BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 41(1): 3–6 2009 10.1111/j.1744-7429.2008.00496.x

Do Terrestrial Tank Bromeliads in Brazil Create Safe Sites for Palm Establishment or Act as Natural Traps for Its Dispersed Seeds?

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ABSTRACT

This study shows for the first time that terrestrial tank bromeliads from Brazilian *restinga* can act as natural traps for dispersed palm *Euterpe edulis* seeds. Such bromeliads, which are shade intolerant, gain benefits by limiting palm recruitment since they hinder canopy formation and, consequently, increase luminosity over its aggregates.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Atlantic Forest; *Euterpe edulis*; facilitation; plant regeneration; *Quesnelia arvensis*; *restinga*; seedling establishment; seed dispersal; seed rain.

FACILITATION IS AN ECOLOGICAL PROCESS that underlies the successful regeneration of many plant species under stressful environmental conditions (Niering *et al.* 1963, Flores & Jurado 2003), and ultimately can play an important role as a biodiversity driver over evolutionary time (Valiente-Banuet & Verdú 2007). Facilitation and competition do not occur in isolation in plant communities; both mechanisms can co-occur within the same community and even for the same individuals. Some theoretical models suggest that facilitation is the predominant interaction under stressful environmental conditions (Lortie & Callaway 2006), although this hypothesis has not always been supported (Maestre *et al.* 2005). Although several studies have shown the co-occurrence of competition and facilitation in temperate and arid environments (Brooker *et al.* 2007), few data are available about these interactions in tropical rain forests.

The main studies about facilitation in Brazilian wet tropical environments have been carried out in *restingas* (Zaluar & Scarano 2000); sandy coastal plains covered by a mosaic of different plant communities, varying from dunes and shrublands to forests, occurring between the sea and the lowland Atlantic forest (Lacerda *et al.* 1993). In some *restinga* habitats, plants can face extreme environmental conditions due to drought, high temperatures, salinity, and nutritional deficiency (Scarano *et al.* 2001). This represents a challenge for plant establishment and may increase competition for the limited resources, although such difficulties can also increase the chances of positive interactions occurring among different plant species.

Bromeliads, one of the most common *restinga* plants (Araújo 1992), can facilitate tree regeneration by increasing nutrient and organic matter content in the soil (Hay *et al.* 1981), and creating suitable sites for seed germination and seedling establishment within them (Fialho 1990, Fialho & Furtado 1993, Scarano 2002). However, bromeliads could also act as natural traps for dispersed propagules if seeds deposited among the rosette of leaves cannot germinate, or if the seedlings emerging there are unable to grow. The root system of emerging seedlings is imprisoned within the hollow of the rosette and can cause bromeliads to decrease plant recruitment. This phenomenon can have far-reaching consequences for plant colonization, establishment, and regeneration in *restinga* habitats where the understory is densely occupied by terrestrial tank bromeliads (Pereira *et al.* 2004).

The main goal of this study is to evaluate if terrestrial tank bromeliads create safe sites for the palm *Euterpe edulis* establishment or act as natural traps for its dispersed seeds, potentially limiting and collapsing plant establishment beneath its aggregates.

METHODS

The research was carried out during March 2007 at Parque Estadual da Ilha do Cardoso, southeastern Brazil, located at 25°03′05″–25°18′18″ S, and 47°53′48″–48°05′42″ W, which comprises an area of 22,500 ha and has a tropical superhumid climate (Af), according to Köppen’s classification. The topography is predominantly mountainous with five main vegetation types: sandy coastal

Received 16 June 2008; revision accepted 14 August 2008.

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dunes, *restinga*, mangroves, lowland tropical Atlantic rain forest, and tropical montane Atlantic rain forest (Bernardi *et al.* 2005).

According to Sugyama (1998), the studied vegetation, known as 'short *restinga*', is comprised of small trees, which form an open canopy up to 4–7 m, with irregular canopies and lacking a vertical stratification, where the understory is predominantly composed of the bromeliad *Quesnelia arvensis* (Vell.) Mez.

To study the effect of bromeliad cover on seedling populations, we chose the palm *E. edulis* Mart. (Arecaceae) as a model species, because it is the most abundant woody species in the neighboring *restinga* forest, representing 19.8 percent of the total individuals (Projeto Parcelas Permanentes 2006), resulting in abundant seedlings in the study area. The large population combined with intense fruit consumption by many species of mammals and birds (Rodrigues *et al.* 1993, Galetti *et al.* 1999, Côrtes 2006) makes the species a remarkable feeding resource for animals and consequently an important component of seed rain. Furthermore, its seedlings are easily identifiable (Reis *et al.* 2000) and the plants do not reproduce vegetatively, which could compromise the evaluation of seedling recruitment resulted from dispersed seeds.

