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BROMELIAD COMMUNITIES IN ISOLATED TREES AND THREE SUCCESSIONAL STAGES OF AN ANDEAN CLOUD FOREST IN ECUADOR

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ABSTRACT. A study conducted in 1996 at Las Palmeras, Ecuador, surveyed bromeliad communities in a 10-year-old secondary forest, in a 30-year-old secondary forest, and in isolated trees in a tropical montane forest. A comparison was made with the bromeliad community in a nearby mature forest to assess the recovery of epiphyte communities following disturbance. Bromeliad abundance, species richness, and volume were greater in the mature forest compared to the two secondary ones. Differences in bromeliad species richness and abundance among and within forests were correlated with host tree diameter at breast height (dbh). Bromeliads on isolated forest trees were less diverse but more abundant than on mature forest trees. No relationship was found between the distance of isolated forest trees from adjacent forest and the abundance or species richness of bromeliads present in their crowns.

RESÚMEN. Se compararon las comunidades de bromelias en un bosque secundario de diez años, un bosque secundario de treinta años, y árboles aislados con las comunidades de bromelias en un bosque maduro, para entender mejor la recuperación de las comunidades del dosel después de la perturbación. Se hizo este estudio en un bosque de niebla localizado en Las Palmeras, Ecuador. La abundancia, diversidad, y volumen de las bromelias fue mayor en el bosque primario que en los dos bosques secundarios. Las diferencias en abundancia y diversidad de bromelias entre bosques fueron corelacionado con el Diámetro a la Altura del Pecho de los árboles anfitriones. La diversidad de bromelias en árboles aislados fue menor y la abundancia mayor que en los árboles del bosque primario. No hubo relación entre la distancia de árboles aislados del bosque y la abundancia o diversidad de bromelias.

Key words: Bromeliaceae, canopy, tropical montane forest, Ecuador, epiphytes, isolated trees, succession

INTRODUCTION

Montane forests in the Neotropics support extreme species diversity and contain the largest proportion of species with narrow elevational distributions (Stotz et al. 1996). Unfortunately these forests are being cut at a rate of 1.1% a year, a faster rate than for the tropical forest biome as a whole (Food and Agriculture Organization 1993). Formerly forested areas are now a patchwork of active fields, active fields with isolated trees, secondary forest, and mature forest. Conservation of biodiversity in these ecosystems may depend upon the ability of species to persist in active fields and recover in regenerating secondary forest.

Studies of tropical forest regeneration have focused almost exclusively on the soil-rooted flora in lowland rain forests (Finegan 1996). Few studies have examined the effects of disturbance on epiphyte communities nor of the ability of these communities to recover following disturbance. Epiphytes in tropical montane rain forests can exceed tree leaves in biomass (Hofstede et al. 1993) and make up one third of the species and almost half of the individual plants (Gentry & Dodson 1987). Epiphytes are crucial to the maintenance of forest diversity as well as to ecosystem processes such as water impoundment and mineral cycling (see review by Nadkarni 1994). Conserving the biodiversity and ecosystem function of tropical montane forests, therefore, depends upon a better understanding of the effects of disturbance on the epiphyte community.

In one of the few studies to examine the effects of disturbance on epiphyte communities, Turner et al. (1994) documented a loss of 62% of epiphyte species during a 200-year period in Singapore. This loss, twice the percentage of plant species lost overall, suggests that epiphytes may be particularly susceptible to disturbance. Little is known, however, about how rapidly epiphyte communities recover their former abundance, species richness, and maturity during forest regeneration. This article compares species richness, abundance, and the phytotelmata volume of epiphytic Bromeliaceae in 10-year-old, 30-year-old, mature forest, and in pasture with isolated trees in a montane region of Ecuador.

