

## PALM SPECIES DISTRIBUTION AND SOIL MOISTURE IN A SWAMPY AREA OF THE ATLANTIC FOREST, SOUTH-EASTERN BRAZIL

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### INTRODUCTION

Environmental patchiness, competition, and distribution of parent plants may result in fine-scale clusters of conspecific individuals and even of individuals of different species. If several species in a community exhibit an aggregated pattern, indicating control by some influencing factors, then a study on patterns of association between them will provide evidence of any grouping of the species into assemblages of similar response to the influencing factors (Greig-Smith 1983). Positive spatial associations may be the result of similar responses to local environmental factors. On the smallest scales, these patterns reflect the interactions between individual plants (Svenning 2001a), whereas on larger scales the spatial distribution of individuals is influenced by variations in edaphic conditions (Hutchings 1997). Recently much attention has been devoted to the effects of spatial heterogeneity on ecological processes occurring at various spatial scales (Clark *et al.* 1995, 1998; Svenning 2001a, b). This environmental heterogeneity of resource distribution may greatly affect the performance and spatial patterns of plant populations and, ultimately, the community structure (Svenning 2001a, b). Variation in soil, topography, and microclimate generates an environmental heterogeneity of resource distribution for plants, which will also create suitable patches for growth and establishment. If recruitment is higher in these patches there will be a spatial association be-

tween plants and patches (Barot *et al.* 1999). Some studies have shown that edaphic variation in palm density is frequent in tropical forests of Central America and Amazonia (Svenning 1999, Pacheco 2001, Vormisto 2002). As pointed out by Clark *et al.* (1998), when the distributions of more species are studied, it will be possible to determine the generality of edaphic effects and to understand the consequences for tropical forest structure and function.

Here, our goals were to assess the relationship between heterogeneity in soil water availability and the spatial patterns of three tropical palm species in an evergreen swampy forest imbedded in a semideciduous forest fragment (Gomes *et al.* 2006). According to Scarano (2006), although South America has the world's largest area of wetlands, including swampy forests and floodplains, Brazilian freshwater wetlands are scarcely studied. Since the study species occur from swampy areas at stream edges to rain and seasonal forests (Henderson *et al.* 1995), we asked whether their abundance was a response to small-scale variation in soil water availability. To develop some hypotheses on the factors that cause spatial population aggregation we analyzed (1) the distribution of soil moisture and its effects on palm density, and (2) the spatial association between each pair of palm species. Our predictions are that (1) population density would be higher in moisture patches if palms are moisture-limited, and that (2) different palm species would be associated in suitable patches if they shared the same requirements in relation to water availability for growth and recruitment.

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## METHODS

**Study area.** This study was carried out in a swampy area of the Santa Genebra Reserve, a 250-ha tropical semideciduous forest fragment situated in São Paulo state, south-eastern Brazil (22°49'45"S, 47°06'33"W; 670 m a.s.l.). The climate shows a rainy season extending from October to March, when there is a mean temperature of 23°C and 74% of the rainfall occurs, and a dry season, with a mean temperature of 17°C, between April and September. The mean annual rainfall is approximately 1400 mm (Silva Matos & Watkinson 1998).

The forest was fragmented in the 1950s, and today most of the area is covered by secondary and old growth (Castellani & Stubblebine 1993, Silva Matos & Watkinson 1998). The swampy area extends to around 10 ha and has a hydromorphic soil with gley features. Typically, water is available in little streams all year round, but during long rainless periods some sections may dry out. Souza & Martins (2004) showed a fine-scale microtopographic pattern of flooded pits and channels delimited by drier mounds for the study area.

**Study species.** Three palm species were included in this study, two canopy and one understory species. *Euterpe edulis* Mart. has a tall (5–12 m), straight, solitary stem (10–15 cm diameter) and is distributed along the Atlantic coast of Brazil in lowland and steep-slope rain forests (up to 1000 m a.s.l.), as well as in forest patches farther inland (Henderson *et al.* 1995). Previous studies have suggested an aggregated pattern in areas of favorable soil water and light conditions (Alves 1994, Silva Matos & Watkinson 1998). The fruits of the palm are an important food resource for birds and

