

SPATIAL DISTRIBUTION AND POPULATION STRUCTURE OF PALMS (ARECACEAE) IN A FOREST FRAGMENT OF LOWLAND DENSE HUMID FOREST IN SOUTH BRAZIL¹

DISTRIBUIÇÃO ESPACIAL E ESTRUTURA POPULACIONAL DE PALMEIRAS (ARECACEAE) EM UM FRAGMENTO DE FLORESTA OMBRÓFILA DENSE DE TERRAS BAIXAS NO SUL DO BRASIL¹

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ABSTRACT

In the state of Rio Grande do Sul, the Dense Humid Forest is reduced to less than 5% of its original cover. However, it still has the highest richness of palms in this state, which constitute an important and economically relevant group. Environmental and demographic aspects of plant populations in forest fragments are of great importance for their management and conservation. We conducted a study on the spatial distribution and age structure of five palm species in a forest fragment at the municipality of Três Cachoeiras, in the north coast of Rio Grande do Sul. We delimited 25 10×10 m plots and counted the number of individuals in the stages of seedling, juvenile and adult for each palm species. Aggregation Indices were calculated with software SADIEShell. We performed variation partitioning analyses among species distribution and environmental variables canopy openness and soil moisture. A total of 1,443 plants were counted and the most abundant species was *Euterpe edulis*. The average density was of 57.72 ind. 100 m⁻². Three species showed a pattern of “inverse J”, which indicated that they have a potential for regenerating in that palm community. The predominant spatial pattern was aggregated ($I_a > 1$) and canopy openness did not influence species abundances. Only the distribution of *Bactris setosa* and *Geonoma gamiova*, both understory species, was explained by soil moisture, suggesting that other abiotic or biotic factors may be influencing the spatial arrangement of the canopy species.

Keywords: Atlantic rainforest; population ecology, soil humidity; canopy openness.

RESUMO

No Rio Grande do Sul, a Floresta Ombrófila Densa está reduzida a menos de 5% da sua área original, porém, apresenta a maior riqueza de palmeiras do estado, que constituem um grupo importante e economicamente relevante. Aspectos ambientais e demográficos de populações de plantas em remanescentes florestais são de grande importância para o seu manejo e conservação. Nós conduzimos o estudo da distribuição populacional e estrutura etária de cinco espécies de palmeiras em um fragmento florestal no município de Três Cachoeiras, no litoral norte do Rio Grande do Sul. Delimitamos 25 parcelas de 10 x 10 m e contamos o número de indivíduos em estágio de plântula, jovem e adulto para cada uma das espécies. Calculamos Índices de agregação (I_a) com o programa SADIEShell. Também desenvolvemos análises de partição de variação entre a distribuição das espécies e as variáveis ambientais, abertura de dossel e umidade do solo. Ao total, foram registrados 1443 indivíduos e a espécie mais abundante foi *Euterpe edulis*. A densidade média foi de 57,72 ind. 100 m⁻². Três espécies apresentaram padrão “J reverso”, o que indica que elas têm um potencial de regeneração nessa comunidade de palmeiras. O padrão espacial predominante foi o agregado ($I_a > 1$) e o grau de abertura do dossel não influenciou a abundância de nenhuma espécie. Apenas

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a distribuição de *Bactris setosa* e *Geonoma gamiova*, ambas de sub-bosque, foi explicada pela umidade do solo, sugerindo que outros fatores abióticos ou bióticos podem estar influenciando o arranjo espacial das espécies de dossel.

Palavras-chave: Mata Atlântica; ecologia de populações; umidade do solo; abertura do dossel.

INTRODUCTION

Because the majority of natural habitats today are confined to fragments, one of the most important aspects when dealing with species conservation is the viability of small remnant populations, considering environmental and demographic characteristics (OOSTERMEIJER, 2000). However, in order to understand many aspects of populations and communities it is necessary to determine the distributions and abundances of organisms across the landscape (CLARK et al., 1995).

