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EFFECTS OF HABITAT STRUCTURE AND PREY AVAILABILITY ON ABUNDANCE OF THE LYNX SPIDER *PEUCETIA VIRIDENS*

JENNY E. JUN AND ANNA R. NOWOGRODZKI

Abstract: To test the hypothesis that *P. viridens* abundance varies with habitat structure and insect abundance, we quantified habitat structure as well as numbers of insects and *P. viridens* caught with sweep nets. Spider abundance varied among habitats and increased with flower number. Neither habitat nor insect abundance in sweep net samples affected *P. viridens* abundance. *P. viridens* abundance may be driven more by pollinator abundance (which probably responds to flower number) than by the abundance of insects within the vegetation.

Key Words: oxyopidae

INTRODUCTION

Spider abundance may respond to physical habitat structure and prey abundance (Arango et al. 2000, Foelix 1996). Some spiders select habitats with greater prey abundance, though some do not (Foelix 1996). We hypothesized that abundance of *Peucetia viridans* (Oxyopidae), the green lynx spider, would increase with increasing prey abundance and would respond to differences in physical habitat structure. Because we focused on physical habitat structure and its effect on prey availability, we examined insects within the vegetation, rather than flying insects visiting the patch.

METHODS

We sampled four 1 m^2 plots in each of three habitat types at Palo Verde National Park in Costa Rica: areas dominated by *Justicia comata* (Acanthaceae), a mix of low grass and *J. comata*, and low grass only. *J. comata* was producing abundant flowers at the time of sampling. In each plot, we counted the number of flowers and visually estimated percentages of green and brown vegetative ground cover. To estimate mean plant height, we measured the height of three haphazardly selected plants in each plot. In *J. comata* plots, we counted the number of stems per plot. In mixed and low grass plots where this was not practical, we counted stems in three haphazardly placed quadrats of 222

cm^2 area, and then estimated total stem density/m^2. We assessed abundance of spiders and insects by sweep netting eight times in a crosshatched pattern covering the entire plot area, and counting all individuals in the samples.

We used JMP 5.0.1 to perform one-way ANOVAs to determine whether habitats differed in structural characteristics, insect abundance, or *P. viridens* abundance. We used linear regression to assess whether *P. viridens* abundance was significantly related to number of flowers, percent vegetation cover, mean plant heights, or insect abundance across habitats.

RESULTS

J. comata plots had greater mean plant height (F = 26.3, df = 2, 9, P = 0.0002, multiple-comparison Tukey test P < 0.05) and total number of flowers (F = 17.8, df = 2, 9, P = 0.0007, multiple-comparison Tukey test P < 0.05) than both mixed and grassy plots. Mixed plots had higher percent green cover than grass plots (F = 5.54, df = 2, 9, P = 0.027, multiple-comparison Tukey test P < 0.05), but the reverse was true for percent brown cover (F = 7.07, df = 2, 9, P = 0.014, multiple-comparison Tukey test P < 0.05). Stem density data were not statistically comparable because of different sampling methods, but stem density appeared much higher in mixed and grassy plots than in *J. comata* plots.

P. viridens abundance was significantly higher in *J. comata* plots than in grass plots (F = 4.46, df = 2, 9, P = 0.045, multiple-comparison Tukey test P < 0.05). Across all three habitats, *P. viridens* abundance increased significantly with increasing total number of flowers (r^2 = 0.39, df = 10, P = 0.029; Fig. 1). There was a marginally significant trend towards increasing *P. viridens* abundance with increasing mean plant height (r^2 = 0.29, df = 10, P = 0.074).

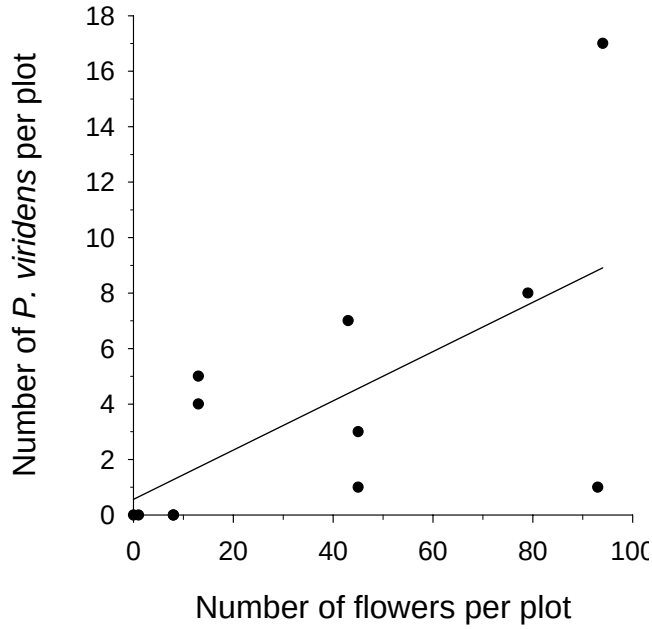

Figure 1. Number of the spider P. viridens per 1 m^2 plot, as a function of number of flowers per plot, including data from three habitat types (J. comata only, a mix of J. comata and low grass, and low grass only) at Palo Verde, Costa Rica.

There was no significant difference among insect abundances in the three habitats (F = 1.23, df = 2, 9, P = 0.34). Insect abundance had no significant effect on abundance of *P. viridens* (r^2 = 0.06, df = 10, P = 0.45).

DISCUSSION

The number of *P. viridens* increased with number of flowers across all three habitats, even though the habitats differed structurally. More flowers may attract more pollinators, and lynx spiders may be responding to the abundance of insects vis-

iting flowers, which are unlikely to be caught in sweep nets. There may also be habitat differences important to *P. viridens* that we did not assess. Our design could be improved by using comparable measures of stem density and foliage height diversity. Our findings suggest that research examining the relationship between pollinator abundance and *P. viridens* abundance across varying flower densities would be informative.

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STRUCTURAL HETEROGENEITY AND NUTRIENT AVAILABILITY EFFECTS ON SIMULATED BROMELIAD INVERTEBRATE COMMUNITIES

TIMOTHY R. MATSUURA, LAKSHMI NARAYAN AND CAYELAN C. CAREY

Abstract: Nutrient availability and structural heterogeneity are important regulators of invertebrate communities. We manipulated these effects separately to understand their relative importance on aquatic invertebrate abundance and diversity in simulated bromeliad tanks. We found that both increased structural heterogeneity and nutrient availability increased invertebrate abundance, but had no effect on community diversity. An interaction between these two factors had a marginal influence on community abundance, suggesting that increased structural heterogeneity may allow invertebrates to better utilize high nutrient availability.

