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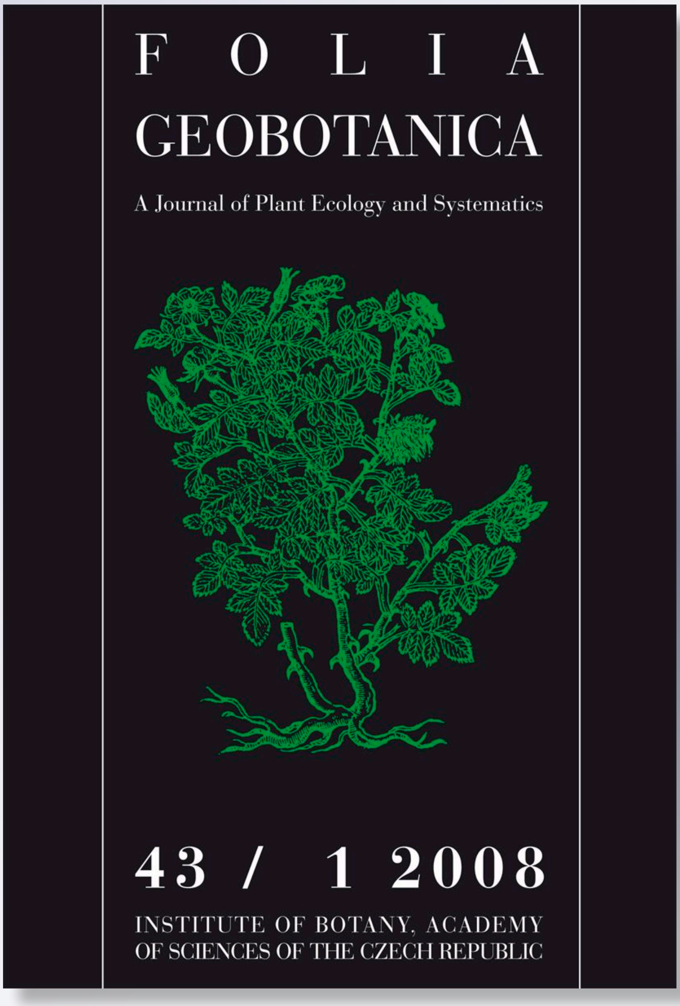

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Abstract Distribution ranges of plant species are related to physical variables of ecosystems that limit plant growth. Therefore, each plant species response to physical factors builds up the functional diversity of an ecosystem. The higher the species richness of an ecosystem, the larger the probability of maintaining functions and the higher the potential number of plant functional groups (FGs). Thus, the richness potentially increases the number of functions of the highly diverse Atlantic Rainforest domain in Brazil. Severe plant growth limitations caused by stress, however, decrease species richness. In the Spodosols of the Mussununga, an associated ecosystem of Atlantic Rainforest, the percentage of fine sand is directly related to water retention. Moreover, the depth of the cementation layer in the Mussununga's sandy soil is a physical factor that can affect the plants' stress gradients. When a shallow cementation layer depth is combined with low water retention in soils and with low fine sand percentage, the double stresses of flooding in the rainy season and water scarcity in the dry season result. This study aimed to

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identify FGs among Mussununga plant species responding to water stress gradients of soil and to verify the effects of the gradients on plant species richness of the Mussununga. A canonical correspondence analysis (CCA) of species abundance and soil texture variables was performed on 18 plots in six physiognomies of the Mussununga. Species richness rarefactions were calculated for each vegetation form to compare diversity. The two main axes of the CCA showed two FGs responding to soil texture and cementation layer depth: stress tolerator species and mesic species. Physical variables affect plant diversity, with species richness rising as the fine sand proportion also rises in the Mussununga. The effect of the cementation layer is not significantly related to species richness variation.

