

SHORT COMMUNICATION

Canopy composition influencing plant patch dynamics in a Brazilian sandy coastal plain

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Competition and predation have often been referred to as key forces regulating community structure. However, in the last decade great attention has been paid to the structuring role of positive interactions between plants, which occur when the presence of one species enhances fitness, survival or growth of another (Bruno *et al.* 2003, Callaway *et al.* 2002). Positive and negative interactions are unlikely to occur separately in nature (Brooker & Callaghan 1998, Holmgren *et al.* 1997), and the overall importance of positive interactions on community structure tends to be higher in resource-poor environments (Callaway *et al.* 2002). Moreover, this balance can be subjected to spatial and temporal shifts (Callaway 1998, Morris & Wood 1989, Tielbörger & Kadmon 1997) linked with plant ontogenetic development and/or changes on resource availability (see Callaway & Walker 1997).

Patchy plant communities, where vegetation islands are separated from each other by empty space, have often been surveyed for the balance of positive and negative plant–plant interactions (Kikvidze & Nakhutsrishvili 1998, Pugnaire *et al.* 1996, Weltzin & McPherson 1999). These environments often show the nurse-plant syndrome (see Franco & Nobel 1989), i.e. pioneer species shelter seedlings, young and/or adult individuals of other species through their ontogeny, which results in the formation of vegetation clumps or islands.

Although this syndrome is well known for the arid zone, there are few examples from tropical environments. One such example has been described for the *restinga*

vegetation in Brazil. Restinga is the name given to the vegetation mosaic that covers the Quaternary sand marine deposits of coastal Brazil (see detailed description in Lacerda *et al.* 1993). In the Restinga de Jurubatiba National Park (22°00′–22°23′S, 41°15′–41°45′W; state of Rio de Janeiro), the most typical vegetation type, out of ten described by Araujo *et al.* (1998), has a patchy vegetation cover scattered over a matrix of white sand and herbaceous clumps. The sandy soil of this open shrub formation has a low capability to retain water and nutrients and the surface of the bare sand can reach up to 70 °C at the peak of radiation on typical summer days. Rainfall averages 1000 mm y⁻¹. *Clusia hilariana* Schltld., a crassulacean acid metabolism (CAM) tree (Franco *et al.* 1999), is the dominant plant and appears as a central tree in most woody vegetation patches, although many patches do not have *Clusia* as the central plant, showing C₃ shrubs instead. Thus, patches dominated by different species are interspersed in the landscape. Since the marine sand deposits upon which these patches grow are quite homogeneous, we assume that patch composition is related to the dominant species in the patch, rather than to topography (which is uniformly flat) and soil characteristics (which is overall sandy and nutrient poor).

It has been suggested that *Clusia hilariana* is an important nurse plant in this study site (Liebig *et al.* 2001, Scarano 2002, Zaluar & Scarano 2000). In order to compare the nurse role of patches with *Clusia* dominance versus patches without *Clusia* dominance, we examined the differences in patch architecture (above-ground vegetation density and stratification) and woody species composition and size structure. Additionally, we performed an experiment of seed introduction for three woody species underneath these two types of patch and

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monitored germination, mortality and seedling growth over a 1-y period.

Thirty vegetation patches, of at least 5-m diameter were randomly chosen within a 4-ha plot. This lower limit of patch size was set because smaller patches tend to have very low frequency, abundance and diversity of seedlings. These patches were classified into two types (1) *Clusia* patches ($n = 19$): patches with dominance of *C. hilariana*, i.e. when the canopy of this species completely covered the canopy of other species; and (2) non-*Clusia* patches ($n = 11$): patches in which the other woody species were dominant. We installed a 1 × 2-m plot in the middle of each patch. The central position of the plots within the patches was chosen to exclude possible edge effects.

