closes, *Alsophila setosa* and *Euterpe edulis* became very abundant (S3) and in old-growth forests (S4) the conspicuous *Euterpe edulis*, *Ficus cestrifolia* and *Coussapoa microcarpa* increase in importance, as do many slow-growing species such as *Hennecartia*

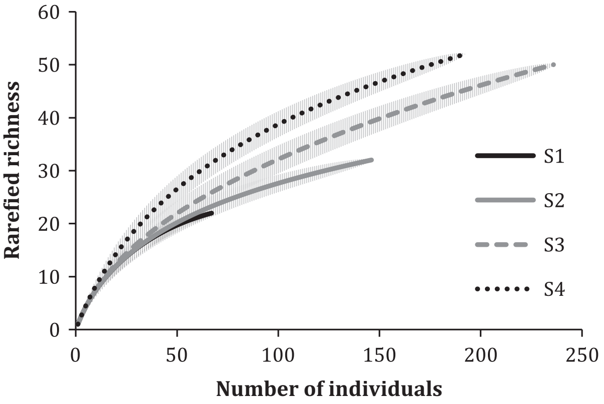

Fig. 2. Rarefied richness curves by the number of individuals sampled within successional stages S1 from 6 to 10 yr since abandonment, S2 = 11–25 yr, S3 = 26–45 yr, S4 = old-growth forest.

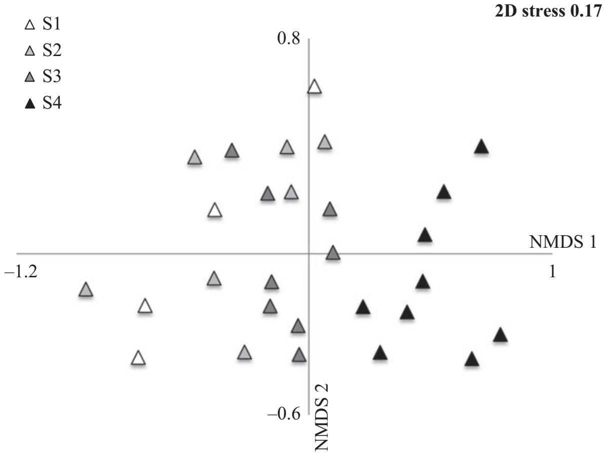

Fig. 3. Non-metric multidimensional scaling of forest plots based on Bray–Curtis dissimilarity, considering square root-transformed data of tree species composition. Shading identifies successional stages: S1 from 6–10 yr since abandonment, S2 = 11–25 yr, S3 = 26–45 yr, S4 = old-growth forest.

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Table 1. List of species characterizing the four successional stages of the Atlantic Forest in southern Brazil, with respective importance values (IV%) and families. The species are in order of decreasing IV (most representative values are in bold), following successional stages 1 (S1), 2 (S2), 3 (S3) and 4 (S4).