MATERIALS AND METHODS

The forest studied is part of La Estación Científica Río Guajalito, located in the village of Las

Palmeras (76°49′W, 0°14′S) at an elevation of 1800 m in the province of Pichincha, Ecuador. Acosta-Solis (1977) classified these forests as lower montane. The area has a June–April dry season (Rudolph et al. 1998) and an average annual precipitation of 2735 mm (Grijalva 1991), and the study was conducted from September to December in 1996. The research station manages several active pastures, abandoned pastures of various ages, and mature forest. Two secondary forests (a 10-year-old clearcut and a 30-year-old clearcut) were selected for study, based on records maintained by the reserve owner. Both areas were ~10 ha in size and surrounded by mature forest. The owner had used these sites as pasture for 2–3 years and then left them to recover without further disturbance. The third site was a section of mature forest not contiguous with any secondary forest, and the fourth site had been cut 10 years earlier but with selected trees left standing to shade cattle.

Quadrats (25 × 25 m) were selected, one at each site, for similar slope, elevation, and aspect. In the pasture, four contiguous 25 × 25 m quadrats were marked to ensure a sufficient number of trees for comparison. Mature forest was at least 500 m away from the closest edge of quadrats in the 10-year-old and 30-year-old clearcuts. Bromeliads were identified in the field using 10× binoculars on all trees greater than 7 cm diameter at breast height (dbh). Despite attempts to locate all bromeliads on every tree, I undoubtedly missed some of the smallest individuals. Measurements for dbh were made at a height of 180 cm. The distance between each isolated tree and the nearest mature forest was measured to examine the effects of proximity of seed source on bromeliad species richness. To compare bromeliad sizes, a 10 × 200 m transect was surveyed along trails in each forest. All trees 7–14 cm dbh within each transect were marked in the 10-year-old, 30-year-old, and mature forests.

Within each transect, I collected all bromeliads on each tree by free climbing. Isolated trees were not included in this portion of the study. Once collected, each bromeliad was filled with water, inverted, and allowed to drain for five minutes into a small tub. The quantity of water was measured in a 50-ml graduated cylinder. Each bromeliad was dried and identified to the species level, where possible, at the Herbario Nacional del Ecuador (QCNE), where voucher specimens were deposited.

The ICE (incidence-based coverage estimator), a non-parametric species estimator (Chao 1984), was used to estimate the aggregate number of species for each forest. Chazdon et al. (1998) demonstrated that ICE is a relatively unbiased estimator of species richness. ICE-estimated species accumulation curves, constructed using Biota (Colwell 1996), averaged 500 random reorganizations for each curve.

Data Analysis

Analyses of variance (ANOVA) were carried out for bromeliad abundance and species richness per tree with forest type (mature/isolated trees/10-year/30-year) and tree dbh as factors. Prior to analysis, bromeliad abundance and species richness per tree were log transformed, using the equation: $\mathrm{Log}_{10}(x + 1)$. Separate ANOVAs were made for bromeliad volume, longest leaf length, and number of leaves per shoot among forests, with forest age as the factor in each case. These ANOVAs included only bromeliads sampled in the study transects. Bromeliad volume, longest leaf length, and leaf number were all log transformed prior to analysis, using the equation: $\mathrm{Log}_{10}(x)$. Post-hoc tests were performed on all significant results using Fisher's Least-Significant-Difference Test (LSD) to compare pairwise differences. Regression analysis was used to compare the effects of distance from forest on the bromeliad abundance and species richness of isolated trees, as well as the relationship between the abundance of some species and tree dbh. All statistical tests were performed using Systat Version 7.0. (Systat Inc. 1997).

RESULTS

Bromeliad Abundance

Abundance per tree ranged from 0 to 33 bromeliad plants. Individuals per tree were ranked: isolated trees > mature forest > 30-year > 10-year, based on the Least Significant Difference Test (LSD). Individuals per ha were ranked: 10-year > mature forest > 30-year > isolated trees (TABLE 1). Forest type and tree size accounted for some of this variation. Larger trees hosted more bromeliads than smaller trees ($P = 0.02$, $F = 9.53$), and trees were largest in the mature forest (tree size: mature forest > 30-year > isolated trees > 10-year, TABLE 1). Interactions of forest type and tree dbh did not influence bromeliad abundance significantly ($P = 0.294$, $F = 1.29$).

