

The population structure of the vascular epiphytes in a lowland forest in Panama correlates with species abundance

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(Accepted 7 February 2007)

Abstract: The long-term dynamics of epiphyte communities are little studied although such baseline data are urgently needed, in particular in the context of global change. Census data of a vascular epiphyte community from 0.4 ha of undisturbed lowland forest in Panama were used to infer future changes in community composition by deducing population growth from the current size class structure of populations. The study includes 11 387 individuals out of 45 species, ranging in abundance from 16 to 1568 individuals. There was a significant negative correlation between the size of a population and the steepness of the size distribution, indicating that more common species are likely to increase in abundance in the future, while rarer species apparently depend on immigration from other populations to allow local persistence.

Key Words: Bromeliaceae, Orchidaceae, population dynamics, rarity, San Lorenzo crane site, size class structure, tropical forests

INTRODUCTION

A central goal of community ecology is to understand the underlying dynamics, i.e. to infer past changes and to predict future changes in species composition (Crawley 1997). Long-term observational and experimental studies, in particular when combined with comparative and theoretical work, are the prime approach to reach this goal (Rees *et al.* 2001), but current variation in demographic traits among the species of a community may already allow predictions of future changes. For example, in forest ecology, high relative representation of a tree species in the forest canopy *and* among saplings in the understorey is interpreted as an indicator that the forest has reached a climax state, whereas the opposite situation is interpreted as an indicator of change (Chao *et al.* 2005, Foster *et al.* 1996). The frequent observation of the second case, in particular in African forests, has led to the idea of cyclical forest succession (Swaine & Hall 1988). Analogously, Oostermeijer *et al.* (1994) proposed, for herbaceous plants as well, that the age/stage structure of species like *Gentiana pneumonanthe* is a useful indicator of likely future population dynamics, and distinguished

‘dynamic’, ‘stable’, and ‘regressive’ populations by a decreasing proportion of seedlings and juveniles.

However, deducing dynamic processes such as population growth rates (λ) from static patterns is an issue of debate. Theoretically, a steeply declining size class distribution of a population could be caused by a high λ , but also result from lower growth rates of juveniles and/or from low survival in any size class (Condit *et al.* 1998). An empirical test for woody plants of a tropical lowland forest in Panama yielded a mixed picture: a significant correlation between past λ and present size class distribution was only found in understorey trees (Condit *et al.* 1998). Similar tests for herbaceous terrestrial or epiphytic plants are lacking. Until this issue is resolved and long-term data are available, the analysis of static population size distributions is arguably the only way to address long-term changes in epiphyte communities.

In the present paper, I use the analysis of the current structure of plant populations to predict the long-term dynamics of an epiphyte community in the lowlands of Panama. Epiphyte assemblages can be extremely species-rich, accounting for up to 50% of the local pool of vascular plants in some tropical forests (Kelly *et al.* 2004), but information on their dynamics in time and space is scarce: there is, for example, only a single published study that directly documents long-term

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community changes in a primary lowland rain forest (Laube & Zotz 2006). That study, which analysed the occurrence of vascular epiphytes on a particular host tree species, *Socratea exorrhiza*, over a period of 5 y, revealed substantial turnover of species and individuals at the level of individual trees, while the overall composition of the epiphyte vegetation on the 99 palm trees studied proved to be remarkably stable. Being limited to a single host tree and to fewer than 1000 epiphytes, the question remains whether this finding can be expanded to an entire local community. This motivated the current analysis of a complete census of 0.4 ha of lowland forest with more than 13 000 individual epiphytes out of 103 species that poses the question whether the relative species composition of an entire community will be similarly stable in time.

METHODS

Field site and census work

This study was conducted at the San Lorenzo Canopy Crane site, which is located within the former Fort Sherman area near the Atlantic coast of the Republic of Panama. The average annual rainfall is estimated to be around 3500 mm. Canopy height of this primary rain forest is quite variable and reaches a maximum of *c.* 40 m. The use of a small gondola allowed access to all strata of the forest.