Keywords Atlantic tropical rainforest · Diversity · Metacommunity ecology · Plant functional types · Richness · Sandy soils · Spodosols · Water retention

Plant nomenclature Forzza et al. (2010)

Introduction

Patterns and distribution ranges of plant species related to physical factors limiting or favoring their occurrence has become a recent subject for studies of the Atlantic Rainforest and its associated ecosystems (Scarano et al. 2004; Geßler et al. 2005a). Plant responses to physical factors are related to functions of ecosystems (e.g., Grime 2001). The higher the species richness of an ecosystem, the higher the probability of maintaining ecosystem functions and the higher the number of functional groups (FGs) of that ecosystem (Tilman et al. 1997). The Brazilian Atlantic Rainforest is among the richest tropical ecosystems on Earth (Rosenzweig 1995; Thomas et al. 2008) and is among the most endangered forest types in Brazil because its distributional range coincides with the regions most disturbed by urbanization, industries, agriculture and roads. There has been an effort to find appropriate models to predict the functioning of this tropical ecosystem with high species and functional diversity (e.g., Geßler et al. 2005b). Nevertheless, most of these studies focused on various woody plants, whereas analyses assessing a wider range of life forms to match conservation, management and restoration requirements of the Brazilian Atlantic Rainforest domain are still lacking. Environmental gradients can affect the diversity of plants, because environmental gradients affect plant growth and ecosystem productivity affects the diversity (e.g., Leigh 1965; Brown 1973). As productivity rises from low to intermediate levels, species richness also rises (Preston 1962; Wright et al. 1993). Diversity is lower in those habitats where low contents of soil nutrients strongly limit plant growth (Hartley and Jones 1997). Similarly, along a water gradient the less productive habitats are those in which water stress causes a severe drought, inducing a stomatal closure (Mooney and Ehleringer 1997). Thus, across a landscape it is expected that gradient extremes of low productivity have lower species richness than moderately productive sites of the same gradient.

The Atlantic Rainforest domain of southern Bahia and northern Espirito Santo states has an associated type of ecosystem, the Mussununga, with physiognomic forms ranging from grasslands to woodlands over sandy Spodosols originated from sandstones of the Barreiras Group from the Tertiary period (ca. 16 million years before present). The vegetation on Tertiary sandy soils are called Mussunungas, an Amerindian Tupi-Guarani word that means “soft and wet white sand” (Meira-Neto et al. 2005) and is sometimes also called Campo Nativo (Araújo et al. 2008). The pedogenesis of tropical Spodosols by podsolization (Horbe et al. 2004) created sandy, slightly convex and circular/amoeboid shaped patches on flat Tertiary terrains. The patches of sandy Spodosols, surrounded by rainforest Podsols, have caused a decrease in the biodiversity and biomass of specialized flora. Mussununga soils are sandy, and their texture strongly influences the water status for plant growth. Sandy soils with finer particles have higher water retention than sandy soils with coarser particles (Mecke et al. 2002). In addition, Mussununga Spodosols have a consistently hard and impermeable cementation layer (ortstein), which causes flooding stress in the rainy season and drought stress in the dry season (Horbe et al. 2004; Meira-Neto et al. 2005). We have hypothesized that the combination of drought and flooding stresses is a strong limiting factor for most rainforest species that prevents them from establishing in the Mussunungas (Meira-Neto et al. 2005; Saporetti-Junior 2009).

Due to the aforementioned Mussununga soil traits and because water availability is the most evident physical factor limiting plant growth in tropical ecosystems (Grace 1997), we hypothesize that FGs in the Mussununga occur as a response to the soil water status for plant growth, and that species richness rises in sites with lower water stress (intermediate productivity) and decreases in areas with higher water stress (low productivity) in Spodosol. This study aimed to assess the textural (water retention) and cementation depth gradients in Mussununga vegetation to *i*) detect functional groups of Mussununga plant species responding to the gradients and *ii*) verify the effects of the gradients on Mussununga plant species richness.

Material and Methods

Study Site

The studied patch of Mussununga is in Caravelas municipality, southern Bahia State, Brazil. The site is on flat terrain that originated from Tertiary sandstones (ca. 16 million years ago), called the Barreiras Group. The patch is located in the evergreen rainforest vegetational zone (Walter and Breckle 2002). The climate is Am according to the Köppen system, humid tropical with mean precipitation around 1750 mm/y. Rainy summers alternate with moderate dry winters, with occasional interannual influence of the El Niño Southern Oscillation (Borchert 1998; Williamson et al. 2000). Thus, flooding and droughts can be much stronger than expected by the climate type.

