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Species richness and abundance of epiphytic Araceae on adjacent floodplain and upland forest in Amazonian Ecuador

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Abstract. Terrestrial plant communities of adjacent upland and floodplain forest of the Amazonian lowland differ from each other in species richness and composition. Epiphytes are generally not considered as being affected by flooding, but we found considerable variation in the communities of epiphytic Araceae of flooded and unflooded forest. Contrary to findings from tree or ground herb communities, no depletion in overall species richness was observed among epiphytic aroids of the floodplains. Abundance and number of epiphytic aroid species per phorophyte were significantly higher than in upland forest, and the species composition varied conspicuously between the two forest types. We suggest that these differences are due to elevated humidity and better soil quality on the floodplains and reject the assumption that flooding has no effect on the epiphytic community.

Key words: Araceae, α-diversity, epiphytes, flooding effects, habitat heterogeneity, lowland rain forest, species composition, species distribution, species turnover

Introduction

The lowland Amazon rain forest is usually seen as consisting of two broad forest types, the unflooded upland forest (terra firme) and the floodplain forest (varzea, ígapo, etc., Prance 1979). Although many different forms within each of these types are recognised, inventories of their tree communities demonstrate that species richness (α-diversity) is higher in the unflooded upland forests than in floodplain forests (Campbell et al. 1986, 1992; Balslev et al. 1987; Junk 1989). The record high tree species richnesses reported from the western Amazon are indeed from sites in upland forests (Gentry 1988; Valencia et al. 1994). The lower species richness in the floodplain forest has been interpreted as the result of stress from flooding. On sloping floodplains, length of inundation influences species richness – the longer the flooding period, the lower the tree species richness (Campbell et al. 1992; Ferreira 1997). This trend has also been demonstrated for the terrestrial herb community (Junk and Piedade 1993).

Araceae, a family of herbaceous monocotyledons, includes about 3000 species distributed mostly in the tropics and subtropics, with a few reaching temperate latitudes. The estimated number of Araceae species in the Neotropics is 2206 (Croat 1988). The low to middle elevation moist forest of the Andean region in Colombia, Ecuador, and Peru is a centre of diversity for Araceae (Madison 1978). The epiphytic life-form is very common in the family, and it has been estimated that 86% of Neotropical aroids are epiphytes (Croat 1988). In Ecuador, there are 397 species of Araceae, of which 304 (77%) are epiphytic, and 150 of these are endemic to Ecuador (Jørgensen and Léon-Yánez 1999). Most endemic epiphytic aroid species are found on the coastal plain (84 species) and the Andes (90 species), whereas the Amazon lowlands of Ecuador have only seven. At the community level, Araceae may be important. In a 1-ha study plot on terra firme at Cuyabeno in Amazonian Ecuador, Araceae was the most species rich of all vascular plant families, with 71 species, of which 68 were epiphytic (Balslev et al. 1998).

We studied species richness of the epiphytic Araceae (aroid) community in adjacent upland and floodplain lowland moist forests in Amazonian Ecuador to determine if flooding affects species richness of epiphytes in the same way it affects species richness of the tree and terrestrial herb communities. Except for hemi-epiphytes, epiphytes are independent of the soil and elevated above the ground where flooding directly affects plant growth. We therefore expected that there would be no effect of flooding on epiphytic aroid species richness. Contrary to this expectation, we did find significant differences in species richness of epiphytic aroids in floodplain forest and adjacent upland forest. The difference was, however, inverse to the difference found in the tree and ground-herb communities. On an equal number of sampled phorophytes, the floodplain had more epiphytic aroid species compared to the upland forests, and a higher proportion of trees had epiphytes. The average number of epiphytic aroid species per phorophyte was significantly higher in the floodplain forest compared to the adjacent non-flooded forest, while diversity (measured as species number per individual) was lower.

Study site

The study was conducted in Amazonian Ecuador (Napo province) at the Yasuní Scientific Research Station (0°40′ S, 76°23′ W, Figure 1) from March to June 1999. The station is located in the Yasuní National Park, which covers approximately 982 000 ha of tropical lowland moist forest (Herrera-MacBryde and Neill 1997).

