



Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area

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Population structure;
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Summary

We analyzed the differences in species richness, community composition, population structure and within-tree location of epiphytic bromeliads in contiguous secondary and mature forests in a premontane area in Costa Rica. Diversity in the mature forest was highest, and the communities differed in their composition as well as in the recruitment rates of the dominant species. *Guzmania monostachia* and *Catopsis nutans* dominated the secondary forests, whereas *Tillandsia fasciculata* and *T. tricolor* were more abundant in the mature forest. The secondary forest species showed high rates of seedling recruitment while the opposite was found for the mature forest species. Species presence and abundance among and within habitats did not correlate with their physiological (i.e. CAM vs. C₃ photosynthesis) or morphological attributes. The spatial distribution patterns were similar among habitats; bromeliads tended to aggregate on a few relatively large phorophytes. The species shared a similar vertical stratification within habitats, except for the two dominant species in the early and mid-successional stages, although its ecological implication is not clear. With some exceptions, conspecifics of different ages were located on similar substrate types (i.e. stems, primary, secondary, or tertiary branches) within the tree-crowns, which suggests limited within-tree dispersion. Differences in species composition and rates of seedling recruitment among secondary and mature forest may arise from ecophysiological differences among species; however, the combined effect of seed availability and dispersal differences may have a larger influence. Thus, epiphyte community assembly can only be

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understood when the differences in habitat conditions, the availability of propagules, their dispersal characteristics and requirements for seedling establishment are known.

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Zusammenfassung

Wir analysierten die Unterschiede im Artenreichtum, in der Gesellschaftszusammensetzung, in der Populationsstruktur und die Verteilung innerhalb der Bäume bei epiphytischen Bromelien in zusammenhängenden sekundären und alten Wäldern in einem Bergvorland in Costa Rica. Die Diversität war in dem altem Wald am höchsten und die Gemeinschaften unterschieden sich sowohl in ihrer Zusammensetzung als auch in den Rekrutierungsraten der dominanten Arten. *Guzmania monostachia* und *Catopsis nutans* dominierten den sekundären Wald, während *Tillandsia fasciculata* und *T. tricolor* im alten Wald häufiger waren. Die Sekundärwaldarten zeigten hohe Raten der Keimlingsrekrutierung während für die Altwaldarten das Gegenteil galt. Das Vorkommen und die Häufigkeit der Arten in und zwischen den Habitaten korrelierte nicht mit ihren physiologischen (z. B. CAM vs. C₃-Photosynthese) oder morphologischen Eigenschaften. Die räumlichen Verteilungsmuster waren in den Habitaten ähnlich. Die Bromelien zeigten die Tendenz, sich auf einigen wenigen, großen Phorophyten zu sammeln. Die Arten hatten, mit Ausnahme der zwei dominanten Arten in den frühen und mittleren Sukzessionsstadien, innerhalb der Habitate eine ähnliche vertikale Schichtung, wobei die ökologischen Implikationen unklar sind. Abgesehen von wenigen Ausnahmen befanden sich artgleiche Individuen unterschiedlichen Alters auf ähnlichen Substrattypen innerhalb der Baumkronen (z. B. Stämme, primäre, sekundäre oder tertiäre Äste), was auf eine beschränkte Ausbreitung innerhalb der Bäume hindeutet. Die Unterschiede in der Artenzusammensetzung und den Raten der Keimlingsrekrutierung zwischen den sekundären und alten Wäldern könnten auf ökophysiologische Unterschiede zwischen den Arten zurückgeführt werden. Die kombinierten Auswirkungen der Samenverfügbarkeit und Unterschiede in der Verbreitung der Arten könnten jedoch eine größere Auswirkung haben. Deshalb kann die Anordnung der Epiphytengesellschaften nur verstanden werden, wenn die Unterschiede in den Habitatbedingungen, die Verfügbarkeit von Verbreitungseinheiten, ihre Verbreitungscharakteristik und die Ansprüche der Keimlinge bekannt sind.

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Introduction

The extraordinary diversity and abundance of vascular epiphytes is a particular characteristic of mature tropical montane forests. The contribution of epiphytes to overall diversity (reviewed in Wolf & Flamenco-S 2003) and to forest biomass (Hofstede, Wolf, & Benzing 1993; Nadkarni 1985) has been well documented for some undisturbed forests. Deforestation of tropical forests for agriculture and cattle grazing continues; as soil productivity decreases, lands are abandoned and are subsequently invaded by successional vegetation or secondary forests (FAO 1993). While secondary forest dynamics has received more attention from forest ecologists (Brown & Lugo 1990; Finegan 1996; and references therein), equivalent studies on epiphytes are still rare.

The few studies on epiphytes in secondary forests report a reduction in species richness (Barthlott, Schmit-Neuerburg, Nieder, & Engwald 2001; Dunn

2000; Krömer & Gradstein 2003). Differences in the physical characteristics of secondary forests, such as lower phorophyte (host-tree) structure diversity and a more homogeneous microclimate, supposedly explains that pattern (Barthlott et al. 2001). The availability and dispersability of propagules has also been suggested as an important determinant of community assembly (Benzing 1981; van Dunné 2001; Wolf 1994; Wolf 2005; Yeaton & Gladstone 1982). Comparative studies on epiphyte communities in mature and successional forests provide insights into the process of community assembly during forest recovery. The incorporation of the variables of species richness and composition are important in the identification of trends in floristic diversity, both are useful indicators of vegetation recovery and change independently along the successional stages (Finegan 1996).

Bromeliad (Bromeliaceae), are restricted to the neotropics, where they contribute considerably to the diversity of epiphytic angiosperm communities,

in effect only surpassed by orchids and pteridophytes (Benzing 2000). The few studies of bromeliads in successional habitats have addressed the spatial distribution (Bader, van Dunné, & Stuiiver 2000; van Dunné 2001; Wolf 2005) and the changes in species richness and composition (Barthlott et al. 2001; Dunn 2000; Wolf 2005). Comparative accounts on the population structure of secondary and mature forest species are still scarce. Particularly, there is a tendency to neglect small plants (juveniles) when surveying epiphytes because of limitations that arise from the observational technique and the difficulty in distinguishing and identifying small juveniles in a complex canopy environment.