Family	Species	IV			
		S1	S2	S3	S4
Melastomataceae	*Tibouchina sellowiana* Cogn.	**17.70**	**8.78**	0.65	–
Fabaceae	*Inga marginata* Wild.	**9.78**	**4.19**	1.91	–
Primulaceae	*Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult.	**8.37**	**8.13**	1.84	–
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	**7.55**	**17.84**	**17.37**	**6.46**
Cunoniaceae	*Lamanonia ternata* Vell.	**5.34**	0.98	1.19	–
Ulmaceae	*Trema micrantha* (L.) Blume	**5.16**	**4.34**	1.26	–
Dicksoniaceae	*Dicksonia sellowiana* Hook	**4.78**	–	–	–
Aquifoliaceae	*Ilex brevicuspis* Reissek	**4.58**	1.79	–	–
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	**4.38**	1.69	2.38	–
Solanaceae	*Solanum sanctaecatharinae*	**4.11**	1.36	–	–
Meliaceae	*Cedrela fissilis* Vell.	**3.95**	2.41	0.56	0.59
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	2.82	3.03	**4.67**	1.59
Lauraceae	*Ocotea puberula* (Rich.) Nees	2.76	2.16	2.94	–
Escalloniaceae	*Escallonia bifida* Link & Otto	2.58	1.91	–	–
Lauraceae	*Nectandra oppositifolia* Nees & Mart.	2.39	**7.98**	**4.23**	2.15
Malvaceae	*Luehea divaricata* Mart.	2.19	–	1.18	0.48
Bombacaceae	*Pseudobombax grandiflorus* (Cav.) A. Robyns	2.11	–	–	1.08
Primulaceae	*Myrsine lorentziana* (Mez) Arechav.	1.98	0.94	1.26	–
Moraceae	*Ficus adhatodifolia* Schott ex Spreng.	1.97	1.86	1.91	0.61
Lamiaceae	*Aegiphila sellowiana* Cham.	1.91	–	0.52	–
Asteraceae	*Piptocarpha axilares* (Less.) Baker	1.85	–	0.97	–
Euphorbiaceae	*Tetrorchidium rubrivenium* Poepp.	1.75	**4.19**	**5.81**	3.40
Salicaceae	*Casearia sylvestris* Sw.	–	**4.01**	**5.67**	0.52
Fabaceae	*Machaerium paraguariense* Hassl.	–	3.69	–	–
Fabaceae	*Erythrina falcata* Benth.	–	3.43	1.82	–
Fabaceae	*Lonchocarpus cultratus* (Vell.) A.M.G. Azevedo & H.C. Lima	–	2.56	3.55	0.69
Euphorbiaceae	*Croton macrobothrys* Baill.	–	2.35	–	–
Annonaceae	*Annona rugulosa* (Schltdl.) H. Rainer	–	1.93	1.01	–
Lauraceae	*Nectandra megapotamica* (Spreng.) Mez	–	1.05	3.00	2.02
Euphorbiaceae	*Alchornea glandulosa* Poepp. & Endl.	–	1.00	–	–
Sapindaceae	*Matayba intermedia* Radlk.	–	0.98	–	–
Lauraceae	*Endlicheria paniculata* (Spreng.) J.F. Macbr.	–	0.94	0.51	–
Arecaceae	*Euterpe edulis* Mart.	–	0.92	**5.24**	**7.97**
Urticaceae	*Cecropia glaziovii* Snethl.	–	0.92	–	–
Annonaceae	*Annona glabra* L.	–	0.90	–	–
Aquifoliaceae	*Ilex paraguariensis* A. St.-Hil.	–	0.89	–	–
Rutaceae	*Zanthoxylum rhoifolium* Lam.	–	0.85	–	–
Cyatheaceae	*Alsophila setosa* Kaulf.	–	–	**9.19**	–
Sapindaceae	*Cupania vernalis* Cambess.	–	–	**4.04**	–
Salicaceae	*Xylosma pseudosalzmannii* Sleumer	–	–	1.07	–
Myrtaceae	*Calyptranthes grandifolia* O. Berg	–	–	1.04	0.50
Sabiaceae	*Meliosma sellowii* Urb.	–	–	0.98	**4.37**
Myrtaceae	*Campomanesia xanthocarpa* (Mart.) O.Berg	–	–	0.79	–
Primulaceae	*Myrsine guianensis* (Aubl.) Kuntze	–	–	0.74	–
Aquifoliaceae	*Ilex microdonta Reissek*	–	–	0.72	–
Fabaceae	*Lonchocarpus campestris* Mart. ex Benth	–	–	0.70	–
Lauraceae	*Cinnamomum glaziovii* (Mez) Kosterm.	–	–	0.69	1.96
Proteaceae	*Roupala brasiliensis* Klotzsch	–	–	0.65	–
Myrtaceae	*Myrcia pubipetala* Miq.	–	–	0.59	0.95
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	–	–	0.59	0.56
Solanaceae	*Cestrum intermedium* Sendtn.	–	–	0.58	–
Urticaceae	*Urera nitida* (Vell) P.Brack	–	–	0.57	0.80
Bignoniaceae	*Handroanthus umbellatus* (Sond.) Mattos	–	–	0.56	–
Phyllanthaceae	*Hieronyma alchorneoides* Allemão	–	–	0.54	1.16

Table 1. *(Continued).*

Family	Species	IV			
		S1	S2	S3	S4
Bignoniaceae	*Cybistax antisyphilitica* (Vell.) J.F. Macbr.	–	–	0.53	–
Cardiopteridaceae	*Citronella paniculata* (Mart.) R.A. Howard	–	–	0.52	–
Sapindaceae	*Matayba elaeagnoides* Radlk.	–	–	0.51	–
Sapindaceae	*Allophylus edulis* (A. St.-Hil.,Cambess. & A.Juss.) Radlk.	–	–	0.50	–
Boraginaceae	*Cordia trichotoma* (Vell.) Arrab. Ex Steud.	–	–	0.50	0.60
Lauraceae	*Ocotea stlvestris* Vattimo-Gil	–	–	0.50	–
Annonaceae	*Annona neosericia* Dunal	–	–	0.49	–
NI	*NI3*	–	–	0.49	–
Rosaceae	*Prunus myrtifolia* (L.) Urb.	–	–	0.49	–
Moraceae	*Ficus cestrifolia* Schott	–	–	–	**7.74**
Monimiaceae	*Hennecartia omphalandra* J. Poiss.	–	–	–	**5.39**
Meliaceae	*Trichilia claussenii* C. DC.	–	–	–	**5.05**
Myrtaceae	*Eugenia multicostata* D. Legrand	–	–	–	**4.97**
Urticaceae	*Coussapoa microcarpa* (Schott) Rizzini	–	–	–	**4.49**
Euphorbiaceae	*Actinostemon concolor* (Spreng.) Müll.Arg.	–	–	–	**4.29**
Euphorbiaceae	*Pachystroma longifolium* (Nees) I.M. Johnst.	–	–	–	2.57
Sapotaceae	*Chrysophyllum viride* Mart. & Eichler	–	–	–	2.54
Fabaceae	*Ormosia arborea* (Vell.) Harms	–	–	–	2.52
Moraceae	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanjouw & Boer	–	–	–	2.49
Sapotaceae	*Chrysophyllum inornatum* Mart.	–	–	–	2.26
Lauraceae	*Ocotea indecora* (Schott) Mez	–	–	–	2.01
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi	–	–	–	1.98
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	–	–	–	1.92
Chrysobalanaceae	*Hirtella hebeclada* Moric. ex DC	–	–	–	1.26
Myristicaceae	*Virola bicuhyba* (Schott ex Spreng.) Warb.	–	–	–	1.11
Monimiaceae	*Mollinedia schottiana* (Spreng.) Perkins	–	–	–	0.96
Apocynaceae	*Aspidosperma australe* Müll. Arg.	–	–	–	0.78
Celastraceae	*Maytenus glaucescens* Reissek	–	–	–	0.67
Myrtaceae	*Eugenia verticillata* (Vell.) Angely	–	–	–	0.60
Meliaceae	*Trichilia pallens C. DC.*	–	–	–	0.53
Annonaceae	*Annona neosalicifolia* Ekman & R.E. Fr.	–	–	–	0.53
Primulaceae	*Myrsine loefgrenii* (Mez) Otegui	–	–	–	0.51
Meliaceae	*Guarea macrophylla* Vahl	–	–	–	0.51
Rutaceae	*Esenbeckia grandiflora* Mart.	–	–	–	0.50
Celastraceae	*Maytenus evonymoides* Reissek	–	–	–	0.49
Urticaceae	*Urera baccifera* (L.) Gaudich. ex Wedd.	–	–	–	0.48
Myrtaceae	*Calyptranthes lucida* Mart. ex DC.	–	–	–	0.48
Rubiaceae	*Faramea montevidensis* (Cham. & Schltdl.) DC.	–	–	–	0.48
NI	*NI2*	–	–	–	0.48
Myrtaceae	*Eugenia bacopari* D. Legrand	–	–	–	0.48
Rutaceae	*Pilocarpus pennatifolius* Lem.	–	–	–	0.47

