THE MAINTENANCE OF AVIAN MORPHOSPECIES RICHNESS IN HUMAN MANAGED MICROHABITATS

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Abstract: Conservation often focuses on the restoration or protection of pristine environments. In the Monteverde cloud forests, actively managed and urbanized areas have been integrated into these pristine environments. The aim of this study was to better understand the differences in avian species richness between tropical forest and nearby managed areas. We predicted that a human altered site would contain similar morphospecies richness to a forested area (alpha diversity), possibly because both habitat types would provide unique structures, habitats, and resources. After comparing bird diversity between human managed and forested sites, we found that actively managed sites had significantly more bird morphospecies. Our results indicate that actively managed areas of a tropical cloud forest provide habitats for many bird species and will be important in future conservation strategies.

Key Words: active management, conservation, species richness

INTRODUCTION

The traditional view of conservation is based on the desire to preserve natural environments without human influence or interference, and to restore damaged habitats to their original state (MacMahon and Holl 2000). However, because there is very little undisturbed land left in the world (Vitousek *et al.* 1997), conservation of biodiversity must also incorporate sustainable development.

In the cloud forests of Monteverde, land use and alteration have increased with a booming ecotourism industry (Scrimshaw *et al.* 2000). Although many conservationists believe that the forest should be preserved (Schwartzman *et al.* 2000), the town of Monteverde has also displayed environmentally conscious development by maintaining gardens, trees, and meadows (Scrimshaw *et al.* 2000). Because the managed areas of Monteverde contain diverse habitats, cosmopolitan species may not be able to achieve the dominance seen in more urban environments (e.g., San Jose) (Shochat *et al.* 2006 b).

Our study explored the idea that human-managed land does not necessarily diminish species diversity compared to intact cloud forest because human-managed land may offer a unique environment in which species can colonize. We hypothesized that human-managed land in Monteverde would support

avian species diversity, and we predicted that managed sites and forest would contain comparable avian morphospecies richness.

METHODS

Our study took place on 20-22 January, 2007 near the Estación Biológica Monteverde, Costa Rica. We conducted our study in two habitat classifications: undisturbed forest and human-managed land. Forest locations were near trails to the East and West of the Estación Biológica in areas of primary and secondary forests, respectively. We formulated our definition of human-managed sites based on a compilation of descriptions given by Shochat *et al.* (2006 a). They categorized human land use into three classes: urban, suburban, and rural. Urban areas were either dominated by built structures or were populated by more than 620 persons per km^2. Suburban areas had less land coverage and were on the edge of urban areas, and rural areas were other residential lands. Our managed sites included all three of these classes, including a banana plantation and cleared plots along the access road to the Estación Biológica, the Monteverde town center, and the Hotel Belmar grounds.

With an observation team in each site-type, we simultaneously observed and documented all birds in one-hour time intervals, totaling eight hours per site-type over three days. We recorded as much detail as possible for each bird sighting, ranging from morphotypes to families to species. If we heard bird calls, we used the sound to help locate the bird and, if possible, make an identification. We calculated the total number of different bird morphospecies per observation period for each site. In total, we observed eight separate forest sites and eight separate areas of managed land.

We matched the observations by time and used a paired two-sample t-test to compare bird morphospecies richness in forested and managed lands. We also compiled a Venn diagram of the birds we were able to identify to species-level for both forested and human-managed sites. This allowed us to compare unique morphospecies and overlapping morphospecies between the two site-types.

RESULTS

There were 49.2% more bird morphospecies in the managed sites than in the forested sites (t_7=2.26, P=0.03; Fig. 1). There were three known bird species found in both of the sites, as well as fourteen that were unique to the different habitat types (Fig. 2).

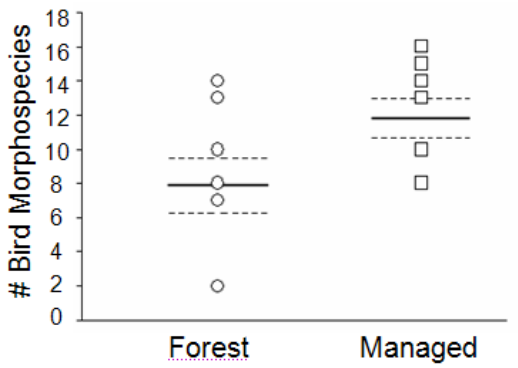

Figure 1. Bird morphospecies richness for both forested and managed sites in Monteverde, Costa Rica. Solid lines represent means, and dotted lines represent ± 1 SE.

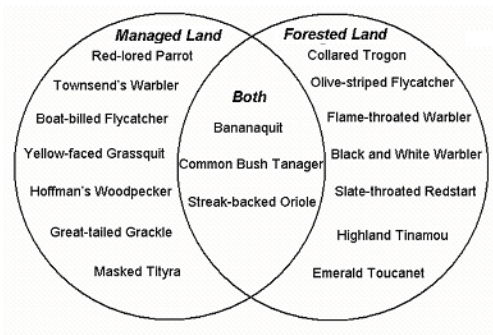

Figure 2. A Venn diagram showing some of the species-identified birds in each of the habitats as well as the species overlap between both.

DISCUSSION

The results support our hypothesis that cleared and managed land would maintain bird species richness comparable to that of forested areas. Morphospecies richness in managed land was actually higher in seven of eight observation periods. Several mechanisms in managed land could be maintaining and possibly increasing avian morphospecies richness, including increased habitat heterogeneity and resource subsidies (e.g., food items or structural complexity; Roth 1976, Freemark and Merriam 1986).

Rarefaction analysis would be necessary to more accurately compare the avian richness between habitat types by standardizing against the number of birds observed. However, because we only considered morphospecies richness data per observation period and did not record morphospecies density, we could not use rarefaction to compare richness between our habitat sites. The low-light and dense flora of the forest sites made this strategy impossible. From a bird watcher's perspective, the managed areas contain a high, visible avian richness that differs in composition between sites. Further studies could investigate the true avian richness of Monteverde's forest habitats and how this compares to the high visible richness in managed areas.