Key Words: aquatic invertebrates, bromeliad tank, phytotelmata

INTRODUCTION

Nutrient availability and structural heterogeneity are important determinants of community diversity and abundance. Heterogeneity of structure and nutrients creates unique combinations of habitat and food resources that can be utilized by varied taxa. For aquatic invertebrate communities, organic matter provides both structural heterogeneity and nutrient availability, making it difficult to assess the relative importance of these factors.

We used simulated bromeliad tanks to assess the effects of nutrient availability and structural heterogeneity on invertebrate communities. We hypothesized that different levels of nutrients and structural complexity would influence both the abundance and diversity of aquatic invertebrates. At increased nutrient availability and increased structural heterogeneity levels, we predicted that abundance and diversity of invertebrates would be greatest due to partitioning of nutrients. Similarly, with low levels of nutrients and decreased structural heterogeneity, competitive exclusion for limited resources would increase, and exhibit the lowest abundance and diversity of invertebrates. In intermediate treatments, we expected that high nutrient availability and low structural heterogeneity would yield higher invertebrate abundance with lower diversity because a competitive dominant would monopolize resources and multiply. Finally, low nutrient availability and high structural heterogeneity would yield lower invertebrate abundance but higher diversity because resources would be limited and highly partitioned.

METHODS

On 21 and 22 January 2005 we applied four treatments to simulated bromeliad tanks: high structural heterogeneity and high nutrient availability, high struc-

tural heterogeneity and low nutrient availability, low structural heterogeneity and high nutrient availability, and low structural heterogeneity and low nutrient availability. We gathered 15 bromeliads from the ground and base of trees close to the Sendero Principal ~300 m northeast of La Estación Biológia Monteverde, in Monteverde, Costa Rica. We collected invertebrates by rinsing the bromeliad leaves with filtered stream water into a homogenized solution. We added 150 mL of this solution to 12 opaque plastic cups with 100 mL of filtered stream water to increase volume.

To create high and low nutrient availability treatments, we cut *Quercus costaricensis* leaves (low nutrient content) and *Ficus* spp. leaves (high nutrient content) (Gonzalez and Seastedt 2001) into 1 cm^2 squares. Low nutrient treatments contained 0.3 g of *Ficus* and 3.9 g of *Q. costaricensis* squares and high nutrient treatments contained 3.9 g of *Ficus* and 0.3 g of *Q. costaricensis* squares. To simulate naturally-occurring structural heterogeneity, we added three squares of 5 cm^2 nylon mesh to each tank. Treatments of low structural heterogeneity contained three squares of 0.20 mm mesh and high structural heterogeneity treatments contained one piece each of 0.50 mm, 0.20 mm, and 0.04 mm mesh. Three cups were assigned to each treatment.

All treatments were placed uncovered at the base of the Sendero Principal for approximately 24 h. Mesh and leaves from each cup were rinsed with filtered water and removed, leaving a solution containing all surviving invertebrates in 250 mL of water. The solution was homogenized and five microscope counting trays were prepared per tank. We used mean abundance and diversity per tray to quantify invertebrates for each cup and identified the invertebrates to order.

Mean invertebrate abundance and diversity for the four treatments were compared with a two-way ANOVA. Diversity was calculated using a species richness index, Simpson's diversity index, Simpson's evenness index, Shannon diversity index and Shannon evenness index.

RESULTS

Total invertebrate abundance per cup was increased with higher nutrient level ($F = 10.25$, $df = 3, 8$, $P = 0.01$, Fig. 1) and structural heterogeneity ($F = 14.20$, $df = 3, 8$, $P = 0.006$), and there was a weak interaction between these parameters ($F = 3.63$, $df = 3, 8$, $P = 0.09$).

For the five most abundant invertebrate orders, we tested for effects of nutrient level, structural heterogeneity, and an interaction between these two factors on abundance of five most abundant invertebrate orders (Table 1). Both nutrient level and structural heterogeneity increased abundances of Coleoptera and Nematoda, while only structural heterogeneity increased Copepoda abundance. Nematoda alone showed increases in abundance from an interaction between resource level and structural heterogeneity. Annelida abundance was not affected by any of the treatments.

All measures of richness, diversity,

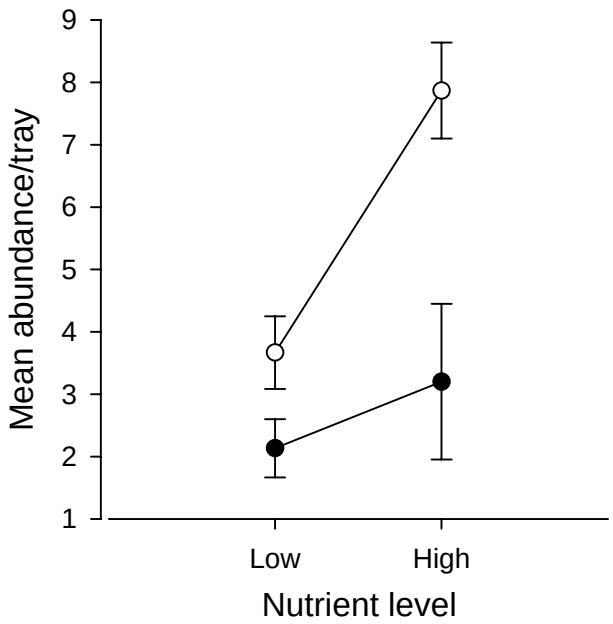

Figure 1. Mean invertebrate abundance per tray increased from low to high nutrient treatments for both low structural heterogeneity (filled circles) and high structural heterogeneity (open circles) treatments. The interaction between these two factors caused a marginally significant increase in invertebrate abundance (see text.)

and evenness showed no effects of nutrients, structural heterogeneity, or an interaction (Table 2).

DISCUSSION

Our study showed that higher nutrient levels and structural heterogeneity independently increase invertebrate abundance. Higher nutrient availability leads to greater total abundance, while increasing structural heterogeneity may increase resource partitioning and provide refugia from predators or interference competitors. High structural heterogeneity also increased the effect of greater nutrient availability on invertebrate abundance, although the test for an interaction between these factors was only marginally significant. This effect could be due to high structural heterogeneity generating an environment where different taxa can exploit increased nutrient availability.

