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Secondary forest expansion over a savanna domain at an ecological reserve in the Southeastern Brazil after 15 years of monitoring

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Abstract Studies report the forest expansion process toward open savanna areas; however, most of them were conducted by means of satellite images and aerial photographs. This study has investigated the forest expansion process through community dynamics over 15 years of permanent plots monitoring. The study was conducted at a forest continuum of three distinct phytophysiognomies (riparian forest, dry forest, and woodland savanna), sampling the trees with diameter at breast height ≥ 4.77 cm, distributed into 211 plots (10 m × 10 m). Density and basal area were compared using a paired t test, and Shannon–Wiener diversity was determined through Hutcheson's t test. The number of dead and recruit trees, and basal area increment and decrement were compared among the phytophysiognomies using variance analysis, followed by Tukey's test. Dynamics rates were calculated for the interval of 15 years, as well as Jaccard and Morisita-Horn's similarity indices among phytophysiognomies. In woodland savanna, density and basal area increased and richness and diversity decreased, whereas in dry forest density decreased and richness and diversity increased. No changes in floristic parameters were observed for riparian forest. The similarity among phytophysiognomies increased over time due to advance of typical dry forests species toward woodland savanna and riparian forest; and local decrease in richness of typical savanna species in woodland savanna (decline of 13 species) and riparian species in the riparian forest (three species). From floristic analysis, our results support the dry forests expansion process toward woodland savanna and riparian forest, which seems to be strongly related to the control of fire and decrease in river flow, respectively.

Keywords Conservation unit · Dry forest · Forest dynamics · Riparian forest · Woodland savanna

Introduction

Several studies have investigated the forest expansion processes toward savannas and grasslands in many parts of South America (Durigan and Ratter 2006; Marimon et al. 2006; Silva et al. 2008, 2013). This process may be explained by multiple factors, such as global climate change (Taylor 1995; Suarez et al. 1999), nucleation process in savannas (Puyravaud et al. 2003; Arantes et al. 2014), intense fire control, and non-logging in protected savanna areas (Durigan and Ratter 2006; Cardoso et al. 2009). Most of these studies are based on analysis of historical sequences of aerial photographs, an important method for determining vegetation dynamics at the landscape scale (Bowman et al. 2001; Durigan and Ratter 2006; Cardoso et al. 2009). However, few studies show how forest expansion occurs at the community and species levels.

Monitoring forest community at permanent plots is a key to understand not only the succession pathways, but also to provide hypotheses and models concerning their mechanisms and causes (Sheil et al. 2000; Lewis et al. 2004). This monitoring allows evaluating the spatial and temporal fluctuations in richness, mortality, recruitment, and growth among the forest communities and populations

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(Oliveira Filho et al. 2007). The forest dynamics studies provide information to identify species that can be more important in the future, as well as those tending to decrease their participation in the community structure (Schorn and Galvão 2006). From studies on forest succession at the community level, it is possible to determine the ecological and physiological mechanisms involved in the community change process and make predictions about short- and long-term changes in tropical forests (Condit et al. 1999; Sheil et al. 2000).

Significant changes in the vegetation cover at *Reserva Ecológica do Panga* (study area, Southeastern Brazil) have been registered by Cardoso et al. (2009), showing through historical sequences of aerial photographs an increase in the woodland savanna cover over savanna and grassland areas, while forest communities (dry forest and riparian forest) have an increase over the savanna domain at the study area (Cardoso et al. 2009). Although how this dynamic forest expansion process occurs at the community level, it is not clearly understood.

Thus, after 15 years monitoring tree communities, we expected that, although the three phytophysiognomies (woodland savanna, dry forest and riparian forest) belongs to the same forest continuum, their dynamics rates will be different, reflecting their differences in successional stage and the "forest expansion process" toward savanna. We expect higher dynamics rates for woodland savanna (transition site), as higher mortality rates for savanna species, higher recruitment and increment of forest species in the woodland, and increase in floristic similarities among the phytophysiognomies.

Materials and methods

Study area

The study was conducted in a forest continuum (19°09′20″S and 48°24′35″W) at *Reserva Ecológica do Panga* (REP) in the Southeastern Brazil (Schiavini and Araújo 1989). Until 1984, the study area was an extensive agricultural farm (Cardoso and Schiavini 2002). In 1986, the farm was acquired by the Federal University of Uberlândia, when it became a REP (conservation unit), with an area of 409.5 ha (Lopes and Schiavini 2007). Before the REP's creation, the savanna domain was used as pasture for livestock and, according to former owners, fire and selective logging were used to decrease the number of wood species and keep these pastures (Cardoso et al. 2009). The REP vegetation is typical of Cerrado (Brazilian Savanna), with a mosaic of plant species ranging from open phytophysiognomies, such as grasslands and cerrado sensu stricto, to forest phytophysiognomies, such as woodland

savanna, dry forests, and riparian forests (Cardoso and Schiavini 2002). The climate is Aw, according to Köppen's classification (Kottek et al. 2006), with strong seasonality and an average annual rainfall of 1482 mm, concentrated within the period from November to March (>70 %) (Cardoso et al. 2009). In general, soil is characterized as deep and loam and it has an intermediate granular texture (Cardoso and Schiavini 2002).

Despite being a forest continuum, others studied have shown that the phytophysiognomies are different from each other in terms of structure, plant species composition, and soil chemical composition (Moreno and Schiavini 2001; Cardoso and Schiavini 2002; Lopes and Schiavini 2007). According to them, the forest continuum consists of a riparian forest (gallery forest) at the bank of Panga's stream, a dry forest (seasonal dry forest), and a woodland savanna (cerradão).

Monitoring dynamics at permanent plots

The first phytosociological study was conducted in 1997 (T_0), when 211 permanent plots (10 m × 10 m) were allocated, distributed into eight parallel transects perpendicular to Panga's stream over continuous forest, ending at the edge between woodland savanna and savanna vegetation (see map of plots distribution in Moreno and Schiavini 2001). Moreno and Schiavini (2001) and Cardoso and Schiavini (2002) divided the permanent plots into the three formations (riparian forest, dry forest, and woodland savanna) in 0.21 ha (21 plots), 1.50 ha (150 plots), and 0.40 ha (40 plots), respectively, based on floristic similarity and soil type. All trees with diameter at breast height (DBH) ≥ 4.77 cm (15 cm of circumference) were tagged with aluminum labels. Stem diameter was measured at 1.30 m aboveground and, for multiple stems, all live stems were separately measured and then data were gathered to calculate the basal area, according the protocol proposed by Moro and Martins (2011). Each tree was identified at the species level, according to the Angiosperm Phylogenetic Group III (APG 2009).