mammal species (Galetti & Aleixo 1998, Silva Matos & Watkinson 1998, Silva Matos & Bovi 2002). *Syagrus romanzoffiana* (Cham.) Glassman is widely distributed in central and south-eastern Brazil, in seasonally dry to swampy forests, and in open, early-growth forests as well as old-growth forests (Henderson *et al.* 1995, Lorenzi *et al.* 1996). Fruits are eaten by squirrels (*Sciurus ingrami*, Thomas, 1901) and primates (*Cebus apella*, Linnaeus, 1758 and *Alouatta fusca*, Saint-Hilaire, 1812) (Galetti *et al.* 1992). *Geonoma brevispatha* Barb. Rodr. presents a multiple-stem growth form, usually forming large clumps (Henderson *et al.* 1995, Souza *et al.* 2003) with more than three stems that are 1–4 m tall (Henderson *et al.* 1995, Souza & Martins 2004). The species is common in central and south-eastern Brazil, from swampy areas at stream edges to the rain and seasonal forests of the Brazilian Plateau region (Henderson *et al.* 1995). Fruits are black and small, possibly consumed by birds. Hereafter the species will be referred to only by their generic names.

**Field sampling.** Within a 1-ha area (100 x 100 m), we randomly established one hundred 25-m<sup>2</sup> (5 x 5 m) permanent plots and recorded all palms with height > 20 cm. Differences between life-stages were not taken into account.

Additionally, in 1993 a soil sample (approximately 975 cm<sup>3</sup>) was taken from each plot during the rainy season (February–March), and another in the dry season (July–August), to calculate soil moisture content. All samples were weighed, dried at 80°C to constant weight and then weighed again. The values from the two samples were averaged to produce soil moisture readings for each plot. Plots were then placed into five classes according to the degree of soil mois-

TABLE 1. Soil moisture content (average  $\pm$  SD) and mean number of individuals of palm species ( $\pm$  SD) for each plot type from a swampy area of the Municipal Reserve of Santa Genebra. N: number of plots in each moisture class. P: probability values of Kruskal-Wallis ANOVA for differences in number of palms/plot among soil moisture classes. Different letters within a column represent significant differences in number of palms per plot type (Dunn's test, P: \*\* < 0.01; \* < 0.05; ns > 0.05).

Plot type (n)	Soil moisture (%)	<i>Euterpe</i>	<i>Geonoma</i>	<i>Syagrus</i>
1 (1)	19.4	0	0	0
2 (62)	33.7 $\pm$ 3.9	6.9 $\pm$ 10.3 a	3.4 $\pm$ 4.9a	1.2 $\pm$ 1.6 a
3 (34)	46.6 $\pm$ 4.7	11.3 $\pm$ 11.6 b	5.0 $\pm$ 6.0a	2.1 $\pm$ 2.0 b
4 (3)	68.3 $\pm$ 7.4	34.0 $\pm$ 18.5 b	6.7 $\pm$ 3.5a	1.3 $\pm$ 1.5 a
P		**	ns	*

ture: 0–20% (class 1), > 20–40% (class 2), > 40–60% (class 3), > 60–80% (class 4). Soil with more than 80% water content was never recorded.

**Statistical analysis.** The number of individuals of each palm species across five different plot types were compared by a non-parametric Kruskal-Wallis test (Zar 1999), followed by Dunn's multiple comparisons tests when appropriate (Zar 1999). Morisita's index ( $I_m$ ) of dispersion (Morisita 1962) was used, as suggested by Krebs (1989) and Hurlbert (1990) to describe the spatial distribution of plants. This index expresses, as a ratio, the chance of finding individuals in the same plot compared with the chance in a random distribution (Krebs 1989, Vandunné 2002). Morisita's index has a value of 1.0 for a random distribution of individuals, while values greater than 1.0 indicate clumping and values less than 1.0 over-dispersion. The significance of each  $I_m$  departure from 1.0 was tested by a chi-square test (Krebs 1989).

We used linear regression and Spearman rank correlations to test the association between the species, considering presence or absence of each species in each plot, and Jaccard's index as a measure of the degree of association between species (Ludwig & Reynolds 1988). Jaccard's index is the proportion of the number of plots where both species occur to the total number of plots where at least one of the species is found. It is equal to zero if there is no association and to 1 at maximum association. Considering that in linear regressions any point describes the density of species  $i$  in the mixed stand, the weighted sum has a maximum which could represent the presence of competition among species. According to Silvertown & Lovett Doust (1993), the simplest way to describe the composition of mixed stands is to plot the density of one species against the density of another (called joint-abundance diagram).