omphalandra, Trichilia claussenii, Eugenia multicostata, Actinostemon concolor and *Meliosma sellowii*.

Structural patterns

As succession proceeds, there was a significant increase in total basal area of live trees, maximum and average height of trees and also in the complexity of vertical structure, detected as variance in tree height (Table 2). Plots at successional Stage 3 did not differ from old-growth plots for the parameters related to tree height, but showed the highest tree density compared to all other stages. Old-growth forests (S4) presented the largest basal cover area of living trees.

The proportion of individuals developed by resprouting (multiple stems below 1.30-m height) diminished with forest recovery from 40% in S1 to 7% in old-growth forests. The proportion of species that are considered as having the capacity to resprout from damaged trunks (field-observed sprouting ability) was 56% for the two initial stages, 32% in the third and 20% in the old-growth forests.

Table 2. Structural parameters of vegetation at each stage of succession. Means followed by the same letter did not differ significantly ($P \leq 0.01$).

Structural parameters	Stage 1 (n = 4)	Stage 2 (n = 7)	Stage 3 (n = 8)	Stage 4 (n = 9)
Maximum height (m)	9.25^{a}	14^{a}	19.19^{bc}	20.33^{c}
Minimum height (m)	4.25	5.21	5.38	4.78
Average height (m)	6.97^{a}	9.15^{a}	11.56^{bc}	11.46^{c}
Height variance	2.79^{a}	6.49^{a}	17.53^{bc}	24.10^{c}
Basal area coverage of standing dead trees ($m^2 \cdot ha^{-1}$)	0.68	0.56	1.02	2.87
Density of standing dead trees (ha)	41.67	23.81	41.67	40.74
Basal area coverage of living trees ($m^2 \cdot ha^{-1}$)	12.85^{a}	20.66^{a}	35.35^{b}	54.79^{c}
Density of living trees (ha)	558.33^{a}	695.23^{a}	983.33^{b}	711.10^{a}

Causal relationships between environment and species composition

Zero-order matrices correlation (Appendix S1) indicated that neither space (**S**) nor relief (**R**) was related to species composition (**C**) or any other set of variables. Thus the variation in space and relief that was not controlled by our chronosequence design did not influence the observed community pattern, and these two matrices were not considered in any final model. The other sets of variables showed significant correlation, so path models were developed based on community (defined by the species composition matrix – **C**), topsoil nutrients (**N**), topsoil texture (**T**) and plot age (**A**).

As previously assumed, age since abandonment (matrix **A**) defines the top of the hierarchy in all tested models. In addition, we expected that successional changes in the communities would be associated with changes in the organic soil portion (topsoil). As our system had fertile soils, the topsoil may better express those changes influencing or being influenced by vegetation cover. This hypothesis was included in the tested models. The forest soil pattern can be see on the ordination diagram of soil variables most correlated to tree species patterns, which also expressed a clear distinction of old-growth forests (Fig. 4). Both axes contributed to express differences among them. Topsoil underneath old-growth forests is more fertile, containing higher values of organic matter and higher available nutrient content (CEC, P, N).