Species Richness

Six species of epiphytic bromeliads in three genera were found within the quadrats: *Racinaea multiflora, Tillandsia complanata, T. truncata, Guzmania variegata, G. squarrosa,* and an

TABLE 1. Mean bromeliad abundance/tree, species richness/tree, tree dbh, and tree density/ha^{-1} by study forest, Las Palmeras, Ecuador, 1996.

Study site	Broms./tree	Species rich./tree	No. broms.	Tree dbh cm	Density trees/ha^{-1}	No. trees
Mature forest	4.9(0.8)	1.7(0.13)	348	18.76(14.97)	1136	71
30-yr-old forest	1.5(0.16)	0.8(0.07)	212	15.37(5.77)	1120	70
10-yr-old forest	0.2(0.04)	0.2(0.03)	38	9.37(2.96)	2608	163
Isolated trees	5.0(0.07)	1.3(0.08)	351	12.86(5.89)	568	142*
F-Stat	10.18	9.36		36.50		
P-Value	0.000	0.000		0.000		

Note: Standard error in parentheses.
* Sampling size = four quadrats because of relative paucity of isolated trees.

unidentified *Tillandsia* species. Species richness varied 0–4 species per tree and 4–6 species per quadrat (TABLE 2). Species richness per tree differed significantly among forest types: mature forest > isolated trees > 30-year > 10-year, based on the LSD test. Estimated bromeliad species richness also differed significantly among forest types: mature forest > 30-year > 10-year > isolated trees (FIGURE 1). Species richness per tree was correlated significantly with host tree dbh (P = 0.001, F = 10.18, R^2 = 0.36). Mean species richness of bromeliads on larger trees exceeded that occurring on smaller hosts. The interaction of forest type and tree dbh did not influence bromeliad species richness significantly (P = 0.294, F = 1.29). Species richness per isolated tree did not vary with distance of the host from mature forest (P = 0.095, R = 0.041, FIGURE 2).

Phytotelmata Volume

In the 10 × 200 m transects, mean phytotelmata volume of bromeliads on small trees (7–14 cm dbh) was highest in the mature forest (P = 0.000, R^2 = 0.201). The forests could be ranked in terms of mean phytotelmata volume per tree and total phytotelmata volume per hectare: mature > 30-year > 10-year (FIGURE 3). The greater bromeliad volume in older forests can be attributed to the presence of larger individuals within all species and to the greater abundance of *Guzmania squarrosa* and *G. variegata,* both large species.

Species Composition

Bromeliad flora also varied among sites. *Racinaea multiflora* was the most common species in all but the 10-year-old forest, where *Tillandsia complanata* and *T. truncata* were the most abundant. *Tillandsia complanata, T. truncata, T. sp.,* and *R. multiflora* were present in all four sites (TABLE 2). The two species that were not present in all sites, *Guzmania variegata* and *G. squarrosa,* were large, rare when present, and not significantly more abundant on large trees than on small ones (TABLE 3).

DISCUSSION

This study constitutes a preliminary examination of the effects of clearcutting and subsequent forest-regeneration on bromeliad communities. It may well be the first such study. By comparing three quadrats, I found that bromeliad species richness and abundance recovered relatively rapidly during forest regeneration. After 30 years, five out of six bromeliad species were present, well before tree species richness might be expected to recover (Finegan 1996). The small size of bromeliad phytotelmata in both the 10-year-old and 30-year-old forests, however, suggests that recovery of ecosystem

TABLE 2. Bromeliad species composition, abundance, and richness at each forest study site.

