Density dependence vs. niche differentiation as explanations for the maintenance of tropical diversity in three understory monocot species

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Abstract: Several hypotheses have been put forth to explain the maintenance of biological diversity in the tropics. We examined two of these hypotheses, density dependence and niche differentiation, in three species of understory monocots with similar morphologies (Araceae, *Spathiphyllum eulvobirens;* Aracaceae, *Asterogyne martiana;* and Heliconiaceae, *Heliconia irrasa*) in the wet lowland forest of La Selva Biological Station, Costa Rica. We hypothesized that folivory and epiphylly would be positively density-dependent, which might have implications for the distribution of the three species. Our second hypothesis was that abiotic factors could affect the distribution of the three plant species, i.e., a species' abundance would change with light availability, soil type, and slope. Our results showed little evidence of density dependence, although *S. eulvobirens* had greater epiphylly in denser patches of conspecifics. Abundances of the three species were not associated with light levels. The distribution of *S. eulvobirens* appeared to be correlated with soil type and slope, but the other two species showed no change with these factors. The coefficients of dispersion for the three species were all greater than one, suggesting that density dependence is not a dominating force in population regulation on the scale we measured. Niche differentiation or other factors such as limited seed dispersal could explain the aggregated dispersion of all three species.

Key Words: Asterogyne martiana, *dispersion, epiphyll,* Heliconia irrasa, *herbivory,* Spathiphyllum eulvobirens

INTRODUCTION

Different hypotheses have been offered to explain the maintenance of biological diversity in the tropics (Wright 1992). Island refugia theory may help explain the generation of new species, but it does not explain why competitive exclusion has not eliminated many of them. One hypothesis suggests that intraspecific, negative density dependence may regulate species at low population levels, thus precluding the ability of any one species to outcompete other similar species (Wright 1992). Another hypothesis argues that niche differentiation occurs on a very fine scale. If microhabitats are finely partitioned, species may be able to coexist because each is a superior competitor in certain conditions (Wright 1992). We attempted to test these two hypotheses in three species of understory monocots with similar morphologies (Araceae, *Spathiphyllum eulvobirens;* Aracaceae, *Asterogyne martiana;* and Heliconiaceae, *Heliconia irrasa*) at La Selva Biological Station, Costa Rica.

We hypothesized that herbivory might be density-dependent, which could affect the distribution of plant species by preventing further increases in population size when abundant (Marquis 1994). If so, individuals found in denser patches of conspecifics should have increased levels of tissue loss to herbivores, (i.e., folivory) and more epiphylls than those at low densities. Further, we hypothesized that differences in abiotic resources could determine the distribution of these three understory species. Therefore, we predicted that the abundance of the three understory plant species would vary with different light levels, soil types, and/or slope.

In addition, we gained further insight into the relative importance of the two hypotheses by examining the spatial distribution patterns of the three species. Aggregated dispersion of a species may reflect patchy resources and niche differentiation. A uniform dispersion could be due to density-dependent forces maintaining a minimum distance between individuals.

METHODS

We sampled populations of *S. eulvobirens, A. martiana* and *H. irrasa* on 18-19 February 1999 in primary tropical rain forests of the La Selva Biological Reserve, Costa Rica. Samples were taken in primary forest along the Camino Experimental Sur and Camino Circular Lejano trails.

Density dependence

To evaluate intraspecific density-dependent interactions for the three species, we sampled 25 m^2 circular plots around a focal individual. For each of the three species, we chose seven plots in which the focal individual was surrounded by a high density of conspecifics, and seven plots in which the focal individual was surrounded by a low density of conspecifics. In all 42 plots, we counted the number of individuals of each species to estimate conspecific and total densities of the three species. We first recorded the individuals within 5 m^2 of the focal individual, and then those within 25 m^2. Since the density of leaves may be a more relevant measure of density experienced by herbivores, we also counted the number of leaves on each individual in a plot.

We looked at folivory and epiphylly on the five conspecific individuals closest to the focal plant in the 5 m^2 subplot. We estimated folivory by calculating the percent leaf loss on each leaf of each individual (see Brayce et al. 1999 for methods). On the same individuals, we estimated epiphylly as the percent of extant leaf surface area that was covered by epiphylls. We also used a penetrometer to measure leaf toughness for five individuals of each species to help explain patterns of herbivory.