We studied the species richness, abundance and community composition of epiphytic bromeliads in two successional forests of different age and one primary forest stand in a tropical premontane locality in Costa Rica (CR). Additionally, we examined the relationship between population structure, vertical stratification and within-tree location with the forest successional stage. Specifically, we addressed the following questions: (i) Is the diversity of epiphytic bromeliads correlated with the forest successional stage? (ii) Do the population structures of the dominant species differ among habitats? (iii) Is the presence and abundance of epiphytic bromeliads among habitats associated with physiological or morphological traits of the species? and (iv) Do the patterns of spatial distribution change with the forest's successional stage?

Materials and methods

Study site

This study was carried out at the Ecolodge San Luis and Research Station, a 62 ha private reserve located on the Upper San Luis River Valley on the Pacific slope of the Monteverde area, Province of Puntarenas, CR (10°17'10"N, 84°47'40"W, 1050 m a.s.l.). The area is classified as humid premontane (bmh-P) according to Holdridge's life-zone system (Haber 2000) and it borders the Monteverde Cloud Forest Preserve and the Children's Eternal Rain Forest Reserve. Weather records from the station report a mean annual rainfall of 3282 mm (± 489), with about 80% of the rain occurring from May to November; the air temperature ranges between 17–25 °C. The terrain is irregular and steep and the original forest cover has been fragmented into a mosaic of different land-uses as consequence of dairy and coffee activities but some mature forest

patches were spared. Recently, several pastures and coffee plantations have been abandoned and subsequently invaded by secondary forest trees which in turn are being colonized by epiphytes. The epiphytic bromeliad flora of this area comprises five genera and some 28 species: *Catopsis* (4), *Guzmania* (6), *Racinaea* (1), *Tillandsia* (11) and *Werauhia* (6) (unpublished data).

Study plots

The station manages several areas in different successional stages, from active pastures to old growth or mature forest. During 2002, a 300 m² area was studied within each of three habitats that differed in their successional stages, located within 700 m from each other. Each sampling area was further divided into three 100 m² plots randomly distributed to encompass the within-habitat variation. The early succession (ES) represents ca. 3 ha pasture abandoned 8–12 yr ago, the distance between plots ranged from 50 to 230 m. The regenerating forest is patchily distributed, in a matrix of grassy areas that enclose the station's facilities. This area is surrounded by active pastures, secondary forests of intermediate age, mature and selectively logged forest patches. The mid-succession (MS) consisted of a (35-) 40-yr-old forest patch along the "Camino Real" trail on a steep slope. The patch is surrounded by selectively logged forest on the eastern and western side, abandoned shaded coffee plantations in the North and a young secondary vegetation patch on the southern side. Due to constraints imposed by shape and size, the three plots were laid out contiguously in this site. The mature forest (MF) is located on the slope to the North of the station facilities. It constitutes a fragment of about 10 ha that is irregular in shape and connected to other forest remnants in the area. The plots were situated away from natural gaps and forest edges and separated from 75 to 150 m.

Host trees characteristics

The woody vegetation in each successional habitat was described by recording the species richness and abundance of trees with a stem diameter ≥ 5.0 cm at breast height (1.3 m, dbh) in the study plots. Voucher specimens were deposited at the National Herbarium of CR. We recorded the number of stems and their diameter (when several stems were present their values were added up), the number of branch bifurcations (forks) thicker than 2.5 cm at the base, and tree height using a

graduated pole or a clinometer (Suunto PM-5/360, Finland).

Bromeliad diversity and community composition

We identified and counted all the bromeliads growing on trees ($\text{dbh} \geq 5.0 \text{ cm}$) within the plots. Their size was measured to the nearest 0.1 cm, as the length of the largest leaves stretched and measured from the base of the rosette. Morphological differences among species and previous knowledge from field experiments were utilized to identify all individuals up to 0.5 cm in size to species level. Ramets from the same genet or plant were recorded separately. Species richness (S), the Shannon (H' , \log_e) and Simpson (D) indices were used to compare bromeliad diversity among the three sampled habitats (Magurran 1988). Vouchers were deposited at the National Herbarium (CR).

We combined rope-climbing techniques (Perry 1978a) and ground-based observations (Flores-Palacios & García-Franco 2001) to census the bromeliads. Small trees were climbed using an extendable aluminum ladder (maximum reach of 6 m) or by free-climbing. In the mature forest, the aforementioned techniques were simultaneously utilized to locate plants higher on the tree. When inaccessible, plant size was visually estimated from the closest accessible point.

Population structure

Individuals of the most abundant species in each habitat were classified into one of the size categories described in Table 1. Size class limits are meant to represent the life stages of the species in the study area and are based on field observations and preliminary data from germination and seedling establishment experiments and

growth rate measurements in the same area (Cascante-Marín et al., unpublished data).

Distribution and abundance

We examined the distribution of bromeliads among trees in each successional habitat by comparing the frequency of occupied and empty trees using the log-likelihood ratio method for contingency tables. Bromeliad abundance and substrate availability per tree (tree size) was examined by calculating "Tree Size" as the summation of the standardized values of stem diameter (cm), tree height (m) and number of branch bifurcations (forks) per tree. This correlation was evaluated by means of a Pearson product-moment correlation test.