	Species abundance/study site (% of total bromeliads/site)							
Forest study site	*Racinaea multiflora*	*Tillandsia complanata*	*Tillandsia truncata*	*Tillandsia* sp.	*Guzmania variegata*	*Guzmania squarrosa*	No. brom.	Species richness
Mature	64.0	20.4	11.7	1.3	2.4	2.0	348	6
30-year	60.9	18.2	15.1	5.2	0.5	0.0	212	5
10-year	10.5	55.2	28.9	5.2	0.0	0.0	38	4
Isolated trees	80.4	12.2	6.9	0.3	0.0	0.0	351	4

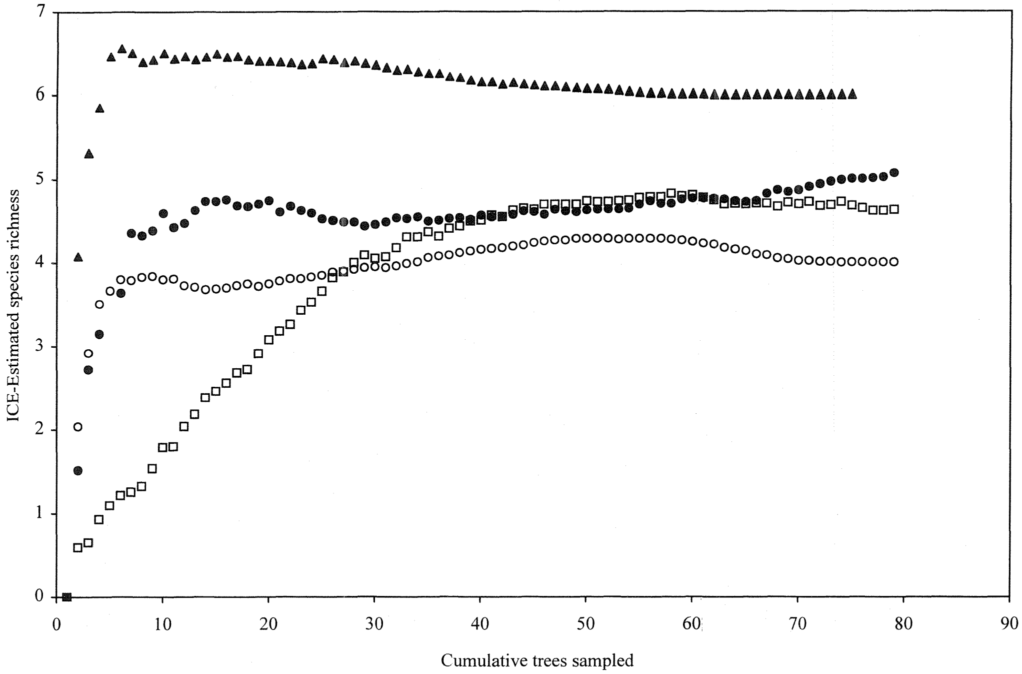

FIGURE 1. ICE-estimated species richness per individual bromeliads sampled in four sites in Ecuador, 1996. Note: ▲ = mature forest, ● = 30-year-old forest, □ = 10-year-old forest, and ○ = isolated trees.