The climate at Yasuní is continuously hot, humid, and aseasonal. Though no long-term measurements are available, data collected at the station during the past few years show that annual precipitation totals about 3000 mm, with monthly means of 102–639 mm (Figure 1); average monthly air temperature was 28.2 °C, while daily minimum and maximum temperatures averaged 21.5 and 34.7 °C, respectively (Nabe-Nielsen 2001). Monthly rainfall is highly variable between years, but no dry season occurs, though irregular fluctuations give occasional dry months.

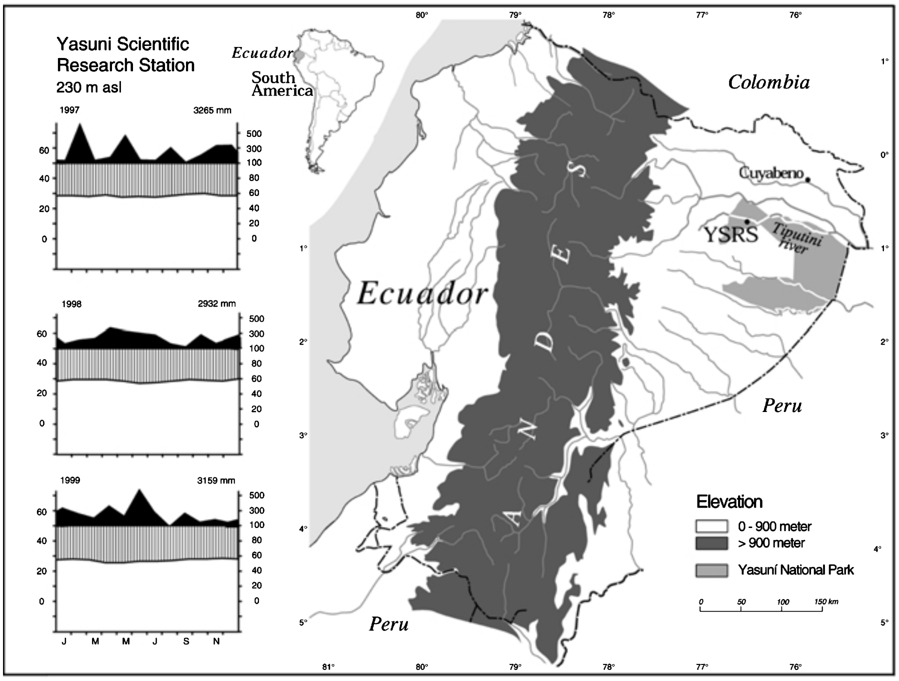

Figure 1. Location of the Yasuní National Park and the Yasuní Scientific Research Station (YSRS) in Amazonian Ecuador. Climatic diagrams for 1997–1999 drawn by Jacob Nabe-Nielsen, based on data collected by YSRS-staff.

The vegetation surrounding the station is mostly old-growth forest (*sensu* Clark 1996), partly replaced on the floodplains by successional forest. The terrain is flat on the irregularly inundated floodplains at about 200 m asl and changes to rolling hills and slopes with ridges reaching up to 250 m asl on adjacent upland areas. The Tiputini river is approximately 30–40 m wide, with fluctuating water levels. During our field work, the floodplain was inundated twice to a depth of up to 2 m.

Tree species richnesses in Yasuní are among the highest in the world with as many as 825 species of free-standing woody plants (dbh $\geq$ 1 cm) in 2 ha of forest (Romoleroux et al. 1997). At the β-level, Pitman (2000) estimated 3141 tree and shrub species for the National Park and the adjacent Waorani Ethnic Reserve (610 000 ha). Liana α-species richness is the highest ever recorded: 96 species in a 0.2 ha terra firme plot (Nabe-Nielsen 2001).