The predominant vegetation of this landscape is tropical rainforest settled mainly on Podsols. There are patches of savannic vegetation, called Mussunungas, over sandy Spodosols surrounded by rainforests, *Eucalyptus* plantations and crop fields (Fig. 1). Caravelas’ Mussununga has sinuous borders and an area of 853 ha at 50 m elevation (S 17°40′44″, S 17°42′15″, W 39°27′40″, W 39°30′19″). It is the largest and best-preserved Mussununga in southern Bahia State.

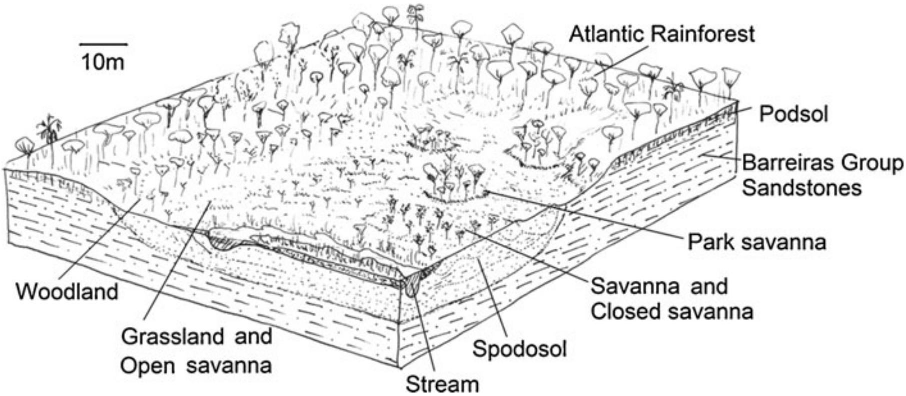

Fig. 1 Diagram of a Mussununga with surrounding Atlantic Rainforest. Soil names are according to the U.S. system of soil classification

Plant and Soil Relations

Plant species abundance data (Table **S1**, Table **S2** in Electronic Supplementary Material (hereafter ESM)) were collected in 18 plots of 4 m^2 (2 × 2 m), in which all individual plants of all life forms were counted. The sampling was performed using three plots in six physiognomies of Mussununga according to the Brazilian vegetation classification (Veloso et al. 1991): grassland, open savanna (grassland and woody *Bonnetia stricta*), savanna (grassland and shrubs), closed savanna (grassland, shrubs and small trees), park savanna and woodland using a systematic and stratified sampling scheme (Figs. **S1**–**S7** in ESM). All samples were taken in the middle of the Mussununga to avoid direct influences of the rainforest. Each physiognomy had three soil samples, each containing a compound sample of ten single samples in 4-m^2 vegetation plots. The texture of 18 compound soil samples (0–20 cm depth) was analyzed at the Soil Laboratory of the Federal University of Viçosa. We used the U.S. soil classification system. Among samples, we measured the ortstein depth in meters (depth m), percentage of coarse sand (%CS) and percentage of fine sand (%FS). These data were compared using the probability area of a normal curve, converting the means and standard deviations to the standard normal distribution using the PNORM function of the R statistical environment (Crawley 2007). The regular soil type of Mussunungas is a sandy Spodosol with an ortstein depth varying from 0.5 to 2 m (Meira-Neto et al. 2005).

Because we wanted to test the relationship of physiognomic variation of Mussununga vegetation to soil traits, a traditional approach was used (Lepš and Šmilauer 2003). A canonical correspondence analysis (CCA) (Ter Braak 1986) was performed using CANOCO 4.5 software (Ter Braak and Šmilauer 2002) to test the relationship of plant abundance with the following physical properties of Mussununga soil: percentage of fine sand (particles finer than 0.2 mm) (%FS), percentage of coarse sand (particles coarser than 0.2 mm) (%CS) and depth from surface to impermeable layer (depth). Because rare species can increase the total inertia of the species dataset (Ter Braak and Šmilauer 2002), only species with at least five individuals were included in the CCA, and the abundance values were logarithmically transformed as species of small life forms tend to be much more abundant than woody species. The CCA was applied as a data-defined approach to address the clustering of sampled species into groups on the basis of soil traits (Leishman and Westoby 1992; Newton 2007). For that approach, overall trends shared by species and plots related to the physical properties of Mussununga soil were grouped using ellipses drawn on charts. The procedure for verifying the length of the largest gradient of the analysis resulted in a value between 3 and 4 (3.09), validating the use of the CCA, a unimodal method (Lepš and Šmilauer 2003).

