Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil

Bruno G. Madeira · Mário M. Espírito-Santo · Santos D'Ângelo Neto ·
Yule R. F. Nunes · G. Arturo Sánchez Azofeifa · G. Wilson Fernandes ·
Mauricio Quesada

Abstract We investigated changes in species composition and structure of tree and liana communities along a successional gradient in a seasonally dry tropical forest. There was a progressive increase in tree richness and all tree structural traits from early to late stages, as well as marked changes in tree species composition and dominance. This pattern is probably related to pasture management practices such as ploughing, which remove tree roots and preclude regeneration by resprouting. On the other hand, liana density decreased from intermediate to late stages, showing a negative correlation with tree density. The higher liana abundance in intermediate stage is probably due to a balanced availability of support and light availability, since these variables may show opposite trends during forest growth. Predicted succession models may represent extremes in a continuum of possible successional pathways strongly influenced by land use history, climate, soil type, and by the outcomes of tree–liana interactions.

Keywords Forest structure · Floristic composition · Succession · Liana–tree interactions · Land use history

B. G. Madeira · M. M. Espírito-Santo (✉) ·
S. D'Ângelo Neto · Y. R. F. Nunes
Departamento de Biologia Geral, Universidade Estadual
de Montes Claros, CP 126, 39401-089 Montes Claros,
MG, Brazil
e-mail: mario.marcos@unimontes.br

B. G. Madeira
Departamento de Biologia Animal, Pós-Graduação em
Entomologia, Universidade Federal de Viçosa,
36570-000 Viçosa, MG, Brazil

G. Arturo Sánchez Azofeifa
Earth Observation Systems Laboratory (EOSL),
Department of Earth and Atmospheric Sciences,
University of Alberta, T6G 2E3 Edmonton, AB, Canada

G. Wilson Fernandes
Ecologia Evolutiva e Biodiversidade/DBG, ICB/
Universidade Federal de Minas Gerais, CP 486,
30161 970 Belo Horizonte, MG, Brazil

M. Quesada
Centro de Investigaciones en Ecosistemas, Universidad
Nacional Autónoma de Mexico, Apartado Postal 27-3
(Xangari), 58089 Morelia, Michoacán, Mexico

Introduction

Seasonally dry tropical forests (SDTFs) are considered as one of the most threatened tropical ecosystems (Janzen 1986) and, in Latin America, $\sim 60\%$ of all SDTFs have already been destroyed (Miles et al. 2006). Current deforestation rates are still high and unknown for many regions. Between 1980 and 2000, approximately 11,000 km^2 (0.6%) of SDTFs disappeared yearly in the Americas (Miles et al. 2006) mainly due to slash-and-burn practices and conversion to agriculture (Murphy and Lugo 1986; Murphy 1995; Miles et al. 2006). Other

potential threats include global climate changes, habitat fragmentation and increasing human population density (Arroyo Mora et al. 2005; Wright et al. 2007). Conservation efforts are concentrated in the creation of conservation units, which has a very limited impact. For example, only 1% of SDTFs in Central America (Janzen 1988; Sánchez-Azofeifa et al. 2003) and 3.9% in Brazil (Sevilha et al. 2004) are under some sort of protection.

During the past few decades, forest restoration after pasture abandonment has increased in importance to complement conservation strategies such as creation of conservation units (Janzen 1983), since it can also minimize global problems, such as climate change (Prentice et al. 1992). However, a fundamental preliminary requirement is to understand how successional processes operate in each forest type. Virtually all the current knowledge in tropical forest succession was obtained in rain forests and may not be applicable to STDFs (Vieira and Scariot 2006). For example, SDTF plant species are predominantly wind dispersed, compared to a high proportion of zoochory syndromes in tropical moist forests (Howe and Smallwood 1982; Gentry 1995; Justiniano and Fredericksen 2000; Morellato et al. 2000). Also, there is evidence that resprouting is relatively more important in SDTF than moist forest natural regeneration (Vieira and Scariot 2006; Vieira et al. 2006; Sampaio et al. 2007). Thus, information on changes in forest composition and structure, as well as the abiotic and biotic interactions driving successional changes is needed for developing successful restoration programs.

Recent studies in Brazilian SDTFs indicate that late successional forests are composed mainly by plant species already present in early succession, due to their high resprouting capacity (Vieira et al. 2006; Sampaio et al. 2007). Thus, succession in SDTFs may not follow the 'relay floristic model' (Egler 1954), which predicts a gradual substitution of pioneer by late species along forest recovery. Instead, these ecosystems may conform to the 'initial floristic composition model', with pioneer species remaining in advanced stages of succession (Egler 1954). However, it is well documented that previous land use history affects the speed and pathway of forest succession in a given area after agricultural land abandonment (Guariguata and Ostertag 2001; Kennard 2002; Chazdon 2003; Vieira et al. 2006;

Sampaio et al. 2007). Thus, SDTFs under different land uses (i.e. agriculture vs. cattle ranching) and management practices (clear-cutting, ploughing and burning frequencies) may show contrasting regeneration patterns.

Studies on succession and efforts to promote natural regeneration of SDTFs also have to recognize the importance of lianas as a key component of forest structure. In tropical forests, lianas can account for up to 40% of leaf area and leaf productivity (Hegarty and Caballé 1991) and can contribute 10–25% of plant species richness (Gentry and Dodson 1987; Gentry 1995; Nabe-Nielsen 2001). Lianas greatly influence tropical forest dynamics, since they reduce tree growth and fecundity and increase tree mortality (Putz 1984; Clark and Clark 1990; Schnitzer and Bongers 2002), rapidly growing in canopy gaps and suppressing sapling growth (Putz 1984). Therefore, they can hinder gap-phase regeneration and impede forest structure recovery, altering patterns of forest succession (Putz 1984; Clark and Clark 1990; Schnitzer et al. 2000; Pérez-Salicrup 2001). Lianas are usually more common in young, secondary forests and fragment edges, where light availability is higher, decreasing in abundance with canopy closure in mature forests (Clark and Clark 1990; DeWalt et al. 2000; Laurance et al. 2001). In spite of that there is very little information on liana community changes with succession (but see DeWalt et al. 2000), specially in SDTFs.