Methods

In each of three different terrain types, characterised as floodplain, transition, and upland, two line transects were laid out. All six transects were placed within an area of 2400 × 1400 m. Floodplain transects were established in frequently inundated areas close to the Tiputini river. Transition transects intersected the contour lines, covering slopes and valleys, occasionally crossing small streams. Upland transects followed the contour lines on top of the hills. Four of the transects were 500 m long; one transition transect was 440 m, and one floodplain transect was 250 m long. In each transect, 25 trees (phorophytes) were sampled for epiphytic aroids. The transects were divided into 20 m units. In the 250 and 440 m transects, all units, or only the last six, were 10 m. In each unit, the tree (dbh $\geq$ 5 cm) nearest to the starting point was chosen for sampling. The distance d of each sampled tree from the starting point was used to estimate tree density per ha by dividing 10 000 m^2 with the mean of all d^2.

For each phorophyte, the following variables were recorded: (1) Diameter at breast height (dbh); (2) altitude above sea level (determined with digital altimeter with accuracy of 5 m); (3) bark texture (smooth, furrowed, rough, peeling); (4) bark hardness (soft, hard); (5) canopy height (measured with an optical rangefinder: 0–5, 5–10, 10–15, 15–20, 20–30, $>$30 m); (6) light intensity 1.6 m above ground at the phorophyte base [modified ‘crown illumination index’ of Clark and Clark (1992): no direct light (CI 1), low, medium or high lateral light (CI 1.5–2.5), some overhead light (CI 3), full overhead light (CI 4), or full lateral and overhead light (CI 5). A transparent plastic plate, with ellipses of 10, 20 or 40 cm^2 painted on it, was used to estimate the sizes of the canopy openings. One small, medium or large lateral hole corresponded to CI 1.5–2.5, and one or two large overhead holes to CI 3 and CI 4, respectively. Two smaller openings equalled one hole of the next category (Brown et al. 2000).

On every sampled phorophyte, all epiphytic Araceae visible from the ground were recorded. All sampled trees were thoroughly observed with binoculars. Herbarium specimens of all studied Araceae species were collected. Voucher specimens (Leimbeck Nos. 1–257) are deposited at AAU, QCA, and QCNE (acronyms according to Holmgren et al. 1990). Many species have leafless climbing stems with terminal foliage only, and height above ground was recorded as height of the lowest leaf above ground. The oldest leaves are often shed, and stem bases frequently rot as the plants grow upwards. Plants that were not connected to each other were treated as separate individuals, even in cases where it was obvious that there once had been a connection.

The term epiphyte is here used in a broad sense, for plants that spend much or all of their lives attached to other plants. This definition includes true epiphytes, or holo-epiphytes, which are exclusively epiphytic, as well as hemi-epiphytes, which have both a terrestrial and an epiphytic phase during their life cycles (Putz and Holbrook 1986; Benzing 1987).

Data analyses

The Mantel test was used to test correlations between the phorophyte variables. Six similarity matrices were constructed for the 150 trees using Gower’s symmetrical similarity coefficient (Legendre and Legendre 1998): (1) An altitude matrix and (2) a dbh matrix (computed from the raw data of these variables); (3) a terrain matrix (created by using the three terrain types as descriptors); (4) a bark matrix (calculated from a combination of bark texture and bark hardness); (5) a canopy matrix (computed using the six canopy height classes); (6) a light matrix (composed of the CI values for canopy openness).

A species composition similarity matrix was constructed from abundance data of epiphytic aroids on sampled phorophytes using the Steinhaus coefficient (Legendre and Legendre 1998). Trees not carrying aroids were given the similarity coefficient $S = 0$ with respect to all other phorophytes. The Mantel test was used to assess correlations with phorophyte variables. The method of Smouse, Long and Sokal (Legendre and Legendre 1998) was used for partial Mantel tests. Probabilities of the Mantel statistic r were in all cases obtained from 1000 permutations.

A principal coordinate analysis (PCoA) was used to assess relationships between species compositions of the epiphytic aroid communities in different transects. The Steinhaus coefficient (Legendre and Legendre 1998), based on species abundances, was chosen as an association measure among the six transects.