We propose two possible mechanisms for differing abundances between treatments. First, Nematoda and Copepoda can reproduce several times in a 24 h period, and their reproduction could be stimulated quickly by increased nutrient availability (Pennak 1953). Second, reduced competition as a result of higher nutrient levels and more varied resource niches from greater structural heterogeneity could decrease competitive exclusion and invertebrate mortality.

The trends for the five most abundant invertebrate orders in our samples follow, generally, the trends found for total abundance. However, Annelida, the fifth most abundant order, did not exhibit any effects between treatments. This difference may be due to this order's preferential feeding on particulate substrate at the bottom of stagnant pools (Pennak 1953). If annelids were not feeding on leaf material or migrating through our simulated bromeliad tank, they would not be affected by varied structural heterogeneity or nutrient availability.

Our tests for differences in diversity across treatments showed no significant effects of nutrient level, structural heterogeneity, or an interaction of these two factors. This could be due to our identification being limited to the level of orders, which would mask diversity at a finer taxonomic scale.

Table 1. Two-way ANOVA results for effects of nutrient availability, structural heterogeneity and an interaction between nutrients and structure on abundances on the five most common invertebrate orders (df = 3, 8 for each test). Mean abundance is the number of invertebrates per tray.

Order	Mean abundance	Effect	F	P
Copepoda	1.59			
		Nutrients	2.00	0.20
		Structural heterogeneity	8.22	0.02
		Nutrients * structural heterogeneity	2.00	0.20
Nematoda	0.81			
		Nutrients	14.79	0.005
		Structural heterogeneity	11.46	0.01
		Nutrients * structural heterogeneity	6.06	0.04
Diptera	0.55			
		Nutrients	1.76	0.22
		Structural heterogeneity	3.67	0.09
		Nutrients * structural heterogeneity	1.76	0.22
Coleoptera	0.43			
		Nutrients	9.95	0.01
		Structural heterogeneity	4.98	0.06
		Nutrients * structural heterogeneity	1.71	0.23
Annelida	0.25			
		Nutrients	0.16	0.70
		Structural heterogeneity	0.02	0.90
		Nutrients * structural heterogeneity	0.45	0.52

Other potential limitations of our study include predation and colonization that could have occurred during the 24 hours when samples were left uncovered. We left our tanks uncovered to simulate the natural processes occurring in bromeliad tanks, but these effects on our tanks may not be indicative of those in natural systems. Further research including replication with predators could extend the conclusions of our study to natural systems.

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Table 2. Two-way ANOVA results for the effects of nutrient availability, structural heterogeneity, and an interaction on richness, diversity and evenness indices, df = 3,8 for each test.

Diversity index	Effect	F	P
Species richness			
	Nutrients	0.57	0.47
	Structural	0.57	0.47
	Nutrients * structural heterogeneity	0.57	0.47
Simpson's diversity index			
	Nutrients	0.70	0.43
	Structural	0.04	0.85
	Nutrients * structural heterogeneity	0.43	0.53
Simpson's evenness index			
	Nutrients	0.12	0.74
	Structural	0.61	0.46
	Nutrients * structural heterogeneity	0.08	0.79
Shannon diversity index			
	Nutrients	0.71	0.42
	Structural	0.27	0.62
	Nutrients * structural heterogeneity	0.33	0.58
Shannon evenness index			
	Nutrients	0.30	0.60
	Structural	0.40	0.55
	Nutrients * structural heterogeneity	0.02	0.89

EFFECTS OF TREE FALL ON MACRO-INVERTEBRATE ABUNDANCE AND DIVERSITY IN A TROPICAL STREAM

DANIEL J. MADIGAN, CHAD M. VALDERRAMA AND GABRIEL H. CALVI

Abstract: Allochtonous inputs can affect invertebrate community structure in streams. We compared the aquatic invertebrate community structure around a recent and an older tree fall in the Quebrada Machina in Costa Rica. We hypothesize that invertebrate communities would change with tree fall age. We found that the branches and leaves of fallen trees supported a more abundant and diverse aquatic invertebrate community than did the rocks around tree falls. We also found a difference in invertebrate functional feeding group composition between the old tree fall and new tree fall, with a greater proportion of filter feeders in the branches of the new tree fall and more gatherers in the old tree fall. We propose that these results reflect a difference in available organic matter between the two sites.

Key Words: functional feeding group, gatherers, shredders, stream invertebrates

INTRODUCTION

In a shallow forest stream, allochthonous inputs of terrestrial organic matter may serve a dominant role in establishing community structure (Fisher and Likens 1972, Minshall et al. 1983). Invertebrate communities are often divided into functional feeding groups including filterers, scrapers, shredders, gatherers, and predators. These feeding groups comprise a variety of trophic levels and have been recognized as essential parts of stream communities (Lehmkuhl 1979).

We studied the aquatic invertebrate community around a recently fallen tree and an older, more decomposed tree fall. We hypothesized that the aquatic invertebrate community structure would be affected by tree falls and would change with the amount of time that the fallen trees had been in the stream. Specifically, we predicted higher invertebrate abundances and diversity in the old tree fall where invertebrates would have more time to colonize. We also expected the proportions of the functional feeding groups to differ between the two tree falls, as their different ages would cause different levels or distributions of nutrient availability between the two sites. We predicted that the older tree fall, with more decomposed leaves, would have more shredders and scrapers than the newer tree fall while the new tree would have more filterers.

METHODS

We surveyed the macro-invertebrate communities around two tree falls of different ages in the Quebrada Machina near the Estacion Biologica Monteverde, Costa Rica. We used a kick-net to sample the benthic fauna at four locations under and around a recent tree fall (new). We collected nine samples of invertebrates: three

from 25 m upstream of the tree fall, three from 25 m downstream, and three from underneath the trunk and crown of the fallen tree. Each sample consisted of all invertebrates collected from under two rocks of similar size. Four other samples were collected from the leaves and branches of each fallen tree by holding the kick-net in front of the branches and shaking them. We repeated these collection methods at the nearest older fallen tree (old) approximately 0.5 km upstream from the new tree fall. The new and old tree falls had similar diameters and were both orientated lengthwise within the stream. The old tree fall had lost all of its leaves, while the leaves were still present on the branches of the new tree fall.

We sorted invertebrate samples and recorded invertebrate abundance, taxa (to family), and functional feeding groups (Lehmkuhl 1979) for each tree fall, and for specific locations within each tree fall. Two-way analyses of variance were used to compare number of individuals in each invertebrate functional feeding group, number of families, and total invertebrate abundances between the two tree falls and between specific locations within each tree fall.