A cover pin frame approach (adapted from Kent & Coker 1992) was used to evaluate differences in vegetation architecture (above-ground branch and foliage density and stratification) between patch types. A thin stick (0.8 cm diameter), subdivided into four 90-cm sections, was positioned vertically in the plots to record: (1) the number of times the stick was touched by vegetation and (2) at which height interval each plant recorded touched the stick. This procedure was repeated each 0.5 m in each plot, adding up to 15 samples per plot. These 15 samples were pooled to comprise the measure of vegetation density (number of touches m^{-1}). Since hardly any data were available for the third and fourth height intervals for non-*Clusia* patches, due to the characteristics of this vegetation, it was not possible to perform multivariate analysis of variance (MANOVA). Thus, t-tests were used to test for differences between patch types in relation to density in each 90-cm height interval separately (Zar 1999). The data series of density on the second height interval was log-transformed so as to obtain homogeneity of variances.

For comparison of understorey species richness and density (individuals m^{-2}) between the distinct patch types, all rooted woody plants within the plots were counted, identified, and classified into three stage classes: seedlings (< 10 cm tall), juveniles (> 10 and < 50 cm tall) and adults (> 50 cm). Differences between patch types in regard to density of seedlings, juveniles and adults were tested with MANOVA and so was species richness of the three stage classes (Scheiner 1993). The data on density and richness of juveniles were log-transformed in order to obtain homogeneity of variances.

We also performed a similarity analysis between adults and understorey individuals (seedlings plus juveniles) within patches as an indirect measure of species establishment due to between-patch dispersal in each patch type, i.e. lower similarity values indicated higher between-patch dispersal, and vice-versa. We used the Jaccard coefficient (Magurran 1988) and t-test of arcsine-transformed data to test for differences between the averages (Zar 1999) of *Clusia* and non-*Clusia* patches. For these ana-

lyses, we used the data of all understorey plants rooted within the plots and for the adult class we also included species that had touched the stick on second, third or fourth height intervals.

Additionally, we performed an experiment of seed introduction to evaluate whether distinct patch types affected seed germination and early seedling growth and mortality. The experiment started on February 2000 when seeds of three woody species with distinct local abundance according to Pimentel (2002) were sown in each of the 30 patches where the diversity patterns had been sampled: *Protium icariba* DC. (Burseraceae), which is a co-dominant shrub to *Clusia*, *Erythroxylum ovalifolium* Peyr. (Erythroxylaceae), which has an intermediate abundance, and *Tapirira guianensis* Aubl. (Anacardiaceae), which has low abundance. Twenty seeds of each species were directly sown within the plot, 1 d after harvest and with no pre-treatment. They were placed underneath the litter of each of the 30 patches (i.e. 600 seeds per species), without any vegetation removal. Individual seeds were placed 5 cm apart and were marked with a small wooden stick, making three small blocks with 20 seeds, one block for each species, per plot. Germination was calculated as the number of germinated seeds divided by the total number of seeds within the plot. Seedling mortality was calculated as the proportion of dead seedlings within a plot at the end of the study. Shoot height of emerged seedlings was measured fortnightly between April and June 2000 and once every 2 mo from July 2000 to April 2001. The relative height growth rate (RHGR) was calculated as a modification of the formula proposed by Evans (1972).

$$RHGR = \frac{\ln H_f - \ln H_i}{T_f - T_i}$$

where H_i is the initial height value, H_f is the final height value and $T_f - T_i$ is the difference between final and initial measurement times. Differences in growth rate were tested using a factorial analysis of variance (ANOVA) with two factors: patch type (with two levels, *Clusia* and non-*Clusia* patches) and species (with three levels, *Protium*, *Erythroxylum* and *Tapirira*). In the analysis of RHGR, only *Protium* and *Erythroxylum* were considered due to the high mortality of *Tapirira* seedlings that resulted in a small number of replicates. Differences in germination and mortality were tested using factorial GLM model with binomial distribution and F values were corrected by the rate of overdispersion (Crawley 2002). Statistical analyses were done with the software R 1.6.2.