Each tree in a roughly square area of *c.* 0.4 ha was inspected for the occurrence of vascular epiphytes (for a detailed account see Zotz 2004). There are a number of species in the Araceae, which may grow either as an epiphyte or a secondary hemi-epiphyte (Croat 1978). At the study site, both life-forms were observed in individuals of *Philodendron radiatum* and *P. sagittifolium*. In these two species, only truly epiphytic individuals were included.

The following data were collected for each individual: height of attachment, leaf/frond number, leaf length, stem length, or number of shoots (depending on species). The delimitation of individual plants is often difficult in vascular epiphytes, and I followed Sanford's definition of an 'individual': a group of rhizomes and leaves belonging to one species, which forms a clearly delimited stand (Sanford 1968). With the exception of small seedlings, which could frequently not be identified to species, all plant sizes were included in the census.

Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), authorities for ferns accord to Lellinger (1989) and Croat (1978). Voucher specimens are deposited in the herbarium of the Smithsonian Tropical Research Institute, Panama (Tupper Center).

Data analysis

The population size-class structures were analysed as suggested by Condit *et al.* (1998). Following this and other studies, only species with >15 individuals were included in the analysis. 'Size' was not consistently measurable in taxa with creeping growth form (e.g. Hymenophyllaceae, Gesneriaceae, most *Peperomia* spp., many ferns), which were consequently excluded. Also excluded were a total of five species of the genera *Ornithocephalus* and *Encyclia*, which could not be reliably distinguished from each other in the field.

The remaining 45 species could not be tallied in identical size classes due to: (1) different non-destructive measures of size (length of the longest leaf or length of the longest stem/pseudobulb, depending on species) and (2) substantial interspecific variation in size by almost two orders of magnitude: there are massive aroids and ferns with leaves of up to 1 m length, e.g. *Elaphoglossum herminieri*, and tiny orchids with leaf sizes of ≤ 0.03 m, e.g. *Trichosalpinx orbicularis*. Lacking a single common measure of size, five relative size classes in 20% steps (0–20%, . . . , 80–100% maximum size) were defined separately for each species, and described the shape of the size distribution by a single parameter, L, which is the slope of the regression of \ln (abundance per size class) vs. size class (Condit *et al.* 1998). All statistical analyses were performed with STATISTICA software (Version 5.1, Statsoft, Tulsa, OK, USA).

RESULTS

Species varied substantially in their size-class distributions (Appendix 1). In general, more common species tended to have a higher proportion of juveniles and smaller size classes, while the opposite was true for rarer species. The fit of the regressions between \ln (abundance in a size class) and size class was quite tight in most cases with a median r^2 of 0.74 (Appendix 1). The slope of these regressions, L, was significantly correlated with the abundance of a species (Figure 1).

The negative correlation between the steepness of the size distribution and species abundance could potentially be an artefact of (1) an increasing likelihood of finding bigger individuals in larger populations, or (2) an underlying correlation of maximum plant and population size. The likelihood of finding a large individual should increase with increasing abundance of a given species, which in turn would lead to a systematic bias towards more negative values of L in common taxa because the width of the five size classes depends upon the largest individual in each species. However, this field sample of 0.4 ha of forest was not

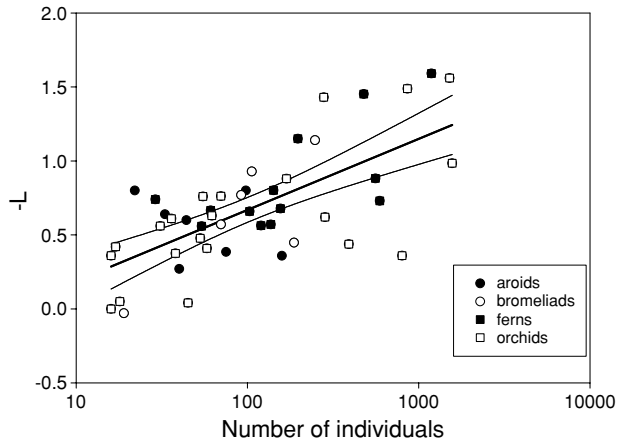


Figure 1. Relationship of population size (number of individuals) and the slope of the size distribution, L . The solid line is the regression line ($L = 0.2 \ln(\text{individuals}) - 0.26$, $r^2 = 0.42$, $P < 0.001$). Different symbols are used for the different taxonomic groups.

