



## Original article

# Water availability determines the richness and density of fig trees within Brazilian semideciduous forest landscapes



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## ABSTRACT

The success of fig trees in tropical ecosystems is evidenced by the great diversity (+750 species) and wide geographic distribution of the genus. We assessed the contribution of environmental variables on the species richness and density of fig trees in fragments of seasonal semideciduous forest (SSF) in Brazil. We assessed 20 forest fragments in three regions in Sao Paulo State, Brazil. Fig tree richness and density was estimated in rectangular plots, comprising 31.4 ha sampled. Both richness and fig tree density were linearly modeled as function of variables representing (1) fragment metrics, (2) forest structure, and (3) landscape metrics expressing water drainage in the fragments. Model selection was performed by comparing the AIC values (Akaike Information Criterion) and the relative weight of each model (wAIC). Both species richness and fig tree density were better explained by the water availability in the fragment (meter of streams/ha):  $wAIC_{richness} = 0.45$ ,  $wAIC_{density} = 0.96$ . The remaining variables related to anthropic perturbation and forest structure were of little weight in the models. The rainfall seasonality in SSF seems to select for both establishment strategies and morphological adaptations in the hemiepiphytic fig tree species. In the studied SSF, hemiepiphytes established at lower heights in their host trees than reported for fig trees in evergreen rainforests. Some hemiepiphytic fig species evolved superficial roots extending up to 100 m from their trunks, resulting in hectare-scale root zones that allow them to efficiently forage water and soil nutrients. The community of fig trees was robust to variation in forest structure and conservation level of SSF fragments, making this group of plants an important element for the functioning of seasonal tropical forests.

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## 1. Introduction

The evolutionary success of fig trees (*Ficus* L., Moraceae) in tropical ecosystems is irrefutable, as denoted by their high diversity (approx. 750 species) and widespread geographical distribution (Berg, 1989). A substantial part of this biodiversity emerged with the rise of the hemiepiphytic habit (subgenus *Urostigma* clade) in Eurasia, approx. 50 million years ago, and posterior dispersion to Africa, America, India, and Australia (Cruaud et al., 2012). In addition to hemiepiphytic species, the subgenus *Urostigma* comprises a diversity of life-forms. Some species (e.g. in section *Galoglychia*, subsection *Platyphyllae*) returned to terrestrial life-form and are able to colonize rocks (rock-splitters) in dry habitats (Berg, 1989). Other species have facultative habit, with freestanding and

hemiepiphytic individuals, such as *Ficus crocata* (section *Americana*) and *Ficus burtt-davyi* (section *Galoglychia*).

Hemiepiphytism in *Ficus* probably conferred wide environmental plasticity to these plants, helping them to obtain light and nutrients (in the organic matter accumulated on the branches of the host tree), as well as escape from fire, flooding and terrestrial herbivores (Putz and Holbrook, 1986; Ingram and Nadkarni, 1993; Putz and Susilo, 1994). However, hemiepiphytes are subjected to higher levels of hydric stress, especially in regions of seasonal climate, as they are not in direct contact with the soil in their initial phase of development (Putz and Holbrook, 1986; Holbrook and Putz, 1996c). Dehydration is the main cause of death of these plants, particularly at the epiphyte phase (Laman, 1995; Zotz and Andrade, 2002). Freestanding fig trees (e.g. *Pharmacosycea* subgenus and some species of *Ficus*, *Sycidium* and *Sycomorus* subgenera), on the other hand, are less water-limited as they are in contact with the soil in their initial development. However, freestanding fig species have less environmental plasticity

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conferred by the hemiepiphytism, and populations are generally constrained near water bodies. Indeed, hemiepiphytic fig species are adapted to water-limited epiphyte phase, using water more conservatively and having leaves more tolerant to drought, whereas freestanding species have a higher potential water use and seem to be more competitive under high water supply (Hao et al., 2010).

In spite of their environmental plasticity, the recruitment of hemiepiphytic fig trees is dependent on a combination of factors related to the characteristics and availability of the host tree. Thus, the structure of tree communities potentially drives the spatial distribution of hemiepiphytes, as their establishment depends on the existence of suitable host trees to support the initial growth of hemiepiphytes. Studies report that hemiepiphytes are more likely to occur on larger trees (Compton and Musgrave, 1993; Athreya, 1999; Male and Roberts, 2005; Mucunguzi, 2007; Orihuela and Waechter, 2010) because of the greater probability of hemiepiphyte seeds arriving on old, large trees (Willians-Linera and Lawton, 1995). On the other hand, hemiepiphytes exert some pressure on the forest structure, as they can negatively affect the growth of their host trees (Clark and Clark, 1990; Zotz and Andrade, 2002; Harrison, 2006), inducing the breaking of branches, and in some cases causing the death of the whole tree (Willians-Linera and Lawton, 1995). Indeed, trees that host hemiepiphytic fig plants are more likely to fall, and falling with its host is the main cause of death for fig trees in the forests of Borneo (Harrison, 2006).

