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Plant-plant associations and population structure of four woody plant species in a patchy coastal vegetation of Southeastern Brazil

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ABSTRACT – (Plant-plant associations and population structure of four woody plant species in a patchy coastal vegetation of Southeastern Brazil). We examined plant population structure and interspecific associations for juveniles and adults of four woody species (*Andira legalis* (Vell.) Toledo*, Clusia hilariana* Schltdl., *Protium icicariba* (DC.) Marchand and *Vernonia crotonoides* Sch. Bip. ex Baker) in a patchy vegetation on a sandy coastal plain (*restinga*) in SE – Brazil. We found 101 vegetation patches in a 0.5 ha grid and these were divided into two distinct size classes, with large patches (> 20 m^2) containing the majority of adult individuals of the species studied. The most abundant species, *P. icicariba* (465 individuals) and *C. hilariana* (312), had actively regenerating populations, whereas *A. legalis* (20) and *V. crotonoides* (338) showed evidence of intermittent regeneration. The regeneration niches of the four species differed as did their investment in vegetative reproduction: for instance, 81% of *C. hilariana* seedlings were found growing inside tank-bromeliads contrasting with only 3% of *P. icicariba* in this habitat. Additionally, 28% of regenerants of *C. hilariana* originated vegetatively, contrasting with only 6% for *P. icicariba*. All significant associations between species found in the study were positive. There was a positive association between adults of *C. hilariana* and *P. icicariba*, as well as between adults of *C. hilariana* and juveniles of both. This suggests that *P. icicariba* is successfully establishing under the canopy of *C. hilariana* and highlights the role of *C. hilariana* in generating vegetation cover that will be later dominated by other woody plant species, as an important process for maintenance of plant diversity in this *restinga* vegetation.

Key words - coastal vegetation, interspecific association, *restinga*, succession

RESUMO – (Associações planta-planta e estrutura populacional de quatro espécies lenhosas em ilhas de vegetação de restinga no sudeste brasileiro). Este estudo examinou a estrutura populacional e as associações interespecíficas entre jovens e adultos de quatro espécies arbustivo-arbóreas (*Andira legalis* (Vell.) Toledo*, Clusia hilariana* Schltdl., *Protium icicariba* (DC.) Marchand and *Vernonia crotonoides* Sch. Bip. ex Baker) numa restinga composta por ilhas de vegetação, no sudeste brasileiro. Foram encontradas 101 ilhas de vegetação numa grade de 0,5 ha e estas foram divididas em duas distintas classes de tamanho, sendo que ilhas grandes (> 20 m^2) contiveram a grande maioria dos indivíduos adultos das espécies estudadas. As espécies mais abundantes, *P. icicariba* (465 indivíduos) e *C. hilariana* (312), apresentaram evidências de ativa regeneração, enquanto para *A. legalis* (20) e *V. crotonoides* (338), esta é possivelmente intermitente ou eventual. Os nichos de regeneração das quatro espécies diferiram, assim como as estratégias de reprodução: por exemplo, 81% das plântulas de *C. hilariana* foram encontradas dentro de tanques de bromélias enquanto apenas 3% das plântulas de *P. icicariba* foram encontradas neste habitat. Adicionalmente, 28% dos regenerantes de *C. hilariana* apresentaram origem vegetativa em contraste com apenas 6% dos regenerantes de *P. icicariba*. Dentre as associações significativas encontradas neste estudo, todas foram positivas. Houve uma associação positiva entre adultos de *C. hilariana* e *P. icicariba*, assim como entre adultos de *C. hilariana* e jovens de ambas espécies. Isso sugere que *P. icicariba* se estabelece sob o dossel de *C. hilariana* e mostra a importância de *C. hilariana* ao gerar área com cobertura vegetal que será posteriormente ocupada por outras espécies lenhosas, o que parece ser um importante processo para a manutenção da diversidade de plantas nesta vegetação de restinga.