Results

Phorophytes

Over the three terrain types, 89% of the trees carried epiphytic aroids, and there were significantly higher numbers of aroid-carrying trees on floodplains (Pearson $\chi^2 = 6.90$, df = 2, $P < 0.05$), where 98% of trees had aroids, compared to 82 and 86% in transition and upland transects, respectively. Trees without epiphytic aroids did not differ from trees with them, with respect to the measured variables. Two aroid-free trees represented *Duroia hirsuta* (Rubiaceae), a myrmecophyte whose ants protect it from epiphytes.

Most epiphytic aroids grew on the lower parts of the trunks, 90% in the first 8 m from the ground; the median epiphyte height above ground was 2.9 m. Aroids were observed up to a maximum height of 22 m above the ground.

Mean tree density in all terrain types was estimated at 1312 trees (dbh $\geq$ 5 cm) per ha. Density was lowest on the floodplain (1012 trees/ha); in transition and upland forest, tree density was 1515 and 1509 trees/ha, respectively. Mean phorophyte dbh was 14.9 cm ($n = 150$, SE = 1.1), with a maximum value of 95 cm. There was no significant difference in phorophyte dbh between transects or terrain types. Other variables such as phorophyte bark hardness and texture, canopy height and light did not differ significantly either. For the likelihood ratio test used, the categories bark texture rough and peeling, canopy height class one and two, and light intensity categories with CI values >1 were lumped.

Species richness

A total of 57 species of epiphytic Araceae was found. Most belonged to *Philodendron* (29 species) or *Anthurium* (20 species), four species belonged to *Monstera*, while *Stenospermation*, *Syngonium*, *Heteropsis*, and *Rhodospatha* each had one species. The mean number of species per transect was 28 (SE = 1.2). Species richness was highest on the floodplains, but the differences between the terrain types were not significant (Figure 2A).

In all six transects together, 1024 individual aroids were sampled, a mean of 6.8 (SE = 6.6) per phorophyte. Numbers of individuals per phorophyte were highest on floodplains and differed significantly among transects (Kruskal–Wallis $\chi^2 = 35.5$, df = 5, $P < 0.0001$). The floodplains accounted for 53% (538) of all individuals, whereas only 27% (281) and 20% (205) were found in transition and upland transects, respectively, corresponding to 10.8 aroids per phorophyte on the floodplains, 5.6 in transition, and 4.1 in upland forest.

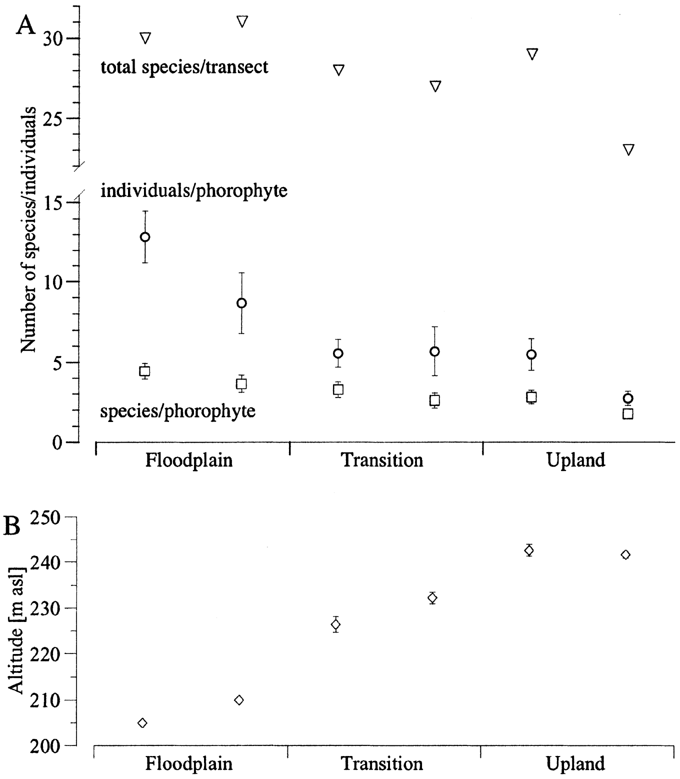

Figure 2. A. Variations of total species numbers per transect (total species/transect), abundance (individuals/phorophyte), and species richness (species/phorophyte) of epiphytic aroids per phorophyte. B. Altitude above sea level of the transects. Bars indicating ±SE.