Subsequently, the individuals were re-measured every 5 years, in 2002, 2007 (Oliveira et al. 2014), and 2012 for conducting the dynamic study. New individuals that met the inclusion criteria (recruits) were measured and identified, and mortality referred to standing dead trees and fallen trees.

Dynamics rates

The community dynamics was based on mortality, recruitment, outgrowth, and ingrowth rates. Annual mortality (M) and recruitment (R) were calculated in terms of annual rates, according to the exponential model (see formulas in

Sheil et al. 1995, 2000; they were adopted by Oliveira Filho et al. 2007). This model considers that the mortality rate is not linear over the years (Sheil et al. 1995) and is considered a good model on monitoring studies of 5–25 years of interval among measurement in tropical forests (Lewis et al. 2004). Annual outgrowth rates refer to the basal area of dead trees plus dead branches and the basal area of living trees (decrement); annual ingrowth rates refer to basal area of recruits plus growth in the basal area of surviving trees (increment) (see formulas in Oliveira Filho et al. 2007). To evaluate forest changes, we computed turnover rates for individuals and basal area through mortality and recruitment rates and outgrowth and ingrowth rates, respectively (see formulas in Oliveira Filho et al. 2007).

Data analysis

Data were regarded as normal by Lilliefors normality test (significance level at 5 %), so we compared tree density and basal area in all phytophysiognomies and throughout the forest continuum between 1997 and 2012 by means of a paired t test. Then, we tested the number of dead trees, recruits, outgrowth, and ingrowth within an interval of 15 years among phytophysiognomies using an ANOVA test, followed by a post hoc Tukey's test, after the data have met the ANOVA test assumptions. All these statistical analyses were conducted using the statistical program SPSS statistics (version 17.0, 2008). These tests allowed us to determine which changes are occurring in the forests community structure.

We used Shannon–Wiener's diversity index (H') to estimate the α diversity of each phytophysiognomy and we also compared diversity in 1997 to that in 2012 in the forest continuum and phytophysiognomies using Hutcheson's t test (Brower et al. 1998); we adopted the software PAST 2.17b (Hammer et al. 2001). The β diversity was evaluated from floristic dissimilarity among phytophysiognomies, calculated through Jaccard and Morisita-Horn's indices (Brower et al. 1998) concerning each measured year. Jaccard and Morisita-Horn's index values were calculated using the software FITOPAC 2.1.2.85 (Shepherd 2010). We did a Euller Venn's diagram displaying the number of species for each phytophysiognomy. In this type of diagram, we may show the number of exclusive species from each vegetation type and the amount of common species among them over the measurement times.

Results

After monitoring over 15 years (1997–2012) the richness decreased from 157 to 144 species, we found a significant decreased in tree density (from 1800 to 1664 ind ha^{-1}) for the forest continuum, whereas an increase in basal area (from 23.94 to 25.63 m^2 ha^{-1}). Shannon–Wiener's diversity index (H') does not significantly change over the years (from 4.10 to 4.08) (see Table 1).

Evaluating the phytophysiognomies separately, the woodland savanna showed significant differences in all the floristic parameters, as an increase in tree density (from 2318 to 2570 ind ha^{-1}) and basal area (from 22.61 to 29.04 m^2 ha^{-1}), and a decrease in diversity (from 3.78 to 3.67) after 15 years (Table 1). The richness in woodland savanna decreased from 94 to 86 species. In the dry forest, the richness change from 110 to 111 species, we found a significant decrease in tree density (from 1675 to 1435 ind ha^{-1}) and increase in Shannon–Wiener's diversity index (from 3.78 to 3.86). Basal area does not change for dry forest (from 23.75 to 24.25 m^2 ha^{-1}) (see Table 1). The riparian forest showed no significant differences after 15 years with regard to tree density (from 1700 to 1576 ind ha^{-1}), basal area (from 27.78 to 29.00 m^2 ha^{-1}), and Shannon–Wiener's diversity index (from 3.60 to 3.55) (see Table 1). The richness in riparian forest increased from 60 to 62 species.

Floristic similarity increased among phytophysiognomies (Morisita-Horn's index) after the 15 years (Table 2). Between woodland savanna and dry forest, it increased from 0.46 to 0.61; woodland savanna and riparian forest from 0.27 to 0.37; and between dry forest and riparian forest, it increased from 0.34 to 0.47. Jaccard's similarity index also increased over the years (Table 2), which is reflected in Euller Venn's diagrams, where the exclusive occurrence of species from woodland savanna decreases from 33 to 20 species (40 % of decrease) and for riparian forest from 13 to 10 exclusive species, (23 % of decrease). Exclusive species for dry forest had just a 3 % decrease (Fig. 1). The number of common species among the phytophysiognomies increased from 30 to 34 species (13 %) (Fig. 1).

The increase in floristic similarity between woodland savanna and other phytophysiognomies occurred due to its reduction of typical savanna species, as 16 species that were present in 1997 were not sampled woodland savanna in 2012 (Appendix). Among them, 13 species were exclusively sampled at woodland savanna (Appendix, see e.g., *Byrsonima pachyphylla*, *Caryocar brasiliense*, *Connarus suberosus*, *Couepia grandiflora*, *Dimorphandra mollis*, *Enterolobium gummiferum*, *Eriotheca gracilipes*, *Kielmeyera coriacea*, *Myrcia variabilis*, *Piptocarpha rotundifolia*, *Schefflera macrocarpa*, *Strychnos pseudoquina*, and *Stryphnodendron polyphyllum*). On the other hand, from the eight new species sampled at woodland savanna, six species also occur in dry forest (Appendix, see e.g., *Heisteria ovata*, *Inga vera*, *Lacistema aggregatum*, *Nectandra cissiflora*, *Protium heptaphyllum*, and *Trichilia pallida*), which also lead to the increase in similarity between woodland savanna and dry forest (Appendix). Besides these species turnover,

Table 1 Results of the paired *t* test concerning structural parameters from 1997 to 2012 in the forest continuum and vegetation types at *Reserva Ecológica do Panga*, Uberlândia, Minas Gerais, Brazil