affected by this theoretical trap: irrespective of species abundance, the maximum plant sizes found at San Lorenzo matched those from nearby Barro Colorado Island (BCI) rather closely (Appendix 1, Croat 1978). The average deviation was about 20%. A regression analysis of the maximum sizes of all species at the two sites ($P < 0.001$, $r^2 = 0.80$) showed no systematic trend of the residuals, and the slope and the y-intercept of the regression equation were not significantly different from 1 and 0, respectively. Population size did not correlate with maximum plant size either. Tested separately for all species with either leaf length or stem length as the measure of size the correlation coefficients were ≤ 0.1 ($P > 0.9$).

Uneven taxonomic participation in the analysis poses another potential problem: the orchids were highly over-represented in the data set with 40% of all species. Therefore, a possible taxonomic bias was tested by separate correlation analyses between the total abundance of a species and L for the four major taxonomic entities (Orchidaceae, Bromeliaceae, Araceae and pteridophytes). With the exception of the aroids ($P = 0.45$), all correlations were significant ($P < 0.05$).

The positive correlation of population size and the proportion of juvenile plants in different species (Figure 1, Appendix 1) was not found when different subpopulations of the same species were analysed. Comparing the proportion of the smallest size class and the number of all conspecifics on a given tree for three haphazardly chosen species (*Scaphyglottis longicaulis*, *Elaphoglossum sporadolepis* and *Vittaria lineata*) yielded no significant results (correlation analysis, $r < 0.1$, $P > 0.55$, Figure 2).

DISCUSSION

At San Lorenzo, the more common epiphyte species tend to have a higher proportion of juveniles, while the opposite is true for rarer species. Species with large populations thus tend to be 'dynamic', species with small populations tend to be 'regressive' (*sensu* Oostermeijer *et al.* 1994). This is not due to population size per se, because subpopulations of the same species on different trees did not show such a trend.

The following discussion rests on the assumption that there is a correlation between size class distributions and population growth rates, λ . Such a correlation has been directly shown for understory tree species on Barro Colorado Island (Condit *et al.* 1998). Yet knowledge of size class structure alone is not sufficient to make inferences on λ (Condit *et al.* 1998, Zotz 2005), because low growth rates of juveniles and lower survival in any size class would also produce steep size distributions. However, unless we assume that currently more-common species have – as a group – slow-growing juveniles and high mortality, while the less-common ones have fast-growing ones and relatively low mortality, we are left with the more parsimonious interpretation: the present dominance structure is likely to be maintained in the future.

Theoretically, population growth rate could be positively or negatively related to current population size or also be independent of it. A negative correlation, a 'rare species advantage' has received considerable attention as a possible mechanism for the maintenance of high plant diversity in tropical forests: rare tree species frequently have an advantage over more common ones

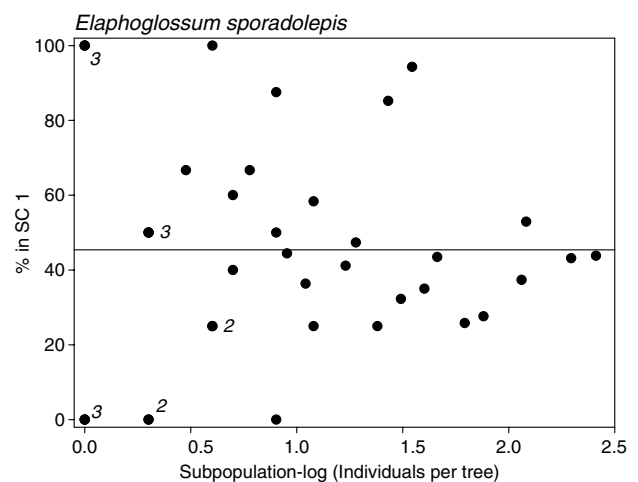


Figure 2. Proportion of juveniles (Size Class 1) in relation to the number of individuals of the 40 subpopulations of *Elaphoglossum sporadolepis*. The solid line represents the average of 45%, the correlation is not significant ($r = 0.1$, $P = 0.55$). Numbers in italics indicate the number of identical data points.