RESULTS

We found a total of 575 individuals from 19 invertebrate families from the two sites (Appendix A). Filterers and gatherers comprised the majority of individuals in all samples, and most of these were black flies (Diptera: Simuliidae) (Appendix A).

We found a significant effect of location on number of individuals per sample More individuals were found on branches than in other locations in the stream at both the new and old tree fall ($F = 2.57$, $df = 3,18$, $P < 0.01$; Fig. 1). There was no effect of tree age on number of individuals per sample ($F = 2.57$, $df = 1, 18$, $P = 0.13$) and no significant interaction between tree age and location for the number of individuals per sample ($F = 0.95$, $df = 3, 18$, $P = 0.44$).

We also detected a significant effect of location ($F = 7.88$, $df = 3, 18$, $P < 0.01$) and tree age ($F = 14.62$, $df = 1, 18$, $P < 0.01$) on the number of taxa (families) per sample. Samples from the new tree branches contained more taxa than the other locations

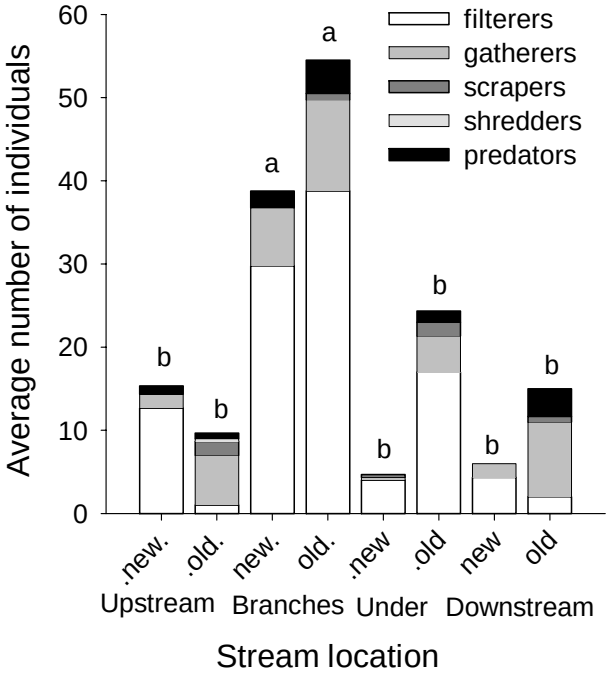

Figure 1. Average number of individuals in each functional feeding group found in each stream location. More individuals were found on the branches of both old and new tree falls. In the new tree, filterers had the same proportion in all locations. In the old tree, filterers had a higher proportion in and under the branches. Different letters (a, b) indicate groups that are significantly different (Tukey multiple comparison test).

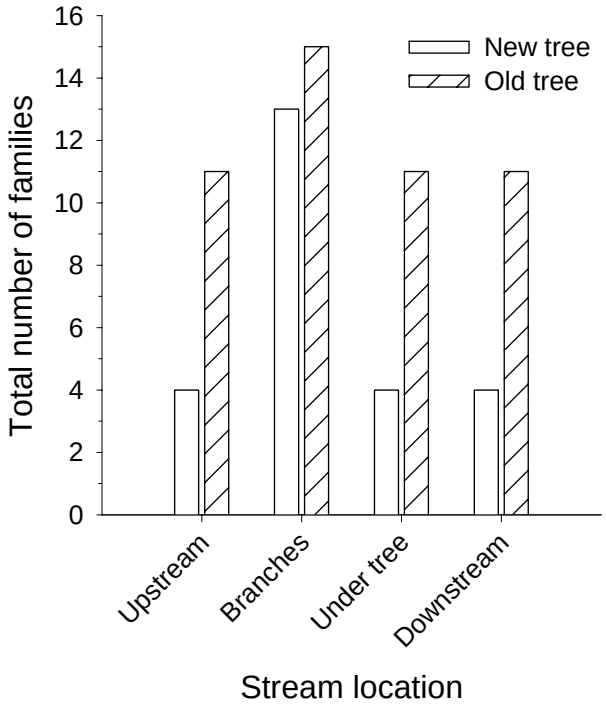

Figure 2. Number of taxa (families) found in each stream location for both a new and an old tree fall. At the old tree site, there were significantly more taxa in the branches than in other locations.

around the new tree (Fig. 2). There was no significant interaction between tree age and location for the taxa per sample ($F = 0.58$, $df = 3, 18$, $P = 0.63$).

There was also a significant effect of location (2-way ANOVA, $F = 3.96$, $df = 3, 18$, $P < 0.01$) and tree age ($F = 15.40$, $df = 1, 18$, $P = 0.03$) on number of (filterers / (filterers + gatherers)) per sample. In the new tree fall, filterers and gatherers were found in approximately the same proportions at all locations (Fig. 3). There was no significant interaction between tree age and location for the taxa per sample ($F = 2.13$, $df = 3, 18$, $P = 0.13$). In the old tree fall, filterers had a marginally significant higher proportion in the branches and the rocks underneath the branches then at other locations within that tree fall (Fig. 3).

DISCUSSION

Tree falls add both structural complexity and nutrients to a stream. This may have contributed to the high aquatic invertebrate abundances found in submerged leaves and branches. In our study, black fly larvae, a filterer, comprised most of these invertebrates, and is a highly mobile and abundant invertebrate in Costa Rican streams (Vargas and Fallas 1983). Its mobility may allow it to colonize quickly after a tree falls into a stream. Since black flies filter fine particulate matter from surrounding waters, they were probably using tree fall branches and leaves as substrate and not as a nutrient