Palavras-chave - associações interspecíficas, restinga, sucessão, vegetação costeira

Introduction

It has been demonstrated that facilitation, as opposed to competition, is the key process regulating the structure and function of plant communities in harsh environments worldwide (Callaway *et al*. 2002, Bruno *et al*. 2003, Brooker *et al.* 2008), and also for some Brazilian vegetation types (Scarano 2002). The occurrence of the nurse plant syndrome, patterns of positive spatial associations between seedlings of one species and sheltering adults of another species (Franco & Nobel 1989), has been reported for some xerophytic habitats, where the vegetation is organised in patches (Pugnaire *et al*. 1996, Flores & Jurado 2003, Scarano 2009). Therefore, nurse plants play a major role in succession in these habitats, since they ameliorate conditions for germination, establishment and/or growth of other plant species.

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The sandy coastal plains in southeastern Brazil consist of a mosaic of vegetation types, ranging from reptant halophytes to forests, collectively called *restinga*. On the northern coast of the state of Rio de Janeiro, one of the most characteristic vegetation types is organised in patches of various sizes, separated by areas of white sand (Pimentel *et al*. 2007). Plants in this area, as in many other open *restingas*, are subject to atmospheric salinity, high solar radiation, soil oligotrophy and low water availability (Scarano *et al*. 2001, 2005). This area is commonly referred to as a *Clusia* scrub, since *C. hilariana* Schltdl. is often a central shrub (not taller than 8 m) nursing understorey plants (Liebig *et al*. 2001, Dias *et al*. 2005, 2006).

A considerable body of work has been developed on this vegetation in recent years, which has led us to formulate the hypothesis that this vegetation undergoes cyclic succession and that facilitation is a key ecological feature in this process (see review in Scarano *et al*. 2004). In short, few species establish directly on the bare sand and provide the nuclei for small vegetation patches that increase in size as when, later in succession, some key shrub or tree species establishes and grows thus facilitating the aggregation of more species in the understory. Two types of large vegetation patches can be distinguished based on the dominance or not of adult *C. hilariana*. Non-*Clusia* patches might originate either from small patches where *Clusia* did not establish or from *Clusia* patches where dominant *Clusia* plants died. Furthermore, *Clusia*'s death might imply a fragmentation of its understory resulting in several small-sized vegetation patches, therefore characterising cyclic succession (see also Dias *et al*. 2005, Dias & Scarano 2007).

However, basic information on population structure and species-specific associations, currently largely unavailable, are necessary to further test the above hypothesis. Thus, in this paper we were particularly interested in species-specific patterns of interspecific association. A negative association pattern between two species might be the result of competition or of differences in habitat preference. A positive pattern might be the result of facilitation or of neutrality and similarity in habitat preference (Kent & Coker 1992). We performed association tests between adults and juveniles of four species key to test the cyclic succession hypothesis. Our premise was that association (positive or negative) between the adult of a given species and juveniles of the same or another species is evidence of interaction (positive or negative) between the former and the latter. The opposite (juveniles faciliting or outcompeting adults) would be unlikely. Additionally, we surveyed the population structure of each of the four species in an attempt to detect preferential germination and establishment sites. This was necessary in order to interpret whether association patterns were related to plant-plant interactions or to plant-habitat interactions, in the absence of manipulative experiments related to species removal or addition (*e.g.* Díaz *et al*. 2003, Kareiva & Levin 2003).

The patchy nature of this *restinga* vegetation provides distinct establishment alternatives and different regeneration niches for the species studied. Thus, they may as adults create different regeneration niches for other species, which is an aspect likely to affect local successional processes not previously examined in depth. For instance, previous statements that germination of *Clusia hilariana* will often take place inside bromeliad tanks (Scarano 2002, Dias & Scarano 2007) and that vegetative reproduction is an important feature for regeneration of many local species (Matallana *et al*. 2005) have not yet been tested quantitatively at population level.