In this study, we compared forest fragments in different successional stages to describe changes in tree and liana communities in a Brazilian SDTF. We used the same approach of Kalácska et al. (2004, 2005) and Arroyo Mora et al. (2005) instead of using age, and our definition of successional stages was based on the forest structural characteristics. One of the main concerns of using age since disturbance or abandonment to define successional stages is that the structure and composition of stands of the same age vary drastically depending on past land use, soil type, topography and propagule availability (Kellman 1970; Sader et al. 1989; Corlett 1994; Guariguata and Ostertag 2001; Chazdon 2003; Vieira et al. 2006; Sampaio et al. 2007). By using a structural approach to successional stages (i.e. vertical and horizontal forest structure), we eliminate potential confounding variables related to the land use history (Arroyo Mora et al. 2005; Kalácska et al. 2005).

We tested the following hypotheses about ecological succession in the studied SDTF: (i) successional dynamics is dominance controlled. In this case, tree diversity would be higher in intermediate stages of succession, due to the competitive exclusion of mid-successional species as the forest matures (Yodzis 1986; Begon et al. 2006). (ii) Succession pathways conform to the 'initial floristic composition model' (Egler 1954), as proposed by Vieira and Scariot (2006) and Sampaio et al. (2007). (iii) Lianas are more abundant in early and intermediate successional stages, decreasing in late forests due to a negative interaction with trees. For this purpose, we compared forest structure and composition among early, intermediate and late successional stages of a SDTF in south-eastern Brazil, simulating the regeneration process that would naturally occur in this ecosystem.

Methods

Study area

This study was conducted in the Parque Estadual da Mata Seca (hereafter PEMS), a conservation unit of integral protection created by merging of four farmlands in 2000, and managed by the Instituto Estadual de Florestas (IEF, State Forestry Institute). The PEMS has an area of 10281.44 ha and is located in the valley of the São Francisco River, Minas Gerais state, Brazil, between 14°48′36″–14°56′59″S and 43°55′12″–44°04′12″W. The original vegetation of the park is SDTFs, growing on flat and nutrient-rich soils (IEF 2000). These forests are dominated by deciduous trees, with almost 90–95% of loss in leaf area during the dry season (May–October). The climate of the region is considered as tropical semi-arid (Köppen's classification), characterized by the existence of a severe dry season during the winter. The average temperature of the study region is 24°C (Antunes 1994), and the average annual precipitation is 818 ± 242 mm (mean $\pm$ standard deviation; data from the meteorological station in the city of Manga, 10 km from the study area). The main economic activities in the area before protection were extensive cattle ranching, and bean and corn plantations inside two central pivots of 80 ha each. Approximately 1,525 ha of the PEMS is covered with abandoned pasture fields in early regeneration stages, while the remaining area supports dry forest fragments in secondary and primary stages (IEF 2000).

Sampling

In January 2006, 20 plots of 20 m × 50 m (0.1 ha each, 2.0 ha in total) were delimited in early, intermediate and late forest fragments. To determine the successional stage of a given forest fragment, we followed the structural approach of Kalácska et al. (2004, 2005) and Arroyo Mora et al. (2005). These authors used the forest vertical structure (i.e. the number of tree crown layers in a vertical profile of the forest) and horizontal structure (the horizontal distribution of tree crowns per area) to define stages, regardless of forest age. In this sense, our early successional stage is characterized by a forest area composed of sparse patches of woody vegetation, shrubs, herbs and grasses with a single stratum of tree crowns composing a very open canopy up to 4 m. This area was used as pasture for at least 20 years and abandoned in 2000, though cattle from adjacent pastures still use the areas occasionally. Intermediate successional stages have two vegetation layers: the first one is composed by deciduous trees with 10–12 m and some emergent trees up to 15 m. The second layer is formed by a dense understory with many young trees and abundant lianas. This area was used as pasture for an unknown period and was abandoned at the late 1980s. Pastures where both early and intermediate successional forests fragments now occur were managed similarly: after clear-cutting, the area was ploughed to plant exotic grasses and burned every 2 years right before the rainy season. The late successional stage is also characterized by two strata, but the first stratum was composed by taller deciduous trees which form a closed canopy 18–20 m high. The second stratum is formed by a sparse understory with reduced light penetration and low density of young trees and lianas. There are no records of clear-cutting in this area for the last 50 years.

Six plots were established in one early successional forest fragment, the same occurring for intermediate succession plots. For late succesional stages, eight plots were established in two forest fragments (~3 km from each other). All forest fragments were located under similar topographic, soil and microclimatic characteristics, thus reducing variation in physical conditions that could affect succession. The

20 plots were located along a 5 km transect encompassing these fragments, between 14°50′–14°51′S and 43°57′–44°00′W. All plots were situated inside the original area of a single farm, in which management practices were similar for all pasturelands in the last 30 years, when the property belonged to the same owner. Plots from the same successional stage were located ∼0.2–1.0 km from each other.

We identified and measured the diameter at breast height (DBH) of all living trees with a DBH equal or greater than 5 cm inside all plots. We also visually estimated the height of these individuals in each plot, using a 2 m graduate stick as reference. Moreover, all independently growing liana stems with a DBH equal or greater than 2 cm had their DBH measured, and their height was estimated as the height of their host tree. Lianas were identified at the morpho-species level, due to difficulties to collect plant vegetative and reproductive parts. Voucher specimens were deposited at the herbarium of the Universidade Estadual de Montes Claros, in Montes Claros, Brazil.

Data analyses

We compared the forest structural characteristics (height, basal area and tree density) for both the tree and liana components among successional stages using general linear models (GLMs) for each characteristic. Then, all factor levels (stages) were compared using contrast analysis by aggregating level and comparing deviance change (Crawley 2002). If the level of aggregation did not significantly alter the deviance explained by the model, the levels were pooled together (amalgamation) simplifying the model. Rejected amalgamation implied that levels were indeed different and no further comparisons were made. Thus, the complete model was simplified by stepwise omission of non-significant terms. All models were submitted to residual analyses, so as to evaluate adequacy of error distribution (Crawley 2002).

We computed the Holdridge complexity index (HCI) (for the tree component only; Holdridge 1967; Holdridge et al. 1971) as a measure of community complexity. This index is calculated by the following equation: C_{HCI} = (Height × Density of stems × Basal area × Number of species)/1,000. The original HCI considers only trees with DBH > 10 cm. Thus, we used a modified version of the index since we sampled trees with DBH ≥ 5 cm (Lugo et al. 1978).

The HCI was compared among successional stages using the same procedure used for the other structural variables.