To check the effect of terrestrial bromeliad density on palm recruitment, we established 70 plots (2 × 2 m) along two parallel trails of *ca* 100 m each, perpendicular to the forest border. Two parallel transects, 5 and 8 m from the trail border, were placed on each side of the trail. Hence, a total of eight transects were set up in the study area. Approximately nine plots, 10 m apart, were placed along each transect.

The following variables were recorded in each plot: (1) area covered by terrestrial tank bromeliads, which was visually estimated in categories according to percentage area cover of bromeliads: 1 = 0–10 percent; 2 = 11–25 percent; 3 = 26–50 percent; 4 = 51–75 percent; 5 = 76–100 percent; (2) number of *E. edulis* palm seedlings found on the ground, considering only individuals with the first leaf insertion up to 20 cm from the ground; (3) distance of *E. edulis* palm seedlings to the center of the closest bromeliad; and (4) canopy cover, measured with a convex densiometer (Lemmon 1957). Average canopy cover per plot was obtained based on four measurements carried out in four opposite directions from the center of the plot.

To assess whether bromeliads facilitate palm establishment and then increase seedling abundance beneath its aggregates, we evaluated the distance from 70 random points to the closest bromeliad. The random points were set up along the same transects used in the previous study and allowed overlapping between points and plots.

We incorporated each seedling–bromeliad distance within the plots as our statistical units ($N = 255$). The distance distribution between *E. edulis* seedlings and the closest bromeliad and between random points and the center of the closest bromeliad were compared by the nonparametric Kolmogorov–Smirnov test, using the software Statistica 7.0 (StatSoft, Inc. 2002).

To understand the ecological implications of the negative relationship between bromeliad cover and palm seedling density, we analyzed the relationship between bromeliad density, palm seedling abundance and canopy cover using structural equation modeling (SEM; Shipley 2000, Pugesek *et al.* 2003). We used this statistical tool because canopy cover could have both direct and indirect bromeliad-mediated effect on palm seedlings, since shading can be particularly important to define the spatial occurrence of the shade-intolerant bromeliad *Q. arvensis* (Fischer & Araújo 1995) and the shade-tolerant palm *E. edulis* (Nakazono *et al.* 2001). We built an *a priori* overidentified saturated model in which the number of palm seedlings was affected both by bromeliad density and canopy cover, and canopy cover also affected bromeliad cover. We also built an alternative, nested model where we constrained the path between canopy cover and palm seedling abundance. Both models were solved by minimizing yield-parameter estimates through an iterative process that used maximum likelihood as discrepancy functions. We used maximum-likelihood estimation (MLE) on the variance-covariance matrix to test the goodness of fit of the model and to calculate the Akaike information criterion (AIC). To select the best-fitting model, we chose the one with the highest P value and the lowest χ^2 and AIC. SEM was performed with SEPATH procedure in Statistica 7.0 (StatSoft, Inc. 2002). The individual plot was used as the sample unit ($N = 70$) in the analyses.

RESULTS

The saturated SEM model describing the interaction among bromeliad density, palm seedling abundance and canopy cover was not adequate ($P < 0.0001$, $\chi^2 = 133.7$); however, the alternative model provided a good explanation of the causal relationship among these variables ($\chi^2 = 1.03$, df = 1, $P = 0.311$). According to this model, bromeliad cover negatively affected palm seedling abundance (Fig. 1). Additionally, canopy cover affected positively palm seedlings indirectly, since it significantly decreased bromeliad density (Fig. 1). Our model suggests, thereby, that plots with denser canopies had more palm seedlings due to decreased bromeliad cover, rather than due to any direct effect of light intensity on palm seedlings (Fig. 1).

