



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

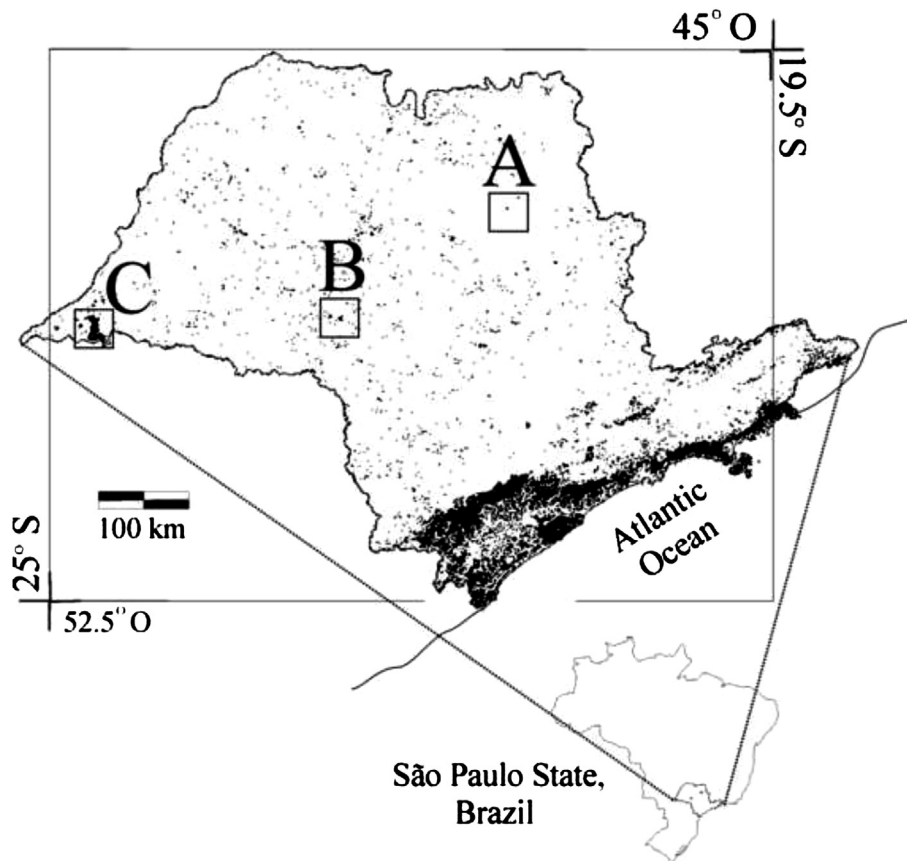


Fig. 1. Location of study areas within São Paulo state, Brazil: (A) Ribeirão Preto, (B) Gália, and (C) Teodoro Sampaio. Modified from Hirota and Ponzoni (2008), with permission from J.F. Ponzoni.

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