To compare tree richness among successional stages, observed species richness was calculated for each plot. Estimated species richness was also calculated using a non-parametric estimator, the incidence-based coverage estimator (ICE) using species-by-sample data (Colwell and Coddington 1994; Chazdon et al. 1998), with the software EstimateS 8.0 (Colwell 2006). We used a GLM to compare the observed species richness among the three successional stages.

In order to assess the variation in species composition between different successional stages (β diversity), we calculated the Morisita–Horn index (quantitative). We also calculated Jaccard's similarity coefficient (C_j) (Magurran 2004) to examine the floristic similarity between all plots of the three successional stages. Then, we used GLMs to test the relationship between similarity in species composition (measured as Jaccard's similarity index between plots) and the distance between plots within and between successional stages in order to determine if plot selection had any influence on species composition within successional stages.

To test the relationship between liana density and tree structural attributes, we used a GLM. The complete model was then simplified following the same procedure used for the other structural variables.

Results

Tree community composition

We identified a total of 1,543 tree individuals, representing 59 tree species and 23 plant families in the 20 plots (2 ha) of the three successional stages (Appendix). In the early stage, we found 296 individuals from 24 species, representing 11 families. Three of these families (Fabaceae = 59.1%, Anacardiaceae = 23.3% and Bignoniaceae = 10.1%) corresponded to 92.6% of all individuals in this stage. From a total of 13 families and 457 individuals (33 species) in the intermediate stage, three families (Bignoniaceae = 31.3%, Combretaceae = 25.6% and Fabaceae = 21.0%) constituted 77.9% of the individuals. In the late stage, we

identified a total of 790 individuals belonging to 42 species and 19 families. Again, three dominant families (Bignoniaceae = 35.8%, Fabaceae = 24.4% and Combretaceae = 19.5%) were responsible for 79.7% of all individuals from this stage.

Individual species dominance changed along the successional gradient, markedly from the early to the intermediate stages, but only slightly from the intermediate to late stages (Fig. 1). In the early stage, *Senna spectabilis* (Caesalpiniaceae) and *Myracrodruon urundeuva* (Anacardiaceae) had high relative abundances, 40.5% and 21.6%, respectively. While *S. spectabilis* was present only in the early

Fig. 1 Number of individuals for the 10 most abundant tree species in early (**a**), intermediate (**b**) and late (**c**) successional stages, by DBH classes of 5–10 and ≥10 cm. Species in bold were represented in more than one successional stage

stage, *M. urundeuva* appeared in all three successional stages and was also a dominant species in the late stage, although with varying abundance/importance (relative basal area) (Fig. 1). There was little change in species dominance from the intermediate to late stages: from the five species, dominant in both stages, four were dominant in the intermediate and late stages: *Anadenanthera colubrina* (Mimosaceae), *Combretum duarteanum* (Combretaceae), *Caesalpinia pyramidalis* (Caesalpiniaceae) and *Tabebuia roseo-alba* (Bignoniaceae) (Fig. 1). The only remarkable change in composition between the intermediate and late stages was the dominance of *Tabebuia ochracea* (28.1%) in the latter, whereas this species was rare (relative abundance of 1.3%) in the former.

The early stage presented a lower species richness than intermediate and late stages, but no significant difference was observed between intermediate and late stages (Tables 1, 2). Observed species accumulation curves and the species richness estimator (ICE) showed contrasting results between successional stages. No stabilization was observed for the early stage, and observed richness accumulation curve was below the estimated richness accumulation curve (Fig. 2a). Both curves indicated stabilization for the intermediate stage at 0.4 ha, although observed species richness showed a slight increase at 0.6 ha (Fig. 2b). For late stages, both curves tended to stabilized at 0.8 ha (Fig. 2c). In contrast with the early stage, the difference between the observed and estimated species richness was much lower for the intermediate and late stages (Fig. 2b, c).

The greatest similarity was observed between the intermediate and late stages, with a Morisita–Horn index of 0.55 (the probability to find an individual of the same species in a sample of the two stages). There was a very low similarity between the early and late stages (Morisita–Horn = 0.062) and, interestingly, an even lower similarity was observed between the early and intermediate stages (Morisita–Horn = 0.014), meaning a high turnover between successional stages. On the other hand, we observed a higher similarity in species composition between plots from the same successional stage than from different successional stages (Fig. 3). Besides, similarities in species composition were not influenced by the distance between plots from the same successional stage ($n = 58$, $F = 0.263$, $P = 0.61$), but decreased with distance between plots from different successional stages
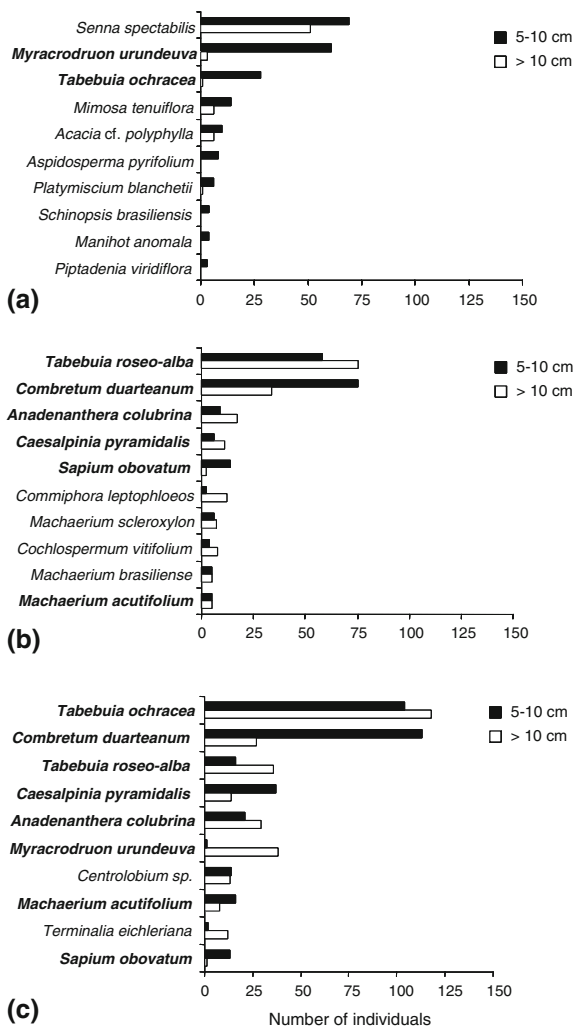
Table 1 Mean values (mean ± standard deviation) of the tree and liana structural characteristics (height, basal area and density) and the Holdridge complexity index (C_{CHI}) in three successional stages in the Parque Estadual da Mata Seca, MG