A mean of 3.1 (SE = 2.3) species was found per sampled phorophyte. Wilcoxon rank sum tests indicated no differences in means among transects of the same terrain type. Grouped data from the same terrain type showed a significant higher mean number of species per phorophyte on the floodplain (Kruskal–Wallis $\chi^2 = 13.3$, df = 2, $P < 0.05$). More than half of all species were found in one or two transects only, and almost one third of the species were recorded in transects of one terrain type only (Table 1). Around 12 species were only found on the floodplain, while transition and upland transects together only had 15 species that were exclusively found there (Table 1).

Phorophyte and microhabitat variables

Altitude above sea level increased from floodplains to transition and upland transects (Figure 2B). Per definition, altitude and terrain type were highly correlated (Table 2), but none of the other habitat variables showed any correlation to either altitude or terrain type. Canopy height was on the borderline of correlating positively with altitude. Bark characteristics correlated significantly with phorophyte dbh and canopy

Table 1. A. Number and percentage of epiphytic aroid species that occurred in n different transects ($n = \{1 \ldots 6\}$) and terrain types ($n = \{1 \ldots 3\}$). B. Number and percentage of epiphytic aroid species that either occurred only on floodplains, only on transition/upland sites or in both habitats. The total number of species was 57.

	n	No.	%
A			
No. of species found in *n* different transects	1	15	26.3
	2	15	26.3
	3	5	8.8
	4	9	15.8
	5	6	10.5
	6	7	12.3
Total		57	100
No. of species found on *n* different terrain types	1	18	31.6
	2	20	35.1
	3	19	33.3
Total		57	100
B			
No. of species found only on either floodplain or transition/upland or both			
floodplain		12	21.1
trans./upland		15	26.3
both		30	52.6
Total		57	100

Table 2. Mantel statistic r obtained from Mantel correlation of different phorophyte variables from 150 sampled phorophytes in six transects.

	Terrain type	Dbh	Bark texture and hardness	Canopy height	Light
Altitude	0.61***	-0.01^{ns}	0.01^{ns}	0.03*	0.04^{ns}
Terrain type		0.00^{ns}	0.00^{ns}	0.01^{ns}	0.00^{ns}
Dbh			0.11***	0.04^{ns}	-0.07^{ns}
Bark texture and hardness				0.06**	0.04^{ns}
Canopy height					0.19***

*$0.05 \leq P \leq 0.06$; **$P < 0.05$; ***$P < 0.01$; ns = not significant.

height, indicating that most trees with small dbh or low canopy had hard and smooth bark, while larger trees or trees in high canopy stands had predominantly soft and not smooth bark. Highly significant correlations were also found between canopy height and light, measured as canopy openness, showing that understorey light intensity decreased with increasing canopy height.

The aroid community

The species composition of epiphytic aroids on individual phorophytes was highly correlated with altitude and terrain type (Table 3). To exclude indirect correlations, the partial Mantel test removed the effect of these variables on each other when comparing with species composition. In both cases, this resulted in a lower test statistic, but the correlations were still highly significant.

Table 3. Mantel statistic r obtained from Mantel and partial Mantel correlations of the species composition similarity matrix of epiphytic aroids (57 species) with phorophyte variables of 150 phorophytes (Matrix B). The effect of matrix C is removed when calculating partial Mantel correlations.