In this paper, while further investigating the cyclic succession and facilitation hypothesis, we expected to find the following results: 1. since *C. hilariana* is a nurse plant and *Clusia*-dominated patches are often earlier in succession than non-*Clusia* patches (Scarano *et al*. 2004), we expected *Clusia* adults to be positively associated with juveniles of the other species; 2. since previous observations linked *Clusia* germination to tank bromeliads (Macedo & Monteiro 1987, Fialho 1990, Fialho & Furtado 1993, Scarano 2002), we expected to provide quantitative confirmation of this pattern in our study site; and 3. since vegetative propagation has been reported to play an important role in plant establishment in this patchy coastal vegetation (Matallana *et al*. 2005, Dias & Scarano 2007), we expected it to be predominant for the study species.

Material and methods

Study site – The study site is located in the Restinga de Jurubatiba National Park, a *ca.* 14,000 ha area which covers part of the municipalities of Macaé, Carapebus and Quissamã (22°00'-22°23' S, 41°15'-41°45' W), approximately 200 km north of the city of Rio de Janeiro, southeastern Brazil. The dry season runs from May to August, mean annual rainfall around 1200 mm and mean annual temperature 23.4 °C, according to data from the National Institute for Meteorology. Araujo *et al*. (1998) described ten different vegetation types for the Park, and this study was conducted in the open shrubby vegetation dominated by *Clusia hilariana*, one of the tallest species in this plant community (up to 8 m; Dias *et al*. 2006). A recent survey found 62 woody species and a Shannon-Wiener diversity index of 3.07 along 600 m transects in 12 different sampling points in the Park (Pimentel *et al*. 2007).

This site has vegetation patches surrounded by open spaces with sparse herbaceous vegetation cover on white sand. The sample plot (0.5 ha; 50 × 100 m) lies 130 m from the sea and is adjacent to one of the sampling points (site 4) of Pimentel *et al*. (2007), which had highest species richness (45) and vegetation cover (56.4%).

Study species – We selected four species to investigate population structure and interspecific associations. These species display distinct dominance patterns along our study site, according to Pimentel *et al*. (2007). *Clusia hilariana* (Clusiaceae) and *Protium icicariba* (DC.) Marchand (Burseraceae) have the highest importance values in our study site (site 4 of Pimentel *et al*. 2007) and throughout the region. *Vernonia crotonoides* Sch. Bip. ex Baker (Asteraceae) has an intermediate dominance and is frequent in small patches (Zaluar & Scarano 2000). The legume *Andira legalis* (Vell.) Toledo (Fabaceae) is rare throughout the region but occurs in low abundance in our study site.

Clusia hilariana is a dioecious plant (Faria *et al*. 2006), has crassulacean acid metabolism (Scarano *et al*. 2005), plays an important role as nurse plant (Dias & Scarano 2007) and has been reported to have a positive effect on plant establishment but not necessarily on plant growth (Dias *et al*. 2005). It has a very characteristic open, many-branched umbrella-shaped crown; large, succulent, glabrous leaves; a superficial root system and aerial roots are often seen growing from the lower branches.

Protium icicariba is a dioecious (Matallana *et al*. 2005), C_3 shrub (Mattos *et al*. 1997), which grows to 3 m tall in the *restingas*. It is co-dominant with *C. hilariana* (Pimentel *et al*. 2007), and forms a dense crown due to profuse branching at ground level. Its pendant leaves often give the visual impression of wilting.

Vernonia crotonoides is a C_3 plant as tall as 3 m in open *restingas* and 4 m in forests. It is a slender shrub, sparsely branching, with greyish pubescent leaves grouped at the apex.

Andira legalis is a C_3 plant ranging from 1-5 m tall as an adult, and grows in both open and shaded environments. It may or may not be intensely branched at ground level, but it often has a thick, woody underground structure (Cirne & Scarano 2001). It is a nitrogen-fixing plant (Scarano *et al*. 2001, Gessler *et al*. 2005) that has been reported to have negative associations with other *restinga* species further south from our study site (Cirne *et al*. 2003), and was chosen also for the possibility of representing this type of effect also here.