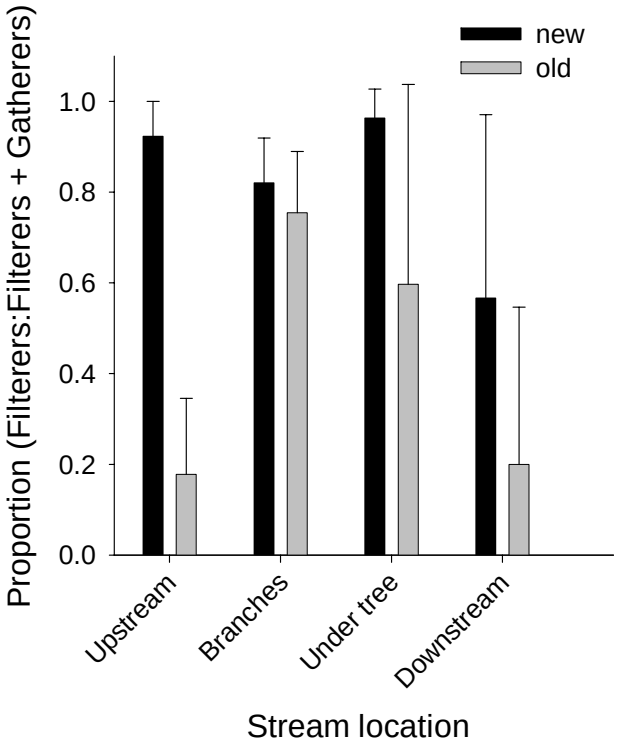

Figure 3. Mean (± 1 SE) proportions of filterers to filterers + gathers in different locations of the old and new tree fall sites (n = 3 samples for upstream, under tree, and downstream, n = 4 for branches). In the new tree fall, filterers have the same proportion in all locations. In the old tree, there were proportionally more filterers in and under the branches.

resource. The high structural complexity of tree fall branches and leaves probably also provided substrate supporting the greater number of invertebrate families found associated with branches and leaves.

Invertebrate gatherers, represented in our study primarily by Elmidae, Chironimidae, Amphipoda, and Baetidae, require undissolved fine particulate organic matter. Higher total abundance of gatherers at the old tree fall (Fig. 1) and higher gatherer abundances relative to filterers at the old tree fall (Fig. 3) suggest a difference in available organic matter between the two sites. Leaves at the new tree fall were still green and unfragmented, a form unavailable for consumption by invertebrate gatherers (Hauer and Lamberti 1996). At the old tree fall the branches served as 'debris dams' in which allochtonous leaf inputs could collect. These leaves were fragmented and partially decomposed, and therefore more available for consumption by gatherers. Thus, as tree falls age, they may act not only as substrate for filterers but also as nutritional resource retainers that support invertebrate gatherers.

The results of our study indicate that structural and nutritional resources provided by tree falls may change with time and that a tree fall in a stream provides complexity that supports high abundance and variety of stream invertebrates.

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Appendix A.

FFG	Family	Tree	Upstream	Branches	Under tree	Downstream
Filterer	Simuliidae	New	38	110	10	11
		Old	2	142	46	6
	Hydropsychidae	New	0	9	2	2
		Old	0	12	5	0
	Polycentropodidae	New	0	0	0	0
		Old	1	1	0	1
Gatherer	Elmidae (small)	New	4	6	1	0
		Old	7	12	0	4
	Elmidae (medium)	New	0	2	0	0
		Old	0	6	1	2
	Elmidae (large)	New	0	4	0	5
		Old	1	2	2	1
	Amphipoda	New	0	2	0	0
		Old	0	15	0	1
	Chironomidae	New	0	6	0	0
		Old	3	1	8	16
	Tricorythidae	New	1	8	0	0
		Old	0	0	0	0
	Baetidae	New	0	0	0	0
		Old	3	7	1	3
	Limnephelidae	New	0	0	0	0
		Old	0	1	0	0
	Platyhelminthes	New	0	0	0	0
		Old	2	0	0	0
Scraper	Psephenidae	New	0	0	1	0
		Old	1	1	0	0
	Leptophilibidae	New	0	0	0	0
		Old	4	1	5	1
Shredder	Odontocera	New	0	0	0	0
		Old	1	0	0	0
Predator	Coenagrionidae	New	2	4	0	0
		Old	0	3	0	0
	Tipulidae	New	0	2	0	0
		Old	0	0	0	0
	Perlidae	New	0	0	0	0
		Old	1	8	1	0
	Libellulidae	New	0	0	0	0
		Old	1	0	1	1
Total		New	45	153	14	18
		Old	23	212	70	36

SUCCESS OF EPIPHYTIC BRYOPHYTES OVER AN ELEVATIONAL GRADIENT

JONATHON C. RAFFENSPERGER AND CHELSEA L. WOOD

Abstract: Bryophyte abundance and success in tropical forests is tightly linked to environmental conditions. We investigated the effects of elevation, canopy openness and wind speed on the percent cover, mat depth and hanging morphology of mosses on the western slope of the Continental Divide near the Estación Biológica Monteverde, Costa Rica. We found that the percent moss cover was positively related to elevation and canopy openness and negatively related to wind. Both mat depth and hanging moss abundance were positively related to elevation. Elevation accounted for the greatest part of the variance in all three response variables. This suggests that moisture level, a correlate of elevation, may be the controlling factor in bryophyte success in this cloud forest landscape.

Key Words: abiotic factors, cloud forest, elevation-moisture gradient, epiphytes, mosses

INTRODUCTION

The abundance and success of epiphytic bryophytes in montane cloud forest vary with several abiotic factors (Nadkarni 2000). Mosses, which lack vasculature for internal water transport, require a very wet environment for growth (Proctor 2000). As photosynthesizers, mosses also require access to light. Exposure to wind should be an important influence as well, since strong gusts could dislodge loosely-attached epiphytes.

During the transitional and dry seasons (November - April), an elevation-moisture gradient exists along the western slope of the Continental Divide near Estación Biológica Monteverde, Costa Rica, with water from clouds, mist and wind-driven precipitation increasing with elevation (Clark et al. 2000). Therefore, we expected that percent moss cover and moss depth would be positively related to elevation in this region. Also, if wind speed is higher on the ridgeline than at lower elevations, then mosses dangling from branches would be more affected than those on tree trunks.

Specifically, we predicted that hanging mosses would first increase with elevation, and then decrease at the highest elevations where their large surface area makes them prone to being dislodged by wind. Conversely, mosses on tree trunks could increase consistently with elevation. We also predicted that canopy openness would be positively related to moss cover, mat depth and abundance of hanging mosses.

METHODS

On 21 January 2005, we examined moss cover and mat depth on 45 trees at varying elevations in the cloud forest around and above the Estación Biológica Monteverde, Costa Rica. We measured epiphytic moss along the Sendero Principal

at 20 m elevational intervals between 1420 m and 1700 m of elevation, sampling three trees at each interval. Trees > 1 m in diameter at breast height were selected haphazardly at each elevation.

