Natural forest regeneration in abandoned sugarcane fields in northeastern Brazil: floristic changes

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Abstract: Surveys were undertaken to examine the floristic changes during secondary succession in three areas of 12 and three of 20-year-old secondary forests in Pernambuco State, Brazil. Two hundred and six species were identified, with 136 being found in the 12-year-old secondary forest and 161 species in the 20-year-old forest. Fabaceae and Myrtaceae were the most important families, increasing in species numbers with regeneration age. Of the 216 species, 115 were trees, 48 shrubs, 16 herbaceous plants, and 24 woody lianas, without significant differences between the two regeneration site ages. NMDS analysis revealed a formation of two floristic groups, distinguishing secondary and mature forests, with a further division within secondary forests in accordance with the time since abandonment. Similarity analysis ANOSIM confirmed the significance of the groups, which had floristic composition significant distinct (R=0.96) and 63% of dissimilarity (SIMPER). However, the sharing of 68 arboreal species between the secondary and mature forests suggests a floristic convergence. DCA analysis of the arboreal component as well as the other plant habits suggested that the separation of the subgroups is correlated with physical and chemical variables of the soils. All of these results indicate that, within the chronosequence analyzed, the velocity and direction of the floristic composition during secondary succession was influenced not only by the time of their abandonment, but also by a wide range of environmental variables.
Keywords: *secondary forests, floristic, secondary succession.*

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Resumo: Com objetivo de detectar mudanças florísticas ao longo da sucessão secundária e subsidiar futuros projetos de recuperação florestal foi realizado levantamento florístico de seis áreas de floresta secundária (capoeira) de 12 e 20 anos em Pernambuco. Foram registradas 206 espécies, sendo 136 nas capoeiras de 12 anos e 161 nas de 20 anos. Fabaceae e Myrtaceae foram as famílias mais importantes, aumentando no número de espécies com a idade de regeneração. Do total de espécies, 115 foram árvores, 48 arbustos, 16 herbáceas e 24 trepadeiras, sem diferença significativa por idade de regeneração. Análise de NMDS indicou a separação dos grupos florísticos das florestas maduras e das capoeiras, assim como a formação de subgrupos de capoeiras (SF1-2-3 e SF4-5-6) com idade de regeneração distinta. A análise de similaridade ANOSIM mostrou que os grupos formados apresentaram composição florística significativamente distintas (R = 0.96) e 63% de dissimilaridade (SIMPER). Entretanto, a presença nas capoeiras de 67 espécies em comum com as florestas maduras indicam uma tendência de convergência florística. A análise de DCA do componente arbóreo e dos outros hábitos sugere que a separação dos subgrupos por idade estaria correlacionada com variáveis edáficas físicas e químicas. Todos esses resultados indicam que, numa análise de cronossequência, não apenas o tempo de abandono, mas todas as variáveis ambientais influenciam a velocidade e direção de formação da composição florística durante a sucessão secundária.
Palavras-chave: *capoeira, flora vascular, sucessão secundária.*

Introduction

The degradation and destruction of natural habitats figure among the principal modern threats to biodiversity (Primack 2008). With the acceleration of the conversion of forests into pasture lands and agricultural fields in recent decades in Latin America (Geist & Lambin 2001) it has come to the point that mature forests altered by anthropogenic actions and regenerating secondary forests now compose approximately half of all remaining forest areas in the tropics (International... 2002). On the other hand, large areas of formerly cleared lands have also been abandoned and are evolving into secondary forests (Wright 2005).

Fragments of mature and secondary forests can be found in many landscapes otherwise dominated by agriculture or pasture lands. This situation can be seen, for example, in the Brazilian Atlantic Forest biome that has suffered negative impacts from a number of economic cycles, resulting in significant landscape modifications and ecosystem destruction (Dean 2002). The conservation of the Atlantic Forest and its biodiversity now presents a significant challenge to conservation efforts, principally due to its advanced state of forest substitution, and depends on the protection of the remaining fragments of mature forest (Tabarelli & Gascon 2005) and the correct management of regenerating forests after abandonment (Dent & Wright 2009). The Atlantic Forest now persists on only between 11% and 16% of its original land area coverage, and even these remnants are extremely fragmented (Ribeiro et al. 2009). This once extensive forest is currently composed of just a few well-preserved mature forest sites with numerous areas of varying ages with diverse use-histories undergoing secondary succession, and these are often surrounded by matrixes of cultivated areas and pasturelands (Ranta et al. 1998, Trindade et al. 2008).

A number of workers have pointed out the importance of secondary forests: as biodiversity reservoirs within fragmented landscapes (Chazdon 1998, 2003, Letcher & Chazdon 2009); as sources of sustenance for wildlife (Parry et al. 2007, Herrera-Montes & Brokaw 2010), providing sites for conservation of rare and endemic species (Liebsch et al. 2008) and wood and non-wood products (Chazdon & Coe 1999); in the accumulation of biomass (Gehring et al. 2004, Grace 2004, Feldpausch et al. 2007); for controlling carbon emissions (Feldpausch et al. 2005); and for diminishing pressure on natural habitats (Wright & Muller-Landau 2006).

The structural attributes of tropical forests such as density, biomass, richness, diversity, and composition can slowly recover after significant natural or anthropogenic disturbances (Brown & Lugo 1990, Guariguata & Ostertag 2001, Chazdon 2003, Finegan & Nasi 2004), but an important question in terms of our understanding of successional processes of secondary forests is if their floristic composition also tends to converge towards that of nearby mature forests or if they maintain their differences. According to Chazdon et al. (2009), convergence seems to be related to the level of anthropogenic disturbance, the duration of the time that the area was used, and the regional landscape context. The interrelations of these parameters make the outcomes of succession less predictable, and measurable differences in the floristic compositions of secondary forests may persist even centuries after they have been abandoned and left to recuperate (Finegan 1996, Aide et al. 2000, Denslow & Guzman 2000, Calvo et al. 2002, Ribas et al. 2003).

Previous researchers (refer to a review by Guariguata & Ostertag 2001) have demonstrated that a number of factors influence the recuperation of the floristic composition after disturbances, although many questions still remain unanswered due, in large part, to the idiosyncratic, non-directional, and largely unpredictable processes of succession in tropical forests (Letcher & Chazdon 2009).

The present work analyzed the floristic composition of 12 and 20-year-old secondary forests (known in northeastern Brazil as capoeiras) growing within a landscape dominated by sugarcane plantations and compared them with mature forest fragments of various sizes and showing varying degrees of disturbance, with the intention of addressing two basic questions: 1) Do 12 and 20-year-old secondary forest tend to floristically converge to resemble neighboring mature forests? 2) Is their time of abandonment/recuperation the principal factor determining this conversion process?

Materials and Methods

Weekly collections were made between June/2006 and July/2009 in six secondary forest fragments (capoeiras) belonging to the Usina São José (USJ) sugar refinery in Igarassu, Pernambuco State (PE), Brazil. The fragments were located between the geographical coordinates 07° 41' 04.9" and 07° 54' 41.6" S and 34° 54' 17.6" and 35° 05' 07.2" W, within a total area of approximately 280 km^2 (Figure 1); 88% of that area was occupied by a monoculture of sugarcane (Trindade et al. 2008). The six forest fragments had sizes that varied from 5 to 11 ha, and they were up to 300 m from mature forest fragments, the latter being considered mature in not having suffered any clear-cutting for at least 60 years.

The local climate is of the type As' (Köppen 1936), characterized as hot and humid, with an average annual rainfall rate of 1687 mm, average temperature of 24.9 °C, and a dry season lasting more than three months (Schessl et al. 2008). The predominant geological formation in the area is the Barreiras Formation of the plio-Pleistocene (the most extensive geologic formation in this region of the coast) that comprises nonconsolidated sandy-clay sediments of continental origin (Companhia... 2003). The landscape is dominated by coastal plateaus 40 to 160 m above sea level that are cut by deep and narrow valleys whose sides have inclinations greater than 30% (Companhia... 2003). The regional vegetation is classified as Dense Ombrophilous Lowland Forest (Veloso et al. 1991).