Matrix B		r
Altitude		0.11***
Terrain type		0.11***
Dbh		-0.03^{ns}
Bark texture and hardness		0.01^{ns}
Canopy height		0.01^{ns}
Light		0.01^{ns}
Matrix B	**Matrix C**	**Partial r**
Altitude	Terrain type	0.06***
Terrain type	Altitude	0.06***

***$P < 0.01$; ns = not significant.

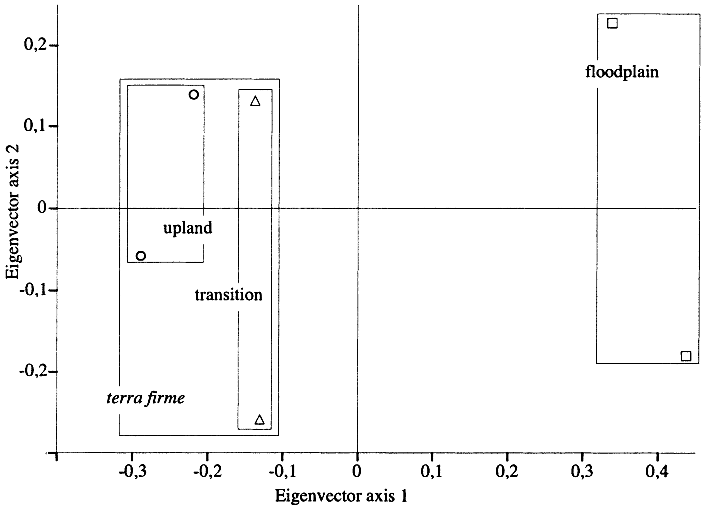

Figure 3. Ordination of six transects from three different terrain types in the space of the first two principal coordinates (Eigenvector axis 1 and 2), based on a principal coordinate analysis (PCoA) of the species composition of the epiphytic aroid community. In each transect 25 phorophytes were sampled for aroids. Differences between transition and upland are too small to justify a fragmentation in separate terrain types, hence they are treated together as terra firme.

Figure 3 displays the ordination of the six transects in the space of the first two principal coordinates. The eigenvalues of axis one and two explained 44 and 18% of the total variation of the dataset. The ordination distinctly separated the floodplain transects from transition and upland sites. Distances between these two groups were largest on the first axis. A calculation of the Spearman's rank correlation coefficient showed that the first principal axis had a significant correlation with altitude (Spearman's $r = -0.89$, $P = 0.0188$).

Discussion

Almost nine of every ten trees in the study area carry epiphytic Araceae, most of them several species. Extrapolating the mean number of aroids per phorophyte to the tree density yields 8922 epiphytic aroids per ha. Although phorophyte density on the floodplain is considerably lower, the number of aroids per ha (10 889) is still higher than in transition (8717) or upland forest (6187), due to the high number of aroids per phorophyte. In comparison, the number of trees and shrubs $\geq$1 cm dbh in Yasuní is 12 287 stems in 2 ha (Romoleroux et al. 1997), and the number of lianas 606 in 0.4 ha (Nabe-Nielsen 2001). In Cuyabeno, ca. 100 km north of Yasuní, there were 10 960 individuals of ground herbs in a 1-ha plot (Poulsen and Balslev 1991), but there Araceae accounted for almost 30% of all species and 20% of the total herb cover. Most of these species were climbers or fallen epiphytes; only three species were obligate terrestrials.

The total number of 57 epiphytic aroid species found on 150 phorophytes in Yasuní is less than the 68 species from the 1-ha Cuyabeno plot (Balslev et al. 1998), where 10× as many trees were sampled. The high species turnover between transects indicates, that larger sample areas would yield far more species. However, in the *Catalogue of the vascular plants of Ecuador* (Jørgensen and Léon-Yánez 1999), only 80 species of epiphytic or climbing aroids were reported from the entire Amazonian Ecuador. This low number of species does not correspond with the findings of this study. It rather reflects the fact that many Amazonian aroid species remain undescribed.

All comparisons of the three terrain types indicate, that in reality there are only two terrain types, separated by the flooding line. Therefore, in the following discussion transition and upland sites are treated together as terra firme, contrasting with the floodplain.