	Forest continuum			Riparian forest			Dry forest			Woodland savanna		
	1997	2012	P	1997	2012	P	1997	2012	P	1997	2012	P
Density	1800 (±601.7)	1664 (±695.0)	<0.01	1700 (±574.5)	1576 (±529.1)	0.082	1675 (±574.4)	1435 (±528.1)	<0.01	2318 (±424.2)	2570 (±586.3)	<0.01
Basal area	23.94 (±9.5)	25.63 (±11.8)	<0.01	27.78 (±10.2)	29.00 (±14.7)	0.547	23.75 (±9.9)	24.25 (±12.0)	0.464	22.61 (±6.9)	29.04 (±7.9)	<0.01
H'*	4.10	4.08	0.519	3.60	3.55	0.458	3.78	3.86	<0.05	3.78	3.67	<0.05

Density (tree ha^{-1}) and basal area (m^2 ha^{-1}) refer to the relativized values per ha. Mean values and number among parents are standard deviation. Number of samples (plots 10 m × 10 m) in forest continuum: 211; riparian forest: 21; dry forest: 150; woodland savanna: 40

H' Shannon–Wiener's diversity index. P values <0.05 are significant. * Hutcheson's t test

density, basal area, and consequently importance of savanna species also decreased in woodland savanna (Appendix, see e.g., *Vochysia tucanorum*, *Bowdichia virgilioides*, *Leptolobium elegans*, *Roupala Montana* and *Qualea multiflora*) and increase of forest species, (see *Cordiera sessilis*, *Coussarea hydrangeifolia*, *Faramea hyacinthine*, and *Siparuna guianensis*).

The increase in floristic similarity between dry and riparian forests was mainly driven by the incoming of 10 new species registered in riparian forest, which eight were sampled in dry forest during this study and are not typical of hydromorphic soils (Appendix see e.g., *Aspidosperma parvifolium*, *Cupania vernalis*, *Senegalia polyphylla*, *Trichilia elegans*, *Garcinia brasiliensis*, *Myrcia tomentosa*, *Hirtella gracilipes*, and *Eugenia involucrata*), as well as increase in density and basal area of common dry forest species (Appendix, see e.g., *Copaifera langsdorffii*, *Eugenia ligustrina*, *Unonopsis guatterioides*, *Trichilia pallida*, and *Faramea hyacinthina*).

Over 15 years, mortality rates were higher than recruitment rates for dry and riparian forests, as well as the forest continuum. For woodland savanna, recruitment rate was higher than mortality (Table 3). Basal area ingrowth was higher than outgrowth for the forest continuum and phytophysiognomies. Moreover, for woodland savanna, ingrowth was almost two times greater than outgrowth, emphasizing the "growth stage" on this phytophysiognomy (Table 3). Among the species with highest increment in basal area, most as typical of dry forests (Appendix, see *Matayba guianensis*, *Platypodium elegans*, *Qualea grandiflora*, *Ocotea corymbosa*, *Faramea hyacinthina*, *Cordiera sessilis*, *Luehea grandiflora*, *Coussarea hydrangeifolia*, *Myrsine umbellata*, *Machaerium acutifolium*, *Copaifera langsdorffii*, and *Anadenanthera colubrina*). The turnover rates of individuals and basal area were similar among phytophysiognomies (Table 3).

Woodland savanna showed the highest values of recruits using *ANOVA* (F = 62.638; P < 0.001), differing from dry and riparian forests. The number of dead trees, ingrowth, and outgrowth among phytophysiognomies showed no significantly differences (F = 1.198; P = 0.304; F = 2.553; P = 0.08; F = 0.466; P = 0.628, respectively).

Discussion

The floristic parameters (e.g., tree density, basal area, and species richness) and dynamics rates (e.g., mortality, recruitment, ingrowth, and outgrowth) found for the forest continuum were similar to other tropical rain forests (Korning and Balslev 1994; Condit et al. 1999) and seasonal dry forests (Batalha et al. 2001; Gomes et al. 2003; Oliveira Filho et al. 2007; Carvalho and Felfili 2011). Since

Table 2 Jaccard and Morisita-Horn's similarity indices among vegetation types in the forest continuum at *Reserva Ecológica do Panga*, Uberlândia, Minas Gerais, Brazil, for 4 years surveyed

	RF				DF				WS			
	1997	2002	2007	2012	1997	2002	2007	2012	1997	2002	2007	2012
RF	–	–	–	–	*0.37*	*0.38*	*0.39*	*0.39*	*0.25*	*0.27*	*0.31*	*0.33*
DF	0.34	0.38	0.41	0.47	–	–	–	–	*0.42*	*0.43*	*0.45*	*0.47*
WS	0.27	0.30	0.33	0.37	0.46	0.48	0.54	0.61	–	–	–	–

Italics Jaccard's similarity index (qualitative, 0–1), upper right; not italics Morisita-Horn's similarity index (quantitative, 0–1), the lower left

RF Riparian forest; *DF* dry forest; *WS* woodland savanna
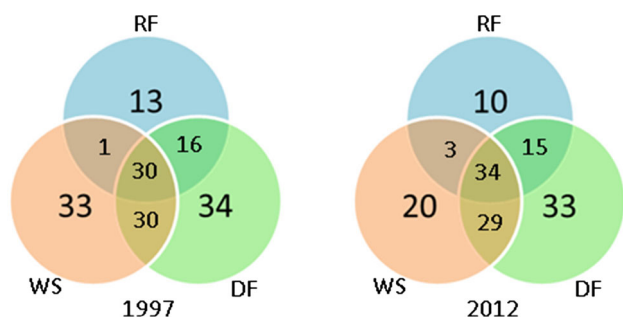
Fig. 1 Euller Venn's diagrams of the number of species for each vegetation type in the forest continuum at *Reserva Ecológica do Panga*, Uberlândia, Minas Gerais, Brazil (1997 and 2012). *RF* Riparian forest; *DF* dry forest; *WS* woodland savanna

1986, when the *Reserva Ecológica do Panga* (REP) became a conservation unit, the entire area was protected and isolated from human disturbances, allowing the forest continuum to advances from early to mature successional stages (Cardoso et al. 2009). The dynamic rates found for the forest continuum are in agreement with other studies, commonly related as a "self-thinning" process, with a decrease in tree density and increase in basal area (Carvalho and Felfili 2011). However, as shown by previous studies based on floristic (Cardoso and Schiavini 2002) and soil comparisons (Moreno and Schiavini 2001), each phytophysiognomy (woodland savanna, dry forest and riparian forest) showed a different dynamic pattern, also reflecting their differences in successional stage and the forest expansion process toward open savanna areas.