Stage	Height	Basal area	Density	No. of species	C_{HCI}
Trees					
Early	3.4 ± 0.8^a	3.1 ± 0.8^a	49.3 ± 21.0^a	8.3 ± 2.4^a	0.6 ± 0.5^a
Intermediate	8.0 ± 4.1^b	15.2 ± 3.4^b	76.2 ± 10.0^b	16.3 ± 1.9^b	15.0 ± 8.3^b
Late	11.8 ± 5.6^c	22.0 ± 6.4^c	98.8 ± 17.2^c	17.3 ± 2.0^b	46.1 ± 25.7^c
Lianas					
Intermediate	8.2 ± 5.2^a	0.56 ± 0.1^a	32.0 ± 4.2^a	–	–
Late	13.3 ± 6.0^b	0.36 ± 0.2^b	15.5 ± 6.9^b	–	–

Height given is measured in metres, basal area in $m^2\ ha^{-1}$, and density in number of individuals $ha^{-0.1}$. Different letters indicate the statistical difference (refer to Table 2)

Table 2 Analysis of variance of the forest structural characteristics (height, basal area and density), number of tree species and of the Holdridge complexity index (C_{CHI}) between three successional stages and of the liana structural characteristics between the intermediate and late stages in the Parque Estadual da Mata Seca, MG

Response variable	Source	d.f.	Deviance	Residual d.f.	Residual deviance	F	P	Errors
Trees								
Height	Stage	1	241.629	17	41.257	49.782	<0.0001	Normal
Basal area	Stage	1	1227.86	17	342.07	30.511	<0.0001	Normal
Density	Stage	1	113.569	17	75.154	13.195	<0.0005	Poisson
Number of species	Stage	1	22.383	17	6.90	26.925	<0.0001	Poisson
Holdridge index	Stage	1	406.56	17	112.43	30.624	<0.0001	Poisson
Lianas								
Height	Stage	1	90.493	12	112.484	9.654	0.009	Normal
Basal area	Stage	1	0.176	12	0.394	5.359	0.039	Normal
Density	Stage	1	40.826	12	25.552	40.826	<0.0001	Poisson

No lianas were found in early plots

($n = 132$, $F = 23.161$, $P < 0.0001$, Fig. 3). Thus, there was no effect of spatial autocorrelation in species composition within successional stages.

Forest structure

All the tree structural variables evaluated in this study varied among the three successional stages (Table 1). For tree diameter, this pattern is clearly demonstrated by the higher frequency of large class diameters (>10 cm) in intermediate and late stages, whereas lower class diameters predominate in early stages (Fig. 1). Although changes in forest structure from intermediate to late stages were statistically significant (Table 2), more dramatic changes were observed from the early to intermediate stage for all structural variables (Table 1). Overall, the HCI increased 30 times from the early (0.5 ± 0.2, mean ± standard

error) to intermediate (15.0 ± 2.1) stage and only 3.1 times between intermediate and late (46.1 ± 9.2) stages (Table 1).

In contrast, liana structure showed a reverse pattern along the successional gradient (Table 1). We sampled 192 liana individuals in 6 intermediate plots and 124 individuals in 8 late plots, representing a significant decrease in stem density along the successional gradient. No lianas were found in the early successional stage. Although the height where lianas were found increased from intermediate to late stages, basal area and liana density were significantly higher in the intermediate stages (Tables 1, 2). Liana density was negatively correlated with tree density, and the correlation was statistically significant for both the intermediate and late stages, indicating that liana density decreases as succession unfolds (Table 3, Fig. 4).

Discussion

Tree structure and diversity: successional changes

Forest structure changed along the successional gradient according to the general pattern of secondary succession described for tropical forests, with a gradual increase in height and basal area (Guariguata and Ostertag 2001; Kalácska et al. 2004; Ruiz et al. 2005). On the other hand, variation on stem density along successional stages observed here did not conform to general patterns observed for both wet and dry forests. Usually, there is a high density of stems with low DBH in early and intermediate stages,
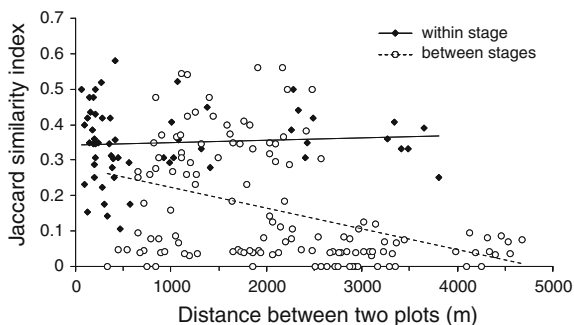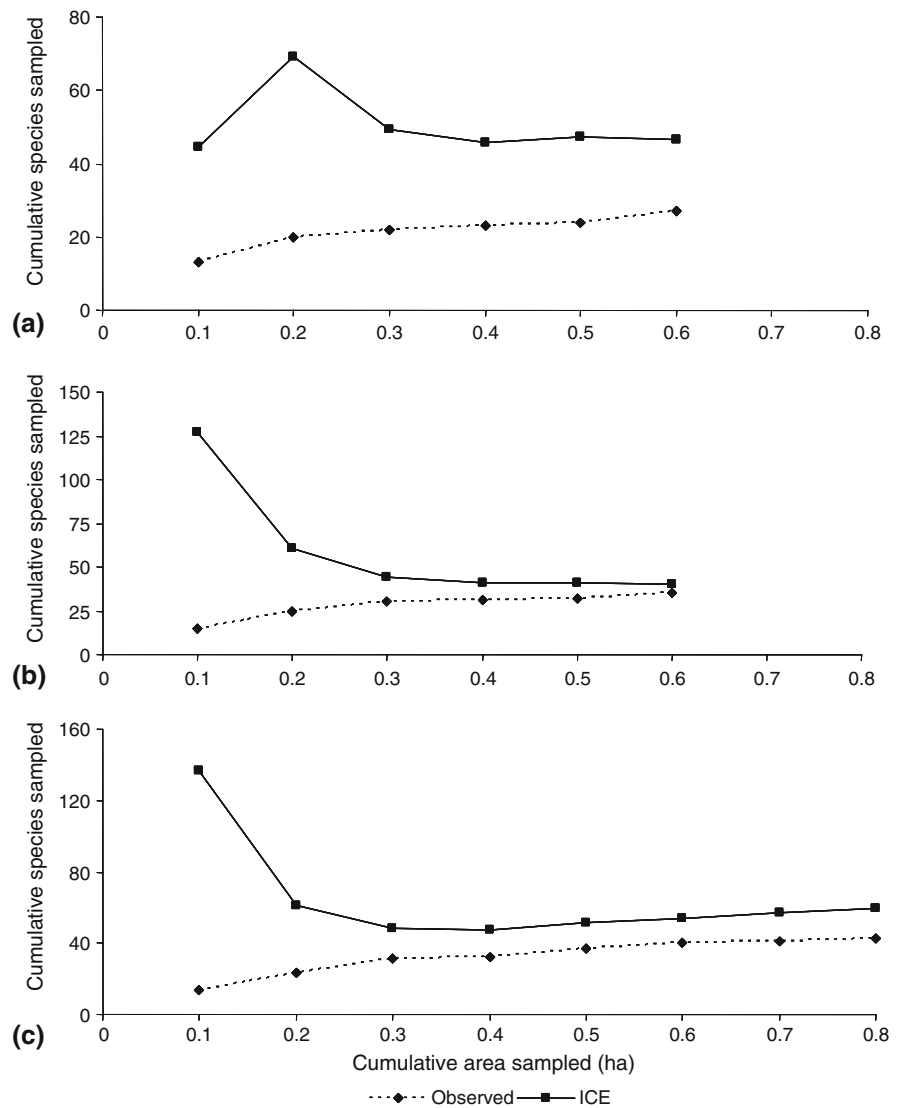
Fig. 3 Linear regression between Jaccard's similarity index (response variable) and distance between plots (explanatory variable) from the same (full line, closed points) and different (dashed line, open circles) successional stages