Site selections considered the approximate ages of the secondary forest (capoeira) remnants based on the vegetational characteristics captured in aerial photographic sequences (CONDEPE/FIDEM) covering the decades of 1960, 1970, and 1980 (at a scale of 1: 30,000), as well as satellite images acquired in 2005 and disturbance histories from the 1990s obtained from interviews with long-time residents in the area.

Of the six secondary forest sites examined, three had been undergoing natural regeneration for approximately 12 years (sites 1, 2 and 6) and three had regenerated for 20 years (sites 3, 4 and 5) after suspending sugarcane cultivation during the 1980s. When they were selected in 2006, the six areas had shrub/arboreal canopy physiognomies varying from 6 to 18 m in height.

Botanical material was collected, using traditional techniques (Mori et al. 1989), crisscrossing the fragment in random walks (Filgueiras et al. 1994) and also examining each plant within one hundred and eighty 10 × 10 m plots installed in the six fragments (30 plots in each fragment). In each fragment, the whole fragment was surveyed, including edge and interior areas. Growth habits examined were arboreal (diameter at breast height, DBH ≥ 15 cm), shrub/subshrubs and terrestrial herbs (DBH < 15 cm), epiphytic herbs and woody lianas, all with reproductive parts, whether flowers or fruits. Seedlings or saplings of arboreal species were not included.

Soil samples were collected in each plot from the first 20 centimeters below the surface and analyzed in terms of their soil texture (sand, silt, and clay), pH in water, P, K^+, Ca^{2+}, Mg^{2+}, and extractable Al^{3+}, according to protocols described in the Manual of Soil Analysis Methods (Embrapa 1997).

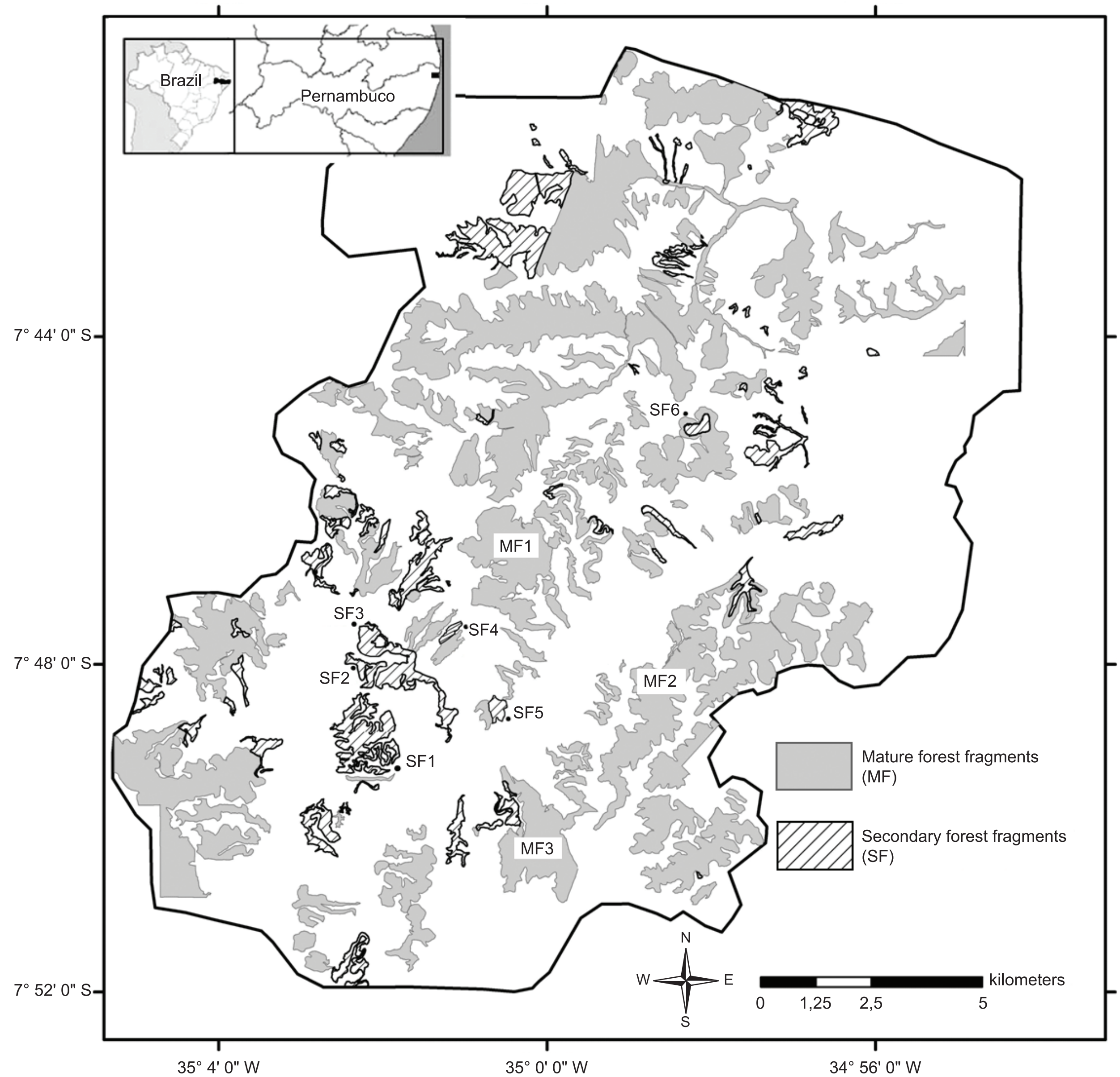

Figure 1. Location of 12-year (SF1, SF2 and SF6) and 20-year secondary forests (SF3, SF4 and SF5) and of mature forests (MF1 = Silva (2004), MF2 = Rocha et al. (2008), MF3 = Silva et al. (2008)) in Usina São José, Igarassu municipality, Pernambuco state, Brazil.

Reference collections were incorporated into the Geraldo Mariz Herbarium (UFP), with duplicates to the Dárdano de Andrade Lima Herbarium (IPA). Species identifications were made by specialists at different Brazilian institutions and by comparisons with collections deposited at the Professor Vasconcelos Sobrinho (PEUFR) and IPA herbaria.

A species list was prepared, listed according to family, with information about plant habits, localities of occurrence, and their herbarium collection numbers. The classification of the angiosperm families followed the recommendations of the APG III (Angiosperm... 2009), and those of the pteridophytes followed Smith & Wolf (2006), with modifications as presented by Smith et al. (2008). The authors' names and scientific names were confirmed using The International Plant Names Index (www.ipni.org) database.

Statistical differences in the soils were tested using one-way ANOVA (Stat Soft 2001). Values were transformed before analysis if they did not exhibit normal distribution or variance homogeneity, following Sokal & Rohlf (1995).

The G test (Sokal & Rohlf 1995) was used to identify changes in the species richness of each plant habit between the 12 and 20-year-old secondary forests.

The floristic compositions of the arboreal component of mature forest fragments in the study area were obtained from the works of Silva (2004), Rocha et al. (2008), and Silva et al. (2008), which included all trees with DBH $\geq$ 15 cm, similarly to the present study. Four types of analyses were performed to examine the arboreal habit data (NMDS, ANOSIM, SIMPER and DCA-Detrended Correspondence Analysis), utilizing the PAST 2.01 (Hammer et al. 2001) and PC-ORD version 4.0 software program (McCune & Mefford 1999).

The NMDS analysis (Non-metric Multi-dimensional Scaling) was used to analyze the degree of floristic difference between the two secondary forest ages (12 and 20-year-old), and between those and nearby mature forests. To that end, a binary matrix (presence/absence) of the secondary forests (115 species) and the mature forests (171 spp.) was constructed. Infra-specific taxa or those without precise identification to the species level (listed as "sp.", "cf." or "aff."), which occurred in at least two areas, were excluded from analysis, resulting in a matrix of 136 species. In the analysis, the Jaccard (J) index coefficient was applied to generate a graph (Legendre & Legendre 1998).