due to frequency-dependent mechanisms (Volkov *et al.* 2005, Wills *et al.* 2006). This apparent discrepancy between co-occurring trees and vascular epiphytes in the tropics may reflect fundamental differences in community processes between life-forms (Benzing 1981). Typical densities in the San Lorenzo area are 2–3 epiphyte individuals m^{-2} bark surface (Zotz & Vollrath 2003). Such low densities make frequency-dependent mechanisms unlikely in structuring communities. In contrast to trees, competitive interactions are probably very limited, and hence there are no ‘inferior competitors’ to take advantage of intense intraspecific competition among the members of dominant species. However, while this reasoning explains the absence of an advantage of rare species, it is unclear why rarer species should do worse.

There is direct evidence for the existence of a rather stable core group of species. Observing the epiphytes on one particular host tree species, *Socratea exorrhiza*, in the same area over a 5-y period, Laube & Zotz (2006) found that there was hardly any rank change among common species in time in spite of considerable turnover of epiphyte individuals. On the other hand, in rare species they observed substantial fluctuations in abundance, sometimes leading to extinction, but immigration events of additional species over-compensated losses. Notably, this relative stability in the composition of the dominant members of the local epiphyte assemblage did not concur with a steady-state in abundance. Rather, there was a continuous increase in abundance, in particular among common species (Laube & Zotz 2006). This highlights that this system is not in equilibrium: by comparing the average longevity of individual trees with epiphyte colonization rates, Laube & Zotz (2006) suggested that many, if not most trees are likely to die before epiphyte assemblages ever become saturated. At least some of the rarer species with a regressive population structure may constitute remnant populations (*sensu* Eriksson 1996), the potential longevity of several decades in many vascular epiphytes (Schmidt & Zotz 2002) allowing for long-term persistence in the absence of sufficient local recruitment. Alternatively, locally rare species may sustain themselves in the long term by occasional immigration from a larger meta-community (the rescue effect *sensu* Brown & Kodric-Brown 1977). In any case, the fact that a few members of almost all species have reached their species-specific maximum size (Appendix 1) suggests that none of the rarer species is a recent arrival: vascular epiphytes are known for their very slow growth rates and larger adults are likely to be decades old (Hietz *et al.* 2002, Larson 1992, Schmidt & Zotz 2002).

The possible reasons for local rarity are diverse (Kunin & Gaston 1997), but the majority of locally rare species are substantially more common in at least part of their geographical range (Murray & Lepschi 2004, Murray *et al.* 1999). Indeed, some of the rarer epiphyte species

in the San Lorenzo plot are extremely abundant in ecologically equivalent forests in central Panama. Good examples are two orchids (*Dimerandra emarginata* and *Caularthron bilamellatum*), which are very abundant in the Barro Colorado Nature Monument (Croat 1978, Zotz *et al.* 1999), or *Werauhia sanguinolenta*, a very common bromeliad in forests along the Caribbean coast of Panama (Zotz, pers. obs.).

In summary, I demonstrate a significant correlation between population size and size class structure in a local community of vascular epiphytes, and interpret this finding as evidence for a core group of species that will maintain the present dominance structure or, if not knocked back by disturbance, will become even more common in the future. However, only direct long-term observations can show whether the composition of epiphyte communities is indeed as stable as the current data suggest.

ACKNOWLEDGEMENTS

The excellent field assistance of Steffen Schultz (Würzburg, Germany) was essential for the success of this study. Funds came from the Smithsonian Tropical Research Institute (STRI, Panama), the United Nations Environmental Program (UNEP), the Deutsche Forschungsgemeinschaft, the FAG, Basel, Switzerland, and the A.F.W. Schimperstiftung, Stuttgart, Germany. Thanks to S. J. Wright, V. Horlyck, J. Herrera and E. Andrade (all STRI) for organizing work at the crane.

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Appendix 1. Size class distribution of 45 epiphyte species. Size classes (SC) were defined in 20% steps from 0–100% maximum size. Also given are population size (individuals), the slope of the size distribution, L (Condit *et al.* 1998), the r^2 of this regression, the maximum size (size SL, in cm) in the San Lorenzo populations (measured organ), and for comparison the maximum size reported by Croat (1978) for each species on Barro Colorado Island (size BCI, cm). n.a. = no data available.