## RESULTS

The average soil moisture was 39% ( $\pm 9.3$  SD), and most plots (63%) showed less than 40% (Table 1). Only one plot was assigned to class 1 (0–25%) and no palm species was recorded there. Density differed significantly between species (Kruskal-Wallis ANOVA,  $H = 29.2$ ,  $P < 0.001$ ). The most abundant palm species was *Euterpe* (9.1 plants/25 m<sup>2</sup>  $\pm 11.9$  SD), followed by *Geonoma* (4.0  $\pm 5.3$  SD) and *Syagrus* (1.5  $\pm 1.7$  SD). The number of palms was significantly different between soil moisture categories, except for

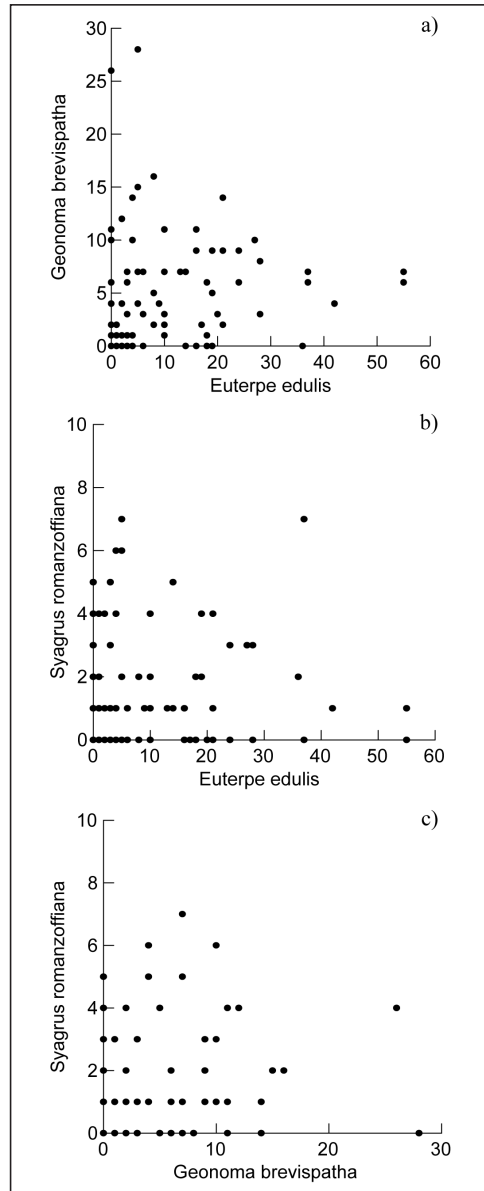


FIG. 1. Relationship between number of palm species found in 100 25-m<sup>2</sup> plots in the swampy area of the Municipal Reserve of Santa Genebra, south-eastern Brazil. The coefficients obtained in a liner regression are: a) *Euterpe edulis* and *Geonoma brevispatha* ( $F = 3.74$ ,  $p = 0.0561$ ,  $r^2 = 0.04$ ); b) *Euterpe edulis* and *Syagrus romanzoffiana* ( $F = 0.01$ ,  $p = 0.9363$ ,  $r^2 = 0.00$ ); c) *Geonoma brevispatha* and *Syagrus romanzoffiana* ( $F = 2.44$ ,  $p = 0.1216$ ,  $r^2 = 0.02$ ).

*Geonoma* (Table 1). *Euterpe* was more abundant in plots with higher water content (Kruskal-Wallis ANOVA,  $H = 12.4$ ,  $P < 0.01$ ). On the other hand, *Syagrus* occurred mainly in plots where moisture was not over 40% (Kruskal-Wallis ANOVA,  $H = 7.5$ ,  $P < 0.05$ ). Although the density of *Geonoma* increased towards more humid plots, we found no significant differences (Kruskal-Wallis ANOVA,  $H = 4.7$ ,  $P > 0.05$ ).

Morisita's index showed that palms ( $I_m = 1.85$ ;  $\chi^2_{(99)} = 135.0$ ,  $P < 0.001$ ) were aggregated in this study area. However, when the species were analyzed independently we observed that *Euterpe* was the most aggregated ( $I_m = 2.57$ ;  $\chi^2_{(99)} = 153.0$ ,  $P < 0.001$ ), followed by *Geonoma* ( $I_m = 2.48$ ;  $\chi^2_{(99)} = 693.0$ ,  $P < 0.001$ ) and *Syagrus* ( $I_m = 1.71$ ;  $\chi^2_{(99)} = 206.0$ ,  $P < 0.001$ ).

The linear regression showed no significance for the relationships between the species (Fig. 1a-c). However, in the case of *Euterpe* and *Syagrus* (Fig. 1b), the distribution of points is structured as a perfect triangle, representing the weighted sum of individuals of these species that could be found in the plots. Also, this result indicates that an increase in density of one species would decrease the density of another. Jaccard's indices showed that all species are positively associated (Table 2), but this association is stronger between *Euterpe* and *Geonoma*. This trend is concordant with the results obtained from Spearman's correlations showing a positive and significant association only between *Euterpe* and *Geonoma* (Table 2).