Measures of Richness

Diversity measures were made using 40 10-m^2 (2 × 5 m) plots in a 400-m^2 (20 × 20 m) grid for each of six vegetation forms (Fig. **S7** in ESM). The Mao Tau estimator (T) was used to estimate the mean number of species. The T was calculated by an interpolation that produces a rarefaction. It consists of systematically enumerating all distinct subsets of quadrats from the total number of quadrats of the sample set and finding the observed richness in each subset of quadrats. The mean species number is then calculated, first for one quadrat, then for two quadrats and so on until reaching the total number of quadrats (Colwell et al. 2004). Thus, the T approach calculates the mean richness and confidence intervals expected for the number of pooled samples, giving a notion of spatiality on the diversity charts. The Mao Tau rarefactions were calculated using Estimates 8.2 software (Colwell 2009). Comparisons were made graphically using probability areas of normal distribution with a confidence interval of 95% (Colwell et al. 2004).

Results

Soil and Functional Groups (FGs)

All plots presented sandy soil containing 90% to 95% sand (Table **1**). The CCA species ordination separated two groups of plant species of the Mussununga ecosystem. One group consists of species tolerant to stress caused by low water

Table 1 Mean values and standard deviations of physical factors of soil in physiognomies of Mussununga vegetation. Depth m – depth of ortstein in meters; %CS – percentage of coarse sand; %FS – percentage of fine sand. Different letters indicate statistical significance of differences among mean values of the same physical factor ($P<0.05$)

Physiognomy	Depth m	%CS	%FS
Woodland	1.21±0.16c	70.66±4.04b	23±5.29ab
Park savanna	2.67±0.52a	78.66±7.77b	16±7.21bc
Closed savanna	2.22±0.09a	68.33±4.04b	25.33±3.78a
Savanna	1.48±0.04b	70.33±6.11b	23.33±4.51ab
Open savanna	0.582±0.06d	72.33±3.51b	20.33±4.16ab
Grassland	1.236±0.08c	86±1a	7.33±1.53c

retention, hereafter named stress tolerators, with the ability to dominate sites more susceptible to drought and containing coarser sand, and with a shallower substrate as a result of more superficial ortstein. These soil traits are the cause of the double stresses of the water regime. Another group of species with an intermediate strategy between stress tolerance and growth ability, hereafter named mesic, dominates sandy soils with a higher proportion of fine sand and a deeper impermeable layer. Therefore, mesic species are subjected to moderate double water stresses (Fig. 2).

The CCA ordination of plots clustered two groups of samples and revealed a pattern for vegetation forms of the Mussununga ecosystem. One group, formed by grassland and open savanna plots, is related to Spodosols with higher proportions of coarse sand and more superficial ortstein. Another group of physiognomies, formed by savanna, closed savanna, park savanna and woodland, is related to soil with deeper ortstein and with higher percentage of fine sand (Fig. 3 and Table 1).

The accumulated variance explained by the two first axes of the CCA was 85%. The probability of all CCA axes being caused by random events was less than 2% ($P<0.02$).

Based on the analysis of 19 species with five or more individuals, stress tolerator species are mainly of therophyte (three species) and chamaephyte (two species) life forms and dominate grassland and open savanna. The mesic group is dominated by eight species of phanerophytes that morphologically influence the vegetation forms