Non-*Clusia* patches showed a greater density of plant touches on the sampling sticks in the first height interval (i.e. the first 90-cm stick segment above the ground), in the second interval and adding up all the intervals, while the third interval did not show a significant difference between patch types (Table 1). It was not possible

Table 1. Stratification of vegetation density (number of touches m^{-1}) of patches with and without *Clusia hilariana* dominance. Vegetation density was recorded within a 1×2 -m plot along four stratified height intervals (i.e. each 90 cm in height). Data comprise mean \pm SE of untransformed data. Bonferroni $\alpha' = 0.013$.

Canopy density	<i>Clusia</i> (n = 19)	non- <i>Clusia</i> (n = 11)	P
0–90 cm	1.19 \pm 0.17	2.39 \pm 0.16	< 0.001
90–180 cm	1.15 \pm 0.20	3.97 \pm 0.52	< 0.001
180–270 cm	1.70 \pm 0.23	0.89 \pm 0.51	0.111
270–360 cm	0.99 \pm 0.15	0.44*	–
Total	1.33 \pm 0.12	2.70 \pm 0.25	< 0.001

*Single value because only one non-*Clusia* patch was tall enough to be recorded in this height interval.

Table 2. Summary table of ANOVA after MANOVA for plant density (individuals m^{-2}) and plant species richness within a 1×2 -m plot in vegetation patches with and without *Clusia hilariana* dominance. The table shows mean \pm SE of untransformed data.

Size class	<i>Clusia</i> (n = 19)	non- <i>Clusia</i> (n = 11)	P
Density			
Seedling	3.24 \pm 0.37	1.94 \pm 0.46	0.072
Juvenile	4.41 \pm 0.57	2.11 \pm 0.22	0.032
Adult	2.53 \pm 0.27	4.00 \pm 0.38	0.011
Richness			
Seedling	3.06 \pm 0.25	2.00 \pm 0.40	0.055
Juvenile	5.41 \pm 0.69	2.89 \pm 0.26	0.052
Adult	3.76 \pm 0.35	5.11 \pm 0.49	0.064

to test for differences in the fourth height interval, because only one non-*Clusia* patch was sufficiently tall to include this interval. *Clusia* patches were on average taller (3.8 ± 0.3 m; mean \pm SE) than non-*Clusia* patches (2.1 ± 0.1 m). *Clusia* patches often had larger area (152.6 ± 43.9 m²) than non-*Clusia* patches (66.8 ± 12.2 m²).

Understorey density was significantly different between patch types ($df = 3$, $F = 6.5$, $P = 0.003$). Density of juveniles, but not of seedlings, was higher in *Clusia* patches. However, adult density showed the opposite pattern, with greater values in non-*Clusia* patches (Table 2). Species richness also differed significantly between patch types ($df = 3$, $F = 3.8$, $P = 0.025$). Species richness of *Clusia* patches was significantly higher for seedlings and juveniles, although only marginally (Table 2). The Jaccard coefficient showed a significantly ($df = 28$, $t = 2.0$, $P = 0.05$) higher similarity between adults and understorey plants in non-*Clusia* patches (0.23 ± 0.03 , mean \pm SE of untransformed data) when compared with *Clusia* patches (0.14 ± 0.03).

The statistical analysis showed differences between species in germination ($df = 2$, $F = 19.9$, $P < 0.001$) and mortality ($df = 2$, $F = 7.6$, $P < 0.001$) and between patch types in RHGR ($df = 1$, $F = 6.8$, $P = 0.016$). No interaction between the two factors was detected for any of the tested variables. *Erythroxylum* showed the highest germination