The non-parametric analyzis ANOSIM (Clarke 1993) was also performed, com 10,000 permutations, aiming at confirming the significance of the groups formed by the NMDS analysis. This method generates a global R-statistic, which is a measure of the distance between groups. An R-value close to 1 indicates strongly dissimilar assemblages, while an R-value close to zero indicates that assemblages are scarcely distinguishable (Clarke 1993). These R-values were used to compare floristic assemblages between secondary vegetation ages. Where ANOSIM revealed significant differences between groups, Similarity percentages (SIMPER) analysis was used to identify those species that contributed most to the observed assemblage distinction (Clarke 1993). Cumulative contributions were cut arbitrarily at 50%. Species with the highest dissimilarity to standard deviation ratios were identified as good discriminators for each comparison (Clarke 1993).

A third analysis (DCA) was applied to determine correlations between the species distributions and environmental variables. Data concerning the presence/absence (0-1) of the arboreal species (115 spp.) and the set of other habits (shrubs, herbs, and woody lianas = 91 spp.) were used to form two primary matrices. A categorical variable matrix was created based of the average values of the chemical (pH, P, K^+, Ca^{2+}, Mg^{2+}, Al^{3+}) and physical (percentages of sand, clay, and silt) analyses of the soils and with the time of vegetation recuperation (12 and 20 years). The Pearson and Kendall correlation was applied to evaluate the representativeness of the variables on the axes; r values ≥ 0.70 were considered high (Cohen 1988, Dancey & Reidy 2006).

Results

Sixty-six families, 120 genera, and 206 species were recorded in the six secondary forests at the USJ. Fifty families and 136 species were identified in the 12-year-old areas, and 57 families and 161 species were encountered in the 20-year-old areas (Table 1), which represented an approximately 15% increase in the number of species. Of the 206 species encountered, 115 were trees (56%), 48 shrubs (23%), 16 herbs (8%), 24 woody lianas (12%), and three were epiphytes (1.5%) (Table 2). In spite of the fact that there was a 20% increase in the number of arboreal species in the 20-year-old

Table 1. Species recorded in six secondary forests (three 12-year and three 20-year old regeneration forests) and mature forests (Silva 2004, Rocha et al. 2008, Silva et al. 2008) in Usina São José, Igarassu municipality.

Species	Growth form	12 years	20 years	Mature
Alliaceae				
Hippeastrum stylosum Herb.	herb		x	
Anacardiaceae				
Mangifera indica L.	tree		x	x
Tapirira guianensis Aubl.	tree	x	x	x
Thyrsodium spruceanum Benth.	tree	x	x	x
Annonaceae				
Anaxagorea dolichocarpa Sprague & Sandwith	tree	x	x	x
Annona montana Macfad.	tree	x		
Guatteria pogonopus Mart.	tree		x	x
Guatteria schomburgkiana Mart.	tree	x	x	x
Guatteria sp.	tree		x	
Xylopia frutescens Aubl.	tree	x	x	x
Apocynaceae				
Allamanda cathartica L.	woody liana	x	x	
Allamanda sp.	woody liana	x		
Aspidospema discolor A.DC.	tree			x
Himathanthus phagedaenicus (Mart.) Woodson	tree	x	x	x
Rauvolfia grandiflora Mart. ex A.DC.	shrub	x	x	x
Rauvolfia ligustrina Willd. ex Roem. & Schult.	shrub	x		
Tabernaemontana salzmannii A.DC.	tree			x
Araliaceae				
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodim	tree	x	x	x
Arecaceae				
Acrocomia sclerocarpa Mart.	palm tree	x	x	
Bactris ferruginea Burret	palm tree			x
Desmoncus polyacanthos Mart.	woody liana	x		
Elaeis guineensis A.Chev.	palm tree	x	x	
Aspleniaceae				
Asplenium sp.	herb	x		

Table 1. Continued...

Species	Growth form	12 years	20 years	Mature
Asteraceae				
Chromlaena sp.	shrub	x		
Conocliniopsis prassifolia (DC.) R.M.King & H.Rob.	shrub	x		
Conyza sumatrensis (Retz.) E. Walker	shrub	x		
Tilesia baccata (L.) Pruski	shrub		x	
Verbesina macrantha A.Rich.	shrub	x		
Vernonia brasiliana (L.) Druce	shrub		x	
Bignoniaceae				
Adenocalymma sp.	woody liana	x		
Lundia cordata (Vell.) DC.	woody liana		x	
Boraginaceae				
Cordia multispicata Cham.	shrub		x	
Cordia nodosa Lam.	shrub	x	x	
Cordia polycephala (Lam.) I.M. Johnst.	tree	x		
Cordia sellowiana Cham.	tree	x	x	
Cordia superba Cham.	tree		x	x
Tournefortia candidula (Miers) I.M. Johnst.	shrub	x		
Boraginaceae 1	shrub		x	
Burseraceae				
Protium arachouchini (Aubl.) Marchand	tree			x
Protium giganteum Engl.	tree		x	x
Protium heptaphyllum L. Marchand	tree	x	x	x
Tetragastris catuaba Soares da Cunha	tree			x
Canabaceae				
Trema micrantha (L.) Blume	tree	x	x	x
Celastraceae				
Maytenus distichophylla Mart. ex Reissek	tree	x	x	x
Maytenus obtusifolia Mart.	tree		x	
Chrysobalanaceae				
Hirtella racemosa Ruiz & Pav.	shrub	x	x	
Clusiaceae				
Clusia nemorosa G.Mey.	tree			x
Symphonia globulifera L.f.	tree	x		
Vismia guianensis (Aubl.) Pers.	tree	x	x	x
Coclospermaceae				
Cochlospermum vitifolium Spreng.	tree		x	
Convolvulaceae				
Ipomoea alba L.	woody liana	x	x	
Cyperaceae				
Cyperus rotundus L.	herb	x	x	
Dilleniaceae				
Davilla aspera (Aubl.) Benoist	woody liana	x		
Doliocarpus dentatus (Aubl.) Standl.	woody liana		x	
Tetracera breyniana Schltdl.	woody liana	x	x	
Dryopteridaceae				
Cystopteris sp.	herb		x	
Erythroxylaceae				
Erythroxylum citrifolium A. St.-Hil.	shrub		x	x
Erythroxylum mucronatum Sw.	shrub	x		x
Euphorbiaceae				
Croton floribundus Spreng.	tree		x	
Pera ferruginea (schott) Mull. Arg.	tree	x	x	x
Pogonophora schomburgkiana Miers ex Benth.	tree	x	x	x
Sapium glandulosum (L.) Morong	tree	x		

Table 1. Continued...