As we predicted, changes in woodland savanna were higher than in the other phytophysiognomies, reflecting its "growth phase" and the forest expansion process. The woodland savanna showed an increase in tree density (>200 trees ha^{-1}) and basal area (>6 m^2 ha^{-1}) and higher dynamic rates, around 3 % year^{-1}. Furthermore, changes in floristic composition were higher in woodland savanna, with reduction of species richness mainly driven by the exclusion of typical savanna species (15 of the 16 species excluded). Among these species, *Brosimum gaudichaudii*, *Byrsonima pachyphylla*, *Caryocar brasiliense*, *Connarus suberosus*, *Dimorphandra mollis*, *Eriotheca gracilipes*, and *Kielmeyera coriacea* occurred in, at last, 50 % of all cerrado areas, and *Casearia grandiflora*, *Enterolobium gummiferum*, *Piptocarpha rotundifolia*, *Schefflera macrocarpa*, and *Strychnos pseudoquina* are regarded as usual in open savannas, too (Ratter et al. 2003).

The forest expansion process in woodland savanna is also observed as colonization of new species that in the first census has been sampled just in dry forest (six of the eight new species). Among them, *Heisteria ovata*, *Inga vera*, *Lacistema aggregatum*, *Nectandra cissiflora*, and *Trichilia pallida* are usual in semideciduous seasonal dry forests within the region (Lopes et al. 2012), but they are not usual in open savanna (occurring very few times; see Ratter et al. 2003). Two other (*Lacistema aggregatum* and *Nectandra cissiflora*) were not found by Ratter et al. (2003), and just *Protium heptaphyllum* is usual in savannas. However, Oliveira Filho and Fontes (2000) have demonstrated that *P. heptaphyllum* is a "supertramp" species, a generalist

Table 3 Dynamics of the forest continuum and vegetation types within intervals (1997–2012) at *Reserva Ecológica do Panga*, Uberlândia. Minas Gerais, Brazil

	Forest continuum	Riparian forest	Dry forest	Woodland savanna
R (% year^{-1})	2.28	2.07	2.03	2.91
M (% year^{-1})	2.79	2.56	3.03	2.24
I (% year^{-1})	2.76	2.43	2.63	3.35
O (% year^{-1})	2.31	2.15	2.50	1.72
Turnover (N)	2.53	2.31	2.53	2.58
Turnover (BA)	2.54	2.29	2.57	2.54

R recruitment rate; *M* mortality rate; *I* ingrowth rate in basal area; *O* outgrowth rate in basal area. *Turnover (N)* turnover rate in number of individuals (% year^{-1}); *turnover (BA)* turnover rate of basal area (% year^{-1})

species observed in many distinct phytophysiognomies. This similarity with dry forest has increased not only in species composition, but also for species representativeness (e.g., density and basal area). Species typical of forests are growing more than savannas species, since nine of the 12 species with highest increment in woodland savanna are typical of forests communities. *Matayba guianensis*, *Ocotea corymbosa*, *Myrsine umbellata*, *Copaifera langsdorffii*, supertramp of forests (Oliveira Filho and Fontes 2000); *Platypodium elegans* is common on sub-montane season forest (Oliveira Filho and Fontes 2000); *Faramea hyacinthina*, *Coussarea hydrangeifolia*, and *Cordiera sessilis* are typical of understory forests on Triângulo Mineiro (Prado Júnior et al. 2014); and *Anadenanthera colubrina* is a typical species of seasonal forest (Linares-Palomino et al. 2011). Thus, the major increment in basal area is due to forest species growth. Their growth makes the environment shaded, creating a more suitable area for colonization by forest species (Arantes et al. 2014). Thus, the "growth phase" in the woodland savanna is not only just a mere growth, but also an increase in the dry forest species at this sector, suggesting, as we predicted, an advance of the forest over the woodland savanna.

Protection against fire has been changing in the woodland savanna, because this phytophysiognomy is undergoing a transition to an open savanna formation, an environment usually altered by fire in a natural situation. The fire absence under forest continuum and neighborhood, according to the book of record of the *Reserva Ecológica do Panga*, is probably the main driver of the increase (not only in richness but also in density and basal area) of tree species typically found in dry and moist forests (Oliveira Filho and Fontes 2000; Durigan and Ratter 2006) over the woodland savanna. Arantes et al. (2014) studying the nucleation process at *Reserva Ecológica do Panga* (*REP*), also demonstrated an increase of colonization by species typically found in dry forest in the open savanna, due to the absence of fire. Without fire, the woodland savanna became taller and thicker, with a well-structured canopy, which is phytophysiognomically very similar to those found in usual dry forest. This "forestation" process due to fire control in the protected areas has also been reported by Briggs et al. (2002) to expansion woody plants in a Biological Station in the United States. Fire-adapted species (such as those savanna species locally extinct) had thick wood with a large amount of suberized tissues that protect the live tissues in case of a fire (Soares et al. 2006). However, the newly established dry forest species had thin bark and they can grow faster than savannas species by not investing so much in sclerenchyma tissues. Thus, without any fire disturbance, dry forests species can grow faster and gradually advance over the woodland savanna (Durigan and Ratter 2006; Arantes et al. 2014). Other works indicate this

forestation process in protected open savannas that become a forest physiognomy in "patches of habitat" close to the Amazon Forest (Mayle et al. 2000; Marimon et al. 2006), in the Australian monsoon tropics (Bowman et al. 2001), and in formerly deforested areas in southeastern Brazil (Durigan and Ratter 2006); however, no study relied on 15 years of monitoring the dynamics.

In the dry forest, we found a significant increase in diversity and a decrease in tree density, suggesting an advance in successional stage ("self-thinning" process) in this phytophysiognomy. As the basal area did not change over the years, the decrease in tree density (and also higher mortality rate) was offset by high increment of survivor's trees. As woodland savanna has been advancing to the open savanna (in 1997 some woodland plots were 0 m from the edge of the forest continuum, and now they are 50–75 m far from the actual edge), the edge effect on the forest continuum is less strong (e.g., reducing wind impacts in the forest community) which helps the advance in successional stage for the dry forest. The increase in floristic similarity with the other phytophysiognomies, leaded mainly by the colonization of dry forests species in woodland savanna and riparian forest and increase in their representativeness (density and basal area) also support the "forestation process" at *Reserva Ecológica do Panga*.