There are remarkable reductions in numbers of individuals and species with increasing altitude (Figure 2). Differences in the total number of species are small among transects. However, the mean number of species per phorophyte on the floodplain is significantly higher than on the other terrain types. The same is true for the abundance (measured as individuals per phorophyte) of epiphytic aroids in floodplain transects. This pattern is contrary to all observations of other life forms in adjacent floodplain and terra firme forests, where the terra firme always has more species per unit area than adjacent floodplain forest (Campbell et al. 1986; Balslev et al. 1987; Duivenvoorden 1994). However, the species/individual curve (Figure 4) shows, that high species numbers on the floodplains are an effect of high numbers of individuals. Species/individual curves of transition and upland forest are very similar and much steeper than the floodplain curve. This means that in floodplains, many more individuals are needed to reach species numbers equivalent to those in terra firme forest. Hence, diversity defined as species per individual is lower on floodplains. This is counterbalanced by the higher number of individuals per area on floodplains, so that diversity defined as species per area or per phorophyte is more or less equal in all terrain types (Figure 4).

It is obvious that the epiphytic aroid community on floodplains is fundamentally different from the one on terra firme. High density and high infestation rates in floodplains indicate that the epiphytic aroid community is phorophyte limited. This is not true for terra firme sites, where apparently much uncolonised space is available. The factors limiting epiphytic aroids in terra firme forest, do not seem to equally influence the floodplain community. How does the floodplain differ from terra firme, and which conditions may be advantageous for epiphytic aroids?

As expected, stress due to flooding does not affect epiphytic aroids in the same manner as it affects obligately terrestrial plants. This may be partly explained by their epiphytic habit and avoidance of inundation by colonising the trunks and the

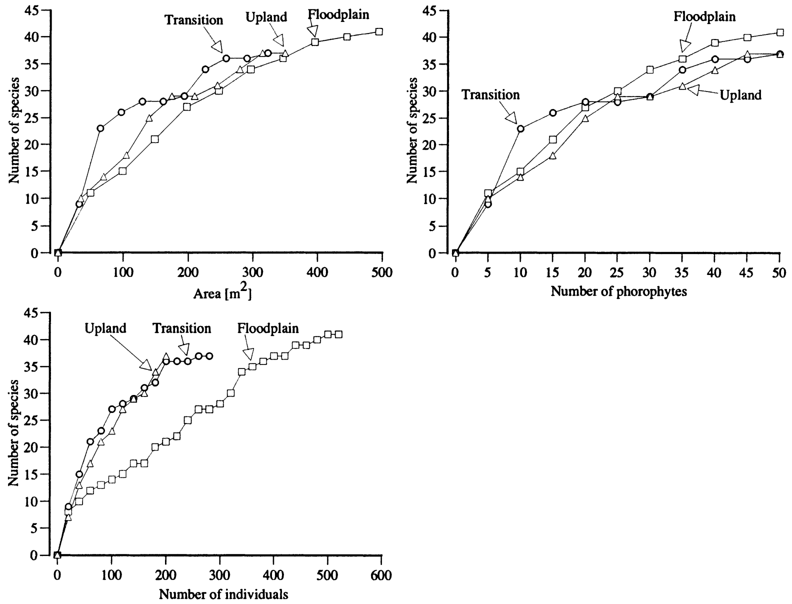

Figure 4. Number of epiphytic aroid species on different terrain types in relation to area, number of phorophytes sampled, and number of individuals sampled. Species/individuals curves of upland and transition forest are much steeper than the floodplain curve, showing that high species richness on the floodplain is an effect of high individual numbers. Due to the high abundance of epiphytic aroids on floodplains, the curves for species richness per area or per number of sampled phorophytes are more or less similar. Species curves are not randomised, but based on the actual sampling order of the species.

canopy. But, as the present study shows, half of the epiphytic aroid individuals are found on the basal 3 m of the phorophyte trunk, where the probability of becoming submerged is high. This indicates tolerance of flooding, resulting in lower mortality or higher recruitment rates. Flooding may also enhance vegetative reproduction, as mechanical damage or separation of plant parts can easily produce independent ramets.