The city of Monteverde and its human-altered surroundings (managed sites) were highly heterogeneous, containing patches of buildings, trees, low brush, meadows, gardens, and ponds. Birds used these areas to socialize, perch, and forage, taking advantage of resource subsidies such as pond insects or fruiting trees (*personal observations*). The species utilizing managed habitats were numerous but may be specifically adapted to colonize only after human alteration

(Stiles and Skutch 1989). For example, the red-lored parrots, golden-browed chlorophonia, and Hoffman's woodpeckers were only seen in managed sites. The Hoffman's woodpecker (Honduras, Nicaragua, Costa Rica) and golden-browed chlorophonia (Cost Rica, Panama) are only found within Central American countries and require habitat outside primary or secondary cloud forest. Other species including the emerald toucanet and collared trogon were seen only in the forest. Further research is necessary to understand the species composition variation between managed habitats and forest, as well as the distribution of rare or endemic species.

Preserving and restoring pristine habitats in the tropics are often emphasized in conservation efforts; however, these habitats are often a small proportion of total land area (Powell *et al.* 2000, MacMahon and Holl 2000). Our findings suggest that rural urbanization and active land management in a tropical cloud forest can maintain avian morphospecies richness in a manner similar to management in temperate zones (Freemark and Merriam 1986). Our study demonstrates that both the forest and managed areas can be centers of avian diversity and therefore important in ecotourism (e.g. bird watching) and environmental education. If further urbanization occurs in Monteverde, it must continue to incorporate trees, gardens, and other areas useful to birds. Environmentally conscious development would allow the managed areas to continue hosting bird species as part of a dynamic landscape (Andren 1994, Schwartzman *et al.* 2000). Further study could follow the urbanization of Monteverde through time and observe the changes in species composition in both nearby forests and newly managed areas.

Urbanization is often considered an invasion of natural habitats; however, it would benefit biodiversity to consider urbanization a dynamic part of a changing environment. A shift in focus may spark an interest in the creative and effective methods of maintaining species richness and environmental health in a cityscape.

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INTERCOMMUNITY PATTERNS OF CLIMBERS AND EPIPHYTES IN PRIMARY AND SECONDARY MONTANE CLOUD FOREST AT MONTEVERDE, COSTA RICA

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Abstract: Tropical forest plant communities and their regeneration in deforested or degraded areas is an important concern in tropical forest conservation. To analyze forest structure with a comparative approach, I characterized patterns of co-occurrence, diversity, and abundance of climbers and epiphytes along 30 m transects in primary and secondary montane cloud forest at Monteverde, Costa Rica (n=4 transects per succession type). I grouped lianas, vines, and climbing epiphytes into one group, hereafter referred to collectively as climbers. I divided epiphytes into three structural groups based on their form and broad taxonomic differences: ferns, bromeliads, and other epiphytes. Structural groups co-occurred less often than expected by chance in secondary forest, but not in primary forest. The diversity of structural groups was not affected by succession type, but total climber and epiphyte abundance was greater in secondary forest. The results of this study suggest that epiphyte communities may recover structural diversity and abundance more quickly than tree communities. Quickly recovering sub-communities in regenerating tropical forest may be important for active management and regeneration of deforested areas.

Keywords: epiphyte, co-occurrence, succession, space competition, structural group, sub-communities

INTRODUCTION

Tropical forests generally have high biodiversity, and populations and communities in the forest change slowly over long time scales (Forsynth and Miyata 1995). In light of modern deforestation, many studies have examined the effects of disturbance on populations and nested communities within forests (Cannon *et al.* 1998, Armbrecht *et al.* 2005). However, few studies have explored the distributions of individual species within plant sub-communities and their relationships with one another. Nevertheless, these dynamics, and especially how individual sub-communities within the forest develop after disturbance, may be crucial for both conservation and renewal of forested lands (Cannon *et al.* 1998). To address variability in distributions for plants in sub-communities in different habitats, I analyzed the structure of climbing plant and vascular epiphyte communities in relation to the successional state of tree communities in montane cloud forest.

Previous research has shown that species richness increases with the age of forest stands (Holtz and

Gradstein 2005). In undisturbed primary forests, extinction and colonization events are common for individual trees, but species composition over large areas remain relatively constant (Laube and Zotz 2006). In spite of local species fluctuations, general structural and functional groups also often remain constant over time (Armbrecht *et al.* 2005, Mayfield *et al.* 2006). Structural plant groups include suites of related or un-related species that can be defined by their method of habitat use, such as the ways in which different plants grow attached to trees. In addition to describing the physical structure and complexity of plant communities growing on trees, these groups also describe the effects that these plants may have on production and nutrient flow in single tree microhabitats (Nadkarni *et al.* 2004, Mayfield *et al.* 2006). For example, climber and epiphyte communities can have large effects on community structure and production in tropical forests, but this effect varies considerably between different succession states (Nadkarni *et al.* 2004). The patterns of co-occurrence and abundance of these groups, though, are not well documented, especially in the context of succession (but see Mayfield *et al.* 2006).

The patterns of co-occurrence in structural and functional groups are increasingly of interest today because rapid forest disturbances are altering the structure of these communities potentially altering biotic interactions among species. Current tropical deforestation rates far exceed reforestation rates, and this disparity is likely to continue to increase well into the future, before sustainable forestry systems can be put in place (Caufield 1993, D. Peart *personal communication*). Tropical countries may one day resemble modern nations in North America and Europe, where the vast majority of forested land is secondary growth (Barry 2007). Climbers and epiphytes can represent a significant portion of the biomass in the canopies of tropical forest (c. 37%), and the vast majority of the rest of the canopy biomass is accumulated as a result of climbing and epiphytic vascular plants growing on the trees (Nadkarni *et al.* 2004). Climber and epiphytes may be crucial for recovering species that depend on them and also for regenerating overall biomass in forest canopies (Nadkarni *et al.* 2004).

In this study, I hypothesized that different distributions of limiting resources, such as light and space, would result in distinct patterns of co-occurrence of structural groups between habitats due to competition for these resources. I expected secondary forest structural groups to co-occur less often than would be expected by random chance because secondary forest offers less space for

attachment onto individual trees and the standing carbon and nutrient levels are low (Nadkarni *et al.* 2004). Because secondary forest has a brighter understory, plants are more likely to be limited by space resources than by light resources. In primary forest, however, I predicted that communities would not be structured by space competition because low light levels should prevent individual groups from fully utilizing the greater space, biomass, and ambient nutrient levels in primary forest.

Because of the difference in ambient light intensities between succession types and the potential differences in space limitation between succession types, I expected that succession type would affect on both the diversity and abundance of structural groups. I expected that secondary forests would harbor more total plants than primary forest, but due to limiting space on secondary forest trunks, I expected diversity per tree to be lower. In addition, I expected trunk diameter and height from the ground to tree canopy to affect both diversity and abundance because they directly represent space for colonization and proximity to the bright canopy, respectively.