Abiotic Factors

To investigate the effects of abiotic factors on the distributions of *S. eulvobirens, A. martiana* and *H. irrasa*, we randomly selected 25 m^2 circular plots on two different soil types as determined by a map generated by the La Selva GIS lab (Matt Clark, *pers. comm.*; 29 plots on alluvial soils, 20 on residual volcanic soils). Nineteen of the alluvial soil plots were surveyed along five randomly selected 50 m transects. At the center of all plots, light availability was estimated with a spherical densiometer. We also recorded whether the slope of the land was greater or less than 8° (sloped vs. flat) At each plot, we counted the number of individuals of each species. We used these densities to determine a dispersion coefficient (SD^2/mean) for each species. A coefficient < 1 indicates uniform dispersion, while a coefficient > 1 indicates aggregated dispersion.

RESULTS

Density dependence

Leaf tissue loss on *S. eulvobirens, A. martiana,* and *H. irrasa* was not associated with the density of conspecific leaves or individuals (*S. eulvobirens*: individuals: r^2=0.0002, df=13, P=0.96, leaves: r^2=0.00005, df=13, P=0.98; *A. martiana*: individuals: r^2=0.04, df=13, P=0.48, leaves: r^2=0.024, df=13, P=0.59; *H. irrasa:* individuals: r^2=0.22, df=13, P=0.09; leaves: r^2= 0.20, df= 13, P=0.11).

In *S. eulvobirens*, epiphylly increased with the density of conspecific leaves (r^2= 0.29, df= 13, P=0.045). In *A. martiana* and *H. irrasa*, however, epiphylly was not affected by the density of conspecific leaves (*A. martiana*: r^2= 0.02, df= 13, P=0.62; *H. irrasa*: r^2= 0.03, df= 13, P=0.53).

There was no evidence for intraspecific competition in any of the species, as measured by the number of leaves/individual vs. number of conspecific individuals (*S. eulvobirens*: r^2= 0.07, df= 13, P=0.36; *A. martiana*: r^2= 0.13, df= 13, P=0.20; *H. irrasa*: r^2= 0.02, df= 13, P=0.59). For interspecific density dependence, we found no changes in the number of leaves per individual with the number of total individuals per plot. (*S. eulvobirens*: r^2= 0.0002, df= 40, P=0.95; *A. martiana*: r^2= 0.0002, df= 41, P=0.77; *H. irrasa*: r^2= 0.06, df= 19, P=0.29).

Abiotic Factors

Densities of *S. eulvobirens, A. martiana* and *H. irrasa* varied across the landscape, but there was no association with light and the density of any of the three species (*S. eulvobirens*: r^2= 0.004, df= 47, P=0.68; *A. martiana:* r^2= 0.06, df= 47, P=0.09; *H. irrasa:* r^2= 0.02, df= 47, P=0.21). There was also no evidence that the total number of individuals per plot increased with light availability (r^2= 0.0005, df= 48, P=0.87).

Table 1. Densities (mean individuals/25m^2 ± 1 SE) and dispersion coefficients of three understory plant species across different abiotic regimes at La Selva Biological Reserve, Costa Rica. * indicates significantly different values with P<0.0001. † indicates significantly different values with P<0.0002.

Species	Density					Dispersion Coefficient
	Mean	Soil Type		Topography		
		Alluvial	Residual	Flat	Sloped	
	(n=49)	(n=29)	(n=20)	(n=36)	(n=13)	
S. eulvobirens	3.6 ± 0.60	1.6 ± 0.60*	6.5 ± 0.87*	2.4 ± 0.58†	7.2 ± 1.2†	5.0
A. martiana	5.9 ± 0.53	5.8 ± 0.63	6.0 ± 0.94	5.8 ± 0.59	6.0 ± 1.2	2.4
H. irrasa	1.4 ± 0.42	1.1 ± 0.45	2.0 ± 0. 79	1.5 ± 0.48	1.3 ± 0.86	6.0

We found that *S. eulvobirens* was significantly more abundant in residual volcanic soils than younger alluvial soils (Table 1; Wilcoxon Ranked Test, $X^2 = 20.36$, df=1, P<0.0001), but these soil types did not affect the abundance of *A. martiana* and *H. irrasa* (Table 1; *A. martiana*: $X^2 = 0.0009$, df=1, P=0.9755; *H. irrasa*: $X^2 = 0.65$, df=1, P=0.42). *S. eulvobirens* abundance was also greater on sloped terrain (Table 1; Wilcoxon Ranked Test, $X^2 = 13.52$, df=1, P=0.0002). There was no association between slope and the abundance of *A. martiana* or *H. irrasa*. (Table 1; Wilcoxon Ranked Test; *A. martiana*: $X^2 = 0.066$, df=1, P=0.08; *H. irrasa*: $X^2 = 0.36$, df=1, P=0.55).