Species	Growth form	12 years	20 years	Mature
Fabaceae-Caesalpinoideae				
Chamaecrista ensiformis (Vell.) H.S.Irwin & Barneby	tree			x
Apuleia leiocarpa (Vogel) J.F. Macbr.	tree	x		
Dialium guianense (Aubl.) Sandwith	tree	x		x
Sclerolobium densiflorum	tree			x
Senna georgica H.S. Irwin & Barneby	shrub	x	x	
Senna quinquangulata (L.C.Rich.) H.S.Irwin & Barneby	woody liana	x	x	
Swartzia pickelii Killip ex Ducke	tree	x	x	x
Fabaceae-Caesalpinoideae 1	tree	x		
Fabaceae-Mimosoideae				
Albizia polycephala (Benth.) Killip.	tree	x	x	
Albizia saman (Jacq.) F. Muell.	tree	x	x	
Inga blanchetiana Benth.	tree			x
Inga capitata Desv.	tree			x
Inga cayennensis Sagot ex Benth.	tree	x	x	
Inga flagelliformis (Vell.) Mart.	tree	x	x	x
Inga ingoides (Rich.) Willd.	tree	x	x	
Inga laurina (Sw.) Willd.	tree		x	
Inga thibaudiana DC.	tree	x	x	x
Inga striata Benth.	tree			x
Parkia pendula (Willd.) Benth. ex Walp.	tree			x
Plathymenia foliolosa Benth.	tree			x
Plathymenia reticulata Benth.	tree		x	x
Fabaceae-Mimosoideae 1	woody liana	x	x	
Fabaceae-Mimosoideae 2	tree		x	
Fabaceae-Papilionoideae				
Andira fraxinifolia Benth.	tree	x	x	x
Andira nitida Mart. ex Benth.	tree	x		x
Bauhinia microstachya (Raddi) J.F. Macbr.	shrub		x	
Bowdichia virgilioides Kunth	tree	x	x	x
Desmodium axillare (Sw.) DC.	herb		x	
Dioclea virgata (L.C.Rich.) Amshoff	woody liana		x	
Dioclea sp.	woody liana	x		
Diplotropis purpurea (Rich.) Amshoff.	tree			x
Indigofera suffruticosa Mill.	shrub		x	
Machaerium hirtum (Vell.) Stellfeld	tree	x	x	
Machaerium salzmannii Benth.	tree	x	x	
Phanera outimouta (Aubl.) L.P. Queiroz	woody liana		x	
Pterocarpus rohrii Vahl	tree		x	
Stylosanthes guianensis (Aubl.) Sw.	shrub		x	
Fabaceae-Papilionoideae 1	shrub	x		
Fabaceae-Papilionoideae 2	tree	x		
Fabaceae-Papilionoideae 3	tree		x	
Fabaceae-Papilionoideae 4	shrub		x	
Heliconiaceae				
Heliconia sp.	herb	x	x	
Hernandiaceae				
Sparattanthelium botocudorum Mart.	shrub	x	x	x
Lauraceae				
Ocotea gardneri Mez	tree		x	
Ocotea glomerata (Nees) Mez	tree	x	x	x
Ocotea limae Vattimo	tree		x	x
Lecythidaceae				
Lecythis pisonis	tree			x

Table 1. Continued...

Species	Growth form	12 years	20 years	Mature
Eschweilera ovata (Cambess.) Miers.	tree	x	x	x
Gustavia augusta L.	tree	x	x	x
Loganiaceae				
Strychnos bahiensis Krukoff & Barneby	shrub	x	x	
Loranthaceae				
Struthanthus sp. 1	shrub		x	
Struthanthus sp. 2	shrub		x	
Malpighiaceae				
Byrsonima sericea DC.	tree	x	x	x
Malpighiaceae 1	woody liana		x	
Malvaceae				
Apeiba tibourbou Aubl.	tree	x	x	x
Eriotheca crenulaticalyx A.Robyns	tree			x
Guazuma ulmifolia Pers.	tree	x	x	x
Luehea paniculata Mart.	tree		x	x
Luehea ochrophylla	tree			x
Triumfetta semitriloba Jacq.	shrub	x	x	
Melastomataceae				
Clidemia capitellata (Bonpl.) D.Don.	shrub	x	x	
Clidemia hirta Cong.	shrub	x		
Henriettea succosa (Aubl.) DC.	tree	x		x
Miconia albicans (Benth.) Triana	shrub	x	x	x
Miconia ciliata (Rich.) DC.	shrub	x	x	x
Miconia minultiflora (Bonpl.) DC.	tree	x	x	x
Miconia prasina (Sw.) DC.	tree	x	x	x
Meliaceae				
Trichilia lepidota Mart.	tree		x	x
Monimiaceae				
Siparuna guianensis Aubl.	tree	x	x	
Moraceae				
Artocarpus heterophyllus Lam	tree	x	x	x
Brosimum guianense (Aubl.) Huber	tree	x	x	x
Brosimum rubescens Taub.	tree			x
Sorocea hilarii Gaudich.	tree		x	x
Myrsinaceae				
Rapanea guianensis Aubl.	tree		x	x
Myrtaceae				
Calyptranthes brasiliensis (Aubl.) DC.	tree		x	x
Campomanesia dichotoma (O. Berg.) Mattos	tree	x	x	
Eugenia candolleana (O. Berg) Kiaersk.	tree	x	x	
Eugenia florida DC.	tree		x	
Eugenia punicifolia (Kunth) DC.	tree		x	
Eugenia sp.	tree	x	x	
Myrcia bergiana O. Berg.	tree		x	
Myrcia guianensis (Aubl.) DC.	tree		x	x
Myrcia racemosa Barb. Rodr.	tree	x	x	x
Myrcia splendens (Sw.) DC.	tree			x
Myrcia sylvatica (G. Mey.) DC.	tree	x	x	x
Myrcia tomentosa (Aubl.) DC.	tree	x	x	
Psidium araca Raddi	tree	x		
Psidium guineense Sw.	tree	x	x	
Psidium guajava L.	tree		x	
Nyctaginaceae				
Guapira laxa (Netto) Furlan	tree	x	x	x
Guapira nitida (Schmidt) Lundell	tree	x	x	

Table 1. Continued...

Species	Growth form	12 years	20 years	Mature
Guapira opposita (Vell.) Reitz	tree		x	x
Neea sp.	tree		x	
Ochnaceae				
Ouratea hexasperma (A.St.-Hil.) Baill.	tree			x
Ouratea polygyna Engl.	tree	x		
Olacaceae				
Schoepfia brasiliensis A. DC	shrub	x		
Orchidaceae				
Orchidaceae 1	herb		x	
Orchidaceae 2	herb		x	
Passifloraceae				
Passiflora alata Curtis	woody liana		x	
Peraceae				
Chaetocarpus myrsinites Baill.	tree			x
Piperaceae				
Piper arboreum Aubl.	shrub	x	x	
Piper colubrinum (Link ex Kunth) Link ex C. DC.	shrub		x	
Piper marginatum Jacq.	shrub	x	x	
Phyllanthaceae				
Margaritaria nobilis L.f.	tree			x
Poaceae				
Lasiacis sorghoidea (Ham.) Hitchc. & Chase	herb		x	
Urochloa fusca (Sw.) B.F. Hansen & Wunderlin	herb	x	x	
Poaceae 1	herb		x	
Poaceae 2	herb	x		
Poaceae 3	herb	x		
Poaceae 4	herb	x		
Poaceae 5	herb		x	
Polygalaceae				
Bredemeyera sp.	woody liana	x		
Polygonaceae				
Coccoloba laevis Casar.	tree		x	
Coccoloba mollis Casar.	tree	x	x	x
Pteridaceae				
Pellaea sp.	herb		x	
Rhamnaceae				
Colubrina glandulosa Perkins	tree		x	
Rubiaceae				
Alseis floribunda Schott	tree	x	x	x
Alseis pickelii Pilg. & Schmale.	tree			x
Genipa americana L.	tree	x		
Palicourea crocea (Sw.) Roem. & Schult.	shrub	x	x	
Posoqueria sp.	tree		x	
Psychotria barbiflora DC.	shrub	x	x	
Psychotria bracteocardia (DC.) Mull. Arg.	shrub	x		
Psychotria capitata Ruiz & Pav.	shrub	x	x	
Psychotria carthagenensis Jacq.	tree			x
Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.)	shrub	x	x	
Sabicea grisea Cham. & Schltdl.	woody liana		x	
Rubiaceae 1	shrub	x		
Rubiaceae 2	shrub		x	
Rubiaceae 3	shrub	x		
Rubiaceae 4	shrub		x	
Rutaceae				
Hortia arborea Engl.	tree			x

Table 1. Continued...

