ISLAND BIOGEOGRAPHY THEORY AS APPLIED TO TANK BROMELIAD COMMUNITIES

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Abstract: Island biogeography theory (IBT) states that isolated and small islands will have lower abundance of organisms and species richness than less isolated and larger islands. We examined isolated and grouped bromeliad tank communities (islands). As predicated by IBT, large bromeliads held more detritus and contained more organisms and morphotypes than small bromeliads. However, we found no significant differences in overall abundance and morphotype richness of invertebrates between isolated bromeliads and those in patches. This suggests that background colonization rates were similar for both types of bromeliads.

Key Words: invertebrates, phytotelmata, richness

INTRODUCTION

Island biogeography theory (IBT) has two components (Begon et al. 1990). Firstly, overall abundance of organisms and species richness of an island should decrease with distance from the mainland or population source, due to higher colonization rates. Secondly, species richness of an island should increase with island area because extinction rates are lower on larger islands. Larger islands will also have larger overall abundances of organisms than smaller islands.

This theory applies to archipelagos and other semi-isolated habitats. For example, greater numbers of herbivorous insects have been found on plants near large numbers of related plant species as compared to rare plant species (Begon et al. 1990). In the case of archipelagos, islands near many other islands should have higher colonization rates than isolated islands, due to colonization among islands.

Epiphytic tank bromeliads support isolated communities of aquatic invertebrates in the water and detritus that collect in their leaf bases (Utley et al. 1983). These tanks may act as islands, where dispersal and colonization processes create patterns similar to those predicted by IBT. In our study, we examined how invertebrate abundance and richness differed between isolated bromeliads and those in patches. We expected greater numbers of invertebrates and greater morphotype richness in bromeliads in patches than in isolated bromeliads, as well as a similar pattern for larger relative to smaller bromeliads.

METHODS

On 21 January 2005, we sampled 20 tank bromeliads in a cloud forest reserve at the Estacion Biólogica Monteverde, in Costa Rica. Ten bromeliads were isolated (no other bromeliads within 2 m) and ten were within a patch (at least one other bromeliad within 1 m). All were located within 2 m of the ground. We measured each plant's largest diameter from leaf tip to tip, number of leaves, and canopy cover.

We collected the water in each plant, and scraped the leaves to gather invertebrates and detritus.

We determined volume of water, strained the contents of each bromeliad, and placed detritus and invertebrates in trays for sorting. We searched each tray for 30 min, removed all invertebrates found, and sorted them by morphotype. Detritus was dried at 150° C for 4 h, and weighed to determine dry mass of detritus. We calculated water content as the difference between initial and dried sample weight.

We compared plant characteristics between patches and the effect of bromeliad size and distribution on number of morphotypes and organisms using one-way ANOVAs. We analyzed relationships between variables using a correlation matrix. We examined the effect of plant characteristics on number of morphotypes and organisms using indicator variables regressions. The regression model was:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon$$

where Y is the response variable (number of morphotypes or organisms), X_1 is the plant characteristic of interest, X_2 is a binary indicator variable of analysis, β_0 is the intercept, β_1 is the slope, β_2 is the change in intercept between patch types, and β_3 is the change in slope between patch types (Neter et al. 1996). We confirmed that data met the assumptions of normality and homogeneity of variances. Data were analyzed using JMP 5.0.1.

RESULTS

We found 44 invertebrate morphotypes in the bromeliads we sampled. These were primarily aquatic insect larvae, with the four most abundant belonging to the orders Diptera, Trichoptera, Dictyoptera, and Coleoptera (in decreasing order of abundance), and isopods. There was no difference in the mean number of morphotypes (patch = 8.7 ± 3.6, isolated = 7.8 ± 3.3; F = 0.34, df = 1, P = 0.57) or in the mean number of total organisms (patch 25.3 ± 14.4, isolated 31.1 ± 19.8; F = 0.56, df = 1, P = 0.46) between bromeliads in patches and those in isolation. Patch and isolated bromeliads also had the same number of leaves, plant width, water volume, and detritus mass (Table 1). However, these traits were all positively correlated to each other and to the number of morphotypes and total organisms per tank (Table 2). Therefore, as bromeliads increased in size, as determined by plant characteristics, the number of morphotypes and organisms significantly increased (Table 2).

For relationships between morpho-

Table 1. Differences in plant traits between patch and isolated bromeliads.