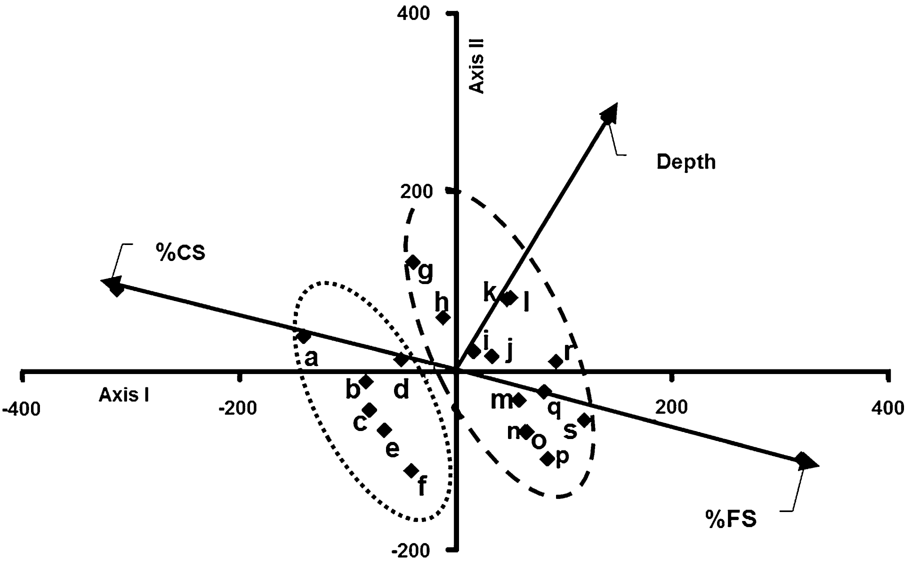

Fig. 2 Correspondence canonical analysis ordination with types of species defined by relationships between three soil variables: depth of impermeable layer (Depth), proportion of coarse sand (%CS) and proportion of fine sand (%FS). The dotted line encircles the functional group (FG) species related to shallower soils with coarser sand, whereas the dashed line encircles the FG species related to deeper soils with finer sand; a – *Panicum trinii* (i), b – *Syngonanthus nitens* (ii), c – *Xyris capensis* (ii), d – *Actinocephalus ramosus* (ii), e – *Comolia ovalifolia* (iii), f – *Sauvagesia erecta* (iii), g – *Myrcia racemosa* (iv), h – *Davilla macrocarpa* (v), i – *Lagenocarpus rigidus* (i), j – *Microlicia* sp. (iii), k – *Guapira pernambucensis* (iv), l – *Paepalanthus klotzschianus* (ii), m – *Bonnetia stricta* (iv), n – *Eugenia ligustrina* (iv), o – *Humiria balsamifera* (iv), p – *Pradosia lactescens* (iv), q – *Ilex psammophila* (iv), r – *Gaylussacia brasiliensis* (iv), s – *Doliocarpus multiflorus* (v). i) Hemicryptophytes, ii) Therophytes, iii) Chamaephytes, iv) Phanerophytes, v) Lianas