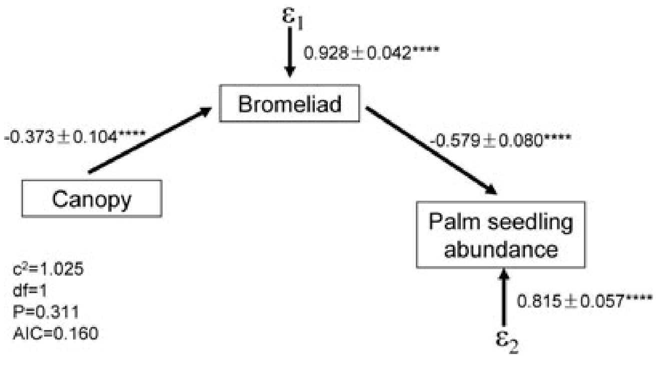

FIGURE 1. Path diagram showing the relations among bromeliads density, palm (*Euterpe edulis*) seedling abundance and canopy cover in the short *restinga* of Parque Estadual da Ilha do Cardoso, Cananéia-SP, Brazil. Numbers above each arrow refer to the path coefficients ± SE (**** = $P < 0.0001$); epsilons refer to the error term of each dependent variable included in the model.

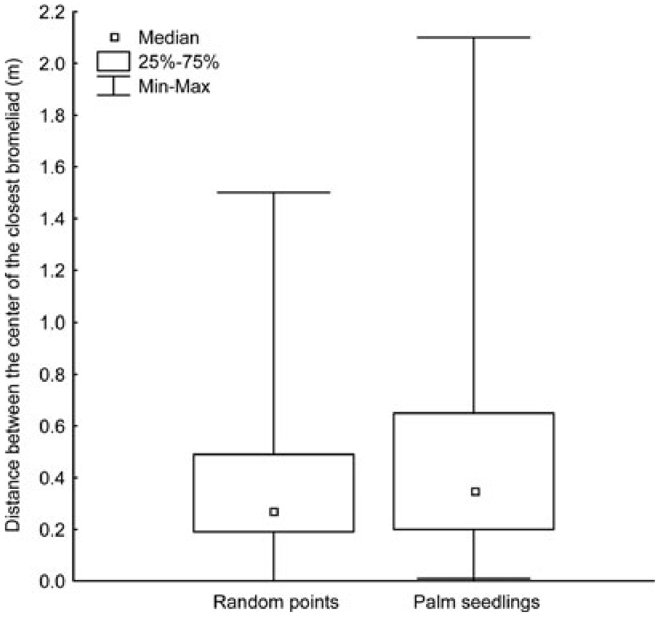

FIGURE 2. Box-plots for the distances between palm (*Euterpe edulis*) seedlings ($N = 255$) and the center of the closest bromeliad, and between random points ($N = 70$) and the center of the closest bromeliad.

The distance between palm seedlings and the closest bromeliads was significantly higher than the distance between random points and their closest bromeliads ($P < 0.05$; Fig. 2), suggesting that palm seeds have more chances to establish if they fall outside microsites directly covered by bromeliads.

DISCUSSION

Our results show that, instead of facilitating plant establishment and increasing seedling abundance beneath its aggregates or within them, bromeliads reduce palm regeneration. Although palm seeds were frequently found inside the tubular hollows formed by bromeliad leaves, no seedlings or juveniles were found growing together with these bromeliads. Because palm seedlings lack roots that are able to grow laterally and escape the bromeliad, we expect that palm seedlings cannot survive more than a few months in bromeliads. Indeed, it was common to find senescent palm seedlings or even completely rotten plants inside bromeliads tubular hollow. Therefore, the causal model fitted to the recruitment data indicates that bromeliads act in our study site as competitors rather than create safe sites for palm establishment.

Even being a shade-tolerant species, the recruitment of *E. edulis* into seedling classes ($\leq$ 10 cm height) is not affected by a more open forest condition (Fantini & Guries 2007), highlighting the lack of any direct effect of light intensity on palm seedling abundance in the study area. Another possibility is that palm seed dispersal varied among plots due to habitat selection by avian frugivores, since a closer canopy cover could offer more perches to birds. Although seed rain was not evaluated in the present study, the results of Fantini and Guries (2007) also indicate that the number of palm seedlings was not affected in sites with different tree density and abundance. Such results reinforce the hypothesis that bromeliad cover is the main factor determining palm density.

Facilitation in the *restinga* through the germination within terrestrial tank bromeliads may occur for some tree species, like *Erythroxyllum ovalifolium* (Fialho 1990, Fialho & Furtado 1993), *Clusia hilariana* (Scarano 2002, cited by Sampaio *et al.* 2005), and *Clusia fluminensis* (M. Macedo, pers. comm.; cited by Fialho & Furtado 1993). However, contrasting with *E. edulis*, these species have adventitious roots that can extend out of the bromeliad interior and reach the soil, continuing their development.