METHODS

Study system.

This study was conducted in a montane cloud forest at Monteverde, Costa Rica. The elevation of four primary forest sites ranged from 1,529 to 1,560 m above sea level, and the elevation at the secondary sites ranged from 1,479 to 1,499 m above sea level. I analyzed four different structural groups for climbers and epiphytes: (1) rooted lianas, vines, and bole climbers (both epiphytic and hemiepiphytic species), (2) epiphytic ferns, (3) epiphytic bromeliads, and (4) all other epiphytes, which included orchids and other small plants. I used these specific groups because each has a unique effect on nutrient flow or habitat structure in epiphytic communities (Nadkarni *et al.* 2004). For example, lianas and other climbers affect the ability of other plants to colonize trees, and they also contribute a large amount to forest biomass (Nadkarni *et al.* 2004). These climbers might facilitate species co-occurrence by creating new locations for epiphyte attachment. Alternatively, if climbers are not suitable substrate for epiphytes, they could decrease available colonizing space. Ferns and bromeliads represent distinct taxonomic groups with markedly different biologies. In addition, they both create different habitats for other organisms (Janzen 1983). Other

epiphytes made up approximately 25% of the remaining vascular plants growing on the study trees. I lumped 'other' epiphytes together because identification from the ground was difficult because non-fern and non-bromeliad epiphytes included many different plant families. In addition, all of the plants in the 'other' epiphyte class were attached to the trees in similar manners and made up small amounts of the total climber and epiphyte biomass on the vast majority of trees (*personal observation*). I chose to analyze only vascular plants that were growing on tree trunks because these communities are more likely to be affected by the changing ambient light levels in the understory of a developing forest than plants growing in the canopy where light levels are more constant through succession.

Data collection.

I collected data from eight 30-m transects in primary and secondary cloud forest (n=4 transects per forest type). I selected transect locations and bearings haphazardly, except that I avoided areas with tree-fall gaps to control for variation in tree density. I collected data for all trees within 50 cm of each transect (i.e., 1 m x 30 m quadrats). I did not record tree species identity because most climbers and epiphytes probably do not discriminate between different tree species (Janzen 1983). For each tree, I measured the diameter at breast height (DBH) to the nearest 0.01 cm, height from the base of the trunk to the start of the canopy to the nearest 0.01 m, and counted the number of individuals in each of the four structural groups up until the start of the canopy. In addition, I counted the number of fissures in a haphazardly selected 5 cm section of the bark of each tree to estimate bark texture. I also noted which trees shed their bark periodically, which could be an adaptation for removing epiphytes (Janzen 1983), and also whether trees had double trunks either above or below breast height.

Statistical analysis: within succession-type variation.

For all analyses, I used trees as independent samples, instead of transect averages, because there was very little variation among transects within succession types. There were no significant differences in DBH or height to the canopy among transects within each succession type (MANOVA: Primary, Wilks' λ=0.78, $F_{6,70}$=1.50, P=0.19; Secondary, Wilks' λ=0.90, $F_{6,68}$=0.64, P=0.70). Moreover, using a van der Waerden nonparametric test, I found that bark index values were not significantly different among transects in primary forest (χ^2_3=4.16, P=0.24) or secondary (χ^2_3=1.25, P=0.74).

For secondary forest, there were no significant differences among transects in total climber and

epiphyte abundance or diversity (MANOVA: Wilks' λ=0.84, $F_{6,68}$=1.06, P=0.40), but there were a significant differences among trasnects in primary forest (MANOVA: Wilks' λ=0.42, $F_{6,70}$=6.26, P<0.0001). Nonetheless, I still used all trees as independent data points because primary forest sites were chosen arbitrarily at approximately the same elevation and close to one another. As a result of the primary transects' close proximities, their plant communities likely have originated from the same gene pool. Future studies could strengthen the statistical power and biological inference by increasing spatial scale sampled.

Statistical analysis: null models.

I tested the degree to which structural groups co-occur in primary and secondary forests. To estimate co-occurrence I calculated a C-score for each habitat type, which averages the proportion of all potential sites (here, trees) that harbor all potential species pairs (here, structural group pairs) (Stone and Roberts 1990). Higher C-scores indicate that species are less likely to occur together in the same site. I ran two null models with 5000 iterations each to calculate C-scores for each forest type, assuming random colonization and extinction of structural groups on individual trees with EcoSim 7.0 (Gotelli and Entsminger 2001). In the simulation, I kept the sums of both the number of structural groups per tree and the number of trees per structural group proportional to the observed data set. With proportional sums, the exact sums of 'species' per tree and trees per 'species' are not fixed, but instead, the relative abundances of species and trees are retained from the observed data set. Proportionality maintains the relative abundances of different functional groups as well as the relative hospitability of individual trees to plant colonization, thus making the model more biologically realistic (Gotelli and Graves 1996). I allowed for degenerate matrices in the simulations (matrices that include trees without epiphytes) because many trees in the field had no vascular plants growing on them.

Statistical analysis: regressions and ANOVAs.

The abundances of many structural groups were correlated with each other (Table 1), so I used total climber and epiphyte abundance for analyses involving abundances. I used linear regressions to analyze the relationship between tree variables (DBH and the bark index) and total climber and epiphyte abundances and diversity.

Table 1. Pair-wise correlations coefficients for abundance of structural groups among trees across succession types.

	Ferns	Climbers	Bromeliads
Other Epiphytes	0.42	0.24*	0.33*
Ferns		0.35*	0.47*
Climbers			0.44*

* indicates significant interactions (P < 0.05), ** indicates highly significant interactions (P < 0.001).

I used two one-way ANOVAs to test whether or not succession type affected total climber and epiphyte abundance and diversity of structural groups. To quantify diversity, I used the Gini diversity index[1] because it is relatively insensitive to low sample size and has better statistical properties than other indices (see Gotelli and Graves 1996).

[1] $1-\sum_{i=1}^{S} p_i^{\,2}$, see and Gotelli and Ellison (2004) and Maguran (2003) for commentary on the strengths and weakness of different diversity indices.

To normalize total climber and epiphyte abundance values, I used a $\log_{10}$ (x+2) transformation because many trees did not have epiphytes. I also squared Gini diversity values to normalize them for analysis.