To assess percent moss cover, we placed a 50 cm X 50 cm string sampling grid, with 100 5 cm X 5 cm squares, on the trunk of each tree. We then counted the number of squares that had > 50% moss cover, and measured mat depth in three randomly selected squares using a ruler. The sampling grid was always placed at breast height on the northwest face of the tree to control for direction of and relative exposure to light and wind. At each tree, we also measured elevation and wind speed with a digital weather station (Skymaster SM-28, Speedtech Instruments), and canopy openness with a spherical densiometer (Model-C, Forest Densiometers). We counted the number of branches with hanging moss for all branches visible from the trail at each sampling interval.

We used stepwise multiple regressions to examine the responses of our dependent variables to measurements of abiotic influences. We put wind speed data into three arbitrary groups based on elevation (i.e., 1420-1500 m, 1501-1600 m and 1601-1700 m) and used a one-way ANOVA and a multiple comparisons post-hoc test to assess differences between them. A linear regression was used to determine the relationship between canopy openness and elevation. Analyses were performed using JMP 5.0.1, and all data met or were transformed to meet the assumptions of parametric tests.

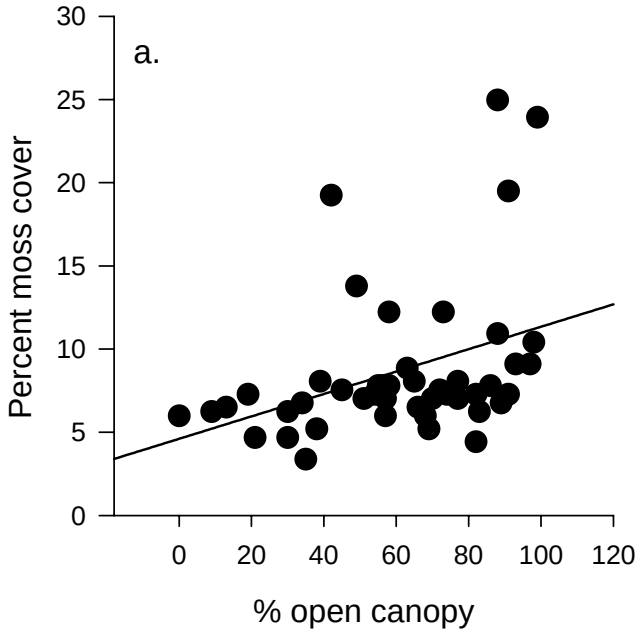
RESULTS

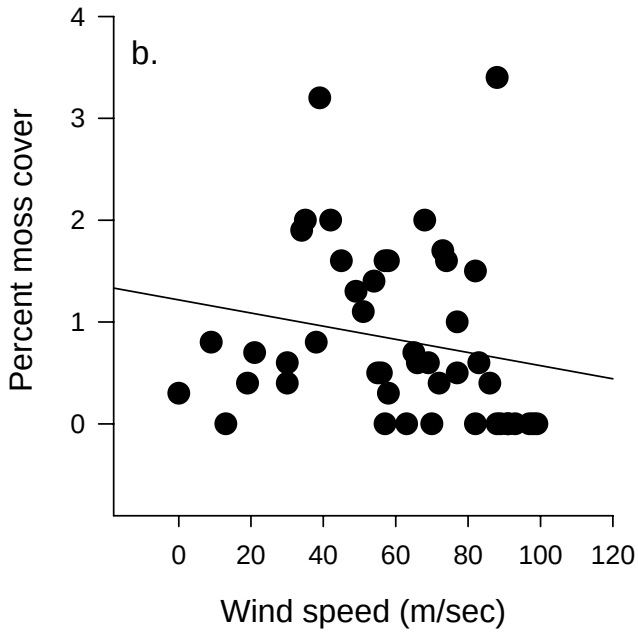
The percent of open canopy was unrelated to elevation ($r^2 = 0.06$, df = 44, P = 0.11). Maximum wind speed was significantly different among the three elevation groups (F = 20.37, df = 2, 43, P < 0.0001). Wind speed was greater at intermediate elevations than at the lower and higher elevations (Tukey HSD post-hoc, $\alpha = 0.05$).

In a stepwise multiple regression, percent moss cover was positively related to elevation and percent of open canopy and negatively related to maximum wind speed ($r^2 = 0.44$, r^2 adjusted = 0.40, df = 3, 41, P < 0.0001; Table 1; Fig. 1). In another stepwise multiple regression, only elevation was positively related to mean moss depth, which had been logarithmically transformed to normalize the data ($r^2 = 0.69$, r^2 adjusted = 0.68, df = 43, P < 0.0001;

Table 1. Results of stepwise multiple regressions for three response variables, each including three predictors.

Predictor	% open canopy		Wind speed (m/sec)		Elevation (m)	
Dependent variable	r^2	P	r^2	P	r^2	P
Percent of area with moss	0.08	0.02	0.05	0.03	0.31	0.0003
Mean moss depth (log)	-	0.35	-	0.29	0.71	< 0.0001
Number of branches with hanging moss	-	0.69	-	0.27	0.61	0.001





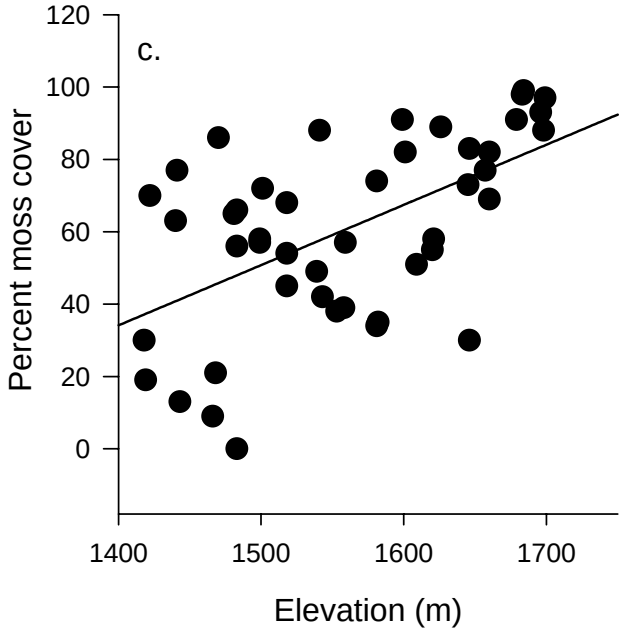


Figure 1. The relationship between percent moss cover on sampled bark area and (a) percent of open canopy, (b) wind speed and (c) elevation, for 45 trees along the Sendero Principal at Estación Biológica Monteverde (n = 45). Lines were fit by least squares linear regression.