Population structure – We numbered, mapped and measured (height, basal diameter) all individuals (plants not visibly connected to others above and up to 10 cm below the soil surface) of the four species inside a 0.5 ha plot. For plants with more than one trunk emerging from the soil, we only measured the height of the tallest and the basal diameter of the largest. For each species, the smallest basal diameter class with a fertile individual was taken as the threshold between juveniles and adults. Adult diameter size (d) was as follows: *C. hilariana*, d ≥ 3.5 cm; *P. icicariba*, d ≥ 1.5 cm; *V. crotonoides*, d ≥ 1.5 cm; *A. legalis*, d ≥ 6.0 cm. Seedlings were defined as individuals that still retained attached cotyledon or displayed the first pair of leaves. For plants up to 50 cm in height we determined their origin (whether from seed or from a vegetative organ) by carefully removing the soil to see if they were connected to other plants underground (clonal growth) or showed a basal diameter disproportionately large in relation to height (resprouts), which were treated as evidences of vegetative reproduction.

Interspecific and intraspecific associations – Patches were used as the sampling unit to test species association, since the vegetation is clearly organised in distinct patches. We separated the patches into two size classes: small (< 20 m^2), and large (≥ 20 m^2). Patch size was calculated as the area of an ellipse, after measuring the largest diameter and the diameter perpendicular to it. This was made to distinguish patches where we found adults of the species studied (≥ 20 m^2) from patches where adults were absent or rare. Thus, for the association tests, we used only data of patches larger that 20 m^2 of area. Each species was divided into two groups: adults and juveniles (including seedlings). The number of individuals per size class for the four study species was counted in each large patch. For adult individuals we tested association between pairs of species using a correlation matrix with Spearman rank order correlation (Zar 1999). Since we can assume that juveniles cannot exert effects on distribution of adults, we used multiple regression analysis to test if the number of juvenile individuals of a certain species was associated with the number of adults and juveniles of other species. We performed Monte Carlo procedure to test if regression coefficients (β) were different from zero (Manly 1997), because data were highly non-normal due to many zero occurrences. We used the *PopTools* add-in for Microsoft Excel (Hood 2008) to compare observed βs with the distribution of values obtained by pairing the y and x values at random. Randomization was done 10,000 times and P values were calculated as the proportion of values higher that observed β values in modules. *Andira* was not included in analysis of association between species, because of its reduced number of individuals.

Results

Population structure – The four species studied had very different population structures (table 1). Among the study species, *C. hilariana* had the highest percentage of juveniles, *P. icicariba* of seedlings and *V. crotonoides* of adults. *A. legalis* had a small population of only 20 individuals in the plot, and all but one were adults.

All *V. crotonoides* less than 50 cm tall were seed originated, as well as the single *A. legalis* plant found in that size class. Only 6% of the regenerants of *P. icicariba* were identified as being asexually originated. Conversely, *C. hilariana* had a higher proportion of asexually originated regenerants (28%).

Table 1. Population structure of the four studied species, in a 0.5 ha-plot of a patchy *restinga* vegetation. Number of individuals and percentage from total (%). Seedlings were newly germinated or sprouted plants; juveniles were intermediate in size as compared to seedlings and adult; whereas adults' size varied according to the species. Adult diameter size (d) was as follows: *C. hilariana*, d ≥ 3.5 cm; *P. icicariba*, d ≥ 1.5 cm; *V. crotonoides*, d ≥ 1.5 cm; *A. legalis*, d ≥ 6.0 cm.

Parameters \ Species	*Andira legalis*	*Clusia hilariana*	*Protium icicariba*	*Vernonia crotonoides*
Nº seedlings	–	32 (10)	283 (61)	9 (3)
Nº juveniles	1 (5)	211 (68)	87 (19)	83 (25)
Nº adults	19 (95)	69 (22)	95 (20)	246 (72)
Total	20	312	465	338
Height range (m)	0.28-2.90	0.05-3.90	0.02-3.20	0.04-3.20
Basal diameter range (cm)	1.0-15.8	0.1-19.0	0.1-15.6	0.1-7.6