Although the host size plays an important role in hemiepiphyte occurrence (Harrison, 2006), the establishment of hemiepiphytes depends on other additional factors. Thus, the host size is not

always correlated with richness of hemiepiphytes (Andersohn, 2004; Mucunguzi, 2007). The availability of micro-habitats suitable for organic matter accumulation, such as forks, cavities and leaf axils (i.e., palm trees), is reported as important places for hemiepiphyte establishment (Todzia, 1986; Putz and Holbrook, 1986; Daniels and Lawton, 1991; Compton and Musgrave, 1993; Laman, 1996; Athreya, 1999; Mucunguzi, 2007). For example, the density of strangler fig trees in India is correlated with the density of the host tree *Vitex altissima* L. (Verbenaceae) due to the high prevalence of hosts with cavities, which accumulate water and nutrients (Athreya, 1999). Palm trees in open, degraded areas are frequently associated with hemiepiphytic fig trees due to the suitable amount of organic matter accumulated in the palm leaf axils (Putz and Holbrook, 1989). Moreover fig species of section *Galoglychia* do not randomly colonize host tree species, but are more likely to occur on species with a combination of morphological structures that apparently confer higher light access to hemiepiphytic fig trees (Michaloud and Michaloud-Pelletier, 1987).

The study of fig tree communities has received little attention in the literature (see Mucunguzi, 2007, for an exception), particularly for hemiepiphytes. Based on the natural history of fig species, it is valid to speculate that their spatial distribution results from a complex combination of factors, many of them related with the microenvironment quality or other abiotic factors and the distribution of suitable host trees. Indeed, freestanding fig tree species (e.g. *Pharmacosycea* section) seem to be constrained by site quality, such as light availability and soil pH (Banack et al., 2002). Hemiepiphytic species depend mainly on water availability; thus, they developed morphological and physiological adaptations related to

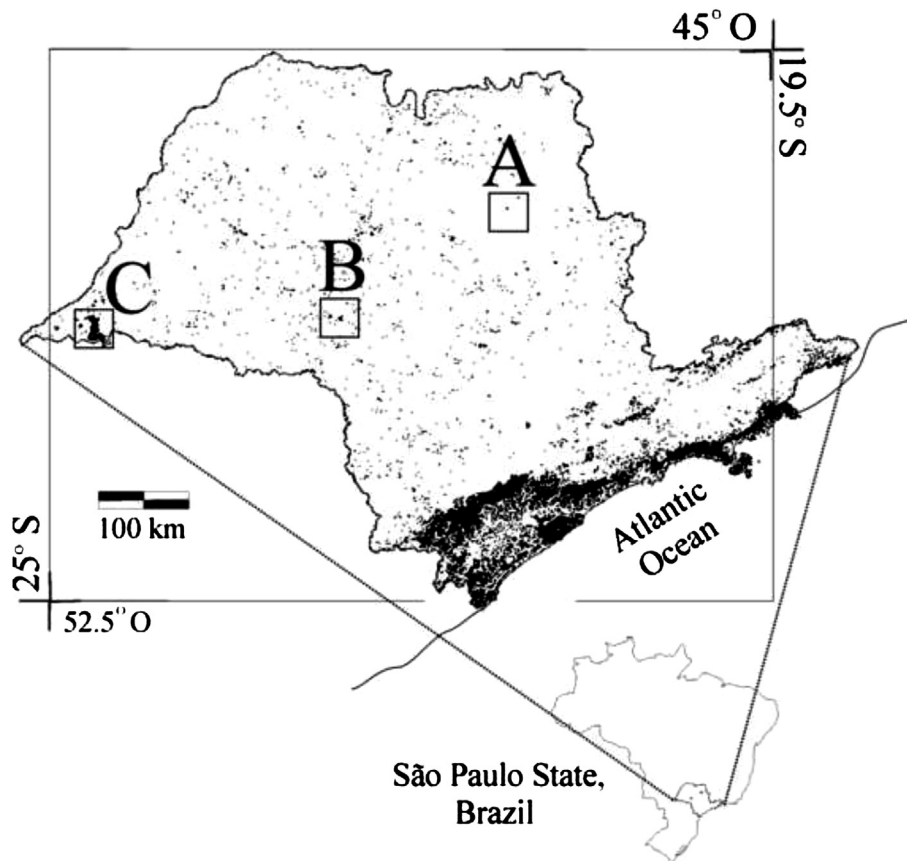


Fig. 1. Location of study areas within São Paulo state, Brazil: (A) Ribeirão Preto, (B) Gália, and (C) Teodoro Sampaio. Modified from Hirota and Ponzoni (2008), with permission from J.F. Ponzoni.

conservative water use (Holbrook and Putz, 1996a, 1996b; Schmidt and Tracey, 2006; Hao et al., 2010). These adaptations include peculiar strategies to disproportionally improve the ability to forage water and nutrients. Roots of individuals of *Ficus schultesii* (Silman and Krisel, 2006) and *Ficus eximia* (LFM Coelho and RAS Pereira, unpublished results) can extend to distances greater than 50 m from the plant, defining a foraging zone exceeding 1 ha.

Fig trees are abundant in humid and riparian forests. However, the environmental factors that drive the diversity and density of these species at the local and landscape levels are under debate. Thus, a formal modeling of variables that express physiological (*i.e.*, water availability) and forest structure (*i.e.*, density of host trees and forest perturbation level) effects on the fig tree community is still missing. In this context, the communities of fig trees in seasonal semideciduous forest (SSF) constitute a formidable model system to be studied. These forests occur in regions with well-defined rain seasonality, resulting in hydric stress during the dry winter (Pennington et al., 2009). We assessed the relative contribution of environmental variables to explain the density and species diversity of fig trees in a large-scale landscape analysis (>500,000 ha) and plot-based sampling in fragments of SSF within Brazil. An AIC-based multiple hypothesis approach (Burnham and Anderson, 2002) was used in order to assess the weight of contribution of ecologically relevant competing models.