Although the conservational effort allocated to the Atlantic Forest biome exceeds the average of tropical forests, most protected areas are too small to ensure long-term species persistence and are too far away from each other to allow species mobility (TABARELLI et al., 2010). Emergent, large seeded and vertebrate-dispersed trees are the plant species most affected by edge effects (MELO et al., 2006; TABARELLI et al., 2010). Palms are among that species and seem a particularly representative group of organisms to study in relation to canopy- understory interactions in tropical forests (TOMLINSON, 1979).

At small spatial scales, neotropical rainforests exhibit high heterogeneity in canopy conditions, soil factors, topography and others, thus affecting directly and indirectly all aspects in the individual performance of palms (SVENNING, 2001). Changes in demography and distribution of palm species have been observed according to topographic variation (VORMISTO et al., 2004; MONTEIRO and FISCH, 2005), soil humidity and composition (MONTEIRO, 2004; SILVA et al., 2009; BAROT et al., 1999), canopy openness or luminosity (SVENNING, 2002; SAMPAIO and SCARIOT, 2008) and biotic variables, such as herbivory (STEVEN and PUTZ, 1985).

An important step towards understanding ecological processes is to identify spatial patterns (FORTIN et al., 2002). Spatial pattern is the arrangement of the members in a given population (TOWNSEND et al., 2006) and is represented

by their frequency in sampling units in the study site (JANKAUSKIS, 1990). Palms are usually aggregated when seedlings, becoming more sparsely distributed with their development (REIS et al., 1996).

In the north coast of the state of Rio Grande do Sul, the Dense Humid Forest physiognomy (DHF), part of the Atlantic Forest biome, has a high landscape and plant diversity, with characteristically tropical species and the richest palm flora among the forest formations in the state (RAMBO, 1956; MARCHIORI, 2002; BRACK, 2006). This study aimed to evaluate age structure and spatial distribution of five palm species located in a fragment of DHF, verifying responses to soil moisture and canopy openness. Our hypothesis was that microhabitat heterogeneity influences the distribution of palm species at the site, through variations in the studied environmental variables.

MATERIAL AND METHODS

Study site and species

The study was conducted in a 6 ha forest fragment at the municipality of Três Cachoeiras (29°24'58.0" S; 49°54' 49.1" W; 21m above sea level), northeast Rio Grande do Sul, Brazil (Figure 1). The area is classified as lowland Dense Humid Forest (TEIXEIRA et al. 1986), part of the Atlantic Rainforest. The vegetation type is marked by the presence of *Ficus cestrifolia* Schott and the geology is originated from fluvial, marine and lake quaternary sediments, up to 30m above sea level (MARCHIORI, 2002). According to Köppen's classification, the regional climate is the Cfa type (temperate subtropical, with the warmest month's temperature superior to 22°C). The soil has organic material with different levels of organic matter and is poorly drained (STRECK et. al, 2002).

We delimited an area of 2,500m² (50 x 50m), divided into 25 plots of 100m² (10 x 10m). We sampled all individuals of the five palm species present at the site: *Euterpe edulis* Martius, *Syagrus romanzoffiana* (Cham.) Glassman, *Bactris setosa*

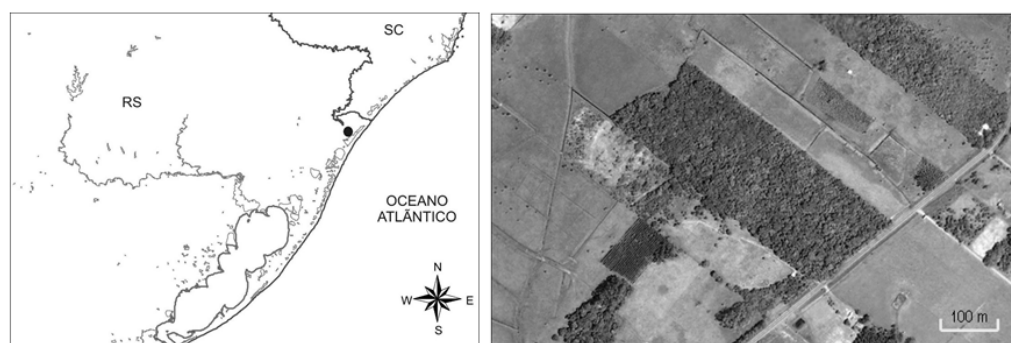


FIGURE 1: Map locating the municipality where the study was developed (black dot) and satellite image of the study site (GoogleTM), oriented according to map.