The vertical stratification of the most abundant species per habitat was determined by measuring the distance from the ground to the bromeliad's attachment point on the host-tree using a tape ruler. When inaccessible, it was estimated to the nearest decimeter with a graduated plastic pole (3 m) from the highest possible tape ruler measurement. The data were sorted according to categories in Table 1 and the differences in vertical distribution were separately tested for each habitat with an analysis of covariance. Species and life stage were entered as main factors and tree height as covariate. Data were square-root or log-transformed when necessary to improve normality and remove heteroscedasticity. Computations were carried out using the program STATISTICA for Windows[®] (Statsoft, Inc. 2000).

Bromeliad location on the host-tree

We examined the bromeliad position within the tree by recording several variables related to the substrate they occupied. 'Substrate type' refers to the location on stems or trunks, or on primary,

Table 1. Size class limits (cm) representing the life-stage categories used in the field to distinguish the previous-year seedlings (PSD), older seedlings (OSD), juveniles (JUV), sub-adults (SAD) and adult plants (ADL) of the most abundant epiphytic bromeliad species in the study site

Category(life stage)	Bromeliad species			
	<i>Catopsis nutans</i>	<i>Guzmania monostachia</i>	<i>Tillandsia fasciculata</i>	<i>Tillandsia tricolor</i>
PSD	≤1.0	≤1.0	≤1.0	≤1.0
OSD	1.1–2.0	1.1–5.0	1.1–5.0	1.1–3.0
JUV	2.1–4.0	5.1–10.0	5.1–10.0	3.1–8.0
SAD	4.1–6.0	10.1–20.0	10.1–20.0	8.1–14.0
ADL	> 6.0	>20.0	> 20.0	> 14.0

secondary or tertiary branches. Since most of the tertiary branches were located near the periphery of the tree crown, no further subdivision was considered necessary. 'Position on the substrate' describes the bromeliad's point of attachment either (1) superior or on the upper surface, (2) lateral or on the sides, or (3) inferior or underneath the branch or stem. 'Substrate inclination' refers to the angle formed by the stem or branch with respect to an imaginary horizontal axis in the vicinity of a bromeliad (about 5 cm on both sides) and divided into four categories: (A) horizontal or nearly so, (B) less than 45°, (C) higher than 45°, and (D) vertical or nearly so.

Using contingency table analyses, we separately determined the association between life stage and each variable, after controlling for species and successional stage. The probability distribution to test for general association in the dataset was calculated by following the Mantel-Haenszel test (Stokes, Davis, & Koch 2000), which is based on randomizations of the column levels among the levels of the row variables while keeping the marginal totals fixed. The statistic (Q_{GMH}) is approximately distributed as chi-square with $(s-1)(r-1)$ degrees of freedom.

Results

Host tree characteristics in the successional habitats

The three successional habitats differed in tree diversity and composition (Table 2). Shannon diversity values (H') increased with the age of the successional vegetation while species dominance (D) decreased. Tree abundance in the ES was lower than in the MS and MF and the species from the younger vegetation were habitat-specific. In the ES

vegetation *Acnistus arborescens* (Solanaceae) represented 78% of the trees. In the MS and MF stages, the dominance of a particular species was less pronounced. *Inga mertoniana* (Fabaceae), *Dendropanax arboreus* (Araliaceae) and *Beilschmiedia brenesii* (Lauraceae) accounted for 52% of all the trees in the MS stage. In the MF, most of the species (74%) were represented by a single tree and the four most common species, *Cupania glabra* (Sapindaceae), *D. arboreus*, *I. mertoniana* and *Lonchocarpus oliganthus* (Fabaceae), constituted 38% of all the recorded trees. Structurally, the trees in the ES were lower in stature (< 6 m) and had on average more stems and a higher stem diameter value than trees in the MS (Fig. 1). The MF vegetation was composed of taller trees, with a higher number of branch bifurcations and larger stem diameters than trees in the other two successional stages (Fig. 1).

Bromeliad diversity and composition

Eleven species (subfamily Tillandsioideae) were identified in the three successional habitats (Table 3). Species richness (S) and Shannon diversity values (H') indicate an increase in diversity of the bromeliad community with age of the successional stage. Species dominance values (Simpson index, D) were similar for the ES and MS but decreased in MF. The identity of the dominant species changed between secondary and mature forest. The frequency of *Guzmania monostachia* and *Catopsis nutans* was significantly higher in the ES and MS stages, while in the MF the dominant species were *Tillandsia tricolor* and *T. fasciculata* ($G = 2\ 791.5$, $df = 6$, $P < 0.001$). The former species together represented 96% and 83% of all the bromeliads in the ES and MS stages, respectively. In the MF, 88% of the plants were *Tillandsia* spp. while

Table 2. Values for the descriptive parameters of diversity and composition of the arborescent vegetation in three forest successional stages at a tropical premontane site, Costa Rica

Parameter	Forest successional stage		
	Early succession	Mid-succession	Mature forest
Species richness, S	6	19	27
Plant families	5	14	22
Shannon index, H'	0.84	2.50	3.09
Simpson's index, D	0.62	0.12	0.06
Total tree abundance (range per plot)	36 (4–20)	67 (20–26)	42 (10–18)

Data from trees ≥ 5.0 cm dbh in three 100 m² plots in each habitat.