## 2. Material and methods

### 2.1. Study areas

We studied three regions (Ribeirão Preto, Gália and Teodoro Sampaio) in the domain of SSFs in São Paulo state, Brazil (Fig. 1). The original SSF extension underwent an intense man-induced fragmentation for agricultural land conversion. SSFs were reduced to less than 10% of their original area and the remaining fragments are surrounded by extensive sugarcane fields. The study areas have a seasonal climate with a dry winter (June–September) and rainy summer (December–March). The mean temperature varies from 17.1 to 19.6 °C during the winter and 24.4–26.3 °C during the summer. The precipitation varies from 25 to 26 mm in the driest month and 170–270 mm in the wettest month (annual precipitation is 1131–1529 mm), with five to six dry months (Brazilian climate database; [www.bdclima.cnpm.embrapa.br](http://www.bdclima.cnpm.embrapa.br)). Each region was delimited by a square area of 42 × 42 km (176,000 ha), totaling 528,000 ha (Figs. S1–S3).

### 2.2. Fig tree sampling

We classified forest patches into three size classes: small (10–45 ha), medium (75–200 ha) and large (>2000 ha). Fig trees were sampled in all three patch size classes, totaling 6, 7, and 7 fragments in Ribeirão Preto, Gália, and Teodoro Sampaio, respectively. We only sampled fragments that had forest physiognomy, thus, fragments intensively disturbed by fire or cattle access were not considered. The location of the fragments in the studied areas is shown in Figs. S1–S3.

We randomly placed plots in the interior and at the edge of the fragments. Inner plots were 0.25 ha in area (125 × 20 m). Edge plots were 0.15 ha in area (150 × 10 m). Edge plots were narrower than the inner ones to overcome sampling difficulties, as the forest edges are dominated by lianas and grasses. The sum of sampled areas per region varied from 4.02 to 4.05 for edge plots and from 4.25 to 7.5 for inner plots, totaling a sampling effort of 31.37 ha for the three regions (Table S1).

We located the plots according to a systematic sampling protocol. For each forest fragment we considered a grid of 100 m

between lines at the inner portion and line segments of 150 m at edges (Fig. 2). We randomly sampled one grid intersection or one line segments to define the first inner or edge plot, respectively, using the function `sample` at R software (R Development Core Team, 2012). The next plots were systematically distributed along the intersections/segments. The grid had approximately half of the total area in small and medium fragments. In large fragments, the grid area was 100 ha.

In each plot, all freestanding individuals ≥50 cm in height and hemiepiphytic fig trees already rooted in the soil were identified to species level and their height of establishment on the host tree recorded using a measuring tape or a topographic abney level (Sokkia™) when established higher than 2 m. When species identification was not possible in the field, we collected a plant branch for further identification in the laboratory. The density of fig trees was estimated from the plot data. To estimate species richness, we considered additional data of species occurrence from random walks in the fragments.

### 2.3. Environmental data

Local and landscape environmental variables were estimated for each forest fragment. These variables were grouped into three categories: (1) landscape, particularly patch area and shape; (2) forest structure and conservation level, and (3) water-related parameters derived from geomorphology and hydrography (see Table 1). The average values of all sampled variables are shown in Table S2. We used the SPRING GIS (Camara et al., 1996) to estimate

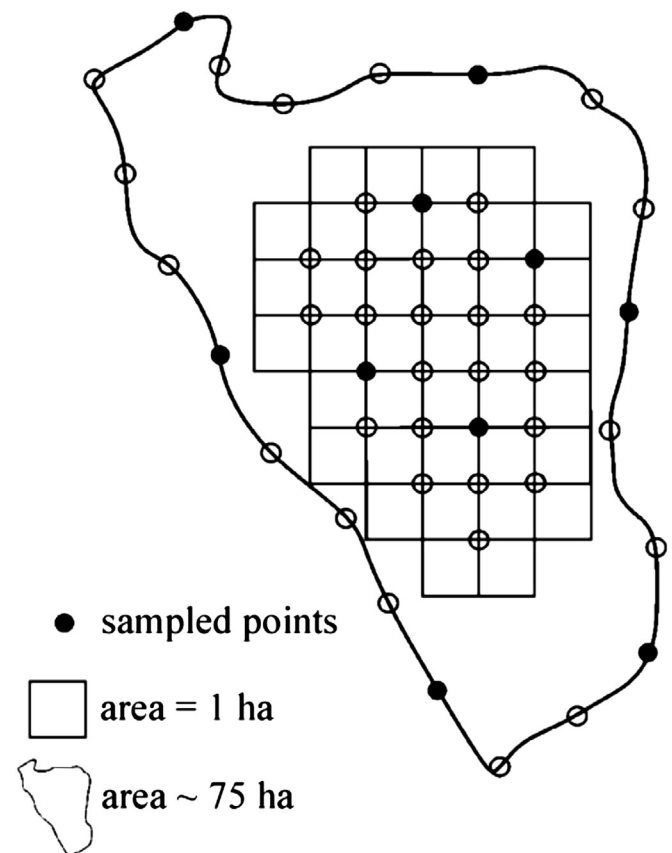


Fig. 2. Systematic sampling schema used to place plots in the forest fragments. The sketch shows the grid and the line segments that defined the points to be sampled.