Although seed rain interception occurs randomly, bromeliads benefit by limiting palm seed germination next to them, since competition for light and resources will be reduced as a result of the lower palm recruitment found in the middle of its aggregates, which potentially may happen for other woody species. The reduced canopy cover in the short *restinga* may stimulate the development of *Q. arvensis* individuals, which are shade intolerant (Fischer & Araújo 1995). In addition, light incidence may be essential to bromeliad seed germination (Mercier & Guerreiro Filho 1990, Pinheiro & Borghetti 2003). Therefore, a more open canopy cover and higher luminosity inside the forest may allow the expansion of bromeliad aggregates, stimulating recruitment by vegetative reproduction, due to the emission of young ramets, and by the production of new individuals as a result of seed germination.

In brief, our results show that terrestrial tank bromeliads play a key role in the dynamics of palm recruitment and regeneration in *restinga*, possibly acting as seed rain sinks. We believe that the distribution of bromeliad aggregates may alter the physiognomy of *restinga* forest and thus determine the structure of plant community in this kind of environment. Despite the situation of abundant terrestrial tank bromeliads being specific to *restinga*, other plant species in the Atlantic Forest, like the native bamboo *Guadua tagoara*, may also negatively influence the occurrence of several woody species (Rother 2006, Fantini & Guries 2007). Thus, plant–plant interactions may play an important role in Atlantic Forest dynamics and probably in other tropical forests, demanding further experimental investigation for the better understanding of the plant–plant competitive processes driving recruitment and spatial distribution of plant species in tropical environments.

ACKNOWLEDGMENTS

We thank M. Melo, M. A. Pizo, F. C. Bechara, and P. Jordano, for thorough comments on a preliminary version of this manuscript, and to M. Galetti, W. Silva, M. A. Pizo, and P. Jordano for allowing us to participate in the 6th Latin American Course on Frugivory and Seed Dispersal. We also fully thank the anonymous reviewers, who gave decisive contributions for the improvement of the manuscript. This study has been partially funded by the CYTED grant *Las interacciones ecológicas entre plantas y animales como generadoras de biodiversidad*: *su papel en la dinámica y conservación de los ecosistemas*.

LITERATURE CITED

Araújo, D. S. D. 1992. Vegetation types of sandy coastal plains of tropical Brazil: A first approximation. *In* U. Deelinger (Ed.). Coastal plant communities of Latin America. pp. 337–347. Academic Press, San Diego, California.

Bernardi, J. V. E., P. M. B. Landim, C. L. Barreto, and R. C. Monteiro. 2005. Spatial study of the vegetation gradient from Cardoso Island State Park, SP, Brazil. Holos Environ. 5: 1–22.

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2007. Facilitation in plant communities: The past, the present, and the future. J. Ecol. 96: 18–34.

Côrtes, M. C. 2006. Variação espacial nas interações entre o palmito *Euterpe edulis* e as aves frugívoras: Implicações para a dispersão de sementes. MSc Dissertation. Universidade Estadual Paulista.

Fantini, A. C., and R. P. Guries. 2007. Forest structure and productivity of palmiteiro (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica. For. Ecol. Manage. 242: 185–194.

Fialho, R. F. 1990. Seed dispersal by lizard and a treefrog – effect of dispersal site on seed survivorship. Biotropica 22: 423–424.

Fialho, R. F., and A. L. S. Furtado. 1993. Germination of *Erythroxylum ovalifolium* (Erythroxylaceae) seeds within terrestrial bromeliad *Neoregelia cruenta*. Biotropica 25: 359–362.

Fischer, E. A., and A. C. Araújo. 1995. Spatial organization of a bromeliad community in the Atlantic rainforest, south-eastern Brazil. J. Trop. Ecol. 11: 559–567.

Flores, J., and E. Jurado. 2003. Are nurse-protégé interactions more common among plants from arid environments? J. Veg. Sci. 14: 911–916.

Galetti, M., V. Zipparro, and L. P. Morelatto. 1999. Fruit phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic forest of Brazil. Ecotropica 5: 115–122.

Hay, J. D., L. D. Lacerda, and A. L. Tan. 1981. Soil cation increase in a tropical sand dune ecosystem due to a terrestrial bromeliad. Ecology 62: 1392–1395.

Lacerda, L. D., D. S. D. Araújo, and N. C. Maciel. 1993. Dry coastal ecosystems of the tropical Brazilian coast. *In* van der Maarel (Ed.). Dry coastal ecosystems: Africa, America, Asia and Oceania. pp. 477–493. Elservier, Amsterdam, The Netherlands.