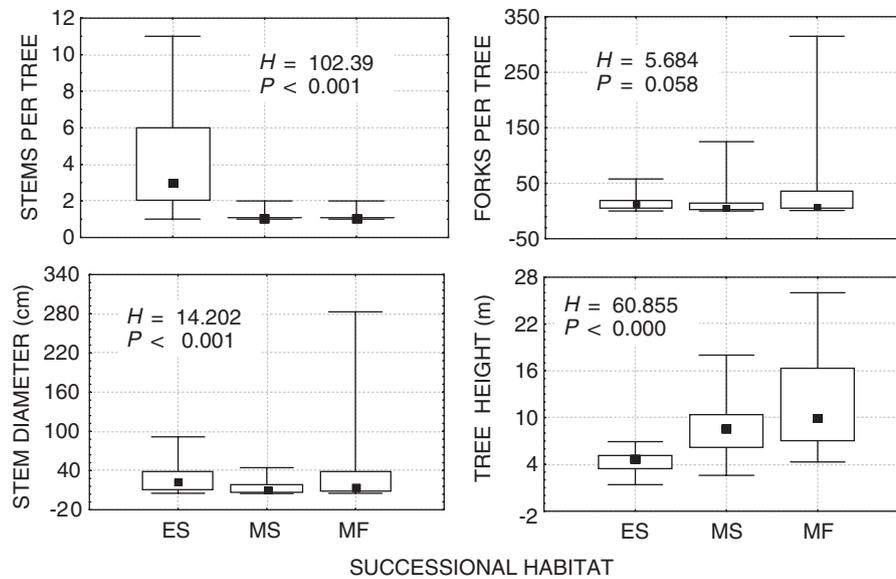


Figure 1. Descriptive values for the parameters of host-tree physiognomy in three successional habitats in a tropical premontane forest, Costa Rica. Each parameter is represented by a graph with habitat on the x-axis: ES – early succession, MS – mid-succession and MF – mature forest. Symbols represent the median (dark square), 25–75% percentiles (box) and minimum and maximum (whiskers). Statistical values from non-parametric tests (Kruskal–Wallis ANOVA) are indicated inside the graphs given in each panel.

Table 3. Species diversity, composition and abundance (number of ramets) of epiphytic bromeliads in three successional stages of a tropical premontane forest, Costa Rica

Bromeliad species	Abundance per habitat (300 m ²)		
	Early succession	Mid-succession	Mature forest
<i>Catopsis nutans</i> (Sw.) Griseb.	934	105	17
<i>C. nitida</i> (Hook.) Griseb.	6	20	1
<i>Guzmania monostachia</i> (L.) Rusby ex Mez	1952	892	15
<i>G. sanguinea</i> (André) André ex Mez	–	–	4
<i>Racinaea spiculosa</i> (Griseb.) M.A. Spencer and L.B. Sm.	2	–	–
<i>Tillandsia fasciculata</i> Sw.	59	45	217
<i>T. juncea</i> (Ruíz and Pav.) Poir.	–	59	19
<i>T. leiboldiana</i> Schltdl.	–	2	–
<i>T. multicaulis</i> Steud.	2	1	2
<i>T. tricolor</i> Schltdl. and Cham.	–	68	338
<i>Werauhia werckleana</i> (Mez) J.R. Grant	–	6	10
Unidentified species	–	–	7
Total abundance	2955	1198	630
Species richness, <i>S</i>	6	9	10
Shannon index, <i>H'</i>	0.74	0.98	1.17
Simpson's index, <i>D</i>	0.54	0.57	0.41

the abundance of *G. monostachia* and *C. nutans* was reduced to 5.1%.

Bromeliad population structure

The relative contribution of each life stage (size class) to the local population (i.e. the population

structure; Fig. 2) is an indicator of the recruitment rate. Populations with high recruitment rates will have a higher number of individuals in the smallest size-classes (seedlings and juveniles). Conversely, populations with a low recruitment will mainly be composed of individuals in the upper size-classes (sub-adults and adults) (cf. Oostermeijer, van 't Veer, & den Nijs 1994). The most abundant species

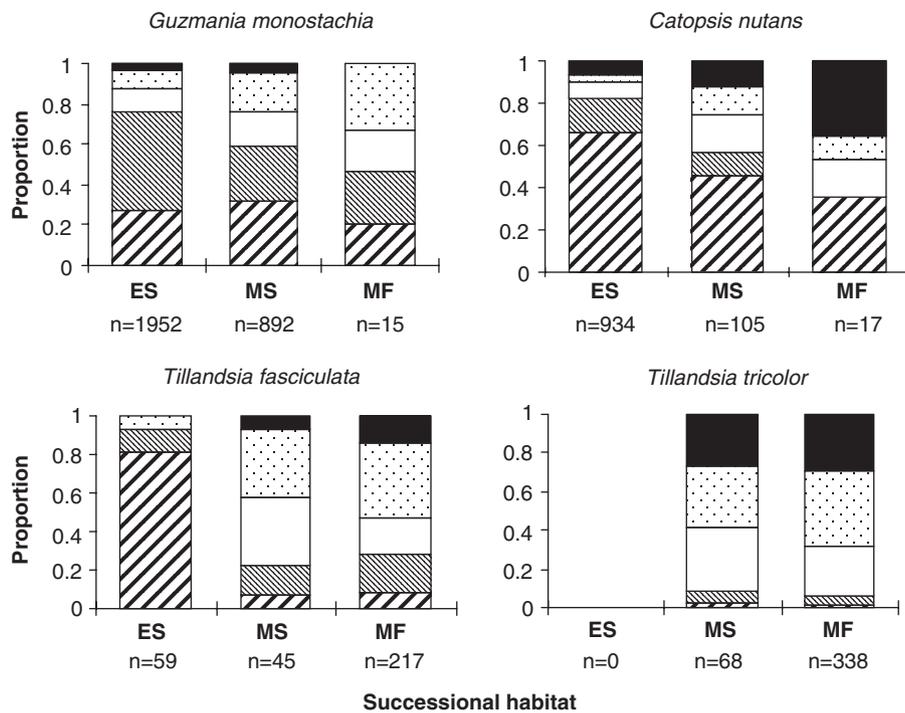


Figure 2. Population structure of the most abundant bromeliad species in three successional habitats in a tropical premontane forest, Costa Rica. Data are proportions per life stage represented by sections in each bar (bottom to top): previous-year seedlings (hatched bold), older seedlings (hatch light), juveniles (white), sub-adults (dotted) and adults (black). Successional habitats (x-axis) are: ES (early succession), MS (mid-succession) and MF (mature forest). Sample sizes (number of ramets) are shown below the x-axis.

in the ES and MS stages, *G. monostachia* and *C. nutans*, showed a population structure characterized by high recruitment (Fig. 2). Contrary, the most common species in MF, *T. fasciculata* and *T. tricolor*, showed different patterns. In the ES stage, the small population of the first species exhibited a high recruitment structure and it presented an intermediate population structure in the MS and MF stages, with similar proportions of individuals in the smallest and largest size classes. For *T. tricolor*, which did not occur in the ES stage, its population structure was nearly intermediate in the MS and MF stages but with proportionally fewer seedlings than the other *Tillandsia*.