**Table 1**  
Environmental variables and competing models used to explain species richness and density of fig trees in the study fragments. Group 1: landscape variables that express area and shape of fragments. Group 2: variables related to forest structure and conservation level. Group 3: variables related with geomorphology and hydrography. Models of group 1 are identified with the prefix LS, group 2 with VS, and group 3 with WT. The fourth group included the null and the Region models (prefix R).

Group	Model	Variable	Numeric meaning	Bio/ecological interpretation
1	LS1	Fragment area (ha)	Ln (area)	Area effect
	LS2	Shape factor (m/m <sup>2</sup> )	Fragment perimeter/fragment area	Edge effect
	LS3	Average distance to the edge (m)	Average distance of each pixel to the fragment edge	Extent of edge effect
2	VS4	Canopy cover (%)	Percentage of canopy opening in a given forest spot	Extent of disturbance
	VS5	Density of trees (ind./ha)	Number of trees with DBH $\geq$ 10 cm in 1 ha	Density of potential host trees and extent of disturbance
	VS6	Basal area (cm <sup>2</sup> /ha)	The summation of trunk sections of trees with DBH $\geq$ 10 cm in 1 ha	Biomass and extent of disturbance
	VS7	Perturbation (binary)	Presence or absence of five or more evidences of anthropogenic perturbation in the fragment	Anthropogenic disturbance
	VS8	NDVI	Mean of NDVI estimated from all pixel (30 m) within the fragment	Vegetation index. Quality of vegetation cover
3	VS9	NDVI (var)	Variance of NDVI	Heterogeneity of vegetation cover
	WT10	Density of streams (m/ha)	Meters of streams in a fragment/fragment area	Water availability
	WT11	Surface slope	Mean of slope estimate using all pixels inside the fragments; data derived from SRTM (90 m) digital elevation model	Complexity of the hydric system and water availability
	WT12	Surface slope (SD)	Standard deviation for the slope surface	Heterogeneity in the hydric system
	WT13	Flux accumulation	Mean of cumulative flow estimated from cumulative flow grid generated from SRTM (90 m resolution)	Water availability
4	R14	Region	Category variable representing the three study regions	Differences in <i>Ficus</i> community due to regional effect
	Null model	Constant	Only $\beta_0$ (average) parameter estimated on regression	Absence of effect

all landscape data. Variables related with area and shape of fragments were estimated from satellite images (see Box S1 for details).

Forest structure was expressed in terms of canopy cover, density, and basal area of trees. These variables were sampled in circular subplots of 3.2 m in radius, systematically placed in each sampling unit (plot). We sampled 8 and 5 subplots per sampling unit in the inner and edge plots, respectively, comprising 10% of the plot area. The percentage of canopy cover was measured on four sides of each subplot (N, S, E, and W) using a spherical forest densiometer (Lemmon, 1956). For the analyzes we used the average value of canopy cover per fragment. The density of trees was estimated by counting all trees of diameter at breast height (DBH)  $\geq$  10 cm. The basal area of trees was calculated by summing the area of the trunk section of all trees of DBH  $\geq$  10 cm and expressed in cm<sup>2</sup>/ha.

The conservation level of fragments was expressed in terms of direct evidence of anthropic perturbation and the vegetation index (normalized difference vegetation index – NDVI) calculated from Landsat-5 images. To assess the anthropic perturbation, we roamed the fragments to count the number of occurrences of evidence of fire, timber extraction or cattle access. Fragments with five or more of these occurrences were scored as “disturbed”. The NDVI is a continuous variable that expresses the vegetation density and varies from –1 (e.g., no vegetation) to 1 (very dense vegetation). Thus, it is a suitable index to estimate the conservation level and spatial heterogeneity.

Water-related condition was expressed through the geomorphology and hydrography of fragments. These variables were extracted from SRTM (Shuttle Radar Topography Mission) data and topographic maps supplied by the Instituto Brasileiro de Geografia e Estatística (IBGE). Thus, we calculated the density of

streams (m/ha), surface declivity, and flux accumulation. In order to include the environmental condition around the area where fig trees were sampled, we estimated water drainage variables and NDVI for forested areas enclosed in squares of 2  $\times$  2 km centered in the location of sampling plots (Fig. S4).

The region where the fragments are located was used as a category variable to assess the regional effects on the species richness and fig tree density.

#### 2.4. Data analysis and competing models

We analyzed data at the fragment level; thus, data from inner and edge plots were combined to produce variables that described the whole fragment.

A multiple hypothesis approach (Burnham and Anderson, 2002) using AIC (Akaike Information Criterion) was used in order to rank ecologically relevant competing models. AIC considers the fitting quality and the number of variables included in the model. Hence, smaller AIC values indicate the better models (Mazerolle, 2006). For each concurrent model we calculated the AICc (AIC corrected for small sample sizes) using the function Ictab available on the package bbmle in the R software (Bolker, 2008). We also estimated the difference between the AICc of each model and the lowest AICc value ( $\Delta AIC_i = AIC_i - AIC_{\min}$ ); therefore, the best model has  $\Delta AIC = 0$ . We estimated the relative weight of each model (wAICc), which represents the likelihood of a given model to be the best one among a set of concurrent models (Johnson and Omland, 2004). Models with  $\Delta AICc \leq 2$  and wAICc  $\geq 0.10$  were considered equally plausible to explain the observed data (Burnham and Anderson, 2002; Johnson and Omland, 2004). As a baseline for comparison,

we included a null model (i.e., dependent variable ~ constant), which refers to the absence of effect.