Table 3 Analysis of variance of the complete and minimal adequate linear models of the density of lianas (response variable) and the forest structural characteristics (tree species richness, basal area of trees and density of trees) between the two sucessional stages in the Parque Estadual da Mata Seca, MG

Source	Errors	d.f.	Deviance	Residual d.f.	Residual deviance	F	P
Complete model							
Density of trees	Quasipoisson	1	26.687	12	39.691	12.16	0.00686
Tree species richness		1	0.447	11	39.243	0.204	0.662
Basal area of trees		1	5.884	10	33.359	2.681	0.136
Stage		1	11.778	9	21.581	5.367	0.0457
Minimal adequate model							
Density of trees	Quasipoisson	1	26.687	12	39.691	13.804	0.00341
Stage		1	16.246	11	23.445	8.403	0.0145
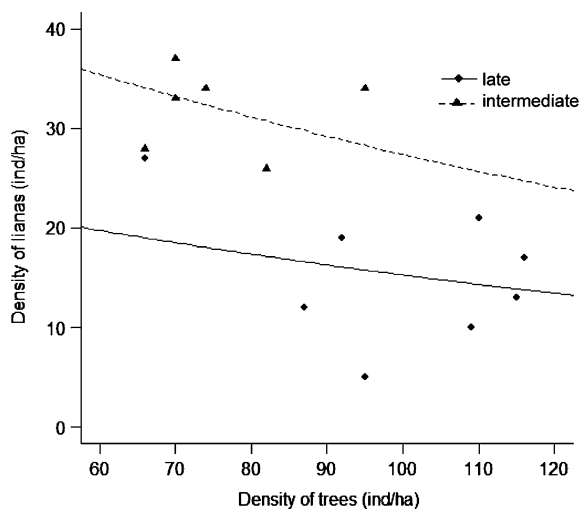
Fig. 4 Linear regression between the density of lianas (response variable) and the density of trees (explanatory variable) in intermediate and late successional stages

and as DBH increases with forest growth, stem density decreases (Mizrahi et al. 1997; Saldarriaga et al. 1988; Denslow and Guzman 2000; Kennard 2002; Kalácska et al. 2004; Ruiz et al. 2005). In spite of the gradual increase in average stem density observed here, the pattern described above is clearly illustrated for one species of the PEMS. *M. urundeuva*, a very common species in Brazilian STDFs (Oliveira-Filho et al. 1998; Pereira et al. 2003; Salis et al. 2004), is the second most abundant species in the early stages, with low DBH values. It was also encountered in the late stages, where this species was the sixth most abundant tree, but with much higher DBH values (see Fig. 1). Nevertheless, the successional changes in stem density observed at the PEMS

were also detected for a STDF in Chamela, Mexico (Kalácska et al. 2005).

In spite of the high species dominance observed for all successional stages, the succession gradient observed here did not conform to the dominance-controlled community model, which predicts higher tree diversity in mid-successional forests (Yodzis 1986; Begon et al. 2006). According to this model, tree species diversity is low in early successional stages, which are colonized by a limited group of pioneers. As succession progresses, other species invade the area and intermediate regeneration stages are composed by a high number of mid- and late successional tree species. As the forest matures towards the climax, late, efficient competitor species oust mid-successional species, causing a decrease in tree community diversity, which is dominated by a lower number of late species (Yodzis 1986; Begon et al. 2006). However, a higher tree diversity in late compared to intermediate stages was described for other STDFs, such as Chamela, Palo Verde (Kalácska et al. 2005) and Providence Island (Ruiz et al. 2005), whereas the successional gradient observed in Santa Rosa conforms partially to the predicted for dominance-controlled tree communities (Kalácska et al. 2005). One likely alternative explanation is that the forest sites considered as late stages in these studies (including the present) are more similar in structure and diversity to secondary forests in an advanced stage of regeneration than to mature forests. In this case, we would expect a decrease in tree diversity in the late stages in the next decades. Indeed, some estimates indicate that the recovery time for lowland dry forest ecosystems is around 150 years (Opler et al. 1977). Nevertheless, the structure of the late

stages in the above-mentioned forests is consistent with that described for mature STDFs (see Murphy and Lugo 1986; Ruiz et al. 2005). Thus, more long-term studies are necessary to test whether succession patterns in STDFs conform to the predicted for dominance-controlled communities.