Bromeliad distribution and abundance

Almost half (45.8%) of the 144 examined trees hosted at least one bromeliad. The proportion of trees supporting bromeliads was higher in the ES (92%) than in the MS and MF (30% and 28%, respectively) ($G = 46.4$, $df = 2$, $P < 0.001$, Fig. 3). Regardless of the successional stage, most epiphytes aggregated on a few trees (Fig. 3). In the ES, seven out of the 36 examined phorophytes contained almost 60% (1770) of all the recorded

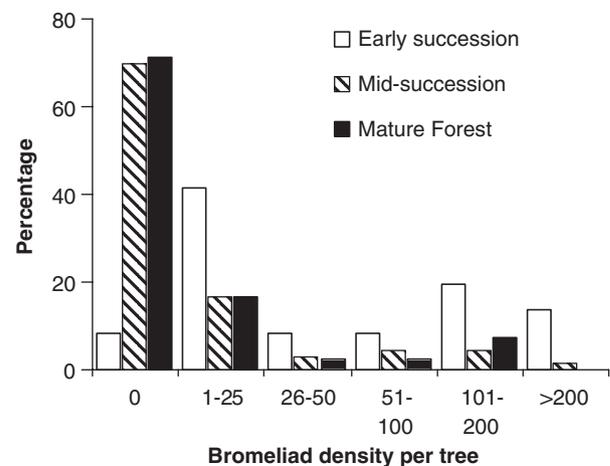


Figure 3. Bromeliad density per host tree in different successional habitats in a tropical premontane forest. Bars represent percentages of trees in each habitat according to bromeliad density categories.

ramets, each tree harbouring from 170 to 407 ramets. Similarly, in MS five out of the 46 sampled phorophytes contained 76% (842) of the bromeliads; from 122 to 302 ramets per tree. In MF, four out of the 46 surveyed trees housed 58% (366) of the bromeliads, each tree having from 43 to 123

ramets. No host-tree specificity was detected in the MS or MF stage; however, 70% of the trees hosting bromeliads in ES belonged to *A. arborescens*. The substrate availability was positively correlated with the bromeliad abundance per tree (Fig. 4). High values of substrate availability usually

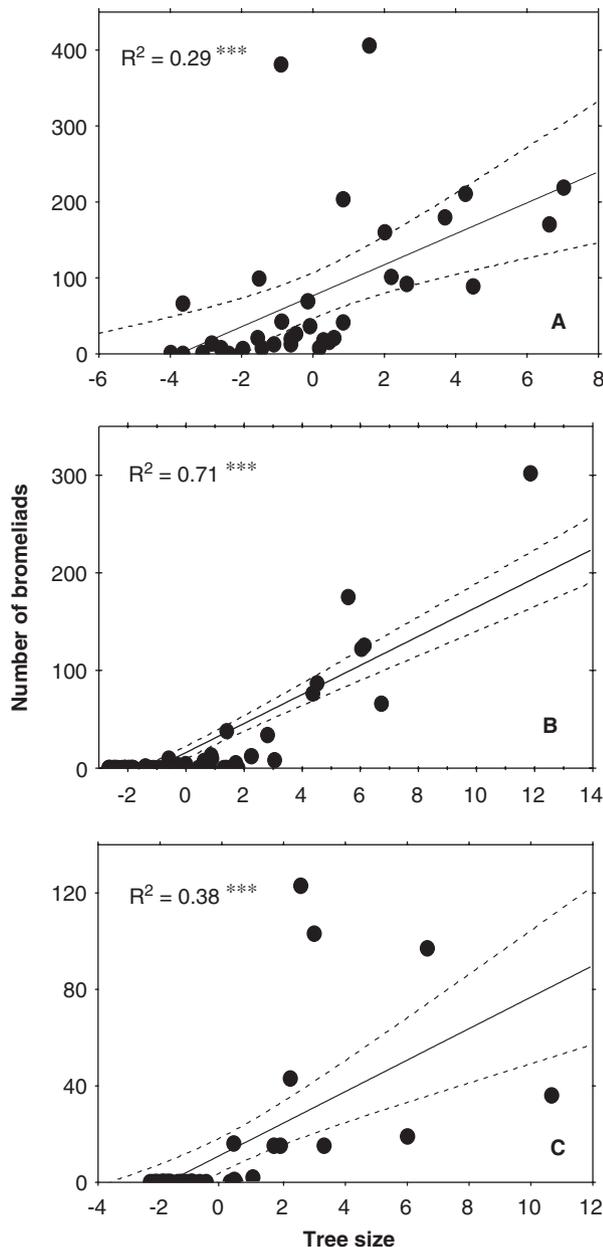


Figure 4. Regression analyses for the standardized parameter of substrate availability (tree size) and the number of bromeliads per host tree in three successional habitats in a tropical premontane forest, Costa Rica. In each graph: (A) early succession, (B) mid-succession, and (C) mature forest, R^2 is the coefficient of determination and its significance after a t -test is indicated by $***P < 0.001$. Dotted lines represent the 95% confidence intervals.

described a relatively tall tree with a thick stem and a wide crown, especially in the MS and MF stages.