None of the measured phorophyte or microhabitat variables correlates with terrain type, except altitude, a consequence of floodplains usually being the lowest sites in a limited area. Furthermore, only terrain type and altitude correlate significantly with species composition, even when the effects of indirect correlations are removed. It is unlikely that differences in elevation between the phorophytes of this study have an influence on growth or survival conditions of epiphytic aroids, as the total altitudinal range is less than 50 m. One important factor might be differences in soil quality. Floodplains that are regularly inundated by rivers with high contents of suspended nutrients (white-water rivers) tend to have more nutrient-rich soils than adjacent terra firme forests (Prance 1979; Campbell et al. 1992). Although the Tiputini river is not of Andean origin, and hence might not be classified a typical white-water river, its often muddy waters are a clear indicator of alluvium suspension, and it usually leaves a considerable layer of sediment on the trunks when water levels decline. However, due to their lack of contact with the ground, true epiphytes are presumably little affected by soil quality, even though Gentry and Dodson (1987) suggested that epiphytes are very sensitive to soil fertility. Hemi-epiphytes and those true epiphytes growing on the lowest parts of trunks may benefit from nutrient-rich depositions. This may especially apply to seedling recruitment. Still, this does not explain a correlation of species composition with altitude.

Furthermore, we suggest that humidity may be a critical factor. Humidity near rivers or in areas with high soil moisture is higher than in drier sites, as indicated by extensive formations of mist in the early morning hours. In addition, these areas are better protected against high winds and desiccation because they occupy the lowest parts of the landscape. Exposed sites, such as forest edges or the upper canopy, are known to have higher levels of air temperature and lower air humidity (Kapos 1989; Parker 1995). This may also be true for the ridges (upland sites) in the present study, which are relatively open and unprotected, compared to the lower sites near the river, in small valleys, or depressions. The fact that species composition correlates with altitude supports this assumption. Most epiphytic aroids are sensitive to desiccation, and prefer to grow on the lower parts of the trunks (Croat 1988), which also explains higher abundances in these sites of elevated humidity. In Colombia, wetter sites have higher aroid species totals than more mesic sites (Croat 1992). Higher occurrences of epiphytes in general are also known from riparian forests in Tanzania (Johansson 1974), and some leafless epiphytic orchids are most frequent in swampy forests along rivers, where humidity is high (Teuscher 1972). Further studies are needed to verify the impact of humidity on the species distribution of epiphytic aroids.

If the conditions for epiphytic aroids are more favourable on floodplains, why then is the species richness per individuals on floodplains so much lower? This might be explained by higher competition on the floodplains. The epiphytic habitat is usually seen as unsaturated, where competition is of minor importance (Nieder et al. 1999). However, as mentioned before, the epiphytic aroid community on floodplains might be space limited due to low phorophyte density, high epiphytic aroid density, and the fact that epiphytes tend to aggregate on the basal parts of phorophytes. This may result in competition for available space, as it has been proposed for non-vascular epiphytes (Wolf 1995). Coexistence of competitively adjacent species requires that inferior competitors are better colonists or have greater longevity than superior competitors (Tilman 1997). For the epiphytic aroid community these requirements may not be met, as many species are very similar ecologically. The result would be the loss of species that are poor competitors.

The ordination of transects supports the above findings and clearly separates the epiphytic aroid flora of the floodplain from that of the more elevated terra firme sites (transition and upland). Even though all investigated transects of the present study were within a distance of 1 km from the river, only a little more than half the species were found in both floodplain and terra firme forest. Higher sampling intensities over larger areas would probably reveal more shared species between terra firme and floodplains. However, species turnover is lower between transition and upland sites on terra firme, than between environmentally less similar terra firme and floodplain sites. This indicates that habitat differences influence the species distribution of epiphytic aroids, and does not correspond with the concept of low habitat heterogeneity for epiphytes in Amazonian lowland forests (Nieder et al. 1999).

This study confirms the assumption that epiphytes in floodplains do not suffer from flood stress (Junk and Piedade 1993), but we have to reject the view that they are unaffected by flooding. In fact, secondary effects of flooding such as elevated humidity and better soil quality in floodplains may enhance the suitability of the habitat, at least for epiphytic aroids, while phorophyte limitation may increase competition.

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