The relative importance of seed colonization and resprouting in forest recovery is controversial, originating opposing succession models. In the 'relay floristics model', a gradual species substitution is expected across time, whereas the 'initial floristic composition model' predicts that pioneer species remain in advanced stages of succession (Egler 1954). The successional gradient analysed in the present study corroborates the former model, since there are striking changes in tree community composition from early to intermediate and late stages. On the contrary, some recent studies on Brazilian SDTFs found that a vast majority of the plant species are present in recently abandoned pastures and remain later in the succession (Vieira et al. 2006; Sampaio et al. 2007). These authors related this pattern to the great resprouting capacity of dry forest tree species, which can be affected by the intensity of pasture management practices such as fire, clear-cutting and tractor use. In our areas, ploughing probably removed the majority of plant roots after clear-cutting, preventing resprouting and reducing the presence of late species in early sites. In areas recovering from this type of pasture management, succession is more likely to conform to the 'relay floristic model'. When resprouting is intense, succession may resemble the predicted by the 'initial floristic composition model'. However, the presence of multi-stemmed trees in early plots and the occurrence of *M. urundeuva* in all three successional stages of the PEMS suggest that regeneration by resprouting is also occurring. Thus, succession models may represent extremes in a continuum of possible successional pathways strongly influenced by land use history.

The great tree species substitution from early to intermediate and late stages is probably related to changes in light penetration through the forest canopy along the successional gradient. Light quality and quantity may have a profound effect in determining the survivorship of shade-intolerant pioneer trees. For instance, *S. spectabilis*, the most abundant species in the early stage, can be considered a pioneer species according to the classification proposed by Swaine and

Whitmore (1988). The plant is a short-lived heliophyte, with rapid growth in height, especially under direct sunlight (Lorenzi 1992). This can explain the absence of this species from the shaded understory of intermediate and late forest fragments. Also, light availability can affect seed germination and seedling growth in early successional stages. Though there is only scattered information on the ecophysiology of the majority of the tree species encountered in this study, some of the dominant species in early successional plots have either positive photoblastic or neutral seeds. For instance, although *M. urundeuva* is considered a climax, shade-tolerant species, it was the second most abundant species in early stage plots, and its seeds may be able to germinate both in gaps, exposed to direct sunlight and daily temperature fluctuations, and in the understory, where diffuse light and lower daily temperature variations predominate (Silva et al. 2002). Similarly, the germinative behaviour of *A. polyphylla*, fifth most abundant species in early stage plots, also indicates that it can germinate in different-sized gaps, exposed to diverse temperature and light conditions (Araújo Neto et al. 2003). Thus, it is likely that most species encountered in early plots are adapted to open canopy conditions, though some late, shade-tolerant species can also regenerate by sprouting in these areas.

Liana structure and liana–tree interactions

Lianas represented a very important structural component of the SDTFs in PEMS, with marked changes along the successional gradient considered in this study, probably related to changes in light and support availability. In the early stages light is not limiting, but there are few branches thick enough to support the growth of lianas with more than 2 cm. In fact, the dependence of large lianas on large trees has been reported in other studies (Clark and Clark 1990; Nabe-Nielsen 2001; Phillips et al. 2002). In the intermediate stages, light availability decreases, but the canopy is still open enough to allow successful liana establishment, due to the presence of adequate support (Sánchez-Azofeifa, unpubl. data). As succession progresses, the canopy increases in height (from 8.2 m in intermediate stages to 13.3 m in late stages, on average) and continuity, reducing the habitat suitability for lianas for two reasons: first, energetic costs associated with ascent may reduce liana capacity to climb a great distance to the canopy (DeWalt et al.

2000); second, lianas are light-demanding (Castellanos 1991; Teramura et al. 1991) and, in closed canopies of late forests, they are only able to establish and grow in tree gaps (Putz 1984; Schnitzer and Carson 2001). These factors may be responsible for the decline in abundance observed here from intermediate to late stages, as well as for the negative relationship verified between liana density and tree density, considering all the sampled plots from both stages.

Our results corroborate other studies, mostly from wet forests, which reported a higher density of lianas in younger forests (DeWalt et al. 2000; Schnitzer and Bongers 2002; Kuzee and Bongers 2005; Schnitzer 2005). We are not aware of any other study comparing liana structural characteristics along a succesional gradient of SDTFs. However, Kalácska et al. (2005) found indirect evidence that lianas are also more abundant in intermediate successional stages. They reported that the proportion of liana leaves collected on leaf traps along a successional gradient in a SDTF in Santa Rosa, Costa Rica, were higher in the intermediate than early and late stages. Thus, there is an urgent need for more studies concerning successional changes in the liana component of SDTFs, in order to understand the regeneration processes in these ecosystems and allow comparisons with the better studied wet forests.

Conclusions

Studies with successional gradients can be very useful to understand natural regeneration patterns in SDTFs, and to compare the consequences of different land use histories for forest recovery. Resprouting can be a very common mechanism of SDTF regeneration, but its intensity may depend on previous land management practices. Pasture colonization through seed germina-tion is more likely in ploughed areas, which can lead to the classical succession pattern characterized by a gradual but marked change in community composi-tion. However, a mixture of both processes is probably the rule for most SDTFs. Many others factors are thought to affect forest regeneration, such as climate, soil type and the abundance of lianas. To our knowledge, this was the first study that analysed changes in liana structure along a successional gradi-ent in SDTFs, providing a possible explanation for their higher abundance at intermediate secondary forests based on trade-offs in support and light availability. Lianas certainly play an important role in SDTF recovery, and the strength of their influence on tree growth needs further attention, with long-term and experimental studies to allow comparisons with the better known wet forests.