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RESULTS

In primary forests, the observed C-scores for the four structural groups were not significantly different from null model communities (P=0.11). However, in secondary forests, the observed C-score was significantly lower than the average null model C-score (P=0.002).

Total climber and epiphyte abundance increased with DBH in both primary and secondary habitats (Table 2, Fig. 1b). Diameter at breast height did not explain variation in diversity among trees in primary forest (Table 2) but it did in secondary forests (Table 2, Fig. 2). The bark index explained a very small amount of the variation in total climber and epiphyte abundance but not in diversity (Table 2).

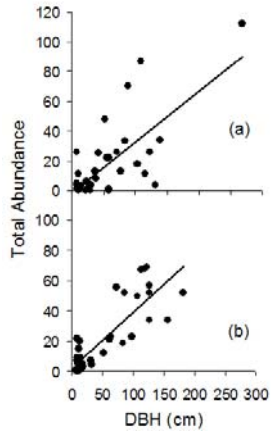

Figure 1. Total climber and epiphyte abundances in primary (a) and secondary (b) forests increases with tree diameter at breast height (regression statistics in Table 2).

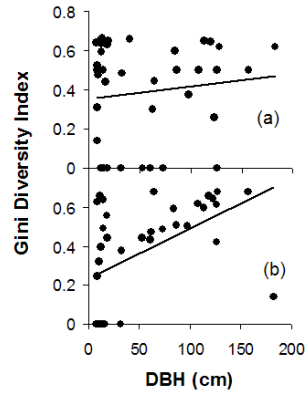

Figure 2. Gini diversity was not significantly correlated with tree diameter at breast height in primary forest (b), but it was in secondary forest (b) (regression statistics in Table 2).

Table 2. Regression statistics for primary and secondary habitats, testing the effect of DBH on climber and epiphyte abundance and diversity. (n=40 trees in primary forest and n=39 trees for secondary forest).

	Primary		Secondary	
	Total Climber and Epiphyte Abundance	Gini Diversity Index	Total Climber and Epiphyte Abundance	Gini Diversity Index
$F_{1,38}$	25.38	1.43	92.75	12.68
r^2	0.40	0.04	0.71	0.26
P	< 0.0001	0.24	< 0.0001	0.001

Succession type did not have an effect on structural group diversity ($F_{1,77}$=0.09, P=0.77) nor total abundance ($F_{1,77}$=2.52, P=0.12).

DISCUSSION

The results of this study suggest that succession type affects the patterns of co-occurrence and diversity in structural groups of climbers and epiphytes. This result is in line with past studies in other Costa Rican tropical forests that demonstrate that the diversity and abundance of structural and functional groups can remain constant after disturbances (Mayfield *et al.* 2006). A noticeable feature of secondary forests, in comparison to primary forests, is that the canopies are much more open, allowing more light to reach the understory. Increased sunlight in secondary forests may allow climbers and epiphytes to increase in abundance, creating competition for nutrients instead of light. Plants growing in

low light environments probably do not compete for nutrients because populations may not be large enough to deplete nutrient resources. Species diversity may be lower on trees with smaller trunk diameters because strong competitors may fill up the space and monopolize them more quickly. In addition, trees with larger trunks were also taller ($r=0.58$, $P<0.0001$), which suggests that trees may also be older and may have had more time to accumulate biomass and nutrients to facilitate epiphyte growth (Nadkarni *et al.* 2004).

Contrary to my prediction that climber and epiphyte diversity would be greater in primary forests, there was no difference in structural group diversity between succession types. The results of this study suggest that the diversity of structural groups in secondary forest may quickly recover to the same levels in primary forest climbers and epiphytes, at least on the trunks of forest trees. This pattern may be due to the relatively short generation times of climbers and epiphytes in comparison with trees. Although longer periods of time may be required for climber and epiphyte communities to build up large deposits of canopy organic matter (Nadkarni *et al.* 2004), it appears that the structural framework of climber and epiphyte communities may recover quickly. This quick recovery may make it possible for other plant and animal species that are dependent on climbers and epiphytes to repopulate regenerating forests (Forsyth and Miyata 1985). Future studies should test how the patterns of climber and epiphyte repopulation vary over longer time scales. In addition, future studies should address the effect of this potentially quick recovery of structural groups on nutrient cycling. Finally, studies should test whether or not these structural group patterns and their effects on nutrient cycling hold at the species level.

The loss of biodiversity has become a prominent topic in tropical forest conservation (Cannon *et al.* 1998, Armbrecht *et al.* 2005, Laurance *et al.* 2006), but the structural stability of recovering sub-communities may be equally important for understanding how to maintain healthy functional ecosystems (Cannon *et al.* 1998, Mayfield *et al.* 2006). The management of quickly regenerating functional sub-communities within the forest may improve nutrient flow and the overall rate biodiversity recovery in regenerating forest systems.

While the results of this study suggest that climber and epiphyte communities may recover quicker than tree communities, long term studies on structural groups, functional groups, and species are needed to test whether these patterns are due to light and nutrient availability or propagule pressure

and recruitment rates. Further research is also needed to evaluate the differences in nutrient cycling between tree communities and vascular plant communities growing on trees and how this may feed back into the regeneration process. Research from the past decade has shown that succession in tropical communities is much more complicated than once thought, and understanding these processes may be critical for proper management of deforested and degraded forest areas in the tropics (Cannon *et al.* 1998, Mayfield *et al.* 2006).

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ROOSTING BEHAVIOR OF THE EXPLODING BUTTERFLY, *MANATARIA MACULATA*

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Abstract: Although the structure of highly organized social insect societies, such as those of Hymenoptera and Isoptera, has been extensively studied, little is known about the structure of Lepidopteran social groups. In Lepidoptera, sociality is evident in clustered egg laying, larval foraging groups, and group roosting in adults. The daytime group roosting behavior of *Manataria maculata* at Monteverde, Costa Rica is acknowledged but not well understood. Our study attempted to determine whether this migratory butterfly exhibits site and group fidelity when roosting. Based on observations of group and nest fidelity in other insect families, we predicted that *M. maculata* would a) not mix between roosting groups and b) be found at the same roost sites on consecutive days. We performed a mark-recapture study over four days and determined that the social behavior of *M. maculata* is more fluid than predicted. Our results demonstrate that site fidelity is low and that individuals not only move between groups, but also can potentially travel large distances (over 300 m) in the course of one day.