Table 1; Fig. 2). In the final stepwise multiple regression, only elevation was positively related to the number of branches with hanging moss (r^2 = 0.63, r^2 adjusted = 0.60, df = 13, P = 0.0004; Table 1; Fig. 3).

DISCUSSION

The responses of all three dependent variables included in this study (elevation, percent open canopy and wind speed) supported our prediction that moss success would increase with increasing elevation. The mechanism producing this pattern is probably not related to light availability because percent of open canopy was unrelated to elevation. Wind speed may also be discounted as a potential explanation because the highest wind speeds were recorded at intermediate elevation. Recalling the link between elevation and rainfall in the Monteverde region (Clark et al. 2000), we propose that water availability is probably the correlate of ele-

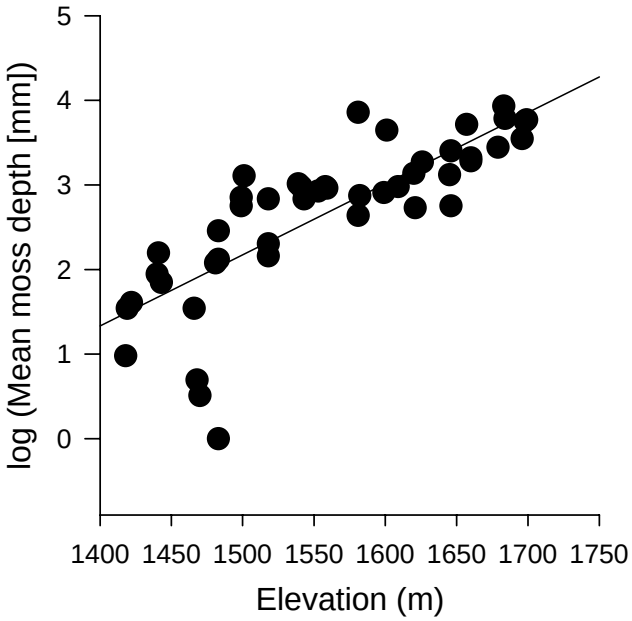


Figure 2. Relationship between mean depth and elevation for tree bark moss epiphytes on 45 trees along the Sendero Principal at Estación Biológica Monteverde. Line was fit by least squares linear regression.

vation which best explains the patterns we found in moss success.

The influence of wind on moss success is less clear. The data did not support our prediction that hanging moss would be less prevalent in high wind environments than more compact mosses. Instead, we found a negative relationship between wind speed and the percent of bark area covered in moss. We propose that this pattern may be created by increased transpiration in high wind locations, which results in increased costs of moss colonizing open bark. Wind may not be an influential disturbance for hanging mosses in this region, or our brief measurements of momentary wind conditions might not have accurately assessed the severity of wind disturbance.

Neotropical forests possess high beta (i.e., between habitat) diversity, particularly where gradients (e.g., elevation) produce changes in habitat structure over small spatial scales (Kricher 1997). Our results suggest that moss productivity may be highest at greater elevations, where water is less limiting. The productivity-resources hypothesis of tropical diversity states that high productivity permits accommodation of more species (Kricher 1997). To the extent that our measurements are correlated with moss productivity, moss diversity may also increase along the examined elevational gradient. Our informal observations of moss morphotypes are consistent with this prediction. Future research examining moss diversity along this gradient might provide useful information about patterns in tropical diversity.

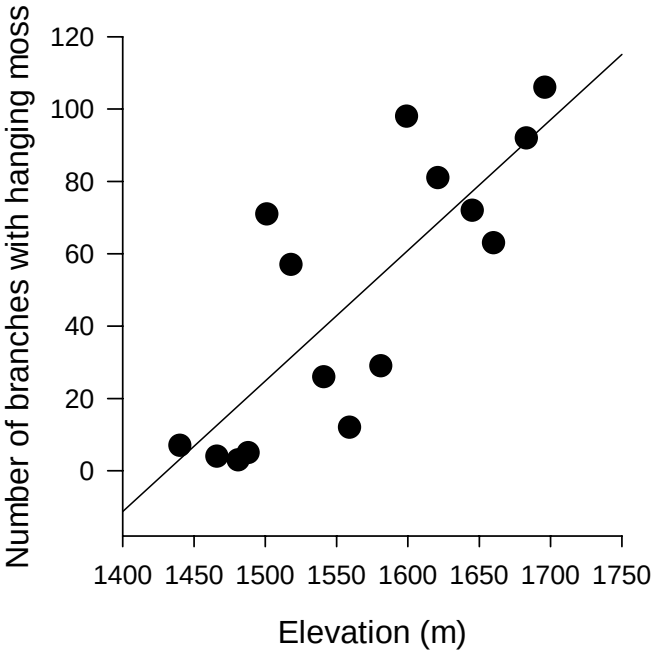


Figure 3. Relationship between the number of branches with hanging moss and elevation for 15 elevational intervals along the Sendero Principal at Estación Biológica Monteverde. Line was fit by least squares linear regression.

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DECEITFUL POLLINATION IN *BEGONIA ESTRELENSIS*

ELVINA C. CHOW, EMILY L. SHARP AND MELISSA A. BARGER

Abstract: Begonia estrelensis is a monoecious plant that uses a deceitful pollination mechanism, in which female flowers produce no nectar or pollen reward but imitate the pollen-producing male flowers with stigmas that look and smell like anthers. There are two traits that are indicative of deceitful pollination, the ratio of male and female flowers and the difference in petal width between the sexes. Assuming that patches with more flowers have more potential pollinators, we hypothesized that number of flowers in a patch would affect sex ratio and flower petal width. We found, as predicted, a negative relationship between number of flowers and percent males, an indicator of sex ratio. However, contrary to our expectations, we found a positive relationship between number of flowers and the difference between petal widths. These relationships suggest the importance of balancing male and female fitness in order to maximize overall fitness.

Key Words: monoecious plants, sex ratio, tropical cloud forest

INTRODUCTION

The Begoniaceae family is monoecious, with male and female flowers occurring on the same plant. The female flowers produce no nectar and have no pollen reward, yet they imitate the pollen-producing male flowers with stigmas that look and smell like anthers. Thus, female flowers are deceitfully pollinated, because the pollinators are fooled into visiting both sexes (Campbell et al. 2001). This mechanism introduces a tradeoff for the overall fitness of an individual, between attracting pollinators with male flowers and successfully pollinating female flowers and producing seeds. This tradeoff is indicated by the male to female sex ratio. Another trait of deceitful pollination is petal width. Flowers with larger petals are more attrac-

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tive to pollinators (Campbell et al. 2001). Because male and female flowers usually differ in size, petal width may be an important factor in deceiving pollinators.