Lemmon, P. E. 1957. A new instrument for measuring forest overstory density. J. Forest. 5: 667–668.

Lortie, C. J., and R. M. Callaway. 2006. Re-analysis of meta-analysis: Support for the stress-gradient hypothesis. J. Ecol. 94: 7–16.

Maestre, F. T., F. Valladares, and J. F. Reynolds. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. J. Ecol. 93: 748–757.

Mercier, H., and O. Guerreiro Filho. 1990. Propagação sexuada de algumas bromélias nativas da Mata Atlântica: Efeito da luz e da temperatura na germinação. Hoehnea 17: 19–26.

Nakazono, E. M., M. C. Costa, K. Futatshugi, and M. T. S. Paulilo. 2001. Crescimento inicial de *Euterpe edulis* Mart. em diferentes regimes de luz. Rev. Brasil. Bot. 24: 173–179.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The Saguaro: A population in relation to environment. Science 142: 15–23.

Pereira, M. C. A., S. Z. Cordeiro, and D. S. D. Araújo. 2004. Estrutura do estrato herbáceo na formação aberta de *Clusia* do Parque Nacional da *restinga* de Jurubatiba, RJ, Brasil. Acta Bot. Brasíl. 18: 677–687.

Pinheiro, F., and F. Borghetti. 2003. Light and temperature requirements for germination of seeds of *Aechmea nudicaulis* (L.) Griesebach and *Streptocalyx floribundus* (Martius ex Schultes F.) Mez (Bromeliaceae). Acta Bot. Brasil. 17: 27–35.

Projeto Parcelas Permanentes/BIOTA/FAPESP. 2006. IV Relatório Temático do Projeto Parcelas Permanentes – Parte III: A vegetação. http://www.lerf.esalq.usp.br/parrel2005.php; Accessed in 12.06.2008.

Pugesek, B. H., A. von Eye, and A. Tomer. 2003. Structural equation modeling: Applications in ecological and evolutionary biology. Cambridge University Press, Cambridge, UK.

Reis, M. S., A. C. Fantini, R. O. Nodari, A. Reis, M. P. Guerra, and A. Mantovani. 2000. Management and conservation of natural populations in Atlantic Rain Forest: The case study of palm heart (*Euterpe edulis* Martius). Biotropica 32: 894–902.

Rodrigues, M., F. Olmos, and M. Galetti. 1993. Seed dispersal by tapir in southeastern Brazil. Mammalia 57: 460–461.

Rother, D. C. 2006. Chuva de sementes e estabelecimento de plântulas em ambientes com bambus na Mata Atlântica. MSc Dissertation. Universidade Estadual Paulista. 107 pp.

Sampaio, M. C., F. X. Picó, and F. R. Scarano. 2005. Ramet demography of a nurse bromeliad in Brazilian *restinga*s. Am. J. Bot. 92: 674–681.

Scarano, F. R. 2002. Structure, function and floristic relationship of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Ann. Bot. 90: 517–524.

Scarano, F. R., H. M. Duarte, K. T. Ribeiro, E. M. Rodrigues, B. Barcellos, A. C. Franco, J. Brulfert, E. Deléens, and U. Luttge. 2001. Four sites with contrasting environmental stress in south-eastern Brazil: Relations of species, life form diversity, and geographical distribution to ecophysiological parameters. Bot. J. Linn. Soc. 136: 345–364.

Shipley, B. 2000. Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference. 317 pp. Cambridge University Press, Cambridge, UK.

StatSoft, Inc. 2002. Statistica for Windows: computer program manual, Version 6.0. StatSoft, Inc, Tulsa, USA.

Sugyama, M. 1998. Estudo das florestas da *restinga* da Ilha do Cardoso, Cananéia, São Paulo, Brasil. Boletim do Instituto de Botânica 11: 119–159.

Valiente-Banuet, A., and M. Verdú. 2007. Facilitation can increase the phylogenetic diversity of plant communities. Ecol. Lett. 10: 1029–1036.

Zaluar, H. L. T., and F. R. Scarano. 2000. Facilitação em *restinga*s de moitas: Um século de buscas por espécies focais. *In* F. A. Esteves, and L. D. Lacerda (Eds.). Ecologia de *restinga*s e Lagoas Costeiras. pp. 3–23. NUPEM, Universidade Federal do Rio de Janeiro, Rio Janeiro, Brazil.