FIGURA 1: Mapa localizando o município onde o estudo foi desenvolvido (ponto preto) e imagem de satélite do local de estudo (GoogleTM), orientada de acordo com o mapa.

Mart., *Geonoma gamiova* Barb. Rodr. and *Geonoma schottiana* Mart. The first two are canopy species and the other three are understory, clonal species.

Sampling and data analysis

Individuals from each population were classified into three ontogenetic stages: seedlings (with leaves but without aerial stem); juveniles (with a visible stem, height up to 1 cm shorter than the shortest adult observed) and adults (minimum height stipulated from the shortest fruiting individual observed). For clonal species, the stage of the genet was determined considering the stage of the oldest ramet, which defines the function of the entire genet in the population (SOUZA and MARTINS, 2002).

For an indirect measure of light availability, hemispheric photographs of the canopy were taken at the center of each plot, at breast height, with fisheye lenses attached to a digital camera. Photographs were converted into percentage values of canopy openness with the software *Gap Light Analyzer* 2.0 (FRAZER et al., 1999). We also measured soil humidity (% water) with a HH2 *Moisture Meter* attached to a Theta Probe ML2X sensor. We calculated an average for each plot, based on four measurements per plot.

We calculated total and mean species densities per plot and estimated a density per hectare for all populations. Spatial distribution of individuals was measured through the Aggregation Index (I_a) calculated in the software SADIEShell (PERRY et al., 1996) at a significance level of 0.05. SADIE measures the degree of overall aggregation across the sampling site through indices that represent either aggregated ($I_a > 1$), random

($I_a = 1$), or regular ($I_a < 1$) distribution patterns. The statistic significance is provided by the program using a form of randomization test.

In order to observe the relative contribution of each environmental variable to species distributions, we performed a variation partitioning analysis, which consists of partial regressions that allow us to analyze the exclusive effect of one factor by controlling the effect of the other. Also, this analysis shows through a possible interaction of both explanatory variables how much of soil humidity was structured by canopy openness. We also tested for relations between both environmental variables using Spearman correlation. Both analyses were carried out in the R environment, using the package *Vegan* (OKSANEN et al. 2010).

RESULTS

We surveyed a total of 1,443 individuals in all species. The average density was of 57.72 ind. 100 m⁻² and *Euterpe edulis* was the most abundant ($n = 690$), followed by *Bactris setosa* ($n = 432$), *Geonoma gamiova* ($n = 202$), *Syagrus romanzoffiana* ($n = 77$) and *Geonoma schottiana* ($n = 42$). For clonal species *Bactris setosa* and *Geonoma gamiova*, we counted a total of 562 and 225 ramets, respectively.

Population structure

For all individuals counted and measured, 1,134 (78.6%) were seedlings, 153 (10.6%) juveniles and 156 (10.8%) adults. In all populations, the number of seedlings exceeded that of juveniles. Except for *Bactris setosa* and *Syagrus*

romanzoffiana, all populations had more juveniles than adults (Table 1).

The majority of seedlings belonged to the species *Euterpe edulis* (Table 1). This species also had the most plants in the juvenile stage, together with *Geonoma gamiova*. *Bactris setosa* presented the largest adult population.

The most frequent species, found in all 25 plots, was *Euterpe edulis* and the least frequent was *Geonoma schottiana*, present in only 12 plots. As we expected, the most frequent stage were seedlings, since it was also the most abundant stage.

Spatial distribution

Considering the total number of individuals, all species showed a significantly aggregated pattern, except for *Syagrus romanzoffiana* (Table 1).

Euterpe edulis had a higher aggregation at the seedling stage, which also occurred for both

species of *Geonoma*. *Bactris setosa* and *Syagrus romanzoffiana* were more strongly aggregated at the adult and juvenile stages. Juveniles of *Bactris setosa* and *Geonoma schottiana*, as well as the seedlings of *Syagrus romanzoffiana* showed a tendency toward a random pattern (Ia~1).

Influence of the environment on spatial distribution

Canopy openness ranged from 10.82% to 24.13% and soil humidity varied from 23.25% to 96.03%. There was a significantly positive correlation between these variables ($r_s = 0.63$; $p < 0.01$).