Key Words: Monteverde, cloud forest, Costa Rica, social behavior, roosting, Lepidoptera, Nymphalidae, Satyrinae

INTRODUCTION

The advantages of sociality for insects include early warning against predators, reduced likelihood of predation per individual, social facilitation of foraging, kin-associated fitness benefits, thermoregulation, and improved mating opportunities. Disadvantages include increased conspicuousness, greater transmission of pathogens and parasites, and intraspecific competition for resources (Costa and Pierce 1997, Altringham 1996). Social behaviors, such as laying eggs in clusters and communal roosting, have been observed in some species of Lepidoptera. Social communication and cooperation in this order are generally simpler than in the more behaviorally complex eusocial societies of Hymenoptera and Isoptera. Nonetheless, Lepidopteran aggregations are not as well studied, perhaps because they are eclipsed by the more elaborate behavior of eusocial insects (Costa and Pierce 1997).

The tropical butterfly *Manataria maculata* (Nymphalidae: Satyrinae) is an altitudinal migrant that is frequently observed roosting in shaded embankments, tree holes, and other dark hiding places.

Manataria maculata roost in groups during the day, leaving the roost occasionally to forage. At night, they roost individually in the canopy. Daytime group size can range from only a few individuals to over four dozen. Although the larval life history of *M. maculata* is relatively well understood (DeVries 1987, Nadkarni and Wheelwright 2000), studies of the social behavior of adults are rare.

The aim of our study was to understand the structure of *M. maculata* social groups. Several insect families, including Lepidoptera, have been shown to exhibit fidelity to a roosting site over a variety of time periods (Adams 1999). Therefore, we hypothesized that *M. maculata* would have distinct daytime social groups which do not mingle and which exhibit site fidelity. We predicted that we would not find *M. maculata* from one roost site mixed with those from another, and that we would find butterflies returning to the same roost sites over several consecutive days.

METHODS

Field site.

We conducted our study on 19-22 January, 2007, between 0730 and 1630 each day, in the cloud forest immediately surrounding the Estación Biológica Monteverde (elevation 1560 m). We used a total of six roost sites located along various trails around the station (Table 1, Figure 1). A typical roost site of *M. maculata* is located underneath a small overhang in a damp earth bank, about 1.5 m above the ground, surrounded by roots and vegetation. The average dimensions of the six roost sites were 22 cm x 13 cm x 11 cm.

Table 1: Descriptions of six *Manataria maculata* roosting sites located in the sides of damp embankments and rotting trees at the Estación Biológica Monteverde.

Site #	Description
1	Under an overhang in a very damp earth bank, surrounded by vegetation (moss and ferns), on the uphill side of the trail directly above the bridge.
2	Under an overhang in a damp earth bank, a 5 minute walk down the first right fork above the bridge, on the uphill side of the Jilquero Trail.
3a	Inside a very moist hollow log on the left of the Principal Trail leading uphill from the bridge, a 15 minute walk up the first left fork above the bridge.
3b	Under a large root in an earth overhang in a bank on the uphill side of the Principal Trail, about 4 m beyond site 3a.
5	Beneath overhanging bromeliads and orchids at the top of a rotten upright tree stump, located along a trail in the forest behind the field station, near the zipline tower. Unlike the areas around the other sites, the area around this site did not appear to offer alternative roost sites (such as earth overhangs).
6	Under a moist earth overhang in the bank on the uphill side of the trail 30 m short of the waterfall pool.

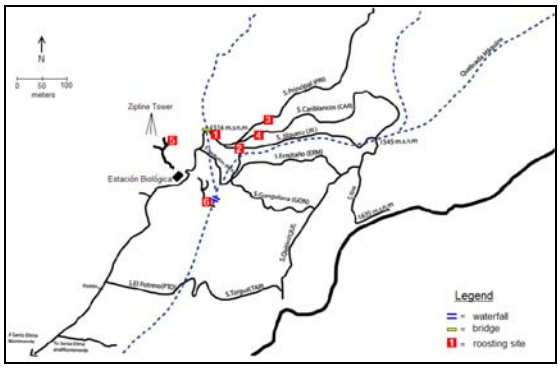

Figure 1: *Manataria maculata* roosting sites we studied were located along the trails around Estacion Biologica at Monteverde. Additional site descriptions are provided in Table 1.

Field methods.

When roosting *M. maculata* are disturbed, the entire group emerges simultaneously; our procedure took advantage of this behavior. After locating *M. maculata* in a roost, we netted the entire group as it flew out. We then removed each individual and processed it at the site of capture, either marking both hindwings with a permanent marker or noting the presence of previous markings. We used unique markings for each site. We recorded the total number of unmarked individuals, the number of previously marked individuals, and the site where each marked individual originated. If we failed to capture any individuals at a given site, or if no *M. maculata* were present, we allowed a minimum of two hours to pass before re-visiting the site.

Ideally, we would have visited each site at the same time each day. However, the inclusion of new sites over the course of the study, the realization that *M. maculata* take several hours to return to their roost after being disturbed, and our academic schedule at the field site all combined to prevent us from visiting the roosts at the same time each day. On the afternoon of Day 1 (19 January) we visited sites 1 through 5. On Day 2, we visited the sites in the morning and the afternoon, discarding Site 4 due to an absence of *M. maculata*, and adding Site 6. On Day 2 we released 53 unmarked individuals, but afterwards switched to marking all captured individuals because we realized that we would not have enough replicates unless we continued marking over the remaining days of the study. On Days 3 and 4, we only visited the sites in the morning and split Site 3 into Site 3a and Site 3b. We attempted to control for time of day by beginning our sampling at approximately 0730. *Statistical analysis:* We used our mark-recapture data to obtain an estimate of the population size of *M. maculata* within the study area (about 40,000 m^2, Fig 1) using the Lincoln Index.

RESULTS

We observed a total of 302 *M. maculata* at all the roosts over four

days. Of those, 97 individuals escaped, 205 individuals were captured, and we marked 152 individuals. Eighteen of the butterflies we marked were subsequently recaptured. Of those 18 butterflies, 15 butterflies were found at the sites at which they had been marked; the remaining three butterflies were found at other sites. One individual was marked at Site 5 and recaptured at a later date at Site 3, approximately 300 m away (Figure 1). Over the four days of the study, we also observed a general decrease in the number of *M. maculata* roosting in each site (Figure 2).