Percent foliage loss was not significantly different between plants (*A. martiana* = 10.0 % ± 1.8, *S. eulvobirens* = 10.0 % ± 1.3, *H. irrasa* = 6.3 % ± 0.94; Wilcoxon Ranked Test, v=5.27, df=2, P=0.07), despite the fact that leaf toughness differed significantly among the three species (Wilcoxon Ranked Test, $X^2 = 12.59$, df=2, P=0.018), being highest in the palm species and lowest in the aroid species (*A. martiana* = 476.5 ± 18.4 g, *H. irrasa* = 297.5 ± 15.9 g, *S. eulvobirens* = 175.0 ± 22.3 g).We found the dispersion of all three species to be aggregated across the landscape, with *H. irrasa* more clumped than *S. eulvobirens*, which was more clumped than *A. martiana* (Table 1).

DISCUSSION

We found little evidence of intraspecific, negative-density-dependent forces acting on the three understory plant species studied. The increase in individual epiphylly with conspecific density in *S. eulvobirens* suggests density-dependent transmission of the epiphylls, although the effect of epiphylls on the fitness of their hosts is not clear (Kricher 1997). Density dependence, at least as we measured it, may not contribute to the patterns of population distribution of *S. eulvobirens*, and does not seem to explain the coexistence of the three species in the forest understory.

We also predicted that abiotic (density independent) factors may contribute to the distribution of these populations. We were surprised to find no increase in plant densities with increases in light, especially since species in the family Heliconiaceae are often found in high light environments, such as gaps (Stiles 1983). Understory species often attain their maximum photosynthetic rates at PAR levels less than direct sunlight, so it is possible that none of these three species would have a competitive advantage in high light conditions.

There was some evidence that other abiotic factors are more important in determining the spatial distributions of the different species. Our categorization of soil type as rich alluvial soil vs. residual volcanic soil surely oversimplifies the diversity and patchiness of soil types in the area we sampled. Yet, we found that *S. eulvobirens* was more common in residual soils. *S. eulvobirens* also appeared to be more abundant on sloped areas. These data suggest that soil and slope may be two axes along which *S. eulvobirens* differentiates its niche from *A. martiana* and *H. irrasa*.

Our abiotic sampling did not help explain the distribution of *A. martiana* and *H. irrasa*. However, soil type and other resources certainly vary (both spatially and temporally) on scales that we were unable to measure in two days. Other factors may be important in determining species distribution as well. First, morphological or physiological differences between species may indicate that they exploit different niches. For example, there were differences in leaf toughness among the species, which is often a strong determinant of a plant's resistance to herbivory. However, we found almost identical folivory rates between *S. eulvobirens* and *A. martiana*, even though the toughness measure for the palm was about twice that of the aroid. This indicates that leaf toughness may affect plant fitness in other ways. Secondly, interspecific interactions among these three plant species could also be important in understanding their distribution in the forest understory. However, the lack of association for leaves per individual of a species with the total number of individuals in a plot does not offer support for interspecific competition as an important factor.

As mentioned above, negative density dependence and niche differentiation have been two hypotheses used to explain the maintenance of diversity in the tropics. Our data indicate that niche differentiation might be more important than density dependence in determining the distribution of these three understory species, at least in terms of light, soil type, and slope. Although other variables could affect the relative importance of the two proposed mechanisms, the aggregated dispersion of all three species does not support negative density dependence. It could be that individuals of a species were aggregated because of patchy resources and niche differentiation, but it is also quite possible that limited dispersal or local disturbances could lead to clusters of individuals throughout the landscape. We feel the complexities demonstrated in attempting to determine the distribution of only three understory plant species is testament to the many factors that must be operating in the maintenance of biological diversity in the tropics.

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