DIVERSITY AND COLONIZATION RATES IN EPIPHYTIC TANK BROMELIADS AT VARYING LIGHT LEVELS AND ELEVATIONS IN A TROPICAL CLOUD FOREST

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Abstract. Epiphytic tank bromeliads contain small, confined aquatic communities. The areas in which these bromeliads grow are variable among light levels and elevations. We examined these two factors as potential determinants in invertebrate diversity within the bromeliad tank communities. In thirteen bromeliad tanks, we found an increase in both abundance and number of morphotypes as volume of the bromeliad tanks increased. Although we found fewer morphotypes at low than at high elevations, no significant relationships were found among light levels. Light levels may not be an influential factor due to the constant shifting of light through the canopy, whereas elevational gradients and the associated environmental conditions remain constant. We also attempted to quantify colonization rates on natural bromeliad tanks (n=13) and on "uninhabited" island aquatic ecosystem (cups of water; n=12). In 24 hours, a total of 19 invertebrates colonized the 25 uninhabited communities, but these data were insufficient to analyze statistically.

Key Words: colonization rate, island biogeography, species abundance, species diversity, species richness

INTRODUCTION

The term "island" can be applied either to a geographically-isolated land mass or to other ecologically-isolated habitats. An example of the latter is the aquatic community contained within epiphytic bromeliads in tropical forests.

Previous studies have considered the effect of tank size on the composition of the aquatic communities in these bromeliad islands. Shaw (1993) found a positive correlation between diversity of microinvertebrates and increasing tank size, while Bizzarro et al. (1992) found the opposite relationship. In both of these studies, bromeliad tank size was the only factor examined as a potentially influential factor in determining the diversity of organisms in these aquatic communities. Perhaps the contradictory conclusions of these two studies are due to other compounding factors inherent in the sites from which the bromeliads were sampled. In this study, we examined the possible influence of elevation and light levels on bromeliad microinvertebrate diversity in a tropical cloud forest.

We hypothesized that bromeliad tank communities would have greater microinvertebrate diversity at low light levels relative to those in high light areas, and at low elevations relative to those at high elevations. We based these predictions on the assumption that a more stable habitat will increase community diversity. We assumed that a more stable community might occur at lower light levels due to lower evaporation rates of the bromeliad tank and at lower elevations due to the more constant temperate conditions (light, temperature, wind, etc...). Differences in colonization rates at high and low light levels and high and low elevations were examined through the use of both natural and artificial island ecosystems. We used the Shannon-Weiner index, which takes into account both species richness and relative abundance, to assess diversity of the systems. Species richness was defined as the number of invertebrate morphotypes present in the tank community.

METHODS

This study was performed on 21-22 January 1997 along the trails of the Estación Biologica Monteverde in Monteverde, Costa Rica. Samples were taken at low (1480 - 1520 m) and high elevation (1635 - 1665 m) and low and high light conditions. Low light was defined as a site under a dense forest canopy that probably remained in constant shade. High light was defined as a site in direct sunlight (usually within a tree-fall gap).

On 21 January, 13 bromeliads in all four categories were located (two at high elevation/high light, five at high elevation, low light, three at low elevation/high light, and three at low elevation/low light). The volume of water of each bromeliad was removed with a turkey baster, and its volume was measured. The sample was then saved for microscopic analysis. The bromeliads were then flushed clear of debris and refilled to their original level with tap water. Twelve 16 oz plastic cups were used to create artificial island communities. Six cups were placed in high elevation sites and six in low elevation sites; three in each light level. These cups were taped at a height of approximately 2 m above the ground and filled with 75 ml of tap water. After 24 hours, the water was collected from the bromeliads and from the plastic cups. All collected water was examined under an dissection microscope, and all invertebrate morphotypes were categorized.

activity by an individual during each sample period. Observations of behavior after 08:30 on 10 January were not analyzed because the entire group entered a resting period that differed greatly from behavior during other sampling periods. We pooled the data from all other observational periods for analyses, and used Kruskal-Wallis ranked sums tests to compare the proportion of time spent in each activity across different age and sex classes.

RESULTS

The Shannon diversity index was calculated for each of the initial bromeliad samples. The Shannon diversity values ranged from 0 to 0.53, and the volume water in bromeliads ranged from 0.5 to 52 ml. Through a regression analysis, no relationship was found between diversity and volume of bromeliad ($r2=0.043$, df= 1, 11, $P=0.49$). A two-way analysis of variance was run to test for an interaction between elevation and light level. No relationships were found between diversity and elevation ($F= 1.40$, df= 1, $P= 0.26$) or diversity and light level ($F= 0.17$, df= 1, $P= 0.69$).

