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

JAMES A. MARLOW

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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).

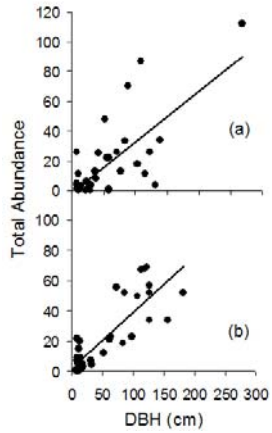

Figure 1. Total climber and epiphyte abundances in primary (a) and secondary (b) forests increases with tree diameter at breast height (regression statistics in Table 2).

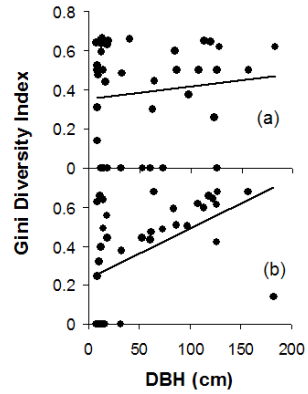

Figure 2. Gini diversity was not significantly correlated with tree diameter at breast height in primary forest (b), but it was in secondary forest (b) (regression statistics in Table 2).

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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