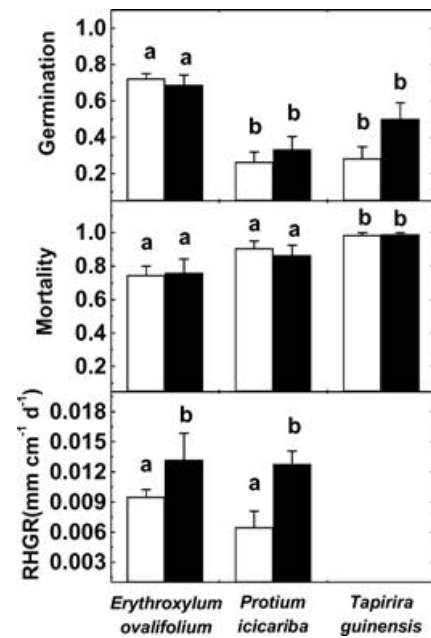


Figure 1. Germination, mortality and relative height growth rate (RHGR) for the three species used in the seed introduction experiment performed on *Clusia* patches (hollow columns) and non-*Clusia* patches (filled columns). Bars represent standard error. Different letters mean significant differences ($P < 0.05$) between patch types or species.

followed by *Tapirira* and *Protium*. *Tapirira* had the highest mortality: out of 228 germinated seeds only five seedlings survived in three patches (one *Clusia* and two non-*Clusia* patches). There was a higher RHGR in non-*Clusia* patches than in *Clusia* patches (Figure 1). These differences were due to the growth of the first 9 wk of the experiment, since from this point on there was hardly any growth.

The positive association between adult *Clusia hilariana* and juvenile density of other woody species supports previous evidence of the role of *Clusia* as a nurse plant on this site. Furthermore, patches dominated by *Clusia* were structurally different from those with no *Clusia* dominance. *Clusia* patches were more stratified, while non-*Clusia* patches were flatter and with a higher vegetation density. These architectural differences can lead to distinct environment conditions underneath the canopy and also distinct attractiveness to potential seed dispersers.

In spite of the higher juvenile density in *Clusia* patches, there were no differences in germination rate and seedling mortality between the two patch types. This suggests that the understorey of *Clusia* patches is not necessarily a better environment for germination and seedling survival than non-*Clusia* patches. The higher juvenile density and higher species richness of seedlings and juveniles on *Clusia* patches could result from a higher visitation of potential seed dispersers to this patch type. *Clusia* patches may provide preferential shelter and nesting sites for animals such as birds and bats in the restinga, because its height and architecture makes it the most conspicuous plant in

this vegetation type (Liebig *et al.* 2001). Moreover, the lower similarity between adults and understorey in *Clusia* patches suggests that there is a higher species invasion in this patch type, which probably resulted from a greater activity of dispersers.

Our results shall require further examination on the mechanisms that drive plant interactions within patches. The higher growth rates of introduced plants in non-*Clusia* patches seem to contrast with the general observation that *Clusia* acts as a nurse plant. The fact that seedling growth took place only during the first 9 wk suggests that the differences found may reflect the intrinsic capabilities of seedlings to grow until seed reserves were exhausted, which rules out the possibility of etiolation due to the denser canopy of the non-*Clusia* patches. Furthermore, higher seedling growth under non-*Clusia* patches is in agreement with the higher density of adults found in this patch type as compared to *Clusia* patches. Therefore, despite possibly favouring seed arrival by improving the activity of dispersers (see also Liebig *et al.* 2001), *Clusia* may later suppress plant growth in its understorey. Indeed, it has often been shown that preferred sites for germination are not always the best sites for plant growth (Morris & Wood 1989, Walker & Vitousek 1991) as competitive interactions may increase with time (Callaway & Walker 1997).

We suggest that the senescence and death of *Clusia* in a given patch could promote the growth of understorey juveniles and a change in architecture to a short and dense vegetation type. Thus, we believe that *Clusia* may have dominated some of the current non-*Clusia* patches in the past. This study confirms the role of *Clusia* as a nurse plant in this site, but suggests that competitive interactions may later take place between *Clusia* and understorey plants.

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