In a regression analysis, we found strong trends between abundance and volume ($r2= 0.28$, df= 1, 11, $P= 0.07$) and between number of morphotypes and volume ($r2= 0.28$, df= 1, 11, $P= 0.06$). Because number of morphotypes increased with volume, we used a new index (defined as morphotypes/volume) in a two-way ANOVA to compare the bromeliad contents to light and elevation. These analyses revealed a relationship between elevation and morphotypes/volume ($F= 4.83$, df= 1, $P= 0.06$); in which low elevations had fewer morphotypes per volume than high elevation samples (Fig. 1). No relationship was found between light level and morphotypes/volume ($F=6.76$, df= 1, $P= 0.40$) or between light and elevation ($F= 1.76$, df= 1, $P= 0.22$).

After 24 hours, we found a total of 19 invertebrates (Table 1) in the 25 experimental island communities (13 bromeliads and 12 cups of water). Although interesting, these data were too few for statistical tests to evaluate colonization rates.

DISCUSSION

We predicted that bromeliads at lower light levels and lower elevations would have more morphotypes than those at higher light levels and higher elevations. According to the theory of island biogeography, increased distance from potential colonizing sources should decrease faunal immigration (Pielou 1979). Bromeliads in lower light and lower elevation forests may have more colonization because the climate in which these bromeliads are found is less extreme, enabling a more stable aquatic community to develop. In areas of high sun exposure, evaporation rates may be high enough to completely eliminate the water tank within the bromeliads. The colder temperatures and higher winds found at high elevations could possibly inhibit community development within the bromeliad tanks. Additionally, lower elevation bromeliads may have more potential colonizers because more organisms may exist at lower levels where the climate is less extreme. The relationship between morphotypes per volume and elevations supports our hypothesis.

We did not find any difference between morphotypes per volume in bromeliads at different light levels. It is possible that the high and low light samples were too similar in light levels to detect changes in species richness in response to light. It was difficult to find bromeliads at high light levels in the cloud forest. Also, many of the high light bromeliads were sampled in a tree fall gaps. The disturbance inherent in these areas may have affected the bromeliad communities.

According to the island biogeography theory, larger islands should have more species richness than smaller islands because larger islands have more resources to support a greater number of organisms. This was supported by our results showing a relationship between number of morphotypes and volume. However, we did not find a relationship between diversity and volume. Though larger islands may have more species richness, they may not necessarily have a more equal numeric distribution of species than small islands. Similarly, even if species richness is expected to be greater at low elevations or low light levels, diversity may not be greater at lower elevations or lower light levels as we indeed found.

Many factors besides elevation, size, and light

may affect colonization rate in bromeliads. A future study might investigate influences of other independent variables such as species of bromeliad or bromeliad height above ground on colonization rate.

We were only able to analyze 24 hour samples from the artificial and natural islands. Observing species establishment over a longer period of time is necessary to obtain a true understanding of island colonization. Interestingly, several organisms that were found to colonize the bromeliads immediately after they were flushed were quite different from the organisms that were in the original bromeliad samples. These initial species may be the primary successors enabling future species to colonize the bromeliad.

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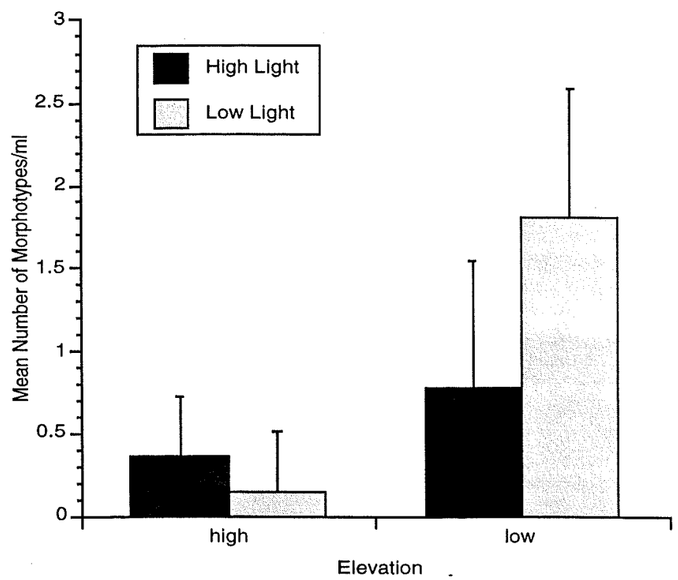

FIG. 1. Species richness (mean number of morphotypes/ml) in bromeliad tanks at high and low elevations and high and low light levels (error bars =1 S.E.)

Table 1: Colonization of natural bromeliads and artificial islands*

		Elevation		
	Low/Low	Low/High	High/Low	High/High
Bromeliads (n=13)				
Volume (ml)	10.5	19.5	11.5	14
Ostracod	1			
Diptera		1	3	1
Coleoptera		2		
Cups of Water (n=12)				
Volume (ml)	225	225	225	225
Diptera	2	6		
Nematoda	1			
Hymenoptera			1	
Trichoptera				1

*Volumes refers to volume of water sampled.