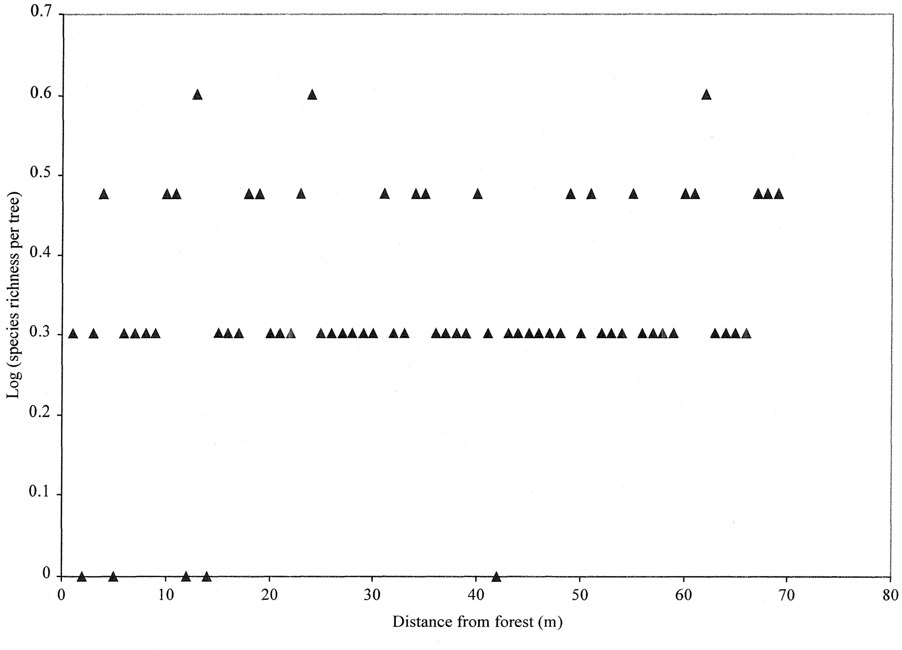

FIGURE 2. Bromeliad species richness per tree and distance of tree from forest edge.

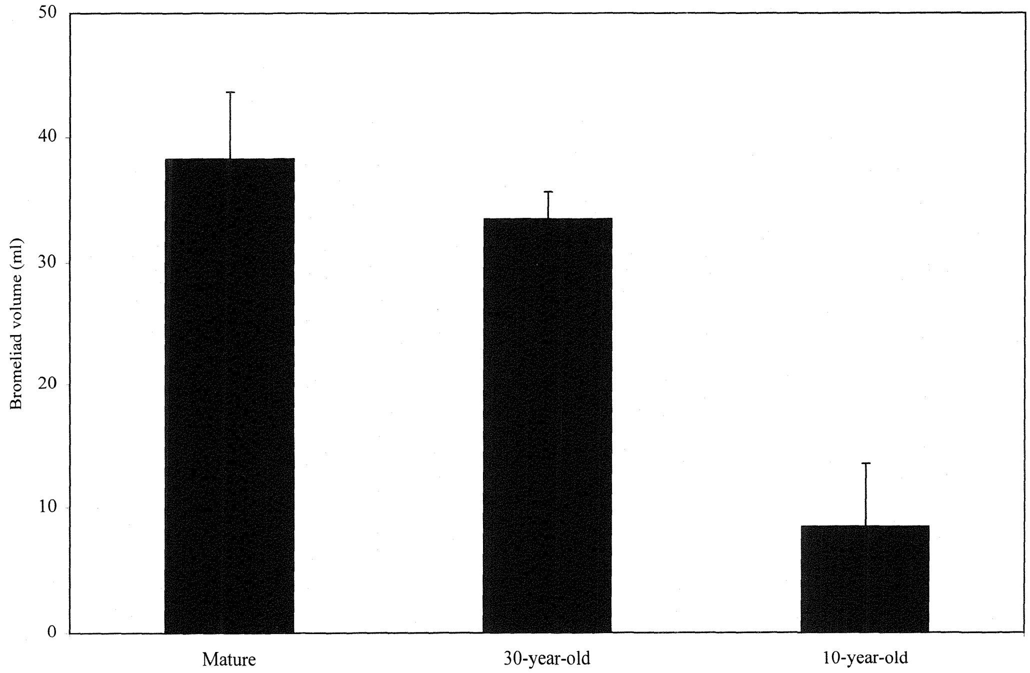

FIGURE 3. Mean bromeliad volume in different forest types. Error bars indicate standard error.

functions, such as water impoundment and mineral cycling, may lag significantly behind the recovery of species richness.