Species	Growth form	12 years	20 years	Mature
Zanthoxylum rhoifolium Lam.	tree		x	x
Salicaceae				
Banara brasiliensis (Schott) Benth.	tree	x	x	
Banara guianensis Aubl.	tree		x	
Casearia arborea (Rich.) Urb.	tree			x
Casearia hirsuta Sw.	tree	x	x	
Casearia javitensis Kunth	tree	x	x	x
Casearia sylvestris Sw.	tree	x	x	x
Sapindaceae				
Allophylus edulis (A.St.-Hil., Cambess. & A.Juss.) Radlk.	tree	x	x	x
Cupania oblongifolia Mart.	tree	x	x	
Cupania paniculata Cambess.	tree	x	x	
Cupania racemosa (Vell.) Radlk.	tree	x	x	x
Cupania revoluta Radlk.	tree	x	x	x
Paullinia pallida L.	woody liana	x		
Paullinia pinnata L.	woody liana	x	x	
Paullinia trigona Vell.	woody liana	x	x	
Serjania salzmanniana Seem.	woody liana		x	
Talisia elephantipes Sandwith	tree			x
Talisia esculenta (A. St.-Hil) Radlk.	tree	x		
Sapindaceae 1	woody liana	x	x	
Sapotaceae				
Diploon cuspidatum (Hoehne) Cronquist	tree			x
Pouteria bangii (Rusby) T.D.Penn.	tree			x
Pouteria gardneri (Mart. & Miq.) Baehni	tree	x	x	x
Pouteria grandiflora (A.DC.) Baehni	tree			x
Pouteria peduncularis (Mart. & Eichler ex Miq.) Baehni	tree			x
Pouteria reticulata (Engl.) Eyma	tree		x	
Pradosia lactescens (Vell.) Radlk.	tree			x
Sapotaceae 1	tree	x	x	
Sapotaceae 2	tree		x	
Scrophulariaceae				
Scrophulariaceae 1	shrub	x		
Simaroubaceae				
Simarouba amara Aubl.	tree	x	x	x
Smilaccaceae				
Smilax sp.	woody liana	x		
Solanaceae				
Solanum asperum Rich.	shrub	x	x	
Solanum paludosum Moric.	shrub	x		
Solanum sp.	shrub		x	
Solanaceae 1	shrub	x		
Trigoniaceae				
Trigonia nivea Cambess.	woody liana		x	
Urticaceae				
Cecropia pachystachya Trécul	tree	x	x	x
Verbenaceae				
Aegiphila pernambucensis Moldenke	shrub	x	x	
Aegiphila vitelliniflora Walpers.	shrub	x	x	
Lantana camara L.	shrub		x	
Violaceae				
Amphirrhox longifolia (A.St.-Hil.) Spreng.	tree	x	x	
Paypayrola blanchetiana Tul.	tree	x		x
Family undetermined				
Undetermined	tree		x	

secondary forest, there were no significant overall differences in terms of the habits of the plants in the two regeneration ages (G test, p = 0.55, Table 2).

The NMDS analysis, applied for all arboreal species of secondary forests (12 and 20 years) and mature forests, revealed the formation of three groups, with stress of 0.093 (Figure 2). The first group was composed by the 12-year secondary forests (SF 1, 2 and 3), the second by the 20-year secondary forests (SF 4, 5 and 6), and the third, by mature forests (Silva 2004, Rocha et al. 2008, Silva et al. 2008).

When the ANOSIM was performed, the three groups previously formed by NMDS were found to be significant (R = 0.983, p = 0.0036), with dissimilarity (SIMPER) of 63%. The two groups composed by secondary forests (SF 1-2-3 and SF4-5-6) differed in floristic composition, with dissimilarity of 57%. Floristic differences were larger when 12-year secondary forest group was compared to mature forests (MF 1-2-3), with R = 1 and dissimilarity of 78% (Table 3). The high dissimilarity on floristic composition between mature and secondary forests was shaped by the presence of tree species exclusive to mature forests, such as: *Aspidosperma discolor*, *Chamaecrista ensiformis*, *Parkia pendula*, *Inga blanchetiana*, *I. capitata*, *Pouteria bangii*, *P. peduncularis*.

The physical and chemical parameters of soil varied significantly between the secondary forest ($p < 0.05$), regardless of age. The secondary forests differed significantly ($p < 0.05$) in their soil physical and chemical parameters and the differences were not related to the forest age. SF1, SF2, and SF3 (20-years) had similar values differing from SF6 (12-years), SF4, and SF5 (Table 4).

This separation of the secondary forests independent of their times of recuperation as observed in the grouping analysis (sub-groups A and B) was confirmed by the DCA analysis, indicating on axis I (eigenvalue = 0.43) that the concentrations of K^+ (r = 0.92), Ca^{2+} (r = 0.64), Mg^{2+} (r = 0.83), and the percentages of clay (r = 0.89) and silt (r = 0.96) were responsible for the formation of the secondary forest groups 1-2-3, while pH (r = –0.74) and sand (r = –0.93) were responsible for the formation of the secondary forest groups 4-5-6 (Table 4; Figure 3a).

The DCA analysis for the other plant habits indicated the formation of two groups with distinct ages (Figure 3b). On axis 1 (eigenvalues = 0.82) there was a correlation of the first group (SF 1-3) with variables K^+ (r = 0.57), clay (r = 0.68), and silt (r = 0.69) and of the second group (SF 2-4-5-6) with pH (r = –0.97) and sand (r = –0.69), Table 4.

Discussion

The difference in the numbers of families between the two regenerating forest ages may seem small, although the presence of families typical of mature forests (such as Aspleniaceae, Dryopteridaceae, Orchidaceae, and Pteridaceae) in the oldest sites and the increases in the numbers of species of Fabaceae, Myrtaceae, Annonaceae, and Sapotaceae indicated that there was a significant floristic enrichment over the years – even though this was not as notable when considering the plant habits.

The occurrence of a large number of species (206) in secondary forests with different times since abandonment within the same landscape, experiencing the same climate, geology and history, could be attributed to spatial heterogeneity, which allows that a high number of plant species persists due to the high resource supply (Tilman & Pacala 1993). According to Connell (1978), different successional stages can be seen as moderately disturbed scenarios, in which disturbance occurs with moderate frequency, duration and intensity, enabling that pioneer and secondary species cohabit the same area, resulting in larger species richness, when compared to less disturbed sites (Castillo-Campos et al. 2008).

The low level of floristic similarity between the secondary and mature forests indicates that they are in distinct successional stages and corroborates with the hypothesis that the recuperation of the floristic composition of secondary forests occurs only slowly (Chazdon 2003, Chazdon et al. 2009, Piotto et al. 2009, Powers et al. 2009). However, the sharing of 68 arboreal species between the secondary and mature forests suggests that the flora of the secondary forests at the USJ tends to convergence to that of the mature forests – as has been observed

Table 2. Number of families and species of different growth habits in six secondary forests (three 12-year and three 20-year old regeneration forests) in Usina São José, Igarassu municipality, Pernambuco state, Brazil (G test, 2.09, p = 0.55, non-significant).

Habit	12 years		20 years	
	Families	Species	Families	Species
Tree	31	78 (57,4%)	34	98 (60,8%)
Shrub	16	35 (25,7%)	15	35 (20,5%)
Herb	4	7 (5,1%)	9	13 (8,1%)
Woody liana	9	16 (11,8%)	10	17 (10,5%)
Total	50	136	57	161

Table 3. Values of R obtained in the similarity analysis (ANOSIM, upper diagonal) and percentages of dissimilarity (SIMPER, lower diagonal) between areas, using binary data of the arboreal component of of 12-year (SF1, SF2 and SF6) and 20-year secondary forests (SF3, SF4 and SF5) and mature forests (MF1= Silva (2004), MF2 = Rocha et al. (2008), MF3 = Silva et al. (2008)) in Usina São José, Igarassu, Pernambuco, Brazil.

Group	SF 1-2-3	SF 4-5-6	MF 1-2-3
SF 1-2-3	0	0.963	1
SF 4-5-6	57%	0	1
MF 1-2-3	78%	53%	0

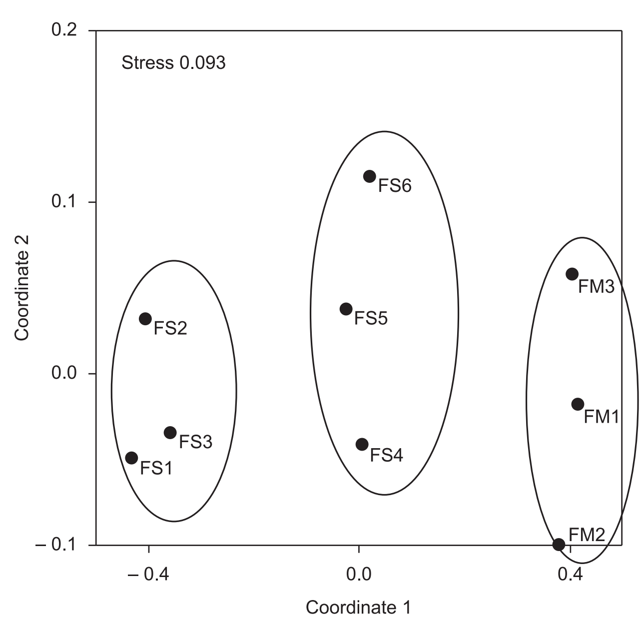

Figure 2. NMDS analysis, using the index of Jaccard, of 12-year (SF1, SF2 and SF6) and 20-year secondary forests (SF3, SF4 and SF5) and mature forests (MF1= Silva (2004), MF2 = Rocha et al. (2008), MF3 = Silva et al. (2008)) in Usina São José, Igarassu municipality, Pernambuco state, Brazil.