Most of the variation was not explained by the environmental variables (Table 2). Soil humidity had significant influence on the distribution of *Bactris setosa* and *Geonoma gamiova* (Table 2). We did not observe a significant relation of

TABLE 1: Number of individuals (N.I.), frequency (number of sample plots in which the species was found), estimated density in a hectare (Ind. ha⁻¹) and Aggregation Index (Ia) for all age classes of *Euterpe edulis* (EE), *Bactris setosa* (BS), *Geonoma gamiova* (GG), *Geonoma schottiana* (GS) and *Syagrus romanzoffiana* (SR) in a fragment of Dense Humid Forest in Rio Grande do Sul, Brazil.

TABELA 1: Número de indivíduos (N.I.), frequência (número de unidades amostrais nas quais a espécie foi encontrada), densidade estimada em um hectare (Ind. ha⁻¹) e Índice de Agregação (Ia) para todas as classes etárias de *Euterpe edulis* (EE), *Bactris setosa* (BS), *Geonoma gamiova* (GG), *Geonoma schottiana* (GS) e *Syagrus romanzoffiana* (SR) em um fragmento de Floresta Ombrófila Densa no Rio Grande do Sul, Brasil.

Age class	Value	EE	BS	GG	GS	SR
Seedlings	N.I.	576	319	139	28	72
	Frequency	25	24	16	8	20
	Ind. ha ⁻¹	2304	1276	556	112	288
	Ia	1.56**	1.49**	1.37*	1.5**	1.09
Juveniles	N.I.	63	38	42	8	2
	Frequency	21	19	14	6	2
	Ind. ha ⁻¹	252	152	168	32	8
	Ia	0.81ns	1.03ns	1.27ns	1.09ns	1.41*
Adults	N.I.	51	75	21	6	3
	Frequency	21	22	12	4	2
	Ind. ha ⁻¹	204	300	84	24	12
	Ia	1.28*	1.71**	1.2ns	1.29*	1.3*
Total	N.I.	690	432	202	42	77
	Frequency	25	24	17	12	20
	Ind. ha ⁻¹	2760	1728	808	168	208
	Ia	1.63**	1.56**	1.44**	1.54**	1.12ns

Em que: * p < 0.05; ** p < 0.001.

TABLE 2: Variation of species distribution partitioned between the environmental variables in a fragment of Dense Humid Forest in Rio Grande do Sul, Brazil. Values are adjusted R^2 . S: seedlings, J: juveniles and A: adults.

TABELA 2: Variação da distribuição de espécies particionada entre as variáveis ambientais em um fragmento de Floresta Ombrófila Densa no Rio Grande do Sul, Brasil. Valores são R^2 ajustados. S: plântulas; J: jovens; A: adultos.

Species	Stage	Humidity	Interaction of both	Canopy Openness	Unexplained
<i>Bactris setosa</i>	S	0.06	0	0.378	0.562
	J	0.085*	0.13	0	0.8
	A	0.29**	0.06*	0	0.741
<i>Euterpe edulis</i>	S	0.044	0	0.02	0.99
	J	0	0	0	1
	A	0.07	0	0	0.93
<i>Syagrus romanzoffiana</i>	S	0	0	0	1
	J	0.02	0	0.29	0.73
	A	0.092	0	0.119	0.88
<i>Geonoma gamiova</i>	S	0.216**	0.04	0	0.77
	J	0.331**	0	0.05	0.68
	A	0.248*	0	0.09	0.79
<i>Geonoma schottiana</i>	S	0.321	0	0.356	0.64
	J	0.01	0	0	0.99
	A	0.027	0	0.363	0.67

Em que: * $p < 0.05$; ** $p < 0.01$.

canopy openness with any population distribution. However, there was a slight interaction between the two variables for adults of *Bactris setosa*, so canopy openness might have had an influence there.