The riparian forest showed no significant differences after 15 years in floristic parameters (tree density, basal area, and diversity). Besides, all the dynamic rates were lower compared to the forest continuum. Nevertheless, some typical water saturation-adapted species were not found in 2012 (*Croton urucurana* and *Inga marginata*) and many species tolerant to dry season and already established in the dry forest colonized the riparian forest (*Aspidosperma parvifolium*, *Cupania vernalis*, *Senegalia polyphylla*, *Trichilia elegans*, *Garcinia brasiliensis*, *Myrcia tomentosa*, *Hirtella gracilipes*, and *Eugenia involucrata*) and other that were sampled in the first census increased their representativeness (*Copaifera langsdorffii*, *Eugenia ligustrina*, *Unonopsis guatterioides*, *Trichilia pallida*, and *Faramea hyacinthina*). This phenomenon has been occurring, perhaps, due to decreased river runoff over the years (Lopes and Schiavini 2007). As a consequence of decreased river flow, there are much less flooding events, usual in this forest sector (Lopes and Schiavini 2007) and soil moisture has become scarce over the years, facilitating colonization by species tolerant to a driest environment.

We may conclude that dry forest is advancing toward the woodland savanna and the riparian forest, as a consequence of protection against fire events and dryness Panga's stream. The turnover of typical savanna species to typical dry forest species, increase in basal area, tree density, and similarity among the physiognomies support the "forest expansion process" toward savanna. Although the

three physiognomies belong to the same forest continuum, we showed that each one has a different dynamic pattern, reflecting their differences in successional stage, structure, and environments' conditions. Besides, even the dry and riparian forests have lower dynamic rates than the woodland savanna, the turnover rates (higher than 2 % per year) determine changes of up to 35 % during the observed period (considering exponential projections, in accordance with the model used for the calculation of charges), showing how this phytophysiognomies are dynamics. The "forestation process" at *Reserva Ecológica do Panga* has been showed by analysis of historical sequences of aerial photographs, but in this study, we showed how this process occurs at community's level. Understanding how this process occurs is important to the future management of Brazilian Savanna conservation.

Appendix

See Table 4.

Table 4 Structural parameters of species in 1997 ($t1$) and 2012 ($t2$) in vegetation types at *Reserva Ecológica do Panga*, Uberlândia, Minas Gerais, Brazil

Species	Riparian forest				Dry forest				Woodland savanna			
	D ($t1$)	D ($t2$)	BA ($t1$)	BA ($t2$)	D ($t1$)	D ($t2$)	BA ($t1$)	BA ($t2$)	D ($t1$)	D ($t2$)	BA ($t1$)	BA ($t2$)
Acalypha gracilis Spreng.	–	4.8		0.02	–	–	–	–	–	–	–	–
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	–	–	–	–	5.3	3.3	0.24	0.16	–	–	–	–
Aegiphila integrifolia (Jacq.) Moldenke	–	–	–	–	0.7	0.7	0.01	0.01	–	–	–	–
Agonandra brasiliensis Miers ex Benth. & Hook.f.	–	–	–	–	0.7	1.3	0.01	0.01	2.5	–	0.01	–
Albizia niopoides (Spruce ex Benth.) Burkart	–	–	–	–	1.3	2.0	0.01	0.02	–	–	–	–
Allophylus sericeus (Cambess.) Radlk.	–	–	–	–	1.3	–	0.00	–	–	–	–	–
Anadenanthera colubrina (Vell.) Brenan	19.1	14.3	0.25	0.32	65.3	57.3	3.09	3.66	20.0	27.5	0.15	0.37
Aniba heringeri Vattimo-Gil	19.1	9.5	0.13	0.09	–	–	–	–	–	–	–	–
Annona crassiflora Mart.	–	–	–	–	–	–	–	–	7.5	5.0	0.11	0.12
Apeiba tibourbou Aubl.	–	–	–	–	1.3	1.3	0.10	0.17	–	–	–	–
Apuleia leiocarpa (Vogel) J.F.Macbr.	–	–	–	–	1.3	1.3	0.04	0.03	–	–	–	–
Aspidosperma cuspa (Kunth) S.F.Blake ex Pittier	9.5	9.5	0.08	0.12	51.3	48.7	0.63	0.79	45.0	35.0	0.43	0.56
Aspidosperma cylindrocarpon Müll.Arg.	71.4	76.2	2.19	2.70	16.7	19.3	0.29	0.37	7.5	12.5	0.08	0.18
Aspidosperma parvifolium A.DC.	–	4.8	–	0.01	24.0	21.3	0.34	0.48	–	–	–	–
Aspidosperma subincanum Mart.	–	–	–	–	18.0	14.7	0.25	0.31	12.5	12.5	0.23	0.41
Astronium fraxinifolium Schott	–	–	–	–	2.0	2.0	0.02	0.03	7.5	7.5	0.13	0.15
Bauhinia ungulata L.	4.8	4.8	0.01	0.01	12.7	10.7	0.04	0.03	2.5	–	0.01	–
Bowdichia virgilioides Kunth	–	–	–	–	–	–	–	–	20.0	12.5	0.49	0.46
Brosimum gaudichaudii Trécul	–	–	–	–	0.7	–	0.00	–	5.0	–	0.01	–
Byrsonima laxiflora Griseb.	–	–	–	–	–	–	–	–	5.0	2.5	0.04	0.01
Byrsonima pachyphylla A.Juss.	–	–	–	–	–	–	–	–	2.5	–	0.02	–
Calophyllum brasiliense Cambess.	57.1	71.4	1.36	0.63	–	2.7	–	0.01	–	–	–	–
Calyptranthes widgreniana O.Berg	47.6	38.1	0.25	0.22	–	–	–	–	–	–	–	–
Campomanesia velutina (Cambess.) O.Berg	–	–	–	–	92.7	33.3	0.64	0.24	–	–	–	–
Cardiopetalum calophyllum Schltdl.	–	–	–	–	2.0	–	0.01	–	10.0	5.0	0.03	0.02
Cariniana estrellensis (Raddi) Kuntze	–	–	–	–	6.7	7.3	0.15	0.28	–	–	–	–
Caryocar brasiliense Cambess.	–	–	–	–	–	–	–	–	5.0	–	0.03	–
Casearia gossypiosperma Briq.	–	–	–	–	4.0	4.0	0.04	0.07	2.5	5.0	0.02	0.02