Differences in tree dbh accounted for almost half of the variation in bromeliad species richness and abundance. Several other authors have reported correlation between epiphyte diversity and abundance and tree size within mature forests (Zimmerman & Olmsted 1992, Tewari et al. 1985, Bartareau & Skull 1994). Larger trees provide a greater surface area for colonization, more time for colonization, and rougher bark (Tewari et al. 1985). Regeneration of bromeliad communities in young forests also may be limited by seed-dispersal (Wolf 1995), as suggested by the low abundance of even young bromeliads in the 10-year-old forest.

The composition of the bromeliad flora in this report was similar to that of a nearby forest at a similar elevation of 1800–2000 m (J. Nieder pers. comm.). Species richness at these sites was identical (six species), and three species (*Til-*

TABLE 3. Mean volume, number of leaves, and length of longest leaf in each bromeliad species and effects of tree size (dbh) on species abundance.

Bromeliad species	No. broms.	Volume cm*	Leaf no.**	Leaf length cm*	Correlation with tree dbh
Racinaea multiflora	182	27.3(3.5)	12.1(0.5)	15.7(0.7)	$P < 0.001$ $R^2 = 0.180$
Tillandsia sp.	8	74.1(25.5)	18.1(1.9)	45.2(7.0)	$P = 0.145$ $R^2 = 0.005$
Tillandsia truncata	30	57.1(13.9)	13.9(1.0)	30.0(4.0)	$P < 0.001$ $R^2 = 0.112$
Tillandsia complanata	55	13.6(0.8)	13.6(0.9)	21.7(2.4)	$P < 0.01$ $R^2 = 0.027$
Guzmania squarrosa	34	74.2(16.6)	16.7(1.4)	34.1(3.6)	$P = 0.631$ $R^2 = 0.001$
Guzmania variegata	8	52.0(19.2)	13.4(1.2)	33.1(5.6)	$P < 0.001$ $R^2 = 0.030$

* $P < 0.01$; ** $P < 0.05$; standard error in parentheses.

landsia truncata, T. complanata, and *Guzmania squarrosa*) overlapped. Rudolph et al. (1998) at the same site studied by Nieder, found that *T. complanata* was able to establish on bare bark, a capacity consistent with its higher relative abundance in the 10-year-old forest of my study. Nieder also found two *Guzmania* species (*G. variegata* and *G. bakeri*) to be the rarest species, with *G. bakeri* established mostly on thick substrate. If also true for *G. variegata* and *G. squarrosa,* this need for thick substrate might explain the absence of these species in the secondary forests.

My results add to the growing body of literature demonstrating that isolated trees can play a major role in maintaining plant and animal biodiversity in agro-ecosystems (Guevara et al. 1986, Hietz-Seifert et al. 1996, Sillet 1992, Sillet et al. 1995, Greenberg & Saldago Ortiz 1994). Bromeliad abundance per tree, especially that of *Racinaea multiflora,* was actually highest on isolated trees. Such trees receive more lateral light than those within forests (Sillet et al. 1995) and as such may provide more habitat or more favorable habitat for heliophylic epiphytes. Such increased sun may not be as favorable, however, for other vascular epiphytes, such as orchids (S. Engwald pers. comm.). Hietz-Seifert et al. (1996) found a weak correlation between species richness and distance from nearby forest for some epiphytes, but this was not the case in my study. Part of the explanation may be that the seed supply for bromeliads on isolated trees is epiphytes on nearby isolated trees not in nearby forest. Alternatively too small a distance may have been included in this study for distance effects to be seen.

This study demonstrates that the species richness and abundance of bromeliads can recover relatively quickly in secondary forests and be partially maintained on isolated trees. Because many canopy-dependent fauna use bromeliad phytotelmata (Nadkarni 1994), epiphyte recovery may signal parallel recoveries in animal communities. Highly diverse, managed ecosystems may be able to mitigate problems related to forest fragmentation (Perfecto & Snelling 1995). Areas with isolated trees can facilitate dispersal of organisms from forest patch to patch and provide long-term habitat for many species.

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