In order to account for differences in tree height, the vertical distribution is graphically expressed as a relative measurement of the bromeliad position with regard to the respective tree height. Tree heights were divided in ten equally distributed bands and the bromeliad distribution was partitioned accordingly (Fig. 5). The vegetation structure greatly determined the bromeliad's vertical stratification. In the ES stage, the majority of bromeliads (>90%) grows at 1.3–3.1 m above the ground with an average host-tree height of 4.4 m. In MS, most bromeliads occurred at 7.3–11.0 m above the ground with an average host-tree height of 12.2 m and in MF, bromeliads were at 9.7–17.5 m above the ground with an average host-tree height of 19.4 m. *G. monostachia* significantly occupied relatively lower strata of the phorophytes, while *C. nutans* occurred higher in the canopy of the ES and MS stages (Table 4, Fig. 5). *T. tricolor* and *T. fasciculata* had intermediate positions when present. In the MF stage, *T. fasciculata* occurred at lower positions than *T. tricolor*.

Regarding the life stages, no particular or consistent pattern was detected. In the ES stage, seedlings of *G. monostachia* were on average located significantly higher in the canopy than older plants; seedlings occupied lower positions in the MS and the developmental stages showed no significant differences in distribution in the MF. In contrast, seedlings of *C. nutans* occupied lower positions than juveniles and adults in ES and MF, while no differences were detected in the MS stage. As for the two *Tillandsia* species, only *T. fasciculata* seedlings were significantly lower than the juvenile and adult plants in the canopy of the MF.

Location on the host-tree

Bromeliads showed a significant association between life stage and 'substrate type'; this relationship, however, was affected by the habitat condition and species ($Q_{GMH} = 40.5$, $df = 6$, $p < 0.001$). *G. monostachia* and *C. nutans* showed the clearest difference in the ES: the first species was mostly found on stems and primary branches (marginally significant) while the second one was more common on tertiary branches (Fig. 6). As the forest became more complex, the pattern of within-tree location changed. Seedlings in the MS were comparatively more frequent on stems and primary branches than older plants, whereas in the

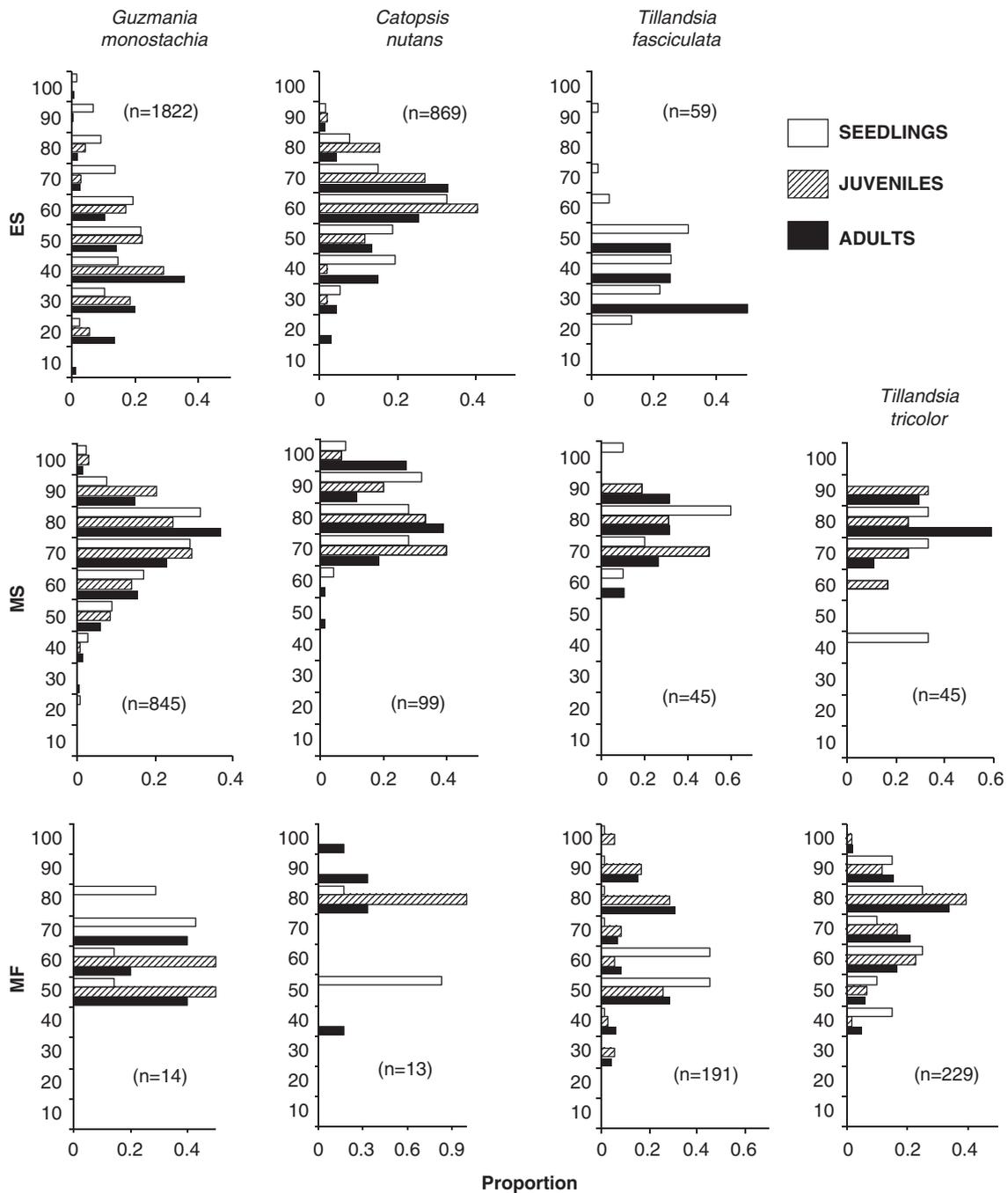


Figure 5. Vertical distribution of the most abundant bromeliad species in three successional habitats in a tropical premontane forest, Costa Rica. Data represent the proportion of individuals (y-axis) in the different life stages (SEEDLINGS: previous-year and older seedlings; JUVENILES; ADULTS: sub-adults and adults) according to host tree height (x-axis). The bromeliad position is expressed as a relative measure of the total tree height divided into ten equally distributed ranges. Successional habitats (rows): early succession (ES), mid-succession (MS) and mature forest (MF).