Table 4 continued

Species	Riparian forest				Dry forest				Woodland savanna			
	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)
Casearia rupestris Eichler	4.8	–	0.01	–	9.3	6.7	0.07	0.05	–	–	–	–
Casearia sylvestris Sw.	14.3	9.5	0.07	0.05	45.3	24.0	0.32	0.16	30.0	27.5	0.13	0.22
Cecropia pachystachya Trécul	14.3	4.8	0.08	0.01	1.3	–	0.01	–	10.0	12.5	0.04	0.07
Celtis iguanaea (Jacq.) Sarg.	–	–	–	–	1.3	0.7	0.00	0.00	–	–	–	–
Cheiloclinium cognatum (Miers) A.C.Sm.	9.5	9.5	0.02	0.04	3.3	7.3	0.02	0.03	–	–	–	–
Chionanthus trichotomus (Vell.) P.S. Green	23.8	19.1	0.29	0.23	4.0	5.3	0.02	0.04	–	–	–	–
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	52.4	47.6	0.41	0.47	185.3	105.3	1.69	1.19	50.0	52.5	0.23	0.34
Coccoloba mollis Casar.	–	–	–	–	0.7	0.7	0.05	0.01	5.0	2.5	0.02	0.02
Connarus suberosus Planch.	–	–	–	–	–	–	–	–	10.0	–	0.02	–
Copaifera langsdorffii Desf.	57.1	71.4	2.22	3.11	14.7	23.3	0.25	0.57	30.0	32.5	0.18	0.44
Cordia alliodora (Ruiz & Pav.) Cham.	–	–	–	–	0.7	0.7	0.02	0.04	–	–	–	–
Cordia trichotoma (Vell.) Arráb. ex Steud.	–	–	–	–	2.7	1.3	0.05	0.05	5.0	5.0	0.02	0.01
Cordiera sessilis (Vell.) Kuntze	52.4	100.0	0.17	0.39	98.0	190.7	0.36	0.76	87.5	225.0	0.34	0.79
Couepia grandiflora (Mart. & Zucc.) Benth.	–	–	–	–	–	–	–	–	2.5	–	0.04	–
Coussarea hydrangeifolia (Benth.) Müll.Arg.	52.4	38.1	0.20	0.18	4.0	7.3	0.01	0.02	65.0	167.5	0.29	0.63
Coutarea hexandra (Jacq.) K.Schum.	–	–	–	–	2.0	2.7	0.01	0.03	–	–	–	–
Croton urucurana Baill.	4.8	–	0.04		1.3	–	0.03	–	–	–	–	–
Cupania vernalis Cambess.	–	4.8		0.01	72.7	40.0	0.58	0.46	10.0	10.0	0.06	0.10
Cybistax antisyphilitica (Mart.) Mart.	–	–	–	–	–	–	–	–	2.5	2.5	0.01	0.01
Dalbergia miscolobium Benth.	–	–	–	–	–	–	–	–	2.5	2.5	0.41	0.42
Dendropanax cuneatus (DC.) Decne. & Planch.	28.6	28.6	0.34	0.30	3.3	6.7	0.02	0.04	–	–	–	–
Dilodendron bipinnatum Radlk.	–	–	–	–	14.7	11.3	0.38	0.43	–	–	–	–
Dimorphandra mollis Benth.	–	–	–	–	–	–	–	–	5.0	–	0.04	–
Diospyros hispida A.DC.	–	–	–	–	124.7	101.3	1.51	1.70	62.5	50.0	0.56	0.68
Duguetia lanceolata A.St.-Hil.	4.8	4.8	0.14	0.16	–	–	–	–	–	–	–	–
Endlicheria paniculata (Spreng.) J.F.Macbr.	90.5	57.1	0.38	0.24	2.7	6.0	0.01	0.02	–	–	–	–
Enterolobium gummiferum (Mart.) J.F.Macbr.	–	–	–	–	–	–	–	–	2.5	–	0.01	–
Eriotheca candolleana (K.Schum.) A.Robyns	–	–	–	–	4.0	6.7	0.03	0.07	–	–	–	–
Eriotheca gracilipes (K.Schum.) A.Robyns	–	–	–	–	–	–	–	–	2.5	–	0.07	–
Erythroxylum deciduum A.St.-Hil.	14.3	4.8	0.09	0.02	7.3	4.7	0.07	0.03	–	–	–	–
Eugenia aurata O.Berg	–	–	–	–	–	–	–	–	2.5	2.5	0.01	0.01
Eugenia florida DC.	23.8	28.6	0.09	0.17	9.3	9.3	0.09	0.08	2.5	5.0	0.01	0.02
Eugenia involucrata DC.	–	23.8		0.11	10.7	13.3	0.04	0.07	–	–	–	–
Eugenia ligustrina (Sw.) Willd.	19.1	42.9	0.08	0.17	3.3	12.7	0.01	0.05	–	–	–	–
Faramea hyacinthina Mart.	33.3	42.9	0.32	0.44	2.7	16.0	0.01	0.06	22.5	102.5	0.08	0.57
Ficus enormis Mart. ex Miq.	–	–	–	–	–	–	–	–	2.5	2.5	0.03	0.05
Garcinia brasiliensis Mart.	–	9.5	–	0.02	1.3	2.7	0.01	0.02	–	–	–	–
Guapira noxia (Netto) Lundell	–	–	–	–	–	–	–	–	5.0	5.0	0.03	0.03