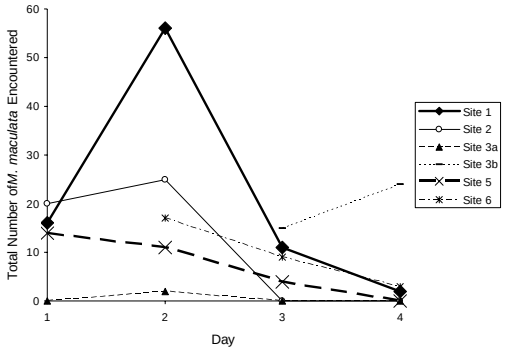

Figure 2. We observed a general decrease in the number of *Manataria maculata* per site over the four days of our study (day 1 = 19 January, 2007). Here, we exclude data collected in the afternoon of days 1 and 2 because afternoon data were not consistently collected across all four days of the study period.

On Day 4 we captured 25 butterflies, three of them marked. Given that we marked a total of 152 individuals, we calculated the population in our 40,000 m^2 (0.04 km^2) study area to be 1267 individuals.

DISCUSSION

Our data refute our hypotheses that *M. maculata* have distinct daytime social groups and exhibit site fidelity. Instead, our results show that site and group fidelity was not steadfast. Rather, the roosting groups intermingled, and the population of *M. maculata* that used a roost was larger than the number of butterflies found there at any given time. Although we observed many small overhangs in the banks along the trails in the study area, only a few appeared to be consistently used by *M. maculata*. Therefore, we believe there are specific features of these roosting sites, such as nutrient concentrations or pheromone markers, which encourage *M. maculata* to return. This hypothesis warrants further investigation.

Based on our observation that the number of butterflies roosting in the morning tended to decline over the four days of study, we suggest that *M. maculata* could 1) periodically change roosting location, or 2) abandon roosts if frequently disturbed. These possibilities are not mutually exclusive. Despite our efforts to minimize disturbance to the roosts, we may have discouraged *M. maculata* from returning to our study sites each day. Trauma or

injury from being handled, a large source population, and the release of 53 unmarked individuals on Day 2 could also explain our low recapture rate.

Our estimate of population size may violate several of the assumptions of mark-recapture population size estimates, including random mixing and equal survival of marked and unmarked animals. These factors could result in either an underestimate or an overestimate of population size, respectively. We consider our estimate of population size to be surprisingly high, especially since rarity is common in the tropics.

A number of questions concerning the social behavior of *M. maculata* remain unresolved. Studies on the foraging behavior of this species could examine how *M. maculata* sociality varies throughout the day. Further, a genetic analysis of roosting groups would reveal whether or not kinship determines group composition. Finally, it is unknown whether the roosting behavior exhibited at Monteverde persists at the lower elevations of *M. maculata*'s range. More detailed knowledge of the group roosting behavior of *M. maculata* could contribute to the sparse literature on Lepidopteran sociality in the adult insects (Costa and Pierce 1997, Murillo and Nishida 2003).

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HANGING WITH MY PHAT BRO(MELIADS): THE NEGATIVE EFFECTS OF INCREASING ACIDITY ON AQUATIC INVERTEBRATE ABUNDANCE IN *GUZMANIA MONOSTACHYIA* (BROMELIACEAE)

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Abstract: Acid rain has had profound effects on aquatic ecosystems worldwide. Decreases in rain pH have lowered the biomass of aquatic organisms in lower trophic levels that are unable to tolerate higher acidities. Invertebrate communities living in bromeliad tanks may be particularly susceptible to changes in rain pH because they obtain water by directly collecting precipitation, and therefore, they have no buffering capacity from surrounding geological substrates. We predicted that increasing water acidity would negatively affect invertebrate abundance in bromeliad tanks. We first measured the natural variation in pH and invertebrate abundance in nine bromeliads from the Estación Biologia Monteverde in Puntarenas, Costa Rica. We found that bromeliad pH naturally varied between 3 and 4.9, and natural invertebrate abundance was marginally negatively correlated with acidity. We then manipulated pH in 27 bromeliad tanks (three levels: pH = 2.4, 3.1, and 5.6) to experimentally test the effects of pH on invertebrate abundance. When pH was experimentally manipulated, invertebrate abundance was significantly lower in treatments with a pH of 2.4 compared to both 3.1 and 5.6. The pH levels of 5.6 and 3.1 did not significantly differ from each other. These data suggest that lower levels of acidity than naturally found in bromeliad tanks can lead to lower invertebrate abundance. Further studies are needed to fully understand the implications of increasing acidity of rain in neo-tropical environments for ecosystem processes relating to bromeliad tank communities.

Key Words: acid rain, phytotelmata, Monteverde, bromeliad

INTRODUCTION

Acid rain and its effects on biological systems are becoming increasing apparent as the pH of rain continues to drop. Rain was once believed to have a pH of 5.6, as this represents the pH of distilled water saturated with CO_2 (Schindler 1988). However, rain water commonly has a pH near 5.0 (Schindler 1988). Regions with high levels of human activity (e.g., areas of manufacturing density or high levels of emissions) have even lower rain pH values because of anthropogenic sulfur emissions (Schindler 1988). In addition, sulfur emissions can affect rain pH globally because atmospheric sulfur pollution can migrate between countries and across oceanic barriers (Schindler 1988; Raven et al. 1999).

Increases in acid rain during the last century have lowered the pH of many aquatic ecosystems in North

America and Northern Europe, resulting in the disappearance of some invertebrates in lower trophic levels (Schindler 1988). Acid rain can also lead to increases in aluminum concentrations through increased leaching, which negatively affects fish and other aquatic organisms, by changing the solubility of aluminum in water (Raven et al. 1999). Although organisms in higher trophic levels may be relatively resilient to pH values less than 5.5, organisms in lower levels may be less able to acclimate to these changes (Schindler 1988). The reasons for increased susceptibility to acid rain of organisms in lower trophic levels are unknown, but their declines in response to acidity are well documented (Schindler 1988). While the United States and Canada have reduced sulfur emissions in the last fifty years, acid rain is still a major problem in other North American countries, such as those in Central America (Schindler 1988; Pringle et al. 1993). Therefore, further increases in acid rain could have drastic effects on invertebrate communities worldwide.

Many species in the bromeliad family host complex aquatic invertebrate communities in their central tanks and surrounding leaves (Morales 2001). These communities are particularly vulnerable to changes in rain pH because they do not have the buffering capacity from the weathering of geological substrates that are present in freshwater communities (Schindler 1988). Additionally, epiphytic bromeliads are more susceptible to direct effects of rain pH changes because they obtain their moisture either by absorption from the air or direct collection of rainwater (Morales 2001).