MF all individuals of the different species were mainly found on stems and primary branches. Bromeliads' attachment on the substrate was proportionally higher on the sides or below the branches or stems ($Q_{GMH} = 38.4$, $df = 4$, $P < 0.001$),

irrespective of species or habitat condition. Nevertheless, the seedlings and juveniles of *C. nutans* were anchored more frequently on top of their substrates in the MS and MF stages, respectively (data not shown). Similarly, bromeliads were more

Table 4. Results of the analyses of covariance (ANCOVA) on the vertical distribution of epiphytic bromeliads (genets) in three successional forest stages in a tropical premontane site, Costa Rica

Effect	Early succession			Mid-succession			Mature forest		
	df	F-ratio	P	df	F-ratio	P	df	F-ratio	P
Tree height	1	774.2	<0.001	1	862.4	<0.001	1	250.4	<0.001
Species	1	93.1	<0.001	3	10.4	<0.001	3	3.5	0.014
Life stage	2	17.6	<0.001	2	2.4	0.09	2	2.7	0.07
Species × life stage	2	54.6	<0.001	6	2.1	0.05	6	1.9	0.08
Error	2684			1022			435		

Tree height was used as covariate, with species and life stages as main factors.

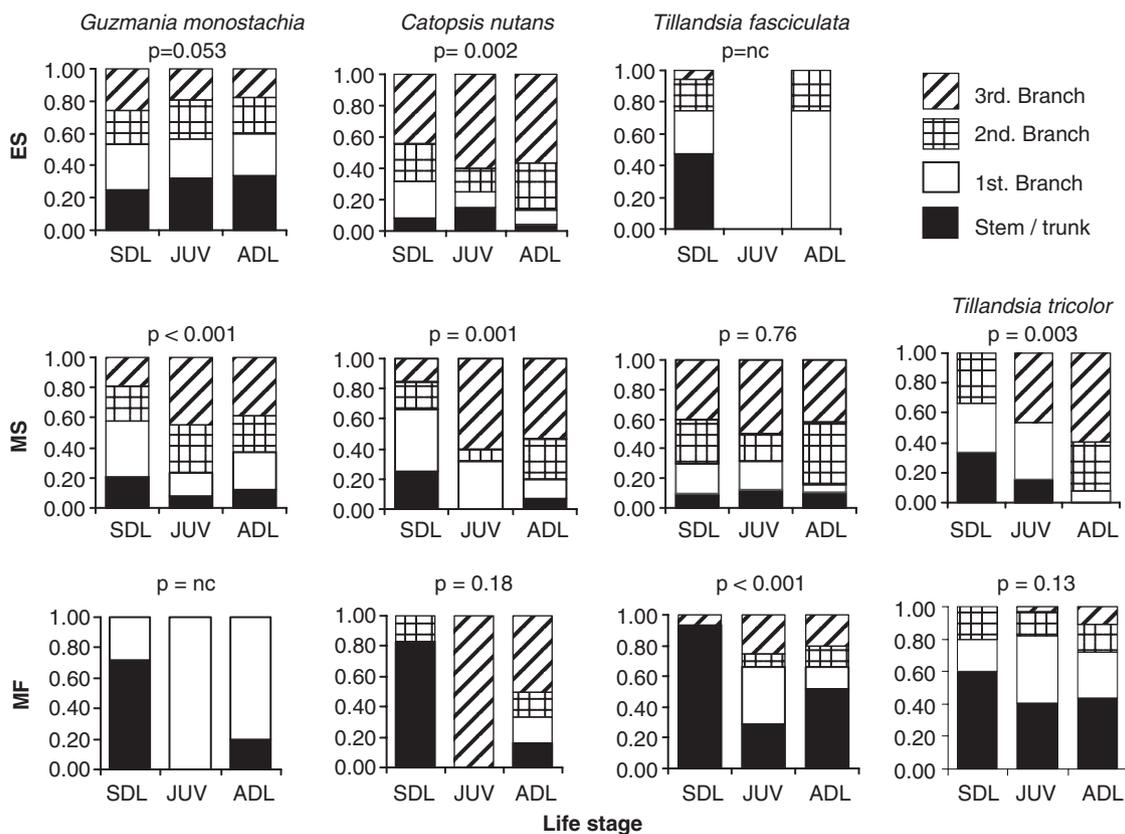


Figure 6. Within-tree location (by substrate type) of the most abundant bromeliad species in three successional habitats in a tropical premontane forest, Costa Rica. Data are proportions (y-axis) per life stage on each substrate represented by sections in each bar: SDL (previous-year and older seedlings), JUV (juveniles) and ADL (sub-adults and adults). Successional habitats (rows): ES (early succession), MS (mid-succession) and MF (mature forest). Above each graph: *P*-values after chi-squared tests were considered significant when $p < 0.05$; 'nc' means tests not computed due to zeros in rows or columns.

common on branches or stems with steep inclinations ($>45^\circ$) ($Q_{GMH} = 71.7$, $df = 6$, $P < 0.001$). However, the seedlings of *G. monostachia* and *T. tricolor* did not show a preference for a substrate inclination in the MS stage (data not shown).

Discussion

The lower diversity of epiphytic bromeliads in the secondary forests, when compared to the nearby mature forest (Tables 2 and 3), coincided

with patterns described for vascular epiphytes from other neotropical areas (Barthlott et al. 2001; Krömer & Gradstein 2003; Wolf 2005). These studies have suggested that epiphyte diversity is positively associated with the diversity of phorophytes (trees) and microclimatic conditions in each habitat. Other aspects related to the distribution of epiphytic bromeliads at each habitat were not affected or did not show any consistent or clear pattern regarding the forest successional stage. Nevertheless, the specific community composition and recruitment rates of the dominant species were noticeably different between secondary and mature forest.