Appendix

Table 4 List of tree species (DBH ≥ 5 cm) identified in the 20 plots in three successional stages in the dry forest of the Parque Estadual da Mata Seca, MG

Family	Species	Stage		
		Early	Intermediate	Late
Anacardiaceae	*Astronium fraxinifolium* Schott	x		
	Myracrodruon urundeuva All.	x	x	x
	Schinopsis brasiliensis Engl.	x		
	Spondias tuberosa Arruda		x	x

Table 4 continued

Family	Species	Stage		
		Early	Intermediate	Late
Apocynaceae	*Aspidosperma pyrifolium* Mart.	x		x
	Aspidosperma polyneuron Mull.Arg.			x
	Aspidosperma subincanum Mart.		x	x
Araliaceae	*Aralia warmingiana* (Marchal) J. Wen		x	x
Arecaceae	*Syagrus oleracea* (Mart.) Becc.			x
Asclepiadaceae	*Calotropis procera* (Aiton) W.T. Aiton	x		
Asteraceae	*Vernonia* sp.	x		
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC.) Standl.		x	x
	Tabebuia ochracea (Cham.) Standl.	x	x	x
	Tabebuia roseo-alba (Ridl.) Sandwith		x	x
	Zeyheria tuberculosa Bureau ex Verlot	x		
Bombacaceae	*Cavanillesia arborea* K. Schum.		x	x
	Chorisia glaziovii (Kuntze) E. Santos		x	x
	Pseudobombax longiflorum (Mart. & Zucc.) A. Robyns.		x	x
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B. Gillett		x	x
Cactaceae	*Cereus jamacaru* DC.		x	x
Cactaceae	*Pereskia grandifolia* Haw.		x	x
Cochlospermaceae	*Cochlospermum vitifolium* Spreng.		x	x
Combretaceae	*Combretum duarteanum* Cambess.		x	x
	Terminalia eichleriana Alwan & Stace		x	x
Euphorbiaceae	*Cnidoscolus pubescens* Pax		x	
	Manihot anomala Pohl	x	x	
	Maprounea guianensis Aublet			x
	Sapium obovatum Klotzsch ex Mull. Arg.		x	x
Fabaceae	*Acacia* cf. *polyphylla* DC.	x	x	x
	Acacia sp. 1	x		
	Acacia sp. 2			x
	Anadenanthera colubrina (Vell.) Brenan		x	x
	Bauhinia sp.	x		
	Caesalpinia pyramidalis Tul.	x	x	x
	Cassia multijuja Rich.	x		
	Centrolobium sp. Mart. Ex Benth.		x	x
	Chloroleucon tortum (Mart.) Barneby & J.W. Grimes	x	x	x
	Enterolobium contortisiliquum Vell. (Morong.)		x	x
	Goniorrhachis marginata Taub.			x
	Machaerium acutifolium Vog.		x	x
	Machaerium brasiliense Vog.		x	x
	Machaerium cf. *floridum* (Mart.) Ducke		x	x
	Machaerium scleroxylon Tul.		x	
	Mimosa tenuiflora Benth.	x		
	Piptadenia viridiflora Kunth. (Benth.)	x	x	
	Plathymenia reticulata Benth.	x	x	
	Platymiscium blanchetii Benth.	x		x
	Pterocarpus rohrii Vahl			x
	Senna spectabilis (DC.) H·S. Irwin & Barneby	x		
Meliaceae	*Cedrela odorata* L.		x	x
Myrtaceae	Myrtaceae sp.			x
Nyctaginaceae	*Ramisia brasiliensis* Oliv.			x

Table 4 continued

Family	Species	Stage		
		Early	Intermediate	Late
Picramniaceae	*Picramnia sellowii* Planch.		x	x
Polygonaceae	*Coccoloba schwackeana* Lindau	x		x
Rhamnaceae	*Zizyphus joazeiro* Mart.	x		
Rubiaceae	*Randia armata* DC.	x		x
Sterculiaceae	*Sterculia striata* A. St.-Hil. & Naudin			x
Ulmaceae	*Celtis iguanaea* (Jaqc.) Sarg.	x		
Vochysiaceae	*Callisthene major* Mart.			x
Total		24	33	42

References

Antunes FZ (1994) Caracterização Climática—Caatinga do Estado de Minas Gerais. Informe Agropec 17:15–19

Araújo Neto JC, Aguiar IB, Ferreira VM (2003) Efeito da temperatura e da luz na germinação de sementes de *Acacia polyphylla* DC. Revta Bras Bot 26:249–256

Arroyo Mora JP, Sánchez-Azofeifa GA, Rivard B, Calvo J (2005) Quantifying successional stages of tropical dry forests using Landsat ETM+. Biotropica 37:497–507. doi:10.1111/j.1744-7429.2005.00068.x

Begon M, Harper JL, Townsend CR (2006) Ecology: individuals, populations and communities. Blackwell, Oxford

Castellanos AE (1991) Photosynthesis and gas exchange of vines. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 181–202

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspect Plant Ecol 6:51–71. doi:10.1078/1433-8319-00042

Chazdon RL, Colwell RK, Denslow JS, Guariguata MR (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier F, Cominsky JA (eds) Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies. Parthenon Publishing, Paris, pp 285–309

Clark DB, Clark DA (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican wet forest. J Trop Ecol 6:321–331

Colwell RK (2006) EstimateS: statistical estimation of species richness and shared species from samples, version 8.0. Available via http://purl.oclc.org/estimates. Accessed 12 August 2008

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos T R Soc B 345:101–118. doi:10.1098/rstb.1994.0091

Corlett R (1994) What is secondary forest? J Trop Ecol 10:445–447

Crawley MJ (2002) Statistical computing: an introduction to data analysis using S-Plus. Wiley, Chichester

Denslow JS, Guzman S (2000) Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. J Veg Sci 11:201–212. doi:10.2307/3236800

DeWalt SJ, Schnitzer SA, Denslow JS (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. J Trop Ecol 16:1–19. doi:10.1017/S0266467400001231

Egler FE (1954) Vegetation science concepts I. Initial floristic composition: a factor in old field vegetation development. Vegetatio 4:412–417. doi:10.1007/BF00275587

Gentry AH (1995) Diversity and floristic composition of Neotropical dry forests. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp 146–194

Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19:149–156. doi:10.2307/2388737

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manage 148:185–206. doi:10.1016/S0378-1127(00)00535-1

Hegarty EE, Caballé G (1991) Distribution and abundance of vines in forest communities. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 313–336

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose

Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JA Jr (1971) Forest environments in tropical life zones: a pilot study. Pergamon Press, New York

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228. doi:10.1146/annurev.es.13.110182.001221

IEF—Instituto Estadual de Florestas (2000) Parecer técnico para a criação do Parque Estadual da Mata Seca. Instituto Estadual de Florestas, Belo Horizonte

Janzen DH (1983) No park is an island: increase in interference from outside as park size decreases. Oikos 41:402–410. doi:10.2307/3544100

Janzen DH (1986) Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, DC, pp 130–137

Janzen DH (1988) Management of habitat fragments in a tropical dry forest: growth. Ann Mo Bot Gard 75:105–116. doi:10.2307/2399468