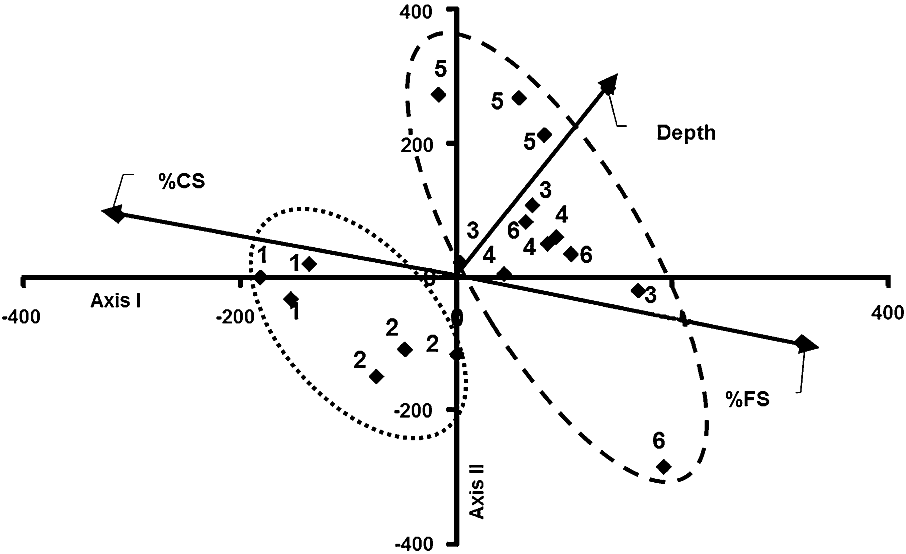

Fig. 3 Correspondence canonical analysis ordination with groups of plots defined by relationships between three soil variables: depth of impermeable layer (Depth), proportion of coarse sand (%CS) and proportion of fine sand (%FS). The dotted line encircles plots of grassland [1] and open savanna (grassland + woody *Bonnetia stricta*) [2], both related to shallower soils with coarser sand, whereas the dotted line encircles plots of savanna (grassland + shrubs) [3], closed savanna (grassland + shrubs + small trees) [4], park savanna [5] and woodland [6] related to deeper soils with finer sand

of savanna, closed savanna, park savanna and woodland. Both groups reveal a trade-off between stress tolerance and growth strategies. Indeed, this trade-off is largely the result of differences among the life forms' abilities to tolerate water stress and to grow (Table S1, Table S2, Table S3; Fig. S1, Fig. S2 in ESM).

Richness

Richness varies across the gradient of the percentage of fine sand (Fig. 4, Tables 1 and 2). Observed richness was lowest in the grassland (the environment with less

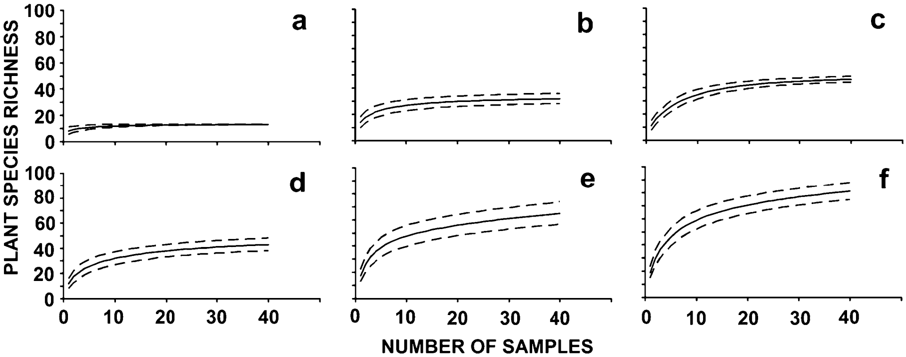

Fig. 4 Estimates of richness using the Mao Tau estimator by means of simulations for 40 plots in each of the six vegetation forms of Mussununga: **a** grassland, **b** open savanna, **c** savanna, **d** closed savanna, **e** park savanna, **f** woodland. Solid lines are mean values of richness; dashed lines are confidence intervals of 95% (±1.96 s.d.)

Table 2 Observed richness (richness) and standard deviation (s.d.) of Mao Tau rarefactions for 40 samples in each physiognomy of Mussununga. Different letters indicate statistical difference among richness ($P<0.05$)

Physiognomy	Woodland	Park savanna	Closed savanna	Savanna	Open savanna	Grassland
Richness	81a	65b	43c	46c	32d	13e
s.d.	3.37	4.39	2.59	1.12	1.96	0.0

fine sand) with 13 sampled species. As the fine sand proportion increases, observed richness significantly rises along the gradient through open savanna, savanna, closed savanna, park savanna and woodland. Only savanna and closed savanna show no significant differences in richness (Table 2). The number of species sampled increased in each habitat with the highest number, 81, sampled in the woodland (Table S4; Fig. S4 in ESM).

Discussion

Functional Groups (FGs)

Two FGs of Mussununga vegetation were detected: *i*) the stress tolerator species related to low percentage of fine sand in the Spodosol; and *ii*) the mesic species related to high proportion of fine sand in the Spodosol. The stress tolerators were also related to more superficial ortstein (Figs. 2 and 3).