The uneven bromeliad distribution among host trees, also reported in other studies (i.e. Zotz, Bermejo, & Dietz 1999; Bader et al. 2000; Benzing 2000; and references therein; Nieder, Engwald, Klawun, & Barthlott 2000; van Dunné 2001), did not change with the successional stage (Fig. 3). In the younger vegetation, the higher frequency of occupied trees may reflect a higher availability of light due to the more homogeneous and scattered vegetation of low height (< 5.5 m). Moreover, the rough and spongy corky bark of the most abundant tree species (*A. arborescens*) in that habitat is likely to enhance seed attachment and seedling establishment because it retains more moisture (sensu Callaway, Reinhart, Moore, Moore, & Penning 2002; Castro-Hernández, Wolf, García-Franco, & González-Espinosa 1999). The distribution of bromeliads along the vertical gradient was clearly a function of the vegetation structure; however, the vertical distribution of conspecifics of different age was not determined by the forest successional condition. The tendency of bromeliad seedlings to establish near their mother plants (Benzing 1978; Zotz 1997; van Dunné 2001) suggests that seed dispersal mostly occurs within trees, both in secondary and mature forest.

The lack of consistent differences in the type of substrate utilized by bromeliads among species and forest stages (Fig. 6) does not suggest a specific ability to colonize different parts of the phorophyte as proposed by Rudolph, Rauer, Nieder, and Barthlott (1998). The preference of most bromeliads to attach laterally on the substrate surface, both in secondary or mature forest, is likely the effect of excessive stem flow caused by heavy rains, which washes most seeds from the top of the branches to their sides, where they germinate. The trampling effect of arboreal mammals that travel along tree limbs (Perry 1978b), cannot be excluded, but is insufficient to explain this pattern, particularly in the younger vegetation where such routes are not yet established. Although not quantified,

the prevalence of bromeliads on inclined substrates (>45°) may just reflect the higher availability of such substrates as reported by Rudolph et al. (1998).

We argue that the specific composition of the bromeliad community in secondary and mature forests is probably not the result of structural and microclimatic differences in the arboreal vegetation. The static data presented here do not offer any information on dynamic processes of seed dispersal, establishment, plant growth and reproduction to elucidate the mechanisms of community assembly. Although these issues are the subject of experiments currently on their way, this paper provides the material to hypothesize on the relative importance of such processes.

Adaptations to a light gradient and water-stress have been postulated to explain the distribution of epiphytic bromeliads (Pittendrigh 1948). The higher light exposure in the canopy of younger vegetation is expected to favour species with CAM-photosynthesis and morphological adaptations to avoid desiccation, as in the case of *T. fasciculata* (Benzing & Renfrow 1971; Griffiths & Smith 1983), and the similar *T. tricolor*. However, these species had small populations in that vegetation or were completely absent and this is a common phenomenon in the entire area. Conversely, the small populations of the facultative C3-CAM species *G. monostachia* (Martin 1994) and *C. nutans* (Benzing 2000) had low recruitment rates in the mature forest, which does not match their supposed ability to deal with the more shady conditions of that habitat. This lack of a direct correlation between the species distribution and their photosynthetic pathway in the latter species has also been reported elsewhere (Zotz 1997; Zotz & Vollrath 2002).

The differences in composition and seedling recruitment between the dominant species of secondary and mature forest probably reflect differences in propagule availability and limited dispersal (sensu Ackerman, Sabat, & Zimmerman 1996; Hurtt & Pacala 1995; Wolf 1994; Wolf 2005; Yeaton & Gladstone 1982) rather than physiological dissimilarities. Recruitment limitation or the failure of species to reach any available favorable habitat due to limited dispersal has been proposed to influence the formation of terrestrial plant communities (see Hubbell, Foster, O'Brien, Harms, Condit, et al. 1999; Svenning 2001; Szentesi & Jermy 2003; Turnbull, Crawley, & Rees 2000; Verheyen, Bossuyt, Hoonay, & Hermy 2004).

All epiphytic bromeliads recorded here (subfamily Tillandsioideae) have small seeds that feature a hairy appendage or coma at one or both ends which enhances air buoyancy and dispersal by wind

(Benzing 2000). The physical separation (<700 m) between the studied secondary and mature forest does not seem to represent an obstacle for seed movement among habitats. Nevertheless, wind-dispersed seeds of epiphytic bromeliads apparently do not disperse very far from the mother plant (García-Franco & Rico-Gray 1998).

Seed-dispersal success is also bound to the reproductive capacity of the species or the number of seeds produced. The probability of establishment increases with the amount of seeds dispersed into a specific area, which in turn depends on the proximity and size of the source population, as well as on factors affecting the movement of seeds (i.e. wind currents). Comparative studies involving the evaluation of growth rates, phenological patterns, seed production, pollination rates and breeding systems are in progress to determine the role of propagule availability in the formation of epiphytic vascular plant communities.

Concluding remarks

Community assembly and distribution of epiphytic bromeliads cannot be solely predicted on the basis of physiological and morphological attributes of the species to exploit certain niches. In this study, we draw attention to the potential effect of seed availability and dispersal in shaping community composition and bromeliad distribution in successional forests. In this view, life-history differences that affect seed production, the location of seed sources, as well as the local wind patterns lead to a non-random dispersal of wind-dispersed epiphytic bromeliads. Therefore, species diversity and composition of the surveyed bromeliad communities is expected to change during forest succession according to site-specific factors that affect seed availability and dispersal, in addition the performance and survival of individual plants, their ability to flower and the time it takes them to do so.

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