TABLE 2. Spearman's rank coefficients and Jaccard's index (values in bold) for association between palm species in the swampy area (P: \*\*\* < 0.001; \*\* < 0.01; \* < 0.05; ns > 0.05.)

	<i>Euterpe</i>	<i>Geonoma</i>	<i>Syagrus</i>
<i>Euterpe</i>	1.0	0.64	0.53
<i>Geonoma</i>	0.44***	1.0	0.53
<i>Syagrus</i>	0.03	0.18	1.0

## DISCUSSION

As observed for palms in Amazonia, we found a clear effect of microhabitat heterogeneity on palm abundance and distribution in a fragment of Atlantic Forest. Studies in other tropical forests, generally using more detailed edaphic characterizations, have also

found associations between palm distribution patterns and edaphic factors (Svenning 1999, 2000, 2001a, 2001b; Souza & Martins 2004, Gomes *et al.* 2006). However, predictions that our species have similar ecological requirements (in terms of soil water availability) are not totally confirmed. As pointed out by Scarano (2006), spatial structure and species abundance may reflect the variation in resistance to flooding of each individual species.

In the analysis of the spatial distribution of each palm species, the general clumping observed might reflect a spatial clumping of wetter sites and, obviously, a net result of biotic interactions involving these species. Seed germination of *Euterpe* is higher in wetter soils but clumping decreases during plant ontogeny (Silva Matos & Watkinson 1998) as a consequence, among other factors, of selective herbivory (Silva Matos 2000) and density-dependent mortality (Silva Matos *et al.* 1999). This tendency in a highly clumped seed shadow towards a less aggregated pattern for adults seems to be a pattern typical for other tropical palms (Sterner *et al.* 1986, Barot *et al.* 1999, Souza & Martins 2002).

Our results extend the findings of other authors who showed that *Euterpe edulis* (Silva Matos & Watkinson 1998) and *Geonoma brevispatha* (Henderson *et al.* 1995, Souza & Martins 2004) are common in wet soils of river margins and swampy forests. Both species are able to germinate and keep seeds viable in saturated soils (Gomes *et al.* 2006). However, at a microhabitat level, we observed differential distributions in relation to soil moisture. Despite the tendency towards wetter soils, *Geonoma* did not show any apparent microhabitat preference, since the population in the study area is restricted to the transitional zones between flooded and well-drained microsites (Souza & Martins 2004). For most tropical palms, a preference for wetter soils could be indicated by both morphological and physiological features, as observed for *Euterpe edulis*. Bovi *et al.* (1978) found that more than half, by weight, of the root system of this palm is concentrated in the top 20 cm of the soil, suggesting a morphological adaptation of the root system to wetter soils, a flood-avoidance strategy *sensu* Scarano (2006). Hence, it might be expected that tolerance to drought in *Euterpe edulis* would be low.

*Syagrus* showed a quite different microhabitat preference than *Euterpe* and *Geonoma*. Such differences between species may occur because many palms establish on moist and nutrient-rich substrates, but recruit

into more advanced stages only within high-light or well drained patches. According to Henderson *et al.* (1995), *Syagrus romanzoffiana* is widespread over a broad edaphic gradient from seasonally dry or swampy to coastal forests. Leaves of seedlings show a reorientation in their growing direction, as well as a bulbous base that is probably an adaptation to unfavorable conditions such as a severe dry season or fire (Tomlinson 1990). According to its initial growing style, it is possible to assume that *Syagrus* retains an ecological relationship with well drained and/or drier habitats.

Further evidence of non-random distribution of palms in a short soil moisture gradient is that palm species were found in the same plots more often than expected by chance. According to Jaccard's index, all three species are positively associated with each other. However, the Spearman correlations showed no evidence of an association between *Syagrus* and the other palm species. The decreased density of *Syagrus* on wetter soil types creates more space for other species, especially for *Euterpe*, which is quite different in terms of growth form. This idea could be an explanation for the findings shown in Figures 1a and 1b. As pointed out by Silvertown & Lovett Doust (1993), competition can change the composition of mixed stands (or stabilize them). Nevertheless, determination of the ecological circumstances affecting the composition of mixed stands is impracticable since competition among species in a plant community is very complex.

In conclusion, the small-scale distribution of palms appeared to be structured by habitat variables, with soil moisture certainly being one of them. Clark *et al.* (1998) found no evidence that canopy palms would coexist by microhabitat specialization in Costa Rican forests. However, the results of our study suggest that microhabitat specialization could be an important factor in the coexistence of canopy palms in swampy forests.

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