DISCUSSION

Population structure

Natural populations are dynamic: births, deaths and individual movements change constantly due to interactions of individuals among them and with the environment (RICKLEFS, 1993). Accordingly, the analyzed populations reflected a temporal heterogeneity on plant recruitment, observed by an inverse J-shape curve population structure in three species (*Geonoma gamiova*, *Geonoma schottiana* and *Euterpe edulis*), i.e. the number of individuals was the highest at the seedling stage. This decrease might be a consequence of ecological factors operating, such as herbivory and density-dependant competition (WEINER and SOLBRIG, 1984; WEINER, 1985; MATOS et al., 1999) and may indicate that these populations can

maintain themselves throughout time (REIS et al., 1996).

The size of a population is influenced by the events that occur in each phase of the life cycle (SAMPAIO, 2006), which can be abiotic (e.g. wind, sunlight, rainfall) or biotic (e. g. seed dispersers or predators). The small size of the study fragment may be favorable to a future increase in the population of *Syagrus romanzoffiana*, due to the partial or complete absence of their seed predators such as rodents, as observed by Fleury and Galetti (2006) in Atlantic forest remnants with less than 100ha in southeast Brazil.

Spatial distribution

The majority of these species showed an aggregated spatial pattern (Table 1), which other studies have also found to be the most frequent pattern amongst tropical palms (ALVES, 1994; SOUZA and MARTINS, 2004). For *Syagrus romanzoffiana* and *Geonoma* spp., this pattern may be related to their low frequencies in the sample plots, since the aggregation is due to the high

variation in number of individuals among plots.

According to the Janzen-Connell model, plant recruitment is benefited by the distance to the parent tree due to a lower density of seedlings (JANZEN, 1970; CONNELL, 1971). For example, predation is commonly density-dependant: the more aggregated, the more visible the individuals are to seed or seedling predators (ROMO et al., 2004). Seed dispersal is thus an important factor in the generation of these spatial patterns: according to the seed dispersal curve, seedlings will be more or less aggregated (BAROT et al., 1999). Thus, frugivorous animals play an important role in spatial distribution of palms, especially vertebrates such as birds and rodents (BARROSO et al., 2010). However, the small fragment size can be a limiting factor for local vertebrate communities. Moreover, due to the low density of individuals, such as the case of *Syagrus romanzoffiana* and *Geonoma schottiana* adults, it may be difficult for their seed dispersers to find them during the fruiting period, so the seedlings might accumulate more under the parent-tree (MEYER and DORNELES, 2003), which in turn can lead to density-related predation. For *Syagrus romanzoffiana* seedlings, which did not have an aggregated pattern, this predation might have already occurred.

A population can have different spatial patterns among developing stages (BAROT et al., 1999). Very often palms have an aggregated pattern at the seedling stage that becomes less aggregated in later stages (REIS et al., 1996). This can be a result (or a combination) of either: 1. a mortality rate exceeding the recruitment rate; 2. the presence of a seedling bank; or 3. intra-specific competition among the adult plants (KAREIVA et al., 1990; STOLL and PRATI, 2001; BEGON et al., 2006).

Bactris setosa had an aggregated pattern for all stages except the juvenile. Monteiro and Fisch (2005) found a similar situation for this species in a lowland forest in São Paulo, southeast Brazil. The multi-stemmed life form of *Bactris setosa*, as well as for other clonal species, can act as a survival strategy for the habitat they belong to, since understory palms are more susceptible to mortality from damages caused by herbivory and tree fall (STEVEN and PUTZ, 1985).

The estimated density for adults of *Euterpe edulis* was high (204 ind.ha⁻¹) when compared to other studies, such as Meyer and Dorneles (2003), who found only 8 ind.ha⁻¹ in the same forest formation in the state of Santa Catarina. However,

similar results were found by Reis et al. (1996) in a primary forest of DHF (315 ind.ha⁻¹) which is an indication that the study fragment may be in an advanced succession stage.

Influence of the environment on spatial distribution

The only two species that responded significantly to soil moisture were understory species. This corroborates with studies that have shown that environmental variation affects understory species more strongly than for larger, canopy species, due to differences in scale such as resource consumption (DUQUE et al., 2002; WIENS, 1989).

Studying the ecophysiology of *Euterpe edulis*, Paulilo (2000) reported that its development was limited only by extremely low or high levels of Photosynthetically Active Radiation (PAR), indicating an ecological plasticity regarding this factor. This could explain why, in our study, this species has not had an influence by canopy openness, which varied between 10.82 and 24.13%.