Table 4. Means and standard deviations of soil chemical and physical variables of 12- and 20-year secondary forests in Usina São José, Igarassu municipality, Pernambuco state, Brazil and their Pearson and Kendall correlation coefficients with the first two axes of detrended correspondence analysis (DCA) for trees and shrubs, herbs and woody lianas. Different letters in rows, in each forest age, indicate significantly different means (ANOVA, $p < 0.05$).

Soil variables	12 years			20 years			Trees		Schrubs, herbs and woody lianas	
	SF1	SF2	SF6	SF3	SF4	SF5	Eigenvalue 1	Eigenvalue 2	Eigenvalue 1	Eigenvalue 2
pH	4.86 ± 0.35^{a}	4.97 ± 0.27^{a}	5.08 ± 0.19^{b}	4.64 ± 0.16^{a}	5.14 ± 0.25^{b}	5.01 ± 0.52^{b}	–0.74	0.24	–0.94	–0.50
P ($mg.dm^{-3}$)	5.07 ± 1.59^{a}	4.07 ± 1.43^{b}	2.80 ± 1.35^{b}	3.63 ± 1.32^{b}	3.23 ± 1.04^{b}	4.37 ± 1.85^{a}	0.80	0.22	0.59	–0.41
K^{+}($mg.dm^{-3}$)	0.27 ± 0.11^{a}	0.20 ± 0.07^{a}	0.08 ± 0.06^{b}	0.14 ± 0.05^{c}	0.07 ± 0.05^{b}	0.09 ± 0.08^{b}	0.92	0.32	0.65	–0.27
Al^{3+}($cmolc.dm^{-3}$)	0.41 ± 0.31^{a}	0.32 ± 0.25^{a}	0.46 ± 0.29^{b}	0.66 ± 0.26^{c}	0.42 ± 0.23^{b}	0.25 ± 0.24^{a}	0.10	–0.61	0.46	0.59
Ca^{2+}($cmolc.dm^{-3}$)	1.79 ± 0.89^{a}	1.69 ± 0.66^{a}	0.95 ± 0.63^{b}	0.77 ± 0.36^{b}	0.96 ± 0.54^{b}	1.14 ± 1.01^{c}	0.65	0.63	0.21	–0.54
Mg^{2+}($cmolc.dm^{-3}$)	1.62 ± 0.54^{a}	1.65 ± 0.45^{a}	0.83 ± 0.29^{b}	1.06 ± 0.29^{b}	0.74 ± 0.18^{b}	1.31 ± 1.31^{c}	0.83	0.63	0.50	–0.25
% Sand ($g.cm^{-1}$)	53.95 ± 7.96^{a}	55.81 ± 6.00^{a}	76.32 ± 6.52^{b}	63.34 ± 6.21^{c}	79.49 ± 5.23^{b}	75.94 ± 5.69^{b}	–0.93	–0.41	–0.73	–0.02
% Clay ($g.cm^{-1}$)	32.61 ± 8.30^{a}	32.38 ± 5.89^{a}	18.78 ± 6.01^{b}	27.48 ± 5.16^{c}	15.77 ± 4.97^{b}	16.17 ± 4.60^{b}	0.89	0.40	0.71	0.09
% Silt ($g.cm^{-1}$)	13.44 ± 4.70^{a}	11.81 ± 2.43^{a}	4.90 ± 2.93^{b}	9.18 ± 2.78^{c}	4.75 ± 1.65^{b}	7.89 ± 1.89^{b}	0.96	0.40	0.74	–0.13

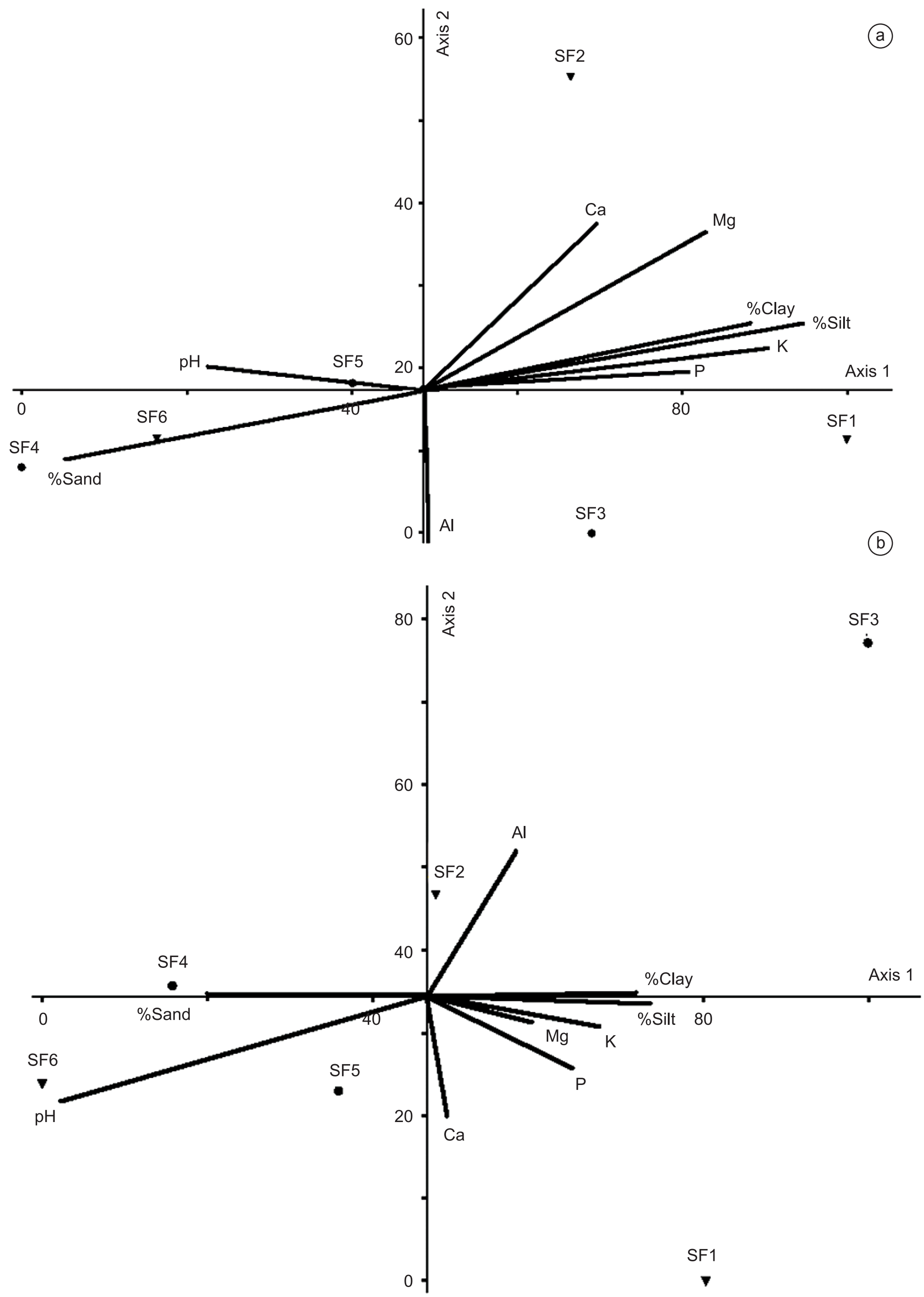

Figure 3. Ordination diagrams (DCA) of trees (a, eigenvalue = 0.43, 0.12) and shrubs, herbs and woody lianas (b, eigenvalue = 0.82, 0.24) of 12-year (SF1, SF2 and SF6) and 20-year secondary forests (SF3, SF4 and SF5) in Usina São José, Igarassu municipality, Pernambuco state, Brazil.

in other tropical forests (Guariguata et al. 1997, Peña-Claros 2003, Capers et al. 2005, Carim et al. 2007, Chazdon et al. 2007, 2009, Liebsch et al. 2007, Castillo-Campos et al. 2008, Norden et al. 2009, Lebrija-Trejos et al. 2010).