We linearly modeled species richness and density of fig trees per fragment as a function of the variables presented in Table 1, plus the simplest model (constant only). First, we generated 15 one-variable concurrent linear models for each dependent variable (i.e., richness or density). As expected from the well-known species-area relationship pattern (Connor and McCoy, 1979) and as postulated by the Island Biogeography Theory (IBT; MacArthur and Wilson, 1967), the fragment area was the best variable to explain the species richness of fig trees in the present study ( $\Delta AICc = 0$ ,  $wAICc = 0.78$ ). Therefore, to assess the effect of the other environmental variables, we included the fragment area in the models 2 to 14 as covariate, plus the null model, totaling 14 multivariate competing models for

species richness. All models were adjusted within R software using linear regression.

### 3. Results

We found eight fig tree species in the surveyed fragments belonging to the *Americana* (*Ficus citrifolia* Mill., *F. crocata* (Miq.) Miq., *F. eximia* Schott, *Ficus lagoensis* C.C.Berg & Carauta, *Ficus luschnathiana* (Miq.) Miq., *Ficus obtusifolia* Kunth e *Ficus trigona* L.f. and *Pharmacosyceae* (*Ficus adhatodifolia* Schott) sections. *F. citrifolia* was the most abundant species in all studied areas. *F. adhatodifolia* (although present in all landscapes) was not sampled in the Ribeirão Preto and Teodoro Sampaio plots because this species did not appear in sampled sites, but was the second most important species in the Gália fragments (Fig. 3).

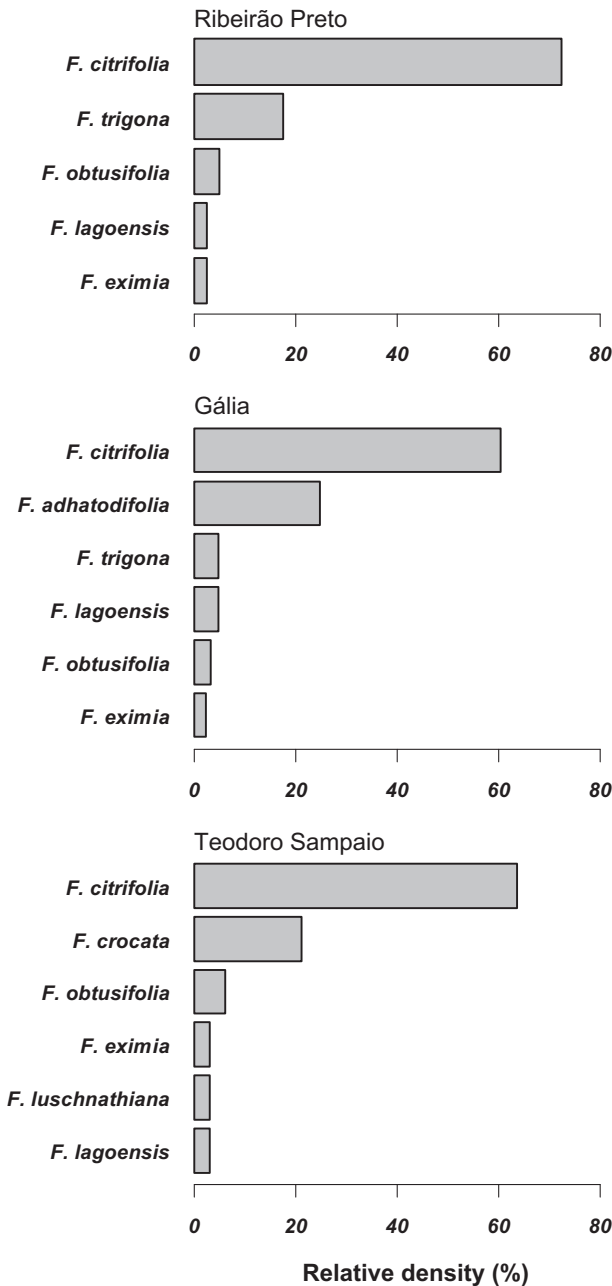


Fig. 3. Relative density (% of total sampled individuals) of *Ficus* species for Ribeirão Preto, Gália and Teodoro Sampaio regions within São Paulo state, Brazil.