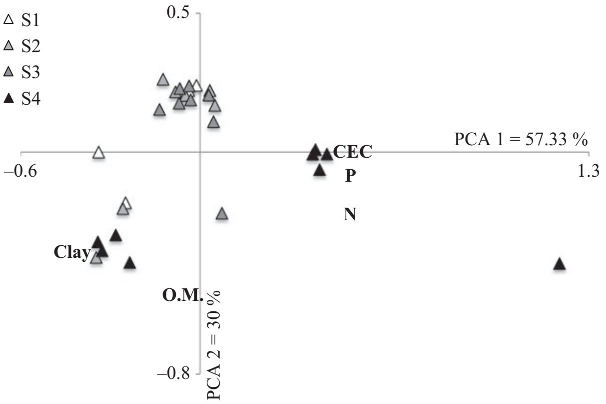

Fig. 4. Principal components analysis of forest plots based on five topsoil variables (matrix N and T) – soil organic matter (SOM), clay fraction, cation exchange capacity (CEC), total nitrogen content (N) and available phosphorus (P) – described for each successional forest plot. The stage description is the same as in Fig. 3.

Three hypothetical models were valid (Fig. 5). In Model 1 we tested communities (matrix **C**) responding to recovery age (**A**) and topsoil conditions (matrices **N** and **T**), and topsoil responding just to recovery age, without direct influence of tree species composition. Model 2 tested the community responding just to age of recovery, while topsoil variables are conditioned by tree species composition and by the recovery age. In Model 3, community is also responding just to recovery age, but only community influences the topsoil properties. All models were valid, but the strongest path-coefficient (0.31) in Model 1 highlighted the importance of recovery age on community assembly and topsoil properties, which further also influence tree species assembly. On the other hand, despite the validity of all models, Model 3 presented the highest P-value ($P = 0.59$), so it was considered the most relevant.

Discussion

Our study is the first to describe the floristic and structural patterns of succession and to assess causal relationships between age, environment and community composition of secondary successional forests for the Atlantic rain forest in a subtropical context (in the southernmost limit of its distribution in Brazil). We found successional forest composition was markedly different from reference areas (old-growth forests). Despite a rapid recovery of forest structure during the early stages of succession, stands between 25 and 45 yr since abandonment did not have similar structural features to those found in old-growth forests, with respect to basal area coverage and live tree density. Our results show that forest age is likely more important than the influence of environmental and spatial differences for species assembly during succession. Forest age is a proxy for other variables that were not included but likely represents an increase in the complexity of structure, processes and interactions over forest succession.

Floristic and structural patterns

Tree species richness increased during succession, especially after the second stage. In the first two stages, *i.e.* after 25 yr of recovery, richness was estimated at 22 species

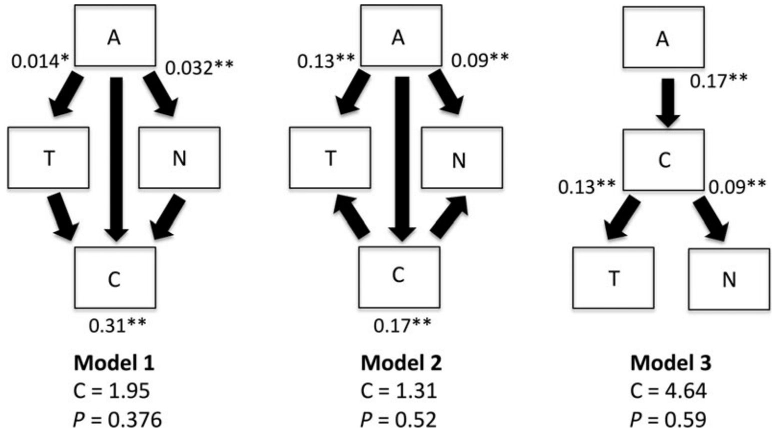

Fig. 5. Valid path models (with the Fischer's C- and respective *P*-values) linking the following matrices: log of plot age (**A**); soil texture (**T**); soil nutrients (N); and species basal area (**C**) in plots. Path coefficients (** $P \leq 0.005$; * ≤ 0.05) between matrices are presented.

given a standardized number of 67 individuals, while the other stages indicate a clear increase in species richness. Although plots did not approach stabilization of richness curves within each stage, we found an increase in species number along the succession. The increase of species richness in the recovery process was also observed in southern (Liebsch et al. 2008) and northeastern (Santos et al. 2008; Piotto et al. 2009) Brazilian Atlantic rain forest, as well as in many other Neotropical forests (Guariguata & Ostertag 2001; Ruiz et al. 2005; Howorth & Pendry 2006; Chazdon et al. 2007). Different trends in species richness across succession are reported for tropical forests in Panama (DeWalt 2003) and in Puerto Rico (Aide et al. 2000), where constant values were found for fallow and old-growth forests. The lack of change in richness across stages of recovery in these studies may be an effect of the large number of individuals usually present at intermediate stages (Gotelli & Colwell 2001), as this was not controlled. It is noteworthy that species richness here increased slowly during succession compared to other forest structural characteristics, and was influenced by the presence of resprouting individuals, land-use intensity and landscape context (Chazdon et al. 2007).