There are two commonly occurring *Begonia* species along trails in the cloud forest at Monteverde, Costa Rica. *B. involucrata* has been extensively studied and has been shown to have a 3:1 male to female flower ratio, and a difference in petal width between the sexes, with males being larger than females (Campbell et al. 2001). These characteristics appear to maximize the deceitful pollination mechanism in this species. Little is known, however, about the other species, *B. estrelensis.* Because this species occurs in patches with more flowers than *B. involucrata*, and because large flower displays may attract more pollinators (Calvi 2005), it seemed that the deceitful pollination traits of *B. estrelensis* might differ from those of other *Begonia* species.

We proposed that *B. estrelensis* in patches with more flowers would be less likely to have a large number of male flowers to attract pollinators. Therefore, the sex ratio of flowers in large patches would be less male-biased. Similarly, female flowers in patches with more flowers would invest less in attracting pollinators, and, therefore, there would be little or no sexual dimorphism in flower size. Specifically, we predicted that patches of *B. estrelensis* with more flowers would have decreased male to female ratio and decreased difference in male and female petal widths, compared to patches with fewer flowers.

METHODS

We sampled 12 *B. estrelensis* patches at similar elevations along the Sendero Principal at the Estacion Biologia Monteverde on 21-22 January 2005. At each patch, we measured number of inflorescences, number of open male flowers, number of open female flowers, petal width for five randomly selected male flowers, and petal width for five randomly selected female flowers.

We calculated the average difference in petal width between male and female flowers by subtracting average male petal width from average female petal width for each patch. Data were analyzed with linear regressions using JMP 5.0.1.

RESULTS

Patch size ranged from 5 and 149 inflorescences, containing 20 and 715 flowers. Male flowers ranged from 13 to 100% of flowers in inflorescences. As number of *B. estrelensis* flowers increased in a patch, the male to female sex ratio, as measured by the percentage of male flowers, decreased ($r^2 = 0.26$, df = 1, 79, $P < 0.0001$, Fig. 1). Usually female flowers were larger than male flowers, with female - male difference ranging from -2.3 mm to 5.2 mm. In patches with more flowers, the difference between female and male flowers was greater ($r^2 = 0.27$, df = 1, 54, $P < 0.0001$, Fig. 2).

DISCUSSION

As we predicted, the male to female flower ratio decreased with an increased number of flowers within a patch (Fig. 1). Assuming that the number of pollinators increases with number of flowers, found for another system by Calvi (2005), a patch can attract pollinators based on number of flowers and not on male pollen rewards, without decreasing male fitness. For this Begonia species, this results in a greater percentage of female flowers in the patch and increased female fitness.

The prediction that average difference in petal width between female and male flowers would decrease with patch size was refuted. Instead, we found that female flowers were larger than male flowers in larger plots. Thus, it is not clear what selective forces influence petal width in this *Begonia* species, and future research will be needed to clarify the relationships between these factors, male and female fitness, and their contributions to overall fitness.

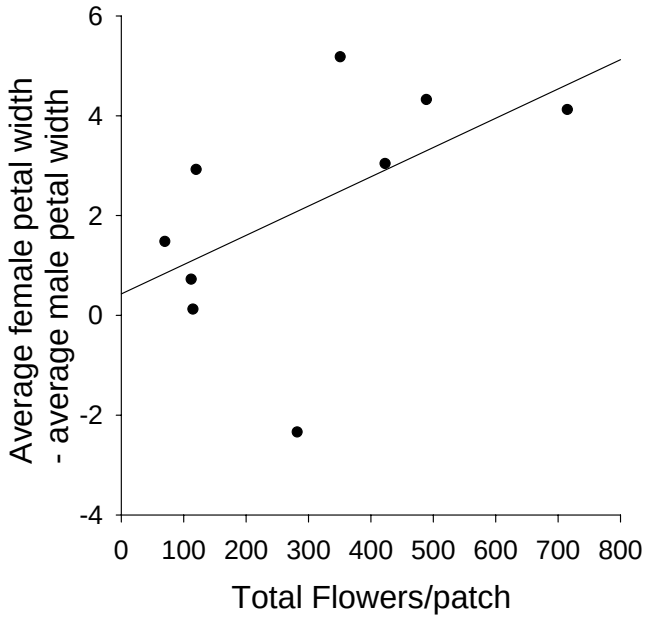

Figure 2. Effect of patch size of *B. estrelensis* on differences in petal width between female and male flowers. As patch size increased, female flowers became larger compared to male flowers.

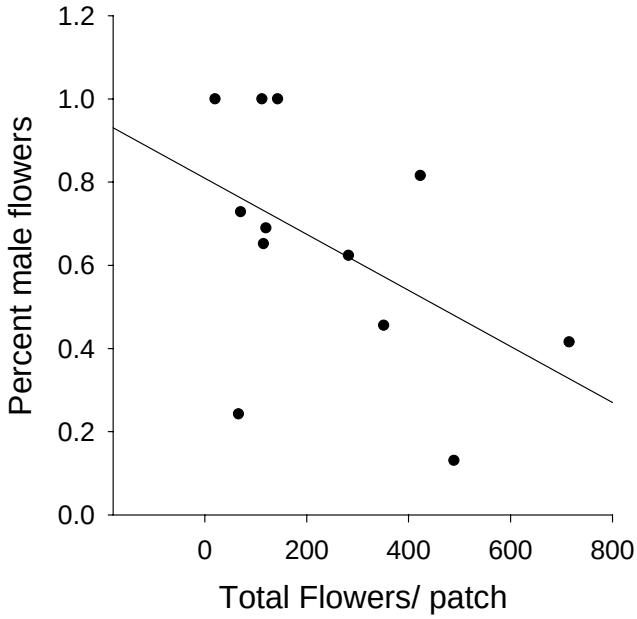

Figure 1. Effect of patch size on sex ratio of *B. estrelensis*. As number of flowers in a patch increased, the percentage of male flowers decreased.

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ISLAND BIOGEOGRAPHY THEORY AS APPLIED TO TANK BROMELIAD COMMUNITIES

RICHARD W. TRIERWEILER, S. ALLIE HUNTER, JENNY E. JUN
AND ANNA R. NOWOGRODZKI

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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