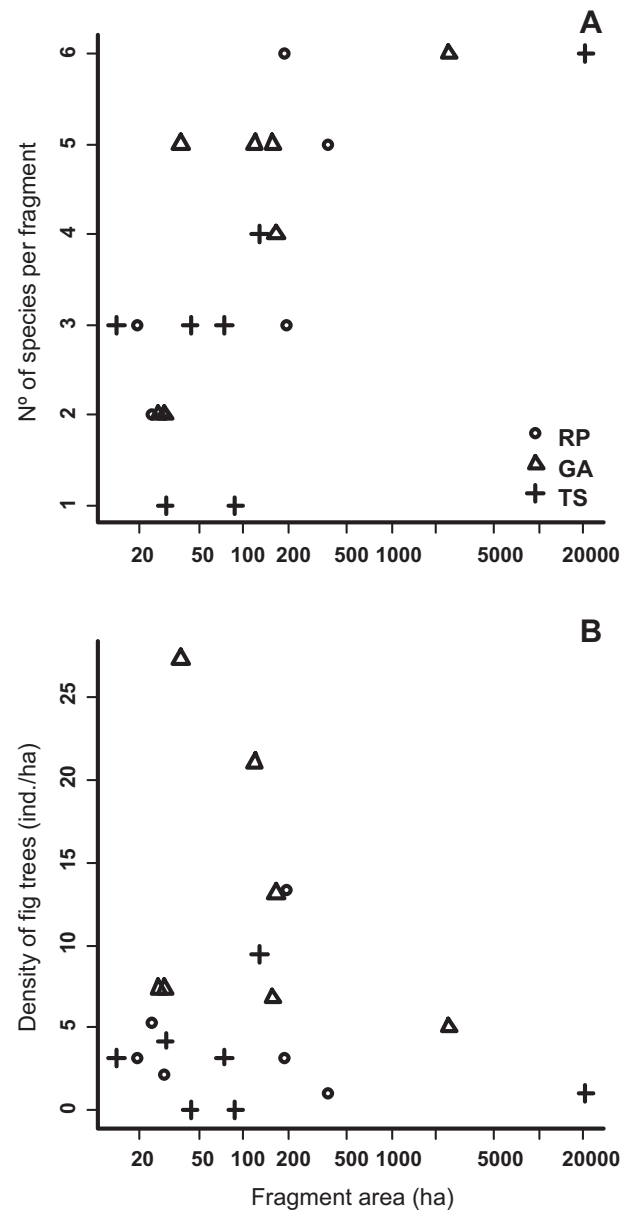


Fig. 4. Species-area (A) and density-area (B) relationships for fig trees studied in forest fragments of São Paulo State, Brazil. RP = Ribeirão Preto; GA = Gália; TS = Teodoro Sampaio. X-axis in logarithm scale.

**Table 2**

Best supported models ( $\Delta\text{AICc} \leq 2$  and  $w\text{AICc} > 0.1$ ) to explain the fig tree richness within forest fragments of São Paulo state, Brazil. Abbreviations: WT – water related, LS – landscape scale, VS – vegetation structure and R – regional scale models.

Models		$\Delta\text{AICc}$	$w\text{AICc}$	Slope sign
WT10:	Richness ~ Ln (area) + Density of streams	0	0.4463	+
WT11:	Richness ~ Ln (area) + Surface declivity	2.2	0.1462	+
WT12:	Richness ~ Ln (area) + Surface declivity (SD)	2.6	0.1226	+
VS6:	Richness ~ Ln (area) + Basal area	3.4	0.0810	+
LS3:	Richness ~ Ln (area) + Distance to the edge	4.9	0.0393	-
VS4:	Richness ~ Ln (area) + Canopy cover	5.7	0.0258	+
R14:	Richness ~ Ln (area) + Region	5.9	0.0235	na <sup>a</sup>
VS5:	Richness ~ Ln (area) + Density of trees	6.1	0.0215	-
VS8:	Richness ~ Ln (area) + NDVI	6.1	0.0211	+
WT13:	Richness ~ Ln (area) + Flux accumulation	6.2	0.0197	+
LS2:	Richness ~ Ln (area) + Shape factor	6.5	0.0175	+
VS7:	Richness ~ Ln (area) + Perturbation	6.5	0.0175	+
VS9:	Richness ~ Ln (area) + NDVI (var)	6.5	0.0175	+
Null model:	Richness ~ Constant	13.8	<0.001	na

<sup>a</sup> na = not applicable.

As described at item 2.4, the number of *Ficus* species was positively correlated with fragment area (species-area effect, Fig. 4A), whereas the density (ind./ha) of fig trees was insensitive to patch area (Fig. 4B). Indeed, the model 'Density ~ Ln(Area)' present the highest AIC among the confronted models (Table 3, see below).

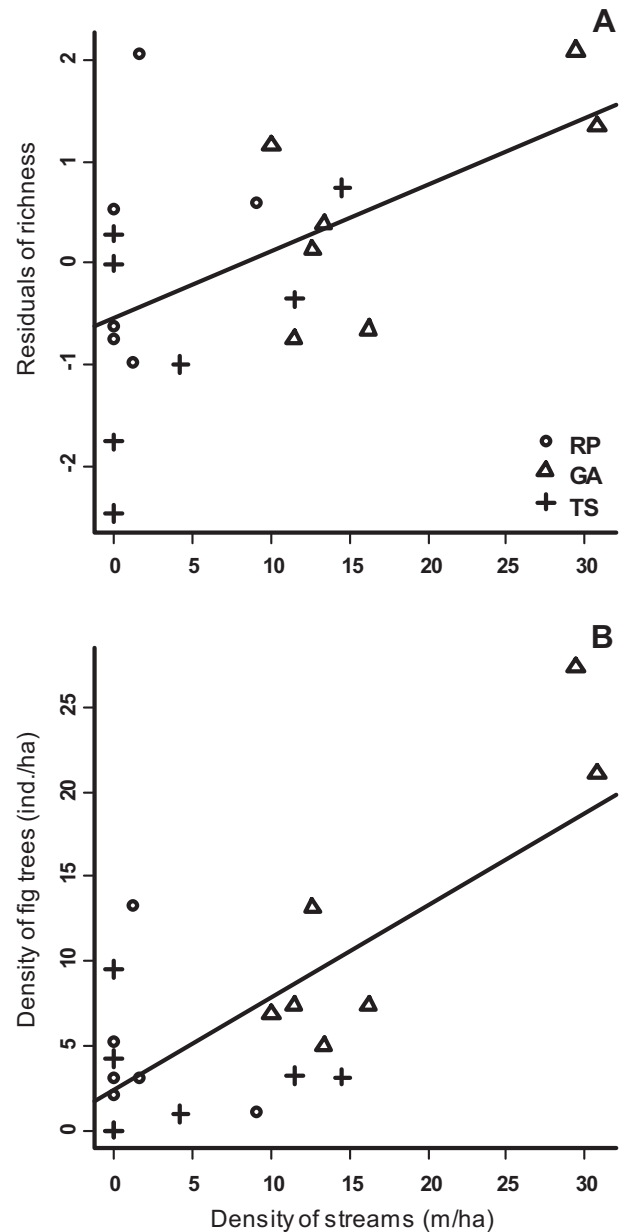
Controlling the area effect, the species richness was positively correlated with the density of streams and surface declivity variables ( $\Sigma w\text{AICc} = 0.72$ , Table 2, Fig. 5A). The other models had little contribution to explain the fig tree richness ( $\Delta\text{AICc} > 3$  and  $w\text{AICc} < 0.10$ ).