Rapid recovery of forest structure is generally described for tropical rain forests (Guariguata & Ostertag 2001; Kennard 2002; Chazdon 2003; Howorth & Pendry 2006; Chazdon et al. 2007; Marín-Spiotta et al. 2007), where stands of 25–80 yr since abandonment reach structural values identical or close to those found in old-growth stands. Our study in the southern limit of the Atlantic rain forest indicates that secondary forests of 25–45 yr old quickly achieve tree heights similar to those found for old-growth forests. Canopy height and the vertical complexity of the tree stratum (height variance) were already similar between stages S3 and S4. Nonetheless, basal area took more time to recover to old-growth values, and the intermediate stage of succession (S3) had a higher tree density than that at the other stages (earlier and later). This may suggest high mortality of shade-intolerant species at the third stage in this subtropical forest, which was also found up until 25 yr of recovery in Caribbean lowland forests (Chazdon 2008). Despite trends in tree species, the species composition of other life forms, woody debris and forest strata complexity are extremely important characteristics for biodiversity and food web structure that may not be fully established in fallows (DeWalt 2003) but were not considered here.

Beyond structural differences, species composition of old-growth forests differed between earlier and intermediate stages. Species such as *Eugenia multicostata*, *Garcinia gardneriana*, *Pachystroma longifolium*, *Actinostemon concolor*, *Meliosma sellowii* and *Henecartia omphalandra* are considered climax species in this region (Backes & Irgang 2009) and were present only in old-growth forests. Although our data suggested some directionality in the successional process, still 68% of the species present in old-growth forests were not present in secondary forests. As pointed out in Finegan (1996), the composition of neighbouring mature and secondary forests is almost completely different, and thus an increase in species richness does not necessarily indicate re-establishment of the original forest community. As expected for tropical forests, the proportion of low-density species in old-growth stands was high. A recent study compiling a series of forest stand data along the Brazilian Atlantic coast indicated an average of ca. 98 tree species for lower montane rain forests (ca. 228 m a.s.l.) in the southern and southeastern regions (Marques et al. 2011). We sampled a total of 52 tree species among all old-growth plots. Another study, just a few kilometers away from our study area, found 72 tree species at an altitude of 220 m a.s.l. and 84 species in stands at 420 m a.s.l. (Moltz 2011). Although the objective of this study was not precisely to compare species richness of late-successional forests, species richness in the narrow strip of the southern subtropical Atlantic rain forest is expected to be lower than in northern areas closer to centres of endemism (Carnaval & Moritz 2008; Werneck et al. 2011). Additionally, some species in these areas may have suffered selective logging in the past, potentially limiting even more so the geographic distribution of extant populations.

Tibouchina sellowiana dominated many early successional and some intermediate stands. Its anemochoric dispersal mode and high number of seeds probably facilitate arrival and establishment at new sites, being excluded only in shady and moist environmental conditions. Other species highly correlated with early stages are zoochoric, with small and attractive fruits for bird dispersal, such as *Myrsine coriacea*, *Ilex paraguariensis*, *Ilex brevicuspis* and *Aegiphila sellowiana*. However, the natural recovery of early stands had idiosyncratic differences from site to site.

Many factors may govern the colonization process, especially differences in conditions for germination (e.g. fertility, drainage and compaction of soil), time of seed arrival, presence of a seed bank and resprouts (Guariguata & Ostertag 2001). The contribution of resprouting stems to the structure and composition of successional forests is not well known, but is an important feature for forest recovery and a trait of many species (Guariguata & Ostertag 2001; Chazdon 2003). In our study, resprouting ability had a key role in forest recovery. The decreasing proportion of resprouted stems through succession was consistent with Kammesheidt (1998) and Oliveira Filho et al. (2004). The high importance of *Cabralea canjerana* at the first stage of succession was probably due to its high resprouting capacity, allowing occupation of space faster than individuals established from seed (Kennard 2002; Simões & Marques 2007). However, it should be noted that the detectability of resprouting capacity is directly linked to disturbance events. Old-growth plots did not suffer homogeneous disturbance and had different species, potentially resulting in the underestimation of resprouting ability for some species (Guariguata & Ostertag 2001).

Differences in species composition between early successional stands may also reflect small differences in historical land use and stochastic factors. Land-use history was controlled as much as possible in our study, such that it is impossible to determine whether small differences may have influenced observed patterns, although stochastic factors surely played some role. Some authors suggest that stochastic processes dominate in the early stages of succession (Coomes et al. 2002; Gravel et al. 2006; Chazdon 2008), while processes mediated by niche prevail at advanced stages (Norden et al. 2009). Only the rules of plant community assembly are related to neutral, niche and stochastic processes (Kraft et al. 2008; Kraft & Ackerly 2010; Ding et al. 2012; Whitfeld et al. 2012), so are these processes important for guiding plant succession? Successional dynamics may involve a 'niche strength continuum', where early stage communities are loosely structured by niche, prevailing abiotic constraints and stochastic forces, and as succession progresses, the role of biotic interactions may increase, resulting in more strongly niche-structured later stages (Chase & Myers 2011; Mutshinda & O'Hara 2011).