The formation of secondary forest groups composed of distinct regeneration ages, as observed in the grouping analysis and ordinations of the arboreal habit, can be justified by the similarities of the soil characteristics within the groups (which is often a consequence of the close proximity of these areas). In terms of the other plant habits, there is also a high correlation within the groups that were formed, principally due to the similarities of soil textures (with the exception of SF 2).

All of these results indicate that not just recuperation times, but many other environmental variables influence the velocity and direction of the formation of floristic composition during secondary succession. Our results corroborate those reported for secondary forests in Costa Rica (Chazdon et al. 2009), Mexico (Powers et al. 2009), and the Brazilian Amazon (Prata et al. 2010) – which also did not encounter any significant correlation between the forest ages and their floristic compositions – with each locality following a distinct and idiosyncratic path of species accumulation driven by edaphic factors (Guariguata & Ostertag 2001), colonizing species (Chazdon 2003, Junqueira et al. 2010), and the landscape matrix (Bierregaard et al. 1992, Nascimento & Laurance 2006). Together these results indicate that the preservation of conserved forest fragments near areas undergoing regeneration permits genetic flux and the continuity of successional processes.

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References

AIDE, T.M., ZIMMERMAN, J.K., PASCARELLA, J.B., RIVERA, L. & MARCANO-VEJA, H. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. Rest. Ecol. 8:328-338. http://dx.doi.org/10.1046/j.1526-100x.2000.80048.x

ANGIOSPERM PHYLOGENY GROUP – APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161:105-121. http://dx.doi.org/10.1111/j.1095-8339.2009.00996.x

BIERREGAARD, R.O., LOVEJOY, T.E., KAPOS, V., SANTOS, A.A. & HUTCHINGS, R.W. 1992. The biological dynamics of tropical rain forest fragments. Bioscience 42:859-866. http://dx.doi.org/10.2307/1312085

BROWN, S. & LUGO, A.E. 1990. Tropical secondary forests. J. Trop. Ecol. 6:1-32. http://dx.doi.org/10.1017/S0266467400003989

CALVO, L., TÁRREGA, R. & DE LUIS, E. 2002. Secondary succession after perturbations in a shrubland community. Acta Oecol. 23:93-404. http://dx.doi.org/10.1016/S1146-609X(02)01164-5

CAPERS, R.S., CHAZDON, R.L., BRENES, A.R. & ALVARADO, B.V. 2005. Successional dynamics of woody seedling communities in wet tropical secondary forests. J. Ecol. 93:1071-1084. http://dx.doi.org/10.1111/j.1365-2745.2005.01050.x

CARIM, S., SCHWARTZ, G. & SILVA, M.F.F. 2007. Riqueza de espécies, estrutura e composição florística de uma floresta secundária de 40 anos no leste da Amazônia. Acta Bot. Bras. 21:293-308. http://dx.doi.org/10.1590/S0102-33062007000200005

CASTILLO-CAMPOS, G., HALFFTER, G. & MORENO, C.E. 2008. Primary and secondary vegetation patches as contributors to floristic diversity in a tropical deciduous forest landscape. Biodivers. Conserv. 17:1701-1714. http://dx.doi.org/10.1007/s10531-008-9375-7

CHAZDON, R.L. & COE, F.G. 1999. Ethnobotany of woody species in second-growth, old-growth, and selectively logged forests of northeastern Costa Rica. Conserv. Biol. 13:1312-1322. http://dx.doi.org/10.1046/j.1523-1739.1999.98352.x

CHAZDON, R.L. 1998. Tropical forests-log 'in or leave 'in? Science 281:1295-1296. http://dx.doi.org/10.1126/science.281.5381.1295

CHAZDON, R.L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspect. Plant Ecol. 6:51-71. http://dx.doi.org/10.1078/1433-8319-00042

CHAZDON, R.L., LETCHER, S.G., VAN BREUGEL, M., MARTÍNEZ-RAMOS, M., BONGERS, F. & FINEGAN, B. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Phil. Trans. R. Soc. 362:273-289. http://dx.doi.org/10.1098/rstb.2006.1990

CHAZDON, R.L., PERES, C.A., DENT, D., SHEIL, D., LUGO, A.E., LAMB, D., STORK, N.E. & MILLER, S.E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23:1406-1417. http://dx.doi.org/10.1111/j.1523-1739.2009.01338.x

CLARKE, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. Aust. J. Ecol. 18:117-143. http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x

COHEN, J. 1988. Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates. Hillsdale.

COMPANHIA PERNAMBUCANA DO MEIO AMBIENTE – CPRH. 2003. Diagnóstico socioambiental do litoral norte de Pernambuco. CPRH, Recife.

CONNELL, J.H. 1978. Diversity in tropical rain forest and coral reefs. Science 199:1302-1310

DANCEY, C.P. & REIDY, J. 2006. Estatística sem matemática para psicologia: usando SPSS para Windows. Artmed, Porto Alegre.

DEAN, W. 2002. A ferro e fogo: a história e a devastação da Mata Atlântica brasileira. Cia das Letras, São Paulo.

DENSLOW, J.S. & GUZMAN, S. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. J. Veg. Sci. 11:201-212. http://dx.doi.org/10.2307/3236800

DENT, D.H. & WRIGHT, S.J. 2009. The future of tropical species in secondary forests: a quantitative review. Biol. Conserv. 142: 2833-2843. http://dx.doi.org/10.1016/j.biocon.2009.05.035

EMBRAPA. 1997. Manual de métodos de análises de solo. Ministério da Agricultura e do Abastecimento, Rio de Janeiro.

FELDPAUSCH, T.R., PRATES-CLARK, C.C., FERNANDES, E.C.M. & RIHA, S.J. 2007. Secondary forest growth deviation from chronosequence predictions in central Amazonia. Glob. Change Biol. 13:967-979. http://dx.doi.org/10.1111/j.1365-2486.2007.01344.x

FELDPAUSCH, T.R., RIHA, S., FERNANDES, E.C.M. & WANDELLI, E.V. 2005. Development of forest structure and leaf area in secondary forests regenerating on abandoned pastures in Central Amazonia. Earth Interact. 9:1-22. http://dx.doi.org/10.1175/EI140.1

FILGUEIRAS, T.S., BROCHADO, A.L., NOGUEIRA, P.E. & GUALA II, G.F. 1994. Caminhamento: um método expedito para levantamentos florísticos qualitativos. Cad. Geoc. 12:39-43.

FINEGAN, B. & NASI, R. 2004. The biodiversity and conservation potential of shifting cultivation landscapes. In Agroforestry and biodiversity conservation in tropical landscapes (G. Schroth, G.A.B. Fonseca, C.A. Harvey, C. Gascon, H.L. Vasconcelos & A.M.N. Izac, eds.). Island Press, Washington, p.153-197.

FINEGAN, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends. Ecol. Evol. 11:119-124. http://dx.doi.org/10.1016/0169-5347(96)81090-1

GEHRING, C., PARK, S. & DENICH, M. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. For. Ecol. Manage. 195:69-83. http://dx.doi.org/10.1016/j.foreco.2004.02.054

GEIST, H.J. & LAMBIN, E.F. 2001. What drives tropical deforestation? A meta-analysis of proximate and underlying causes based on sub-national case study evidence. CIACO, LUCC Report Series n.4. Louvain-la-Neuve.