**Table 3**

Best supported models ( $\Delta\text{AICc} \leq 2$  and  $w\text{AICc} > 0.1$ ) to explain the density of fig trees (ind./ha) within forest fragments of São Paulo state, Brazil. Abbreviations: WT – water related, LS – landscape scale, VS – vegetation structure and R – regional scale models.

Models		$\Delta\text{AICc}$	$w\text{AICc}$	Slope sign
WT10:	Density ~ Density of streams	0	0.9580	+
R14:	Density ~ Region	8.9	0.0115	na <sup>a</sup>
WT12:	Density ~ Surface declivity (SD)	8.9	0.0111	+
WT11:	Density ~ Surface declivity	10.5	0.0049	+
VS9:	Density ~ NDVI (var)	11.4	0.0032	+
VS6:	Density ~ Basal area	12.0	0.0024	+
Null model:	Density ~ Constant	12.3	0.0020	na
VS8:	Density ~ NDVI	12.8	0.0016	+
VS5:	Density ~ Density of trees	13.0	0.0015	+
WT13:	Density ~ Flux accumulation	14.3	<0.001	-
LS3:	Density ~ distance to the edge	14.3	<0.001	-
VS4:	Density ~ Canopy cover	14.6	<0.001	-
LS2:	Density ~ Shape factor	14.7	<0.001	+
VS7:	Density ~ Perturbation	14.9	<0.001	+
LS1:	Density ~ Ln (area)	14.9	<0.001	-

<sup>a</sup> na = not applicable.



**Fig. 5.** Relationship between density of streams and (A) richness residuals and (B) density of fig trees in the studied fragments of São Paulo state, Brazil. Richness residuals were calculated from the linear model 'Richness ~ Constant + Ln(Area)'; see item 2.4 for details. RP – Ribeirão Preto, GA – Gália, and TS – Teodoro Sampaio regions.

The Gália region had the highest density of fig trees (12.9 ind./ha), followed by the regions of Ribeirão Preto (4.7 ind./ha) and Teodoro Sampaio (3.0 ind./ha) (Table S2). The density of fig trees was positively correlated with the density of streams ( $w\text{AICc} = 0.96$ , Table 3, Fig. 5B). The other competing models presented lower power to explain the fig tree density ( $\Delta\text{AICc} > 9$  and  $w\text{AICc} \leq 0.01$ ).

The region where fragments are located was not an important variable to explain either richness or density of fig trees, indicating that our results were not geographically biased.

Hemiepiphytic fig trees established in average at  $2.7 \pm 3.4$  m ( $x \pm \text{sd}$ ,  $n = 83$ ) on their host trees, with more than 80% of them established below 5 m (Fig. 6).

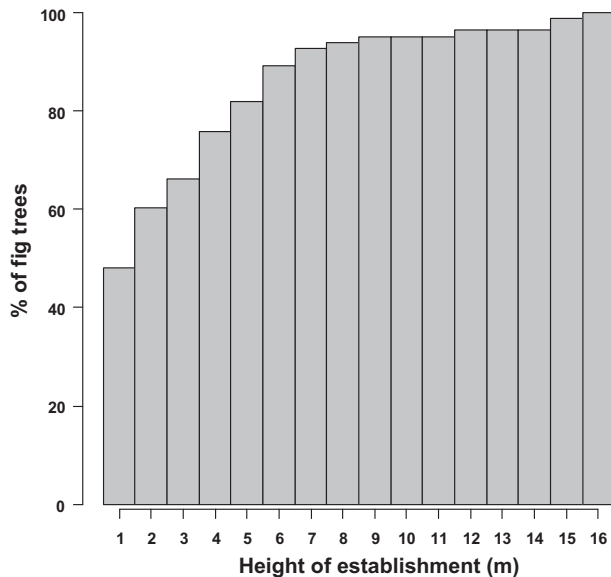


Fig. 6. Cumulative distribution of height of establishment of hemiepiphytic fig trees in seasonal semideciduous forests in São Paulo state, Brazil.