Forest recovery and its relation to age and environmental conditions

Our results indicated that forest age, expressed in years since agricultural abandonment, was the strongest force governing succession. The validity of three path models denotes that topsoil nutrients are influenced by and can influence plant communities. However, we consider that these were more likely than not affected by vegetation development, as expressed in Model 3. As shown in the soil-based ordination, old-growth forests differed from successional stands by higher content of P, N, potential cation exchange capacity and organic matter, which may be related to the ability of tropical rain forests for fast nutrient cycling and its relationship with species composition and respective foliar chemical content (Waring 2012).

Forest age can be seen as a proxy, since it incorporates many processes not directly considered in our study. Recently, the effects of diversity on ecosystem processes were found to be stronger over time, as complementary interactions between species become more important, resulting in less saturating relationships between biodiversity and function (Allan et al. 2013). Such effects of plant species richness were best observed for biomass production, soil water content, the abundance of decomposers, the carbon cycle and the diversity of other organisms, being marginally or not significant for soil N fluxes and pools (Allan et al. 2013). The authors also found that these effects decreased in deeper soils. In a semi-arid ecosystem with poor soils in Spain, Martinez-Duro et al. (2010) found that soil chemical composition (10.5%) and geographic variables (7.2%) were better at explaining variation in species composition through succession than was time since abandonment (3.4%). Nonetheless, less influence of landscape and soil differences on the floristic patterns were reported for secondary tropical rain forests of Costa Rica (Letcher & Chazdon 2009), where time since abandonment was responsible for predictable changes in forest structure and composition. These results suggest that the strength of each of the studied variables may vary under different systems and conditions, and that interactions between plant community and environment are variable over time, leading to specific trajectories through successional stages.

Our study of Atlantic rain forest recovery revealed that species are assembled primarily due to factors or variables related to time post-abandonment, regardless of local topsoil conditions, relief or spatial relationships. It is important to remember that the study region had no apparent limitation to propagule dispersal, as sites were located in a mosaic of traditional slash-and-burn agriculture, successional forests and conservation units, which maintain considerable cover of mature forest. We detected some predictability in the direction of natural forest recovery, in the structure of trees (biomass, i.e. height and basal cover) and in the identity of colonizer species in each phase of regeneration after abandonment. However, stands with 40 yr of recovery still differ from old-growth forests in terms of species composition and richness. As forest age was the major predictor variable for tree species composition, we can conclude that the dynamics of natural forest recovery were driven by autogenic processes not entirely related to local environmental conditions of soil, relief and space.

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References

Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L. & Marcano-Vega, H. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* 8: 328–338.

Allan, E., Weisser, W.W., Fischer, M., Schulze, E.-D., Weigelt, A., Roscher, C., Baade, J., Barnard, R.L., Bessler, H.(…) & Schmidt, B. 2013. A comparison of the strength of biodiversity effects across multiple functions. *Oecologia* 173: 223–237.

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: s.105–s.121.

Backes, P. & Irgang, B.E. 2009. *Árvores do sul: guia de identificação e interesse ecológico*, 2nd edn. Paisagem do Sul, Porto Alegre, BR.

Becker, F.G., Irgang, G.V., Hasenack, H., Vilella, F.S. & Verani, N.F. 2004. Land cover and conservation state of a region in the Southern limit of the Atlantic Forest (river Maquiné basin, Rio Grande do Sul, Brazil). *Brazilian Journal of Biology* 64: 569–582.

Bergamin, R., Müller, S. & Mello, R. 2012. Indicator species and floristic patterns in different forest formations in southern Atlantic rainforests of Brazil. *Community Ecology* 13: 162–170.

Blanc, L., Maury-Lechon, G. & Pascal, J.P. 2000. Structure, floristic composition and natural regeneration in the forests of Cat Tien National Park, Vietnam: an analysis of the successional trends. *Journal of Biogeography* 27: 141–157.

Borcard, D., Gillet, F. & Legendre, P. 2011. *Numerical Ecology with R*. Springer, New York, NY, US.

Brown, S. & Lugo, A.E. 1990. Tropical Secondary Forest. *Journal of Tropical Ecology* 6: 1–32.

Carnaval, A.C. & Moritz, C. 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography* 35: 1187–1201.

Chase, J.M. & Myers, J.A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351–2363.

Chazdon, R.L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71.

Chazdon, R.L. 2008. Chance and determinism in tropical forest succession. In: Carson, W.P. & Schnitzer, S.A (eds.) *Tropical forest community ecology*, pp. 384–408. Wiley-Blackwell, Oxford, UK.

Chazdon, R.L., Letcher, S.G., 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 B: Biological Sciences* 362: 273–289.

Coomes, D., Rees, M., Turnbull, L. & Ratcliffe, S. 2002. On the mechanisms of coexistence among annual-plant species, using neighbourhood techniques and simulation models. *Plant Ecology* 163: 23–38.

Dean, W. 1997. *Ferro e fogo: a historia e a devastacao da Mata Atlantica brasileira*. Companhia das Letras, São Paulo, BR.