As none of the canopy species (*Euterpe edulis* and *Syagrus romanzoffiana*) were significantly related to the measured variables, other indirect effects of the environmental heterogeneity such as animals, physical damage, and interspecific interference (SVENNING, 2001) might be influencing their spatial distribution at the study site. The fact that only one of the *Geonoma* species was affected by soil humidity indicates that, although closely related, they have distinct ecological demands and tolerances, and thus are not competing for this specific resource.

Canopy-generated heterogeneity in light availability has an important role in the ecology of understory palms, by often affecting growth and fecundity (SVENNING, 2001). The absence of significance in the regression of species abundances with canopy openness might be due to the little variation of the canopy cover among plots, considering the area is inserted in a typically tropical forest, containing a dense and continuous tree coverage (TEIXEIRA et al., 1986). However, it is important to bear in mind that the lack of a visible relationship between these variables does not imply that the canopy openness is not affecting the performance of the individuals in some way. Moreover, as pointed out by Souza (2004), leaf layers of a canopy are at least to some point dynamic, so it might be wiser to study its influence

– especially on understory palms – throughout time.

Final Considerations

Soil humidity appeared to be an important variable influencing species distribution in the study site, thus helping maintain the diversity of this palm community through microhabitat specialization.

Based on the population structure, the endangered species *Euterpe edulis*, *Geonoma gamiova* and *Geonoma schottiana* showed a pattern of “inverse J”, which points toward a process of population growth because the number of individuals at the seedling stage was higher than at the following stages. This highlights the importance of maintaining and preserving this forest fragment. *Euterpe edulis* is widely cut down in Brazilian forests, because it is one of the main species from which heart of palm is commercially produced (CARVALHO et al., 1999). Considering we observed signs of logging at the study site, the extraction of this species, although sustainably managed in some cases, must be avoided especially in small forest fragments, due to the high impact on the population viability. This reaffirms the relevance of demographic studies in different forest remnants, so that it is possible to establish an adequate management of this important ecological and economic resource. As for the *Geonoma* species, which suffer extraction of their leaves for ornamental purposes, they also need attention regarding population viability, considering that leaf removal affects several aspects of its ecology.

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REFERENCES

- ALVES, L. F. **Competição intraespecífica e padrão espacial em uma população de *Euterpe edulis* Mart. (Arecaceae)**. 1994. 75 f. Tese (Biologia Vegetal) – Universidade Estadual de Campinas, Campinas, 1994.
- BAROT, S.; GIGNOUX, J.; MENAUT, J. Demography of a Savanna Palm Tree: Predictions from Comprehensive Spatial Pattern Analyses. **Ecology**, v. 80, n. 6, p. 1987-2005. 1999.
- BARROSO, R. M.; REIS, A.; HANAZAKI, N. Etnoecologia e etnobotânica da palmeira juçara (*Euterpe edulis* Martius) em comunidades quilombolas do Vale do Ribeira, São Paulo. **Acta Bot. Bras.** v. 24, n. 2, p. 518-528. 2010.
- BEGON, M.; HARPER, J. L.; TOWNSEND, C. R. **Ecology: From individuals to ecosystems**. 4º ed. Oxford: Blackwell Publishing, 2006. 759 p.
- BRACK, P. Vegetação e Paisagem do Litoral Norte do Rio Grande do Sul: patrimônio desconhecido e ameaçado. In: II ENCONTRO SOCIOAMBIENTAL DO LITORAL NORTE DO RS: ECOSSISTEMAS E SUSTENTABILIDADE. 2006, Imbé. **Livro de Resumos...** Imbé: CECLIMAR, 2006. p. 46-71
- CARVALHO, R.; MARTINS, F.; SANTOS, F. Leaf ecology of pre-reproductive ontogenetic stages of the palm tree *Euterpe edulis* Mart. (Arecaceae). **Annals of Botany**, v. 83, p. 225–233, 1999.
- CLARK, D. A. et al. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. **Ecology**, v. 76, n.8, p. 2581-2594. 1995.
- CONNELL, J. H. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: **Dynamics of populations**. Ed. Centre for Agricultural Publishing and Documentation: Wageningen, 1971. p. 298–310.
- DUQUE, A. et al. Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. **Journal of Tropical Ecology**, v. 18, n. 4, p. 499-525. 2002.
- FLEURY, M.; GALETTI, M.. Forest fragment size and microhabitat effects on palm seed predation. **Biological Conservation**, v. 131, p. 1–13. 2006
- FORTIN, M. J.; DALE, M.; HOEF, J. Spatial analysis in ecology. In: **Encyclopedia of Environmetrics**. Ed. John Wiley and Sons: Chichester, 2002. v.4, p. 2051–2058.
- FRAZER, G. et al. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, British Columbia, e Institute of Ecosystem Studies, New York. 1999.
- JANKAUSKIS, J. **Avaliação de técnicas de manejo florestal**. Belém: SUDAM, 1990. 143 p.
- JANZEN, D. H. Herbivores and the number of tree species in tropical forest. **American Naturalist**. v. 104, p. 501–528. 1970.