In the Monteverde Cloud Forest (MCF), bromeliads are important sources of standing water, providing breeding habitats for many species of invertebrates (Weller and Cushman 2004). MCF is a diverse tropical cloud forest in the Puntarenas region of Costa Rica. Past studies on bromeliads in MCF have focused on the correlations of tank water volume, detritus level, and nutrient availability with invertebrate densities (Weller and Cushman, 2004; Matsuura et al., 2005; Treirweiler et al., 2005). However, no previous studies, to our knowledge, have investigated the repercussions of pH levels on invertebrates inhabiting bromeliad tanks.

To examine the effects of pH on this unique aquatic environment inside bromeliad tanks, we studied the effects of natural and experimental variation in tank water pH on invertebrate abundance. Specifically, we addressed three questions about bromeliad tank communities and acidity: (1) What is the natural pH variation in

bromeliad tanks? (2) How does pH correlate with invertebrate abundance? and (3) How does invertebrate survivorship vary with experimentally manipulated pH? We predicted that increasing acidity would negatively affect invertebrate abundance for both natural and experimental variation in tank pH.

METHODS

We conducted our study in a tropical cloud forest at La Estación Biologia de Monteverde, Costa Rica on 20-22 January, 2007. We collected bromeliads of the species *Guzmania monostachyia* (Bromeliaceae) along the Sendero Principal trail at varying elevations. We were only able to obtain bromeliads that were growing at less than 5 m up the trunk because higher bromeliads were inaccessible. Within the bromeliads, we sampled the diverse community of invertebrates, including adults in the orders Nematoda, Annelida and Copepoda, and larvae from the orders Diptera and Coleoptera.

We measured the natural variations in bromeliad tank pH on nine bromeliads in situ using a Milwaukee SM102 pH Meter, rinsing the probe in tap water between readings to eliminate contamination. We characterized the sizes of the bromeliads by measuring the length of the longest leaf on the outermost ring of leaves, diameter of the bromeliad, depth of the tank from the first separation of the innermost leaves, and diameter of the tank at the point where depth was determined. We took these measurements to see if bromeliad size covaried with invertebrate abundance.

We tested the relationship between the natural pH level of the bromeliads and the invertebrate communities within their tanks. We collected the organic material in 9 bromeliads to sample the aquatic invertebrate community. After removing and washing the detritus in each plant, we cleaned the plant with 15 half-second sprays of water and collected the contents in a cup. We examined the contents of each plant, counting and classifying any remaining live aquatic macroinvertebrates within each cup by order.

For the pH experiment, we collected 27 bromeliads and determined their starting pH, size, and invertebrate community, as described above, and placed them into individual holes in a patch of secondary forest 20 m east of the research station. We removed as much water as possible within each invertebrate sample and returned them to their respective plant. We used three pH treatments: 5.6, 3.1, and 2.4, and randomly assigned nine bromeliads to each. The 5.6 and 3.1 treatments reflect the extremes of natural pH variation of the bromeliads (see Results), and the 2.4

treatment reflects the conditions the bromeliad macroinvertebrates might experience in the event of acid rain. If bromeliads were to encounter acid rain with a pH of 2.4, as has been recorded in nature, their tanks would have the same pH due to their inability to buffer against pH fluctuations (Schindler 1988). To re-saturate the bromeliad tanks, we created three solutions with varying pH using lemon juice and tap water. To the first treatment, we added tap water with a pH of 5.6. To the second and third treatment group, we added lemon juice-water solutions with a pH of 3.1 and 2.4, respectively. Estimates of bromeliad size (as described above) did not differ among the pH treatments (MANOVA: $\lambda = 0.73$, $F_{8, 42} = 0.91$, $P = 0.52$).

After 24 hours, we recollected and analyzed the contents of the bromeliads to determine the change in the invertebrate community. We sampled invertebrates using the methods described above for initial invertebrate sampling. The total number of invertebrates before and after the pH experiment was used to determine the percent change in the number of aquatic invertebrates. We assumed that there was no recruitment of new invertebrate individuals to the bromeliads in our experiment.

Statistical analyses. We used correlation analyses to assess the relationship between the natural variation in pH and the number of invertebrates in the bromeliad tanks. We used a one-way ANOVA to test the effects pH treatments (pH=5.6, 3.1, and 2.4) on the percent change in invertebrates. We used a Tukey Highly Significant Difference multiple comparisons test to test which experimental pH treatments were significantly different from each other at alpha = 0.05. To normalize the data from our bromeliad pH experiment, we arcsine transformed the percent change in invertebrate abundance.

RESULTS

In our observational survey of nine bromeliads in the Monteverde cloud forest, the natural pH varied from 3.0 to 4.9, with a mean of 3.9 ± 0.1. As natural acidity of the water in the bromeliads increased, the number of aquatic invertebrates in the bromeliads decreased; however, this result was not statistically significant ($r = -0.62$, $n = 9$, $P = 0.076$; Figure 1). To have an 80% chance of finding a significant correlation between natural acidity and number of aquatic invertebrates at $\alpha = 0.05$, we would have needed to sample ten more bromeliads.

We also found a marginally significant positive correlation between the tank depth of each bromeliad and the abundance of invertebrates in the bromeliads ($r = 0.59$, $n = 9$, $P = 0.088$). However, tank

depth and acidity were not correlated (r = -0.10, n = 9, P = 0.79). To have an 80% chance of finding a significant correlation between tank depth of each bromeliad and number of aquatic invertebrates at alpha = 0.05, we would nave needed 22 more samples.

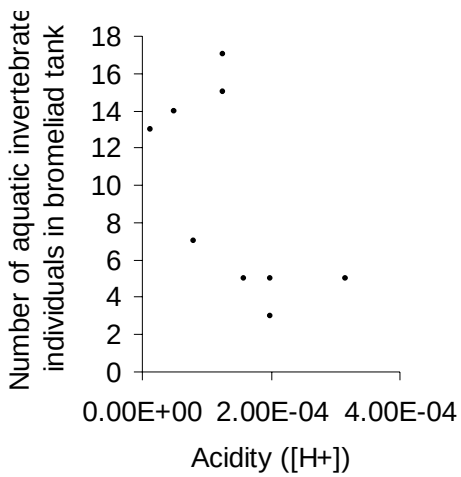

Figure 1: Number of aquatic invertebrate individuals in nine bromeliad tanks across their natural gradient of hydrogen ion concentrations. As the concentration of hydrogen ions increases, the number of invertebrates found in the bromeliads tends to decrease, with marginal significance.