DeWalt, S. 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management* 182: 139–151.

Ding, Y., Zang, R., Letcher, S.G., Liu, S. & He, F. 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos* 121: 1263–1270.

FAO. 2005. *Global Forest Resources Assessment 2005: progress Towards Sustainable Forest Management*. FAO, Rome, IT.

FAO. 2007. State of the world's forests. Food and Agriculture Organization, Rome, IT.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends in Ecology and Evolution* 11: 119–124.

Doi: 10.1111/jvs.12162

Fridley, J.D. 2013. Successional convergence, stochastic assembly and the future of tropical forests. *Journal of Vegetation Science* 24: 415–416.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A. & Sodhi, N.S. 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12: 561–582.

Gotelli, N.J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391.

Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9: 399–409.

Guariguata, M.R. & Ostertag, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185–206.

Hammer, Ø., Harper, D.A.T. & Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 9pp.

Hasenack, H. & Ferraro, L.W. 1989. Considerações sobre o clima da região de Tramandaí - RS. *Pesquisas em Geociências* 22: 53–70.

Hasenack, H. & Weber, E. 2010. Base cartográfica vetorial do Rio Grande do Sul 1: 50.000. In: Série geoprocessamento, 3. IB-Centro de Ecologia. UFRGS, Porto Alegre, BR.

Howorth, R.T. & Pendry, C.A. 2006. Post-cultivation Secondary Succession in a Venezuelan Lower Montane Rain Forest. *Biodiversity & Conservation* 15: 693–715.

ITTO. 2002. *ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests*. Policy and Development Series 13, International Tropical Timber Organization, Yokohama, JP.

Kammesheidt, L. 1998. The role of tree sprouts in the restoration of stand structure and species diversity in tropical moist forest after slash-and-burn agriculture in Eastern Paraguay. *Plant Ecology* 139: 155–165.

Kennard, D.K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *Journal of Tropical Ecology* 18: 53–66.

Klanderud, K., Mbolatiana, H.Z.H., Vololomboahangy, M.N., Radimbison, M.A., Roger, E., Totland, Ø. & Rajeriarison, C. 2009. Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. *Biodiversity & Conservation* 19: 187–204.

Kraft, N.J.B. & Ackerly, D.D. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80: 401–422.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322: 580–582.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*. 2nd edn. Elsevier, Amsterdam, NL.

Letcher, S.G. & Chazdon, R.L. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* 41: 608–617.

Lichstein, J. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology* 188: 117–131.

Liebsch, D., Marques, M.C.M. & 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.

Lopes, A.V., Girão, L.C., Santos, B.A., Peres, C.A. & Tabarelli, M. 2009. Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments. *Biological Conservation* 142: 1154–1165.

Marín-Spiotta, E., Silver, W.L. & Ostertag, R. 2007. Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. *Ecological Applications* 17: 828–839.

Marques, M.M., Swaine, M. & Liebsch, D. 2011. Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest. *Biodiversity & Conservation* 20: 153–168.

Martinez-Duro, E., Ferrandis, P., Escudero, A., Luzuriaga, A. & Herranz, J. 2010. Secondary old-field succession in an ecosystem with restrictive soils: does time from abandonment matter? *Applied Vegetation Science* 13: 234–248.

Metzger, J.P. 2009. Conservation issues in the Brazilian Atlantic forest. *Biological Conservation* 142: 1138–1140.

Mittermeier, R.A., Gill, P.R., Hoffmann, M., Pilgrim, J., Brooks, J., Mittermeier, C.J., Lamourux, J. & Fonseca, G.A.B. 2005. *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. CEMEX, Washington, DC, US.

Moltz, M. 2011. Comunidades arbóreas ao longo de um gradiente altitudinal na floresta atlântica sul-brasileira. *Programa de Pós Graduação em Botânica (Doctoral dissertation)*. UFRGS, Porto Alegre, BR.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York, NY, US.

Mutshinda, C.M. & O'Hara, R.B. 2011. Integrating the niche and neutral perspectives on community structure and dynamics. *Oecologia* 166: 241–251.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Nimer, E. 1990. Clima. In: IBGE. (eds.) *Geografia do Brasil: Região Sul*. pp. 151–187. IBGE, Rio de Janeiro, BR.

Norden, N., Chave, J., Belbenoit, P., Caubère, A., Châtelet, P., Forget, P.-M., Riéra, B., Viers, J. & Thébaud, C. 2009. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. *Journal of Ecology* 97: 186–197.

Oliveira Filho, A.T., Carvalho, D.A., Vilela, E.A., Curi, N. & Fontes, M.A.L.L. 2004. Diversity and structure of the tree community of a fragment of tropical secondary forest of the brazilian Atlantic Forest domain 15 and 40 years after logging. *Brazilian Journal of Botany* 27: 685–701.

Oliveira-Filho, A.T. 2009. Classificação das fitofisionomias da América do Sul cisandina tropical e subtropical: proposta de um novo sistema–prático e flexível–ou uma injeção a mais de caos? *Rodriguésia* 60: 237–258.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-term Studies in Ecology, Approaches and Alternatives*, pp. 110–135. Springer, New York, NY, US.