- KAREIVA, P.; MULLEN, A.; SOUTHWOOD, R. Population dynamics in spatially complex environments: theory and data. **Philosophical Transaction of the Royal Society of London**, v. 330, p.175-190. 1990.
- MARCHIORI, J. N. C. **Fitogeografia do Rio Grande do Sul: enfoque histórico e sistemas de classificação**. Porto Alegre: Est Edições, 2002. 118 p.
- MATOS, D. S.; FRECKLETON, R. P.; WATKINSON, A. R. The role of density dependence in the population dynamics of a tropical palm. **Ecology**, v. 80, n. 8, p. 2635-2650. 1999.
- MELO, F. P. L. et al. Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. **Biological Conservation**, v. 132, n. 1, p.50-60, 2006.
- MEYER, F. S.; DORNELES, S. S. Demografia do palmito *Euterpe edulis* (Arecaceae) na Floresta Ombrófila Densa de terras baixas em regeneração, na região da Vila da Glória, São Francisco do Sul (SC). **Revista Saúde e Ambiente**, v. 4, n. 2. p. 7 - 13, 2003.
- MONTEIRO, E. A.; FISCH, S. T. V. Estrutura e padrão espacial das populações de *Bactris setosa* Mart e *Bactris hatschbachii* Noblick ex A. Hend (Arecaceae) em um gradiente altitudinal, Ubatuba (SP). **Biota Neotropica**, v. 5, n. 2. 2005.
- MONTEIRO, E. A. **Caracteres morfológicos e influência ambiental nas populações de *Bactris hatschbachii* Noblick ex A. Hend e *Bactris setosa* Mart (Arecaceae), no gradiente altitudinal em um trecho de mata Atlântica/Ubatuba-SP**. 2004. Dissertação (Mestrado). – Universidade de Taubaté, São Paulo.
- OKSANEN, J.; KINDT, R.; LEGENDRE, P. et al. Vegan: Community Ecology Package. R package version 1.17-1. Available from URL: <http://cran.r-project.org/package=vegan>. 2010.
- OOSTERMEIJER, J. G. B. Population viability analysis of the rare *Gentiana pneumonanthe*: importance of demography, genetics, and reproductive biology. In: **Demography, and Viability of Fragmented Populations**. Cambridge University Press: Londres, 2000.
- PAULILO, M. S. Ecofisiologia de plântulas e plantas jovens de *Euterpe edulis* Martius (Arecaceae): Comportamento em relação à variação de radiação solar. **Sellowia**, v. 49-52, p. 93-105. 2000.
- PERRY, J. N. et al. SADIE: Software to measure and model spatial pattern. **Aspects of Applied Biology**, v. 46, p. 95-102, 1996.
- PERRY, J. N., et al. Red-blue plots for detecting clusters in count data. **Ecology Letters**, v. 2, p. 106-113, 1999.
- RAMBO, P. B. **A fisionomia do Rio Grande do Sul**. São Leopoldo: Ed. Unisinos, 1956. 473 p.
- REIS, A. Demografia de *Euterpe edulis* Mart. (Arecaceae) em uma Floresta Ombrófila Densa Montana em Blumenau, SC. **Sellowia**, v. 45, p. 5-37. 1996.
- RICKLEFS, R. E. **A economia da Natureza**. 3º ed. Rio de Janeiro: Guanabara Koogan, 1993, 542 p.
- ROMO, M.; TUOMISTO, H.; LOISELLE, B. A. On the density-dependence of seed predation in *Dipteryx micrantha*, a bat-dispersed rain forest tree. **Oecologia**, v. 140, p. 76–85. 2004.
- SAMPAIO, M. B. **Ecologia populacional da palmeira *Geonoma schottiana* Mart. em mata de galeria no Brasil Central**. Dissertação (Mestrado em Ecologia) – Universidade de Brasília. Brasília, 2006.
- SAMPAIO, M. B.; SCARIOT, A. Growth and reproduction of the understory palm *Geonoma schottiana* Mart. in the gallery forest in Central Brazil. **Revista Brasileira de Botânica**, v.31, n.3, p.433-442. 2008.
- SILVA, M. C. P.; MARTINI, A. M.; ARAÚJO, Q. R. Estrutura populacional de *Euterpe edulis* Mart. no sul da Bahia, Brasil. **Revista Brasileira de Botânica**, v.32, n.2, p. 393-403. 2009.
- SOUZA, A. F.; MARTINS, F. R. Spatial distribution of an undergrowth palm in fragments of the Brazilian Atlantic Forest. **Plant Ecology**, v.164, p. 141–155. 2002.
- SOUZA, A. F.; MARTINS, F. R. Microsite specialization and spatial distribution of *Geonoma brevispatha*, a clonal palm in south-eastern Brazil. **Ecological Research**, v. 19, p. 521-532. 2004.
- SOUZA, A. F. **Aspectos da dinâmica populacional de uma palmeira clonal na floresta paludícola da reserva municipal de Santa Genebra (Campinas, SP)**. 2004. 177 f. Tese (Doutorado em Ecologia) – Universidade Estadual de Campinas, Campinas.
- STEVEN, D.; PUTZ, F. E. Mortality rates of some rain Forest palms in Panama. **Principes**, v. 29, n. 4. p. 162-165. 1985.
- STOLL, P.; PRATI, D. Intraspecific aggregation alters competitive interactions in experimental plant communities. **Ecology**, v. 82, n. 2, p.319-327. 2001.
- STRECK et. al. **Solos do Rio Grande do Sul**. Porto Alegre: Emater/RS – UFRGS. 2002.
- SVENNING, J. C. On the role of microenvironmental heterogeneity in the ecology and diversification