Justiniano MJ, Fredericksen TS (2000) Phenology of tree species in Bolivian dry forests. Biotropica 32:276–281

Kalácska M, Sánchez-Azofeifa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH (2004) Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. For Ecol Manag 200:227–247

Kalácska M, Sánchez-Azofeifa GA, Calvo-Alvarado JC, Rivard B, Quesada M (2005) Effects of season and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests. Biotropica 37:486–496. doi:10.1111/j.1744-7429.2005.00067.x

Kellman MC (1970) Secondary plant succession in tropical montane Mindanao. Australian National University, Department of Biogeography and Geomorphology, Canberra

Kennard DK (2002) Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. J Trop Ecol 18:53–66. doi:10.1017/S0266467402002031

Kuzee ME, Bongers F (2005) Climber abundance, diversity and colonization in degraded forests of different ages in Côte d'Ivoire. In: Bongers F, Parren MPE, Traoré D (eds) Forest climbers of West Africa: diversity, ecology and management. CABI Publishing, Wallingford, pp 67–84

Laurance WF, Pérez-Salicrup D, Delamônica P, Fearnside PM, D'angelo S, Jerozolinski A, Pohl L, Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–116

Lorenzi H (1992) Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil, vol 2. Plantarum, São Paulo

Lugo AE, Gonzalez-Liboy JA, Cintron B, Dugger K (1978) Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10:278–291. doi:10.2307/2387680

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Malden

Miles L, Newton AC, Fries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE (2006) A global overview of the conservation status of tropical dry forests. J Biogeogr 33:491–505. doi:10.1111/j.1365-2699.2005.01424.x

Mizrahi A, Ramos-Prado JM, Jimenez-Osorio J (1997) Composition, structure, and management potential of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan Mexico. For Ecol Manage 96:273–282. doi:10.1016/S0378-1127(97)00008-X

Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB (2000) Phenology of Atlantic rain forest trees: a comparative study. Biotropica 32:811–823. doi:10.1111/j.1744-7429.2000.tb00620.x

Murphy PG (1995) Dry forests of Central America and the Caribbean. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp 9–34

Murphy PG, Lugo AE (1986) Ecology of tropical dry forests. Annu Rev Ecol Syst 17:67–88. doi:10.1146/annurev.es.17.110186.000435

Nabe-Nielsen J (2001) Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. J Trop Ecol 17:1–19. doi:10.1017/S0266467401001018

Oliveira-Filho AT, Curi N, Vilela EV (1998) Effects of canopy gaps, topography, and soils on the distribution of woody species in a central Brazilian deciduous dry forest. Biotropica 30:362–375. doi:10.1111/j.1744-7429.1998.tb00071.x

Opler PA, Baker HG, Frankie GF (1977) Recovery of tropical lowland forest ecosystems. In: Cairns J Jr, Dickson KL, Herricks EE (eds) Recovery and restoration of damaged ecosystems. University of Virginia Press, Charlottesville, pp 379–421

Pereira IM, Andrade LA, Sampaio EVSB, Barbosa MRV (2003) Use-history effects on structure and flora of caatinga. Biotropica 35:154–165

Pérez-Salicrup DR (2001) Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. Ecology 82:389–396

Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, Alexiades M, Cerón C, Di Fiore A, Erwin T, Jardim A, Palacios W, Saldias M, Vinceti B (2002) Increasing dominance of large lianas in Amazonian forests. Nature 418:770–774. doi:10.1038/nature00926

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) Special paper: a global biome model based on plant physiology and dominance, soil properties and climate. J Biogeogr 19:117–134. doi:10.2307/2845499

Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724. doi:10.2307/1937767

Ruiz J, Fandino MC, Chazdon RL (2005) Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. Biotropica 37:520–530. doi:10.1111/j.1744-7429.2005.00070.x

Sader S, Waide RB, Lawrence WT, Joyce AT (1989) Tropical forest biomass and successional age class relationships to a vegetation index derived from Landsat TM data. Remote Sens Environ 28:143–156. doi:10.1016/0034-4257(89)90112-0

Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. J Ecol 76:938–958. doi:10.2307/2260625

Salis SM, Silva MP, Matos PP, Silva JSV, Potti VJ, Pott A (2004) Fitossociologia de remanescentes de florestas estacionais deciduais em Corumbá, Estado do Mato Grosso do Sul, Brasil. Rev Bras Bot 27:671–684. doi:10.1590/S0100-84042004000400008

Sampaio AB, Holl KD, Scariot A (2007) Regeneration of seasonal deciduous forest tree species in long-used pastures in Central Brazil. Biotropica 39:655–659. doi:10.1111/j.1744-7429.2007.00295.x

Sánchez-Azofeifa GA, Castro K, Rivard B, Kalascka M, Harriss RC (2003) Remote sensing research priorities in tropical dry forest environments. Biotropica 35:134–142

Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. Am Nat 166:262–276. doi:10.1086/431250

Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends Ecol Evol 17:223–230. doi:10.1016/S0169-5347(02)02491-6

Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913–919

Schnitzer SA, Dalling JW, Carson W (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J Ecol 88:655–666. doi:10.1046/j.1365-2745.2000.00489.x

Sevilha AC, Scariot A, Noronha SE (2004) Estado atual da representatividade de unidades de conservação em Florestas Estacionais Deciduais no Brasil. In: Sociedade Brasileira de Botânica (org) Biomas florestais. Editora da Universidade Federal de Viçosa, Viçosa, pp 1–63

Silva LM, Rodrigues TJD, Aguiar IB (2002) Efeito da luz e da temperatura na germinação de sementes de aroeira (*Myracrodruon urundeuva* Allemão). Rev Arvore 26:691–697

Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86. doi:10.1007/BF00044629

Teramura AH, Gold WG, Forseth IN (1991) Physiological ecology of mesic, temperate woody lianas. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 245–285

Vieira DLM, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. Restor Ecol 14:11–20. doi:10.1111/j.1526-100X.2006.00100.x

Vieira DLM, Sampaio AB, Scariot A, Holl K (2006) Tropical dry forest regeneration from root suckers in Central Brazil. J Trop Ecol 22:1–5. doi:10.1017/S0266467405003135

Wright JC, Sánchez-Azofeifa GA, Portillo C, Davies D (2007) Poverty and corruption compromises tropical forest reserves. Ecol Appl 17:1259–1266. doi:10.1890/06-1330.1

Yodzis P (1986) Competition, mortality and community structure. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 480–491