Pillar, V.D. & Orlóci, L. 1996. On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science* 7: 585–592.

Piotto, D., Montagnini, F., Thomas, W., Ashton, M. & Oliver, C. 2009. Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. *Plant Ecology* 205: 261–272.

Rambo, B. 1956. *A fisionomia do Rio Grande do Sul*. Selbach, Porto Alegre, BR.

Ranta, P., Blom, T.O.M., Niemelä, J., Joensuu, E. & Siitonen, M. 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiversity & Conservation* 7: 385–403.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142: 1141–1153.

Ruiz, J., Fandiño, M.C. & Chazdon, R.L. 2005. Vegetation Structure, Composition, and Species Richness Across a 56-year Chronosequence of Dry Tropical Forest on Providencia Island, Colombia. 1. *Biotropica* 37: 520–530.

Santos, B.A., Peres, C.A., Oliveira, M.A., Grillo, A., Alves-Costa, C.l.P. & Tabarelli, M. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation* 141: 249–260.

Santos, B.A., Arroyo-Rodríguez, V., Moreno, C.E. & Tabarelli, M. 2010. Edge-Related Loss of Tree Phylogenetic Diversity in the Severely Fragmented Brazilian Atlantic Forest. *PLoS ONE* 5: e12625.

Scudeller, V.V., Martins, F.R. & Shepherd, G.J. 2001. Distribution and abundance of arboreal species in the Atlantic ombrophilous dense forest in Southeastern Brazil. *Plant Ecology* 152: 185–199.

Shipley, B. 2002. *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge, UK.

Shipley, B. 2003. Testing Recursive Path Models With Correlated Errors Using D-Separation. *Structural Equation Modeling: A Multidisciplinary Journal* 10: 214–221.

Simões, C.G. & Marques, M.C.M. 2007. The Role of Sprouts in the Restoration of Atlantic Rainforest in Southern Brazil. *Restoration Ecology* 15: 53–59.

Streck, E.V., Kämpf, N., Dalmolin, R.S.D., Klamt, E., Nascimento, P.C., Schneider, P., Giasson, E. & Pinto, L.F.S. 2008. *Solos do Rio Grande do Sul. 2*. EMATER/RS, Porto Alegre, BR.

Tabarelli, M., Lopes, A.V. & Peres, C.A. 2008. Edge-effects Drive Tropical Forest Fragments Towards an Early-Successional System. *Biotropica* 40: 657–661.

Tabarelli, M., Aguiar, A.V., Ribeiro, M.C., Metzger, J.P. & Peres, C.A. 2010. Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. *Biological Conservation* 143: 2328–2340.

Tedesco, M.J., Gianello, C., Bissani, C.A., Bohnen, H. & Enrkweiss, S.J. 1995. *Análises de solo, plantas e outros materiais* 2 ed, pp. 174. UFRGS, Porto Alegre, BR.

Teixeira, M.B., Coura-Neto, A.B., Pastore, U. & Filho, A.R.L.R. 1986. *Levantamento de recursos naturais (Folha SH.22 Porto Alegre e parte das Folhas SH.21 Uruguaiana e SI.22 Lagoa Mirim)*. IBGE, Rio de Janeiro, BR.

Teixeira, A.M.G., Soares-Filho, B.S., Freitas, S.R. & Metzger, J.P. 2009. Modeling landscape dynamics in an Atlantic Rainforest region: implications for conservation. *Forest Ecology and Management* 257: 1219–1230.

Valeriano, M.D.M. 2007. Visualização de imagens topográficas. In: *Anais Simpósio Brasileiro de Sensoriamento Remoto*, pp. 1377–1384. Instituto Nacional de Pesquisas Espaciais (INPE), São José dos Campos, BR.

van Breugel, M., Bongers, F. & Martinez-Ramos, M. 2007. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. *Biotropica* 35: 610–619.

van der Maarel, E. 1988. Vegetation dynamics: patterns in time and space. *Vegetatio* 77: 7–19.

Vieira, I. 2003. Classifying successional forests using Landsat spectral properties and ecological characteristics in eastern Amazônia. *Remote Sensing of Environment* 87: 470–481.

Waechter, J.L. 2002. Padrões geográficos na flora atual do Rio Grande do Sul. *Ciência & Ambiente* 24: 93–108.

Waring, B.G. 2012. A meta-analysis of climatic and chemical controls on leaf litter decay rates in tropical forests. *Ecosystems* 15: 999–1009.

Werneck, M.D., Sobral, M.E.G., Rocha, C.T.V., Landau, E.C. & Stehmann, J.R. 2011. Distribution and Endemism of Angiosperms in the Atlantic Forest. *Naturenza Conservacao* 9: 188–193.

Whitfeld, T.J.S., Kress, W.J., Erickson, D.L. & Weiblen, G.D. 2012. Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. *Ecography* 35: 821–830.

Wildi, O. 2002. Modelling succession from pasture to forest in time and space. *Community Ecology* 3: 181–189.

Supporting Information

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

Appendix S1. Zero-order matrix correlation matrices.