- of neotropical rain-forest palms. **The Botanical Review**, v.67, n.1, p. 1-53. 2001.
- SVENNING, J. C. Crown illumination limits the population growth rate of a neotropical understorey palm (*Geonoma macrostachys*, Arecaceae). **Plant Ecology**, v. 159, p. 185-199. 2002.
- TABARELLI, M. et al. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. **Biological Conservation**, v. 143, n. 10, p. 2328-2340. 2010.
- TEIXEIRA et al. Vegetação. In: **Levantamento de recursos naturais**. Rio de Janeiro: IBGE, v. 33. p. 541-620. 1986.
- TOMLINSON, P. B. Systematics and Ecology of the Palmae. **Annual Review of Ecology and Systematics**, v. 10, p. 85-107. 1979.
- TOWNSEND, C. R.; BEGON, M.; HARPER, J. L. Fundamentos em Ecologia. Artmed, Porto Alegre. 2006.
- VORMISTO, J.; TUOMISTO, H.; OKSANEN, J. Palm distribution patterns in Amazonian Rainforests: What is the role of topographic variation? **Journal of Vegetation Science**, v. 15, n. 485-494. 2004
- WEINER, J. Size hierarchies in experimental populations of annual plants. **Ecology**, v. 66, n. 3, p. 743-752. 1985.
- WEINER, J.; SOLBRIG, O. T. The meaning and measurement of size hierarchies in plant populations. **Oecologia**, v. 61, p. 334-336. 1984.
- WIENS, J. A. Spacial scaling in ecology. **Functional Ecology**, vol. 3, n. 4. p. 385-397. 1989.