Table 4 continued

Species	Riparian forest				Dry forest				Woodland savanna			
	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)
Guapira venosa (Choisy) Lundell	–	–	–	–	1.3	2.0	0.01	0.02	–	–	–	–
Guarea kunthiana A.Juss.	4.8	4.8	0.01	0.01	–	–	–	–	–	–	–	–
Guazuma ulmifolia Lam.	19.1	9.5	0.25	0.22	51.3	15.3	0.63	0.20	5.0	2.5	0.03	0.02
Guettarda viburnoides Cham. & Schltdl.	–	–	–	–	22.7	13.3	0.31	0.21	40.0	32.5	0.29	0.25
Handroanthus impetiginosus (Mart. ex DC.) Mattos	–	–	–	–	1.3	0.7	0.01	0.01	2.5	2.5	0.02	0.02
Handroanthus umbellatus (Sond.) Mattos	19.1	14.3	0.33	0.33	–	–	–	–	2.5	2.5	0.03	0.05
Heisteria ovata Benth.	–	–	–	–	–	0.7	–	0.00	–	2.5	–	0.02
Hirtella gracilipes (Hook.f.) Prance	–	19.1	–	0.08	–	3.3	–	0.01	2.5	5.0	0.01	0.05
Hymenaea courbaril L.	4.8	4.8	1.07	1.75	14.0	13.3	1.33	1.96	–	–	–	–
Inga laurina (Sw.) Willd.	–	–	–	–	1.3	1.3	0.01	0.00	–	–	–	–
Inga marginata Willd.	4.8	–	0.02	–	0.7	–	0.00	–	–	–	–	–
Inga vera Willd.	61.9	38.1	1.05	0.65	2.7	2.7	0.07	0.05	–	2.5	–	0.01
Ixora brevifolia Benth.	4.8	4.8	0.06	0.06	–	–	–	–	–	–	–	–
Kielmeyera coriacea Mart. & Zucc.	–	–	–	–	–	–	–	–	2.5	–	0.04	–
Lacistema aggregatum (P.J.Bergius) Rusby	–	–	–	–	–	1.3	–	0.00	–	2.5	–	0.01
Leptolobium elegans Vogel	–	–	–	–	–	–	–	–	40.0	20.0	0.43	0.29
Licania humilis Cham. & Schltdl.	–	–	–	–	–	–	–	–	2.5	2.5	0.01	0.02
Lithrea molleoides (Vell.) Engl.	9.5	4.8	0.21	0.24	43.3	5.3	1.54	0.12	42.5	22.5	0.67	0.49
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	–	–	–	–	1.3	0.7	0.05	0.07	–	–	–	–
Luehea divaricata Mart. & Zucc.	81.0	61.9	1.94	2.59	7.3	4.7	0.12	0.13	–	–	–	–
Luehea grandiflora Mart. & Zucc.	–	–	–	–	34.7	32.0	0.43	0.44	97.5	112.5	0.81	1.24
Machaerium acutifolium Vogel	–	–	–	–	8.0	5.3	0.08	0.06	95.0	85.0	1.12	1.43
Machaerium brasiliense Vogel	–	–	–	–	6.0	8.7	0.04	0.08	–	–	–	–
Machaerium hirtum (Vell.) Stellfeld	4.8	4.8	0.13	0.14	29.3	15.3	0.46	0.24	2.5	2.5	0.01	0.01
Machaerium stipitatum Vogel	–	–	–	–	5.3	4.7	0.04	0.07	–	–	–	–
Maclura tinctoria (L.) D.Don ex Steud.	–	–	–	–	0.7		0.01	–	–	–	–	–
Magnolia ovata (A.St.-Hil.) Spreng.	38.1	23.8	0.38	0.27	–	–	–	–	–	–	–	–
Margaritaria nobilis L.f.	–	–	–	–	1.3	3.3	0.03	0.09	–	–	–	–
Matayba elaeagnoides Radlk.	81.0	81.0	0.56	0.95	26.0	28.0	0.18	0.26	10.0	12.5	0.03	0.11
Matayba guianensis Aubl.	57.1	38.1	0.30	0.26	76.0	60.7	0.50	0.49	145.0	187.5	0.67	1.25
Maytenus floribunda Reissek	–	–	–	–	26.0	33.3	0.11	0.15	2.5	2.5	0.01	0.01
Metrodorea nigra A.St.-Hil.	–	4.8	–	0.01	–	–	–	–	–	–	–	–
Miconia albicans (Sw.) Triana	–	–	–	–	–	–	–	–	10.0	12.5	0.02	0.04
Miconia calvescens DC.	–	–	–	–	0.7	–	0.00	–	–	–	–	–
Myrcia citrifolia (Aubl.) Urb.	–	–	–	–	–	–	–	–	–	5.0	–	0.02
Myrcia laruotteana Cambess.	4.8	–	0.01	–	–	–	–	–	–	–	–	–
Myrcia splendens (Sw.) DC.	–	–	–	–	20.7	2.0	0.11	0.01	87.5	47.5	0.31	0.22
Myrcia tomentosa (Aubl.) DC.	–	9.5	–	0.02	10.7	9.3	0.04	0.03	57.5	62.5	0.34	0.36
Myrcia variabilis DC.	–	–	–	–	–	–	–	–	5.0	–	0.02	–
Myrcia venulosa DC.	4.8	–	0.01	–	–	–	–	–	–	–	–	–
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	9.5	4.8	0.08	0.04	5.3	2.0	0.11	0.04	12.5	20.0	0.14	0.28
Myrsine umbellata Mart.	–	–	–	–	20.7	14.0	0.28	0.35	72.5	60.0	0.42	0.74
Nectandra cissiflora Nees	76.2	47.6	1.22	0.71	10.7	21.3	0.12	0.29	–	5.0	–	0.02
Nectandra megapotamica (Spreng.) Mez	4.8	4.8	0.36	0.67	–	–	–	–	–	–	–	–