In our pH manipulation, we found a significant difference among pH treatments in the percent change in aquatic invertebrate abundance after 24 hours (Figure 2). The pH=2.4 treatment was significantly different from the pH=3.1 and pH=5.6 treatments at α = 0.05, but the higher pH treatments were not significantly different from each other (Figure 2). In the pH=2.4 treatment, each bromeliad lost an average of 144% more invertebrate individuals than the pH=3.1 treatment, and an average of 234% more invertebrate individuals than the pH=5.6 treatment.

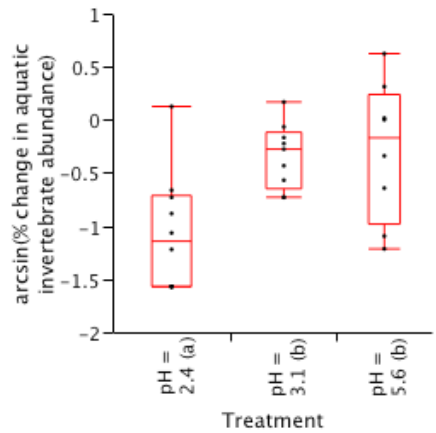

Figure 2: Percent change in aquatic invertebrate abundance in bromeliads across three pH treatments (pH 2.4, 3.1, 5.6). N = 9 plants per treatment. Treatments marked (a) are significantly different from treatments marked (b), which do not differ significantly from each other.

DISCUSSION

Our study suggests that there is a negative effect of acidity on bromeliad tank macroinvertebrate communities. While previous studies have focused on correlations between bromeliad physical characteristics, such as tank depth, with aquatic invertebrate abundance (Weller and Cushman 2004), we have shown that tank acidity is important as well. Additionally, we found that while tank depth and acidity were both correlated with aquatic invertebrate abundance, they were not correlated with each other,

indicating independence of tank depth and acidity effects. Because the two correlations of tank depth and number of invertebrates with acidity were only marginally significant, a future study should increase sample size of bromeliads to substantiate the two correlations described and investigate possible additive vs. non-additive effects of these two factors on number of invertebrates.

Our prediction that experimentally increasing acidity beyond natural levels would negatively affect aquatic invertebrate abundance was also supported. Both the tap water treatment and the lower threshold of the natural range acidity treatment had acidity levels that roughly spanned the natural range of bromeliad tank acidity, whereas the high acidity treatment was well below the natural range found in tanks. We suspect that there is a threshold between a pH of 3.1 and 2.4, below which the mortality of aquatic invertebrates significantly increases. To investigate this threshold prediction, further studies should examine mortality across a gradient of pHs. The percent change in aquatic invertebrate abundance in the tap water treatment indicates a tolerance for slightly higher pH levels than found in natural variation. Since rainfall in undisturbed habitats has a pH near 5.0 (Schindler 1988), invertebrate tolerance of water less acidic than the natural range of pH in bromeliads is important for survivorship.

While we were able to include a larger sample size in our study compared to previous bromeliad studies (e.g., Weller and Cushman 2004), our study is limited by its short time-span. In addition to the effects of acidity on invertebrate mortality, freshwater microhabitats can also experience negative sub-lethal effects (Stucliffe and Hildrew 1989). For example, acidic streams and lakes often affect invertebrate populations by containing less available nutrients or deterring larger predators, both of which alter species composition over time. To understand the sub-lethal effects of acidity on bromeliad communities, experimental studies should observe changes in the inhabitants over a longer time period than our 24 hour time period. Increasing acidity can also negatively affect invertebrate communities by decreasing food availability over longer time periods (Stucliffe and Hildrew 1989). It is possible that both acid treatments pH=3.0 and 2.4 would negatively affect invertebrate communities over a long time period due to time lag effects. Longer-term experimental studies should examine shifts in invertebrate species composition and abundance as a bromeliad tank acidifies over time.

Our study examined only bromeliads growing on the lower 5

m of tree trunks at the Monte Verde cloudforest. However, because invertebrate abundances and species composition in subcanopy bromeliads are similar to those in the upper canopy (Nadkarni and Longino, 1990), our study results may also be applicable to bromeliads growing higher in the canopy. Nonetheless, other tropical rainforests may have very different bromeliad communities and thus different responses to tank acidification. To better test the natural acidification on tropical forests in general, our study could be repeated in multiple different forests. In addition, to achieve natural responses to acidic solution additions, the bromeliads should be left attached to their host tree while the experiment is in progress. Leaving the bromeliads attached to the tree may also facilitate natural invertebrate migration in and out of acidic bromeliads.

Acid rain has the potential to greatly affect tropical habitats. With distinct wet and dry seasons, tropical habitats can experience 50% of their annual rainfall in as little as 15 days (Monte Verde Institute 2004). Shifts in the acidic content of this rain could have immediate detrimental effects on forest fauna. We found that in the acidic treatments, only the smallest aquatic invertebrates, such as nematodes and annelids were still alive. While Costa Rica is only responsible for 1% of Central America's industrial nitrogen and 2% of its sulfuric oxide emissions (Earth Trends 2003), acidic air pollution can travel distances far beyond Costa Rica's borders.

The significance of bromeliad acidification goes beyond acid rain alone. In highly productive tropical environments, sulfite leaching from high concentrations of detritus can acidify soils and habitats to levels equivalent to severe acid rain (Johnson et. al., 1979). Additionally, sulfuric emissions from volcanic activity can create acid rain in nearby microclimates (Pringle et. al., 1993). The acute effects of acidification on aquatic invertebrates have been demonstrated in many freshwater systems (Schindler, 1998), and are even thought to have caused decreases in the abundances of larger animals, such as amphibians (Blaustine and Wake, 1995). The effects of acid on aquatic invertebrates provide examples of the overall effects of acid on microhabitats. Acidification-related invertebrate mortality could rapidly cascade up the food-web, greatly altering all trophic levels in tropical rainforests. With longer-term research on the effects of acid inputs on bromeliad community response, we may be better able to understand how acidity can alter not only the inhabiting invertebrates, but also community food-web dynamics and ecosystem processes.

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