The populations also varied in regard to sites of seedling occurrence. Seedlings of *C. hilariana* occurred mostly (81%; *n* = 32) inside rosettes of the bromeliads *Aechmea nudicaulis* (L.) Griseb. and *Neoregelia cruenta* (R. Graham) L.B. Smith, more typically inside patches and at patch edges, but sometimes also inside fully exposed bromeliads between patches. The remaining 19% were found growing on soil inside the patches or at the edge. We extended this investigation to all plants up to 50 cm tall and observed the same pattern: 70% of the plants were found inside bromeliad rosettes, 25% under bromeliad tanks and only 5% on soil with no neighbouring bromeliads (*n* = 59). Bromeliads were a less common site of occurrence for *P. icicariba* seedlings since only 3% of the seedlings of this species were found inside tanks while the remaining 97% occurred on the ground of dense vegetation patches (*n* = 278). Seedlings of *V. crotonoides* showed a third occurrence pattern: 89% of the seedlings were found in open areas, close to individuals of the geophyte palm *Allagoptera arenaria* (Gomes) Kuntze and/or the cactus *Pilosocereus arrabidae* (Lem.) Byles & G.D. Rowley which form small patches, while 11% occurred inside bromeliad tanks (*n* = 9).

Intraspecific and interspecific association – We found 101 vegetation patches in the sample area. From this total, 30 patches had an area greater than 20 m^2 and were used to perform the association tests. The majority of adult individuals for the four species tested for association were found in large patches: 92% for *C. hilariana*, 99% for *P. icicariba* and 69% for *V. crotonoides*. The correlation matrix showed positive association between adults of *C. hilariana* and *P. icicariba* and between adults of *P. icicariba* and *V. crotonoides*, but no significant association was detected between *C. hilariana* and *V. crotonoides* (table 2). Multiple regression analysis showed a marginal significant positive association between *C. hilariana* juveniles and *C. hilariana* adults ($P = 0.050$) and significant positive association between *P. icicariba* juveniles and *C. hilariana* adults ($P = 0.048$). No association between juveniles was detected (table 3).

Table 2. Correlation matrix between the number of individuals of three studied species in vegetation patches larger than 20 m^2. Spearman rank order correlation coefficients (*$P < 0.05$; **$P < 0.01$, $n = 30$).

	Clusia hilariana	*Protium icicariba*	*Vernonia crotonoides*
Clusia hilariana	–	–	–
Protium icicariba	0.44 *	–	–
Vernonia crotonoides	0.27	0.62 **	–

Table 3. Regression coefficients (β) of multiple regressions tested with Monte Carlo procedure (* marginally significant: $P = 0.05$; **significant at $P < 0.05$). Association of *Clusia*, *Protium* and *Vernonia* juveniles with their own adult individuals and with other species adults and juveniles. Data from vegetation patches larger than 20 m^2.

Y	X	β	*P*
Juveniles			
Clusia	*Clusia* adults	2.24	0.050*
	Protium juveniles	-0.19	0.068
	Protium adults	1.14	0.201
	Vernonia juveniles	-2.42	0.310
	Vernonia adults	0.57	0.166
Protium	*Protium* adults	2.05	0.202
	Clusia juveniles	-0.28	0.134
	Clusia adults	3.90	0.048**
	Vernonia juveniles	-1.98	0.384
	Vernonia adults	1.13	0.163
Vernonia	*Vernonia* adults	0.06	0.110
	Protium juveniles	0.00	0.315
	Protium adults	0.14	0.069
	Clusia juveniles	-0.01	0.251
	Clusia adults	-0.05	0.241

Discussion

Sexual vs. vegetative origin of regenerants – Despite the commonness of a trade-off between sexual reproduction and vegetative propagation (Abrahamson 1975, Bennett 1991) in extreme habitats a combination of sexual and asexual reproduction should give a plant optimal fitness (Abrahamson 1980). *Clusia hilariana*, *Protium icicariba* and *Andira legalis* showed this combination. However, their life strategies were clearly different: *C. hilariana* had a considerable contribution of vegetative reproduction and seedling occurrence was mostly inside tank-bromeliads; *P. icicariba* regenerants were mostly seed-originated, with occurrence inside dense patches, not frequently associated to bromeliads; and *A. legalis* showed no sign of ongoing regeneration, since only 20 individuals were found which were almost exclusively adults.