Table 4 continued

Species	Riparian forest				Dry forest				Woodland savanna			
	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)
Nectandra membranacea (Sw.) Griseb.	–	–	–	–	–	0.7	–	0.00	–	–	–	–
Neea hermaphrodita S.Moore	9.5	9.5	0.04	0.05	–	–	–	–	–	–	–	–
Ocotea corymbosa (Meisn.) Mez	19.1	4.8	0.13	0.03	0.7	1.3	0.04	0.09	15.0	25.0	0.27	0.79
Ocotea minarum (Nees & Mart.) Mez	–	–	–	–	5.3	4.7	0.03	0.02	17.5	17.5	0.33	0.31
Ocotea percoriacea Kosterm.	4.8	–	0.03	–	–	–	–	–	–	–	–	–
Ocotea pulchella (Nees & Mart.) Mez	19.1	4.8	0.26	0.03	20.7	6.0	0.19	0.09	20.0	7.5	0.16	0.13
Ormosia arborea (Vell.) Harms	–	–	–	–	0.7	1.3	0.00	0.01	–	–	–	–
Ouratea castaneifolia (DC.) Engl.	–	–	–	–	4.7	5.3	0.03	0.05	7.5	12.5	0.07	0.11
Phyllanthus acuminatus Vahl	–	–	–	–	0.7	1.3	0.01	0.01	–	–	–	–
Picramnia sellowii Planch.	4.8	–	0.03	–	–	–	–	–	–	–	–	–
Piptadenia gonoacantha (Mart.) J.F.Macbr.	–	–	–	–	4.0	3.3	0.14	0.18	–	–	–	–
Piptocarpha rotundifolia (Less.) Baker	–	–	–	–	–	–	–	–	2.5	–	0.02	–
Platypodium elegans Vogel	4.8	4.8	0.49	0.60	15.3	12.7	0.37	0.51	40.0	55.0	0.74	1.27
Plenckia populnea Reissek	–	–	–	–	–	–	–	–	10.0	5.0	0.20	0.07
Pouteria gardneri (Mart. & Miq.) Baehni	–	–	–	–	6.7	6.7	0.13	0.21	7.5	10.0	0.07	0.17
Pouteria torta (Mart.) Radlk.	–	–	–	–	5.3	7.3	0.08	0.13	–	–	–	–
Prockia crucis P.Browne ex L.	–	–	–	–	0.7	1.3	0.00	0.01	–	–	–	–
Protium heptaphyllum (Aubl.) Marchand	166.7	200.0	1.71	3.21	5.3	14.0	0.05	0.12	–	5.0	–	0.01
Prunus myrtifolia (L.) Urb.	–	–	–	–	–	–	–	–	7.5	2.5	0.03	0.02
Pseudobombax tomentosum (Mart. & Zucc.) A.Robyns	–	–	–	–	1.3	1.3	0.02	0.02	10.0	7.5	0.13	0.27
Psidium rufum Mart. ex DC.	–	–	–	–	6.0	6.0	0.03	0.03	–	–	–	–
Psidium sartorianum (O.Berg) Nied.	–	–	–	–	3.3	5.3	0.02	0.05	–	–	–	–
Qualea dichotoma (Mart.) Warm.	9.5	9.5	0.71	0.92	2.0	3.3	0.04	0.09	7.5	7.5	0.16	0.30
Qualea grandiflora Mart.	–	–	–	–	1.3	1.3	0.01	0.01	220.0	197.5	3.56	4.09
Qualea multiflora Mart.	–	–	–	–	–	–	–	–	7.5	2.5	0.04	0.03
Qualea parviflora Mart.	–	–	–	–	–	–	–	–	10.0	7.5	0.11	0.15
Rhamnidium elaeocarpum Reissek	19.1	9.5	0.06	0.06	28.7	16.0	0.24	0.08	15.0	12.5	0.05	0.05
Roupala montana Aubl.	–	–	–	–	15.3	12.7	0.34	0.28	70.0	47.5	0.75	0.49
Rudgea viburnoides (Cham.) Benth.	–	–	–	–	5.3	4.0	0.03	0.03	70.0	100.0	0.39	0.57
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	–	–	–	–	–	–	–	–	5.0	–	0.04	–
Schefflera morototoni (Aubl.) Maguire et al.	–	–	–	–	–	0.7	–	0.00	–	–	–	–
Senegalia polyphylla (DC.) Britton & Rose	–	4.8	–	0.01	5.3	4.0	0.03	0.05	5.0	12.5	0.01	0.08
Senna silvestris (Vell.) H.S.Irwin & Barneby	4.8	4.8	0.03	0.05	2.0	–	0.01	–	10.0	10.0	0.04	0.05
Simira sampaioana (Standl.) Steyerm.	–	–	–	–	3.3	4.7	0.03	0.08	–	–	–	–
Siparuna guianensis Aubl.	–	–	–	–	–	6.7	–	0.02	5.0	25.0	0.01	0.10
Strychnos pseudoquina A.St.-Hil.	–	–	–	–	–	–	–	–	2.5	–	0.05	–
Stryphnodendron polyphyllum Mart.	–	–	–	–	–	–	–	–	2.5	–	0.01	–
Styrax camporum Pohl	19.1	4.8	0.08	0.03	28.7	16.7	0.53	0.27	67.5	60.0	0.95	1.07
Styrax ferrugineus Nees & Mart.	–	–	–	–	–	–	–	–	2.5	2.5	0.03	0.03
Sweetia fruticosa Spreng.	–	–	–	–	6.0	9.3	0.04	0.08	–	–	–	–
Syagrus flexuosa (Mart.) Becc.	–	–	–	–	–	–	–	–	2.5	2.5	0.01	0.02
Symplocos nitens (Pohl) Benth.	–	–	–	–	–	0.7	–	0.00	–	–	–	–
Symplocos pubescens Klotzsch ex Benth.	14.3	–	0.15	–	6.7	6.7	0.05	0.05	25.0	22.5	0.26	0.30

Table 4 continued

Species	Riparian forest				Dry forest				Woodland savanna			
	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)	D (t1)	D (t2)	BA (t1)	BA (t2)
Tabebuia roseoalba (Ridl.) Sandwith	4.8	4.8	0.04	0.04	8.0	9.3	0.08	0.10	22.5	22.5	0.20	0.31
Tapirira guianensis Aubl.	123.8	66.7	5.83	4.31	30.7	28.0	0.66	0.70	75.0	115.0	1.66	1.76
Tapirira obtusa (Benth.) J.D.Mitch.	–	–	–	–	–	0.7	–	0.00	–	–	–	–
Terminalia argentea Mart.	–	–	–	–	1.3	0.7	0.09	0.01	10.0	7.5	0.36	0.40
Terminalia glabrescens Mart.	14.3	9.5	0.39	0.04	35.3	36.0	1.32	1.61	22.5	27.5	0.26	0.46
Terminalia phaeocarpa Eichler	–	–	–	–	33.3	26.7	0.82	1.03	5.0	2.5	0.02	0.02
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	–	–	–	–	0.7	0.7	0.00	0.00	–	5.0	–	0.01
Trichilia catigua A.Juss.	–	–	–	–	–	–	–	–	2.5	2.5	0.00	0.01
Trichilia elegans A.Juss.	–	4.8	–	0.02	–	6.7	–	0.02	–	–	–	–
Trichilia pallida Sw.	19.1	33.3	0.10	0.08	0.7	2.7	0.00	0.01	–	2.5	–	0.01
Unonopsis guatterioides (A.DC.) R.E.Fr.	14.3	33.3	0.07	0.21	0.7	5.3	0.00	0.02	–	–	–	–
Virola sebifera Aubl.	–	–	–	–	0.7	2.0	0.00	0.03	2.5	25.0	0.01	0.13
Vochysia tucanorum Mart.	9.5	4.8	0.45	0.12	6.0	4.7	0.14	0.12	150.0	85.0	1.46	1.29
Xylopia aromatica (Lam.) Mart.	–	–	–	–	4.7	3.3	0.02	0.03	52.5	72.5	0.33	0.55

D absolute density (tree ha^{-1}); *BA* basal area (m^2 ha^{-1}). Species are in alphabetical order

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