The 85% of variance explained by the two main CCA axes showed physical properties of soil that separated two sets of species, each influenced independently by the amount of fine sand and the ortstein depth of Mussununga soils. Fine sand percentage is related to moisture, which is affected by the water retention capacity. The depth of ortstein drives the drainage regime in Mussununga's Spodosol (Saporetti-Junior 2009) and is related to flooding stress. Nevertheless, if only the variation of fine sand proportion is analyzed, this one-dimensional gradient significantly explains the abundance of species of two FGs: stress tolerator and mesic. Both FGs were named according to the CSR theory of primary and secondary plant strategies (Grime 2001). The abundance of stress tolerators, a primary strategy, is negatively correlated to the fine sand proportion. The abundance of mesic FG species, a secondary strategy between stress tolerators and competitors, is positively related to the amount of fine sand. Sandy soils have high water retention variance as a capillary effect (Huang and Zhang 2005), because finer sand particles have a higher capillary tension head than coarser sand particles. Particle size distribution influences the soil water retention curve, and both fit power-law models. These models are influenced by the power-law relations of surface-volume and surface-void volume (Ghilardi and Menduni 1996; Huang et al. 2006), because water is bonded to soil particles forming water films (Davidson and Janssens 2006), directly related to the particle area. It is important to remember that the higher the proportion of fine sand is, then the lower the proportion of coarse sand in Mussununga

Spodosol is (Table **1**). In the dry season, sandy soils with lower fine sand percentage are subjected to a relatively short, but severe drought that largely constrains not only plant growth, but also plant diversity because it prevents the occurrence of intolerant species (Lomolino et al. 2006) of the metacommunity's adjacent areas.

The effect of flooding as a stressor in the rainy season is greater in patches of Mussununga soils with more superficial ortstein. Flooding fills the void volume of soil and decreases the availability of oxygen, working as an ecological limit to woody species distribution (Crawford 1992). The flooding of the soil is an abiotic constraint on the growth of woody plants (Jackson and Colmer 2005) and limits plant diversity to stress tolerant species (Armstrong et al. 1994). Nevertheless, flooding is a secondary stress on Mussununga vegetation, superimposed spatially to drought. This causes a severe double water stress, especially on the grassland and open savanna physiognomies that have shallower ortstein than other Mussununga forms, and decreases the abundance of the mesic FG, especially woody species. Besides the limitation on mesic species abundance, low productivity imposes low densities on all populations and increases the probability of local extinctions (Rosenzweig 1995).

Species Richness

Species richness increases as fine sand percentage rises in Mussununga vegetation. The richness increases because water content (a resource to plant growth) increases along the gradient, from grassland to woodland (Fig. **4**). Ortstein depths were not significantly related to species richness (Tables **1** and **2**).

We assume that there are no effective barriers to the dispersal of endozoochorous species living in patches with the entire water retention gradient extending from the rainforest to the Mussununga grassland of the Atlantic Rainforest metacommunity. Thus, the two FGs detected in Mussununga vegetation are not delineated by potential differences in dispersion abilities that occur along the water status gradient. Instead, their populations are sympatrically distributed, but with opposite and well-defined preferences. The abundance variation of both FGs along the gradient results in different phytophysiognomies as a response to soil water retention (Figs. **2** and **3**, Table **1**). We are considering the hypothesis that sites where stress tolerators dominate have source populations (Pulliam 1988; Pulliam and Danielson 1991) of this FG. Therefore, where mesic FG dominates, the stress tolerators would have sink populations caused by a decreased ability to compete with better soil water status for growing. In actuality, the gradient from the highest to lowest soil water status for plant growth begins in the rainforest Podsol (not measured in this work) and ends in the grassland Spodosol. Hypothetically, the extremes of the rainforest-grassland gradient have source populations with quite different strategies, most of them completely separated, e.g., grassland species, especially therophytes and chamaephytes that are life forms adapted to unfavorable seasons for plant growth (Crawley 1997). The intermediate position of that gradient would be a habitat of lower quality for source populations from both extremes, but a high quality habitat for those psammophyllous species such as the big sedge *Lagenocarpus rigidus* or the phanerophytes *Gaylussacia brasiliensis*, *Humiria balsamifera* and *Ilex psammophila*. Some of the mesic FG species shown in the CCA are rainforest species including *Pradosia lactescens* and *Eugenia ligustrina*, both endozoochorous phanerophytes which occur in the Mussununga woodland. Thus, their populations in the Mussununga probably receive more immigrants than provide emigrants, and would therefore be considered sink populations.

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