The relevance of vegetative propagation, via clonal growth and/or resprouting, has often been demonstrated for the regeneration of *restinga* species (Sampaio *et al*. 2004, 2005), including *C. hilariana* (Scarano *et al*. 2004) and *A. legalis* (Cirne & Scarano 2001). The absence of young plants of *A. legalis* suggests that widespread vegetative growth for this species may take place only in response to disturbance, as shown by Cirne & Scarano (2001) and Cirne *et al*. (2003) for another population in a *restinga* site subjected to occasional fire events. *Clusia hilariana*, instead, showed a more conspicuous asexual production of plants, which may confer advantages to these regenerants such as physiological integration, i.e. the capacity to share resources with the parent plant and guarantee resource supply during the establishment phase (Kroon & Kwant 1991, Stuefer 1994, Wijesinghe & Handel 1994).

The suitability of bromeliad rosettes for seed germination and seedling establishment has been shown for strangling *Clusia* and *Ficus* species in rain forests (Benzing 1990), for *Tabebuia* tree species in a Brazilian swamp forest (Scarano *et al*. 1997) and for *Clusia fluminensis* Planch. & Triana and *Erythroxylum ovalifolium* Peyr. shrubs among others, in a *restinga* farther south on the Rio de Janeiro coast (Macedo & Monteiro 1987, Fialho 1990, Fialho & Furtado 1993). This is the first time a comparative survey of plant occurrence inside and outside bromeliads has been conducted, and *C. hilariana* clearly is more present in bromeliads (see Sampaio *et al*. 2004, 2005 for bromeliad distribution and clonal growth in this site). It remains to be seen whether these plants will reach the soil later on, to establish and grow until the reproductive phase. The larger proportion of juveniles than seedlings of *C. hilariana* suggests that seedling-juvenile transition may face obstacles. These results are in agreement with reproductive biology studies on this species by Faria *et al*. (2006) and Martins *et al*. (2007), which showed great variation in seed set between years. *Protium icicariba*, conversely, seemed to be actively regenerating as seen by the reversed-J curve of population size structure. Thus, the two dominant species of this vegetation show contrasting reproductive strategies.

Plant-plant associations and succession – All significant associations found in this study were positive. This is in accordance with the reported prevalence of positive interactions between plants under harsh environmental conditions (Callaway *et al.* 2002, Brooker *et al.* 2008). *Clusia hilariana* and *P. icicariba* are co-dominant in the studied vegetation (Pimentel *et al.* 2007), and the great majority of large patches that are not dominated by *C. hilariana* present dominance of *P. icicariba*. Thus, the positive association between adult individuals of *C. hilariana* and juveniles of *P. icicariba*, as well as the positive association between adults of these two species, suggests that *P. icicariba* is successfully establishing under *C. hilariana* canopy. This is further evidence that patches with *C. hilariana* dominance are earlier in succession as compared with *P. icicariba* patches, which often present also a higher density and species richness of adult individuals (Dias *et al*. 2005). This highlights the role of *C. hilariana* in generating vegetation cover that will be later dominated by other woody plant species as an important process for maintenance of plant diversity in the studied vegetation.

In conclusion, facilitation, as assessed here by plant-plant positive associations, appeared to be the predominant interaction among the species studied in this community, although it was clear that not all species studied were nurse plants and that nursing was rather selective. Bromeliads played an important role in nursing *C. hilariana* seedlings, which later, as adults, will nurse a number of woody species (Zaluar & Scarano 2000, Liebig *et al*. 2001, Dias *et al*. 2005). This confirms the first and second expectations of this paper. *Protium icicariba*, despite showing a mutual positive association with *C. hilariana*, showed no nursing role as previously reported (Dias *et al*. 2005). It is noteworthy that vegetative propagation, unlike our third expectation, was not as relevant to the study species as previously reported in other studies. *Vernonia crotonoides* and *A. legalis* did not seem to be potential nurse plants. Thus, it seems that succession leading to an increase in complexity in the *restinga*, *i.e.* whether a given patch will grow in size and diversity along a given time scale, is largely dependent on positive interactions and nursing roles which are played effectively by some species but not by others.

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