Traits	ANOVA Results	Patch	Isolated
# of leaves	F = 0.89, df = 1, 18 , P = 0.36	17.4 ± 1.2	15.8 ± 1.2
width (cm)	F = 0.24, df = 1, 18 , P = 0.63	45.5 ± 4.9	48.9 ± 4.9
water volume (ml)	F = 0.064, df = 1, 18 , P = 0.80	3.9 ± 0.3	4.0 ± 0.3
detritus mass (g)	F = 0.06, df = 1, 18 , P = 0.81	1.5 ± 0.4	1.6 ± 0.4

Table 2. Correlations (x to y) calculated by Spearman's Rho of tank bromeliad characteristics (patch and isolated combined) and number of invertebrate morphotypes and total organisms. (All variables except width and # of leaves were log-transformed)

X	Y	Spearman's Rho	P
# of leaves	width (cm)	0.48	0.03
detritus mass (g)	width (cm)	0.68	0.0009
	# of leaves	0.52	0.019
water volume (ml)	width (cm)	0.7	0.0005
	# of leaves	0.63	0.003
	detritus mass	0.89	< 0.0001
organisms	width (cm)	0.68	0.0009
	# of leaves	0.54	0.015
	detritus mass	0.72	0.0003
	water volume	0.73	0.0003
morphotype	width (cm)	0.61	0.004
	# of leaves	0.79	< 0.0001
	detritus mass	0.66	0.0016
	water volume	0.78	< 0.0001
	organisms	0.71	0.0004

types and organisms and plant characteristics, we tested for equality of slopes and intercepts between patch and isolated bromeliads using indicator variables regressions. No significant differences in slope or intercept were detected for any of these relationships (Table 3).

DISCUSSION

We found that large bromeliads, which held more detritus, contained more morphotypes and total organisms than small bromeliads. These results support the prediction of IBT that large islands harbor greater morphotype richness and overall organism abundances than small islands. A similar result was found by Yanoviak (2001) and Licona et al. (2003).

We found no significant differences in overall abundance and morphotype richness between isolated bromeliads and those in patches. Therefore, clumped and isolated bromeliads do not function as islands or archipelagos, at least on the scale at which we measured them. Background colonization from the surrounding forest, which applies to bromeliads both in patches and alone, appears to be fairly high. This would mean that single bromeliads in this forest at Monteverde do not function as isolated islands with infrequent colonization, and inter-island colonization rates are negligible compared to back-

Table 3. Parameter estimates of slopes and intercepts of regression of morphotype and number of organisms on plant characteristics. The comparison between the intercepts of isolated and patch bromeliads was insignificant (all P > 0.20). The comparison of their slopes was also insignificant (all P > 0.33).

Y	X	Intercept Isolated (P)	Intercept patch (P)	Slope Isolated (P)	Slope patch (P)
Morphotypes	Detritus	1.45 (0.0006)	1.37 (<0.0001)	0.31 (0.06)	0.45 (0.0004)
	Water vol.	-0.11 (0.85)	0.13 (0.80)	0.52 (0.004)	0.50 (.003)
	# of leaves	0.08 (0.87)	0.23 (0.83)	0.12 (0.004)	0.11 (0.01)
	Plant width	0.68 (0.06)	0.90 (0.13)	0.03 (0.003)	0.03 (0.06)
Number of Organisms	Detritus	2.3 (<0.0001)	2.16 (<0.0001)	0.57 (0.003)	0.57 (0.004)
	Water vol.	0.13 (0.83)	0.58 (0.47)	0.78 (0.0007)	0.63 (0.01)
	# of leaves	1.7 (0.13)	0.77 (0.45)	0.10 (0.16)	0.13 (0.05)
	Plant width	1.73 (0.01)	0.91 (0.14)	0.03 (0.02)	0.05 (0.004)

ground colonization.

As indicated above, another possible reason we saw no differences in number of organisms or morphotypes between patch and isolated bromeliads was because we measured bromeliad communities at too small of a spatial scale. We defined isolated and patch bromeliads based on the assumption that 1 m was close enough for aquatic invertebrate dispersal by crawling between bromeliads but 2 m was too far. However, while aquatic insect larvae cannot travel far between bromeliads, adult insects of the same species can travel large distances to lay their eggs. Adult insects may be equally able to reach isolated and patch bromeliads as we defined them.

Our results support that IBT applies to bromeliad communities on a small scale, where size is important but distance is not. It would be interesting to examine colonization rates of tank bromeliads on a larger scale (i.e., between distinct forest patches or different mountain ranges) to see if the effect of distance on bromeliad community composition is consistent with IBT.

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