GRACE, J. 2004. Understanding and managing the global carbon cycle. J. Ecol. 92:189-202. http://dx.doi.org/10.1111/j.0022-0477.2004.00874.x

GUARIGUATA, M.R., CHAZDON, R.L., DENSLOW, J.S, DUPUY, J.M. & ANDERSON, L. 1997. Structure and floristic of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecol. 132:107-120. http://dx.doi.org/10.1023/A:1009726421352

GUARIGUATA, M.R. & OSTERTAG, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148:185-206. http://dx.doi.org/10.1016/S0378-1127(00)00535-1

HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Paleont Electronica 4: 9p. http://www.paleoelectronica.org/2001_1/past/issue1_01.htm.

HERRERA-MONTES, A. & BROKAW, N. 2010. Conservation value of tropical secondary forest: A herpetofaunal perspective. Biol. Conserv. 143:1414-1422. http://dx.doi.org/10.1016/j.biocon.2010.03.016

INTERNATIONAL TROPICAL TIMBER ORGANIZATION – ITTO. 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. International Tropical Timber Organization, Yokohama.

JUNQUEIRA, A.B., SHEPARD JUNIOR, G.H. & CLEMENT, C.R. 2010 Secondary forests on anthropogenic soils in Brazilian Amazonia conserve agrobiodiversity. Biodivers Conserv. 19:1933-1961. http://dx.doi.org/10.1007/s10531-010-9813-1

KÖPPEN, W. 1936. Das geographische system der klimate. Handbuch der Klimatologie, Band 5, Teil C. Gebrüder Bornträger, Berlin.

LEBRIJA-TREJOS, E., MEAVE, J.A., POORTER, L., PÉREZ-GARCÍA, E.A. & BONGERS, F. 2010. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. Perspect. Plant. Ecol. 12:267-275. http://dx.doi.org/10.1016/j.ppees.2010.09.002

LEGENDRE, P. & LEGENDRE, L. 1998. Numerical Ecology. 2nd ed. Elsevier, Amsterdam.

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. http://dx.doi.org/10.1111/j.1744-7429.2009.00517.x

LIEBSCH, D., GOLDENBERG, R. & MARQUES, M.C.M. 2007. Florística e estrutura de comunidades vegetais em uma cronoseqüência de Floresta Atlântica no Paraná. Acta Bot. Bras. 21:983-992. http://dx.doi.org/10.1590/S0102-33062007000400023

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. Biol. Conserv. 141:1717-1725. http://dx.doi.org/10.1016/j.biocon.2008.04.013

McCUNE, B. & MEFFORD, M.J. 1999. PC-ORD - Multivariate Analysis of Ecological Data. version 4.0. MjM Software. Gleneden Beach, Oregon.

MORI, S.A., SILVA, L.A.M., LISBOA, G. & CORADIN, L. 1989. Manual de manejo do herbário fanerogâmico. Centro de Pesquisas do Cacau, Ilhéus.

NASCIMENTO, H.E.M. & LAURANCE, W.F. 2006. Area and edge effects on forest structure in Amazonian forest fragments after 13-17 years of isolation. Acta Amazon. 36:183-192. http://dx.doi.org/10.1590/S0044-59672006000200008

NORDEN, N., CHAZDON, R.L., CHAO, A., YI-HUEI JIANG, Y. & VÍLCHEZ-ALVARADO, B. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecol. Letters 12:385-394. http://dx.doi.org/10.1111/j.1461-0248.2009.01292.x

PARRY, L., BARLOW, J. & PERES, C.A. 2007. The conservation value of secondary forests for large vertebrates in the Brazilian Amazon. J. Trop. Ecol. 23:653-662.

PEÑA-CLAROS, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 35:450-461.

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 Ecol. 205:261-272.

POWERS, J.S., BECKNELL, J.M., IRVING, J. & PÈREZ-AVILES, D. 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. For. Ecol. Manage. 258:959-970. http://dx.doi.org/10.1016/j.foreco.2008.10.036

PRATA, S.S., MIRANDA, I.S., ALVES, S.A.O., FARIAS, F.C., JARDIM, F.C.S. 2010. Floristic gradient of the northeast paraense secondary forests. Acta Amazon. 40:523-534. http://dx.doi.org/10.1590/S0044-59672010000300011

PRIMACK, R.B. 2008. A primer of conservation biology. Sinauer Associates, Sunderland.

RANTA, P., BLON, T., NIEMELÃ, J., JOENSUU, E. & SIITONEN, M. 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. Biodivers. Conserv. 7:385-403. http://dx.doi.org/10.1023/A:1008885813543

RIBAS, R.F., MEIRA NETO, J.A.A., SILVA, A.F., SOUZA, A.L. 2003. Composição florística de dois trechos em diferentes etapas seriais de uma floresta estacional semidecidual em Viçosa, Minas Gerais. Rev. Arvore 27:821-830. http://dx.doi.org/10.1590/S0100-67622003000600008

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. Biol. Conserv. 142:1141-1153. http://dx.doi.org/10.1016/j.biocon.2009.02.021

ROCHA, K.D, CHAVES, L.F.C., MARANGON, L.C. & LINS E SILVA, A.C.B. 2008. Caracterização da vegetação arbórea adulta em um fragmento de floresta atlântica, Igarassu, PE. Rev. Bras. Cien. Agra. 3:35-41.

SCHESSL, M., DA SILVA, W.L. & GOTTSBERGER, G. 2008. Effects of fragmentation on forest structure and litter dynamics in Atlantic rainforest in Pernambuco, Brazil. Flora. 203:215-228. http://dx.doi.org/10.1016/j.flora.2007.03.004

SILVA, A.G. 2004. Fisionomia e estrutura da comunidade arbórea, na Mata dos Macacos Município de Igarassu-PE. Dissertação de Mestrado. Universidade Federal Rural de Pernambuco, Recife.

SILVA, H.C.H., LINS E SILVA, A.C.B., GOMES, J.S. & RODAL, M.J.N. 2008. The effect of internal and external edges on vegetation physiognomy and structure in a remnant of Atlantic Lowland Rainforest in Brazil. Bioremed. Biodivers. Bioavail. 2:47-55.

SMITH, A.R., PRYER, K.M., SCHUETTPELZ, E., KORALL, P., SCHNEIDER, H. & WOLF, P.G. 2008. Fern classification. In The Biology and Evolution of Ferns and Lycophytes (T.A. Ranker & C.H. Haufler, eds.). Cambridge Univ. Press, Cambridge, p.417-467. http://dx.doi.org/10.1017/CBO9780511541827.017

SMITH, A.R. & WOLF, P.G. 2006. A classification for extant ferns. Taxon 55:705-731. http://dx.doi.org/10.2307/25065646

SOKAL, R.R. & ROHLF, F.J. 1995. Biometry: the principles and practices of statistics in biological research. New York: Freeman.

STATSOFT. 2001. STATISTICA. version 6.0. Stat Soft Inc., Tulsa.

TABARELLI, M. & GASCON, C. 2005. Lessons from fragmentation research: improving management and policy guidelines for biodiversity conservation. Conserv. Biol. 19:734-739. http://dx.doi.org/10.1111/j.1523-1739.2005.00698.x

TILMAN, D. & PACALA, S. 1993. The maintenance of species richness in plant communities. In Species diversity in ecological communities (R.E. Ricklefs & D. Schluter, eds.). University of Chicago Press, Chicago, p.13-25.

TRINDADE, M.B., LINS E SILVA, A.C.B., SILVA, H.P., FILGUEIRA, S.B. & SCHESSL, M. 2008. Fragmentation of the Atlantic rainforest in the Northern Coastal Region of Pernambuco, Brazil: recent changes and implications for conservation. Bioremed. Biodivers. Bioavail. 2:5-13.

VELOSO, H.P., RANGEL-FILHO, A.L.R. & LIMA, J.C.A. 1991. Classificação da vegetação brasileira, adaptada a um sistema universal. IBGE, Rio de Janeiro.

WRIGHT, S.J. & MULLER-LANDAU, H.C. 2006. The future of tropical forest species. Biotropica 38:287-301. http://dx.doi.org/10.1111/j.1744-7429.2006.00154.x

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