#### 4. Discussion

Controlling the species-area effect, our results showed that water availability seems to be the most important factor to explain species richness and density of fig trees in fragments of SSF. In addition, surface declivity and its standard deviation also figured between the best models to explain species richness, suggesting that complexity of drainage system is important to species richness. On the other hand, variables related to forest structure and disturbance level were of little importance to explain the diversity and density of fig trees in SSF fragments. The importance of water availability to fig trees is also noted when the studied areas are compared. Gália has a more complex drainage system and also the highest density and richness of fig trees (Table S2). Moreover, the freestanding species *F. adhatodifolia* (sect. *Pharmacosycea*) was the second most abundant species in the Gália fragments, with a relative density of approx. 24%. In SSF the dry season probably constrains the fig tree recruitment in both hemiepiphytic (*i.e.*, sect. *Americana*) and freestanding species. Indeed, water stress is the most important cause of death for the epiphyte phase of fig trees (Putz and Holbrook, 1986; Laman, 1995; Holbrook and Putz, 1996c; Zotz and Andrade, 2002). Perennial water bodies seem to be essential for freestanding species, such as *F. adhatodifolia*, as these species have more limited habit plasticity, which constrains the tree recruitment to the more humid and fertile microhabitats close to the water body (Banack et al., 2002).

The rainfall seasonality in SSF may favor both establishment strategies and morphological adaptations in the hemiepiphytic fig tree species. During the dry season about 50% of tree species in SSFs drop their leaves as adaptation to spare water by reducing transpiration rates. This deciduousness increases light and ventilation understory, potentially reducing light constraints. Thus, it allows the hemiepiphytic fig trees to establish at lower heights, where epiphytic-phased plants are less exposed to hydric stress. In the studied areas ca. 80% of the hemiepiphytic fig trees established up to 5 m in height on their host trees. In evergreen forests where moisture is less restrictive, but seed germination is light constrained understory, hemiepiphytic fig trees are more likely to establish higher in their host trees (Todzia, 1986; Laman, 1996; Coelho, 2005). In fact, the behavior of *Galoglychia* species (sister

group of *Americana*) inhabiting an evergreen forest in Ivory Coast is quite different to the hemiepiphytic figs in SSFs. Michaloud and Michaloud-Pelletier (1987) observed that *Galoglychia* hemiepiphytes were more likely to grow on tall trees, preferentially those with less dense foliage and whose first branch was above the canopy.

The lower establishment height in SSF can result from a vertical selection at seed germination. Seeds deposited at lower heights could be more likely to survive due to higher humidity near the forest floor and less time for the fig roots to reach the soil. This hypothesis is supported by the observation that most hemiepiphytic fig trees in the studied areas established on fallen trunks (Coelho, 2011), which probably have better germination conditions. Moreover, in those fragments, individuals of hemiepiphytic species frequently grow as freestanding trees, mainly at the fragment edges. This plasticity seems to be widespread in the *Urostigma* subgenus (Berg, 1989). For example, *F. burtt-davyi* (section *Galoglychia*) tends to be hemiepiphytic when growing in forest environment but occurs as a freestanding small tree in open areas (Compton and Musgrave, 1993). Concerning morphological adaptations some canopy emergent *Americana* species, such as *F. schultesii* (Silman and Krisel, 2006) and *F. eximia* (this study), have evolved a specialist adaptation to capture moisture. Both species have superficial roots extending up to 100 m from their trunks, resulting in a root zone larger than 1 ha. This hectare-scale root zone allows these species to efficiently forage water and soil nutrients in order to sustain their large plant size. This wide root complex is probably common in many other fig species.

Considering spatial scale is essential when extending our findings to other *Ficus* groups or regions. We described species richness and abundance relationships that operate at local scales, which reflect ecological mechanisms at the community level. In a regional wider scale (*i.e.*, continental scale) historical and evolutionary mechanisms are likely more important to explain biodiversity (Willig et al., 2003). In this context, the richness of eight *Ficus* species observed in the studied SSF fragments seems to represent a latitudinal pattern since the same number of fig tree species was observed in an Atlantic rainforest area of similar latitude (*i.e.*, 21°–25°S) but with annual rainfall 1.5–2 times higher (Table S3, Coelho, 2005). On the other hand, in a region of the Amazon rainforest at latitude 3°S, 19 *Ficus* species were reported (Ribeiro et al., 1999). Therefore, the diversity of fig trees at the regional scale in Brazil is not well correlated with water availability but seems to follow the classic latitudinal diversity gradient (Willig et al., 2003).

Our results showed that environmental variables related to water availability are the main determinant of species richness and individual density in local communities of fig trees in SSF, although particular species population (*e.g.*, the environmentally generalist *F. citrifolia*) may respond differently to environmental conditions. Density of *F. citrifolia* in SSF was positively correlated with the variance of NDVI ( $\Delta AICc = 0$ ,  $wAICc = 0.7$ ; Table S4), which represents structurally heterogeneous fragments. Moreover, we showed that the *Ficus* community can persist even in highly fragmented landscapes, evidencing that the fig–fig wasp mutualism is resilient this level of disturbance. This trait makes fig trees potentially suitable for restoration projects in isolated areas. As the *Ficus* community was robust to variation in forest structure and conservation level of fragments, our results also indicate that fig trees are important elements for the functioning of seasonal tropical forests, playing a role in diverse ecological aspects, such as with frugivorous vertebrates (Shanahan et al., 2001), associated insects (Weiblen, 2002) and interaction with host trees. This study is also the first to describe a species-area pattern for hemiepiphytic plants.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2013.02.002>.

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