Species	Family	Individuals	SC 1	SC 2	SC 3	SC 4	SC 5	L	r^2	Size		
										SL	Size BCI	Organ
<i>Scaphyglottis longicaulis</i>	Orchidaceae	1568	61.2	20.9	13.9	2.9	1.2	-0.98	0.98	35	30	stem
<i>Scaphyglottis behrii</i>	Orchidaceae	1514	67.3	20.2	9.3	2.7	0.5	-1.18	0.98	45	45	stem
<i>Elaphoglossum sporadolepis</i>	Lomariopsidaceae	1187	42.2	48.0	9.7	0.0	0.1	-1.59	0.91	38	40	leaf
<i>Maxillaria uncatata</i>	Orchidaceae	859	64.8	30.3	3.5	0.8	0.2	-1.49	0.98	15	n.a.	stem
<i>Pleurothallis brighamii</i>	Orchidaceae	800	13.6	41.5	32.1	7.5	5.3	-0.36	0.41	10	9	leaf
<i>Anantherocorus angustifolius</i>	Vittariaceae	592	39.9	30.9	18.9	8.3	2.0	-0.73	0.91	40	30	leaf
<i>Dicranoglossum panamense</i>	Vittariaceae	559	32.9	40.1	20.6	5.3	1.1	-0.88	0.85	33	40	leaf
<i>Niphidium crassifolium</i>	Polypodiaceae	478	61.5	27.7	9.3	1.3	0.2	-1.45	0.97	70	85	leaf
<i>Trichosalpinx orbicularis</i>	Orchidaceae	391	18.2	22.3	42.7	14.1	2.6	-0.44	0.43	4	n.a.	leaf
<i>Scaphyglottis prolifera</i>	Orchidaceae	284	39.4	33.8	15.5	6.0	4.2	-0.62	0.96	22	25	stem
<i>Dichaea panamensis</i>	Orchidaceae	279	85.9	10.8	2.5	0.4	0.4	-1.43	0.94	20	18	stem
<i>Tillandsia anceps</i>	Bromeliaceae	248	64.5	19.0	10.7	5.0	0.4	-1.14	0.92	45	40	leaf
<i>Elaphoglossum</i> sp.	Lomariopsidaceae	197	58.4	27.4	10.2	3.6	0.5	-1.15	0.97	50	n.a.	leaf
<i>Tillandsia bulbosa</i>	Bromeliaceae	187	71.1	7.5	7.0	5.9	8.6	-0.45	0.47	31	30	leaf
<i>Sobralia fragrans</i>	Orchidaceae	169	17.5	41.2	36.1	4.1	1.0	-0.80	0.64	30	23	leaf
<i>Anthurium friedrichsthali</i>	Araceae	159	21.5	27.2	29.1	17.7	4.4	-0.40	0.54	45	56	leaf
<i>Asplenium juglandifolium</i>	Aspleniaceae	156	66.7	16.7	8.3	3.2	5.1	-0.68	0.82	60	n.a.	leaf
<i>Asplenium serratum</i>	Aspleniaceae	142	47.9	34.5	10.6	2.1	3.5	-0.80	0.86	60	70	leaf
<i>Campyloneurum occultum</i>	Polypodiaceae	137	35.6	33.3	20.7	5.2	5.2	-0.57	0.87	40	40	leaf
<i>Campyloneurum phylliditis</i>	Polypodiaceae	120	51.7	26.7	8.3	7.5	5.8	-0.56	0.90	85	100	leaf
<i>Vriesea gladioliflora</i>	Bromeliaceae	106	45.7	37.2	9.6	6.4	1.1	-0.93	0.93	58	60	leaf
<i>Elaphoglossum herminieri</i>	Lomariopsidaceae	103	60.2	16.5	10.7	9.7	2.9	-0.66	0.91	60	100	leaf
<i>Anthurium acutangulum</i>	Araceae	98	17.5	41.2	36.1	4.1	1.0	-0.80	0.64	45	40	leaf
<i>Catopsis sessiliflora</i>	Bromeliaceae	92	28.3	43.5	22.8	3.3	2.2	-0.77	0.80	18	22	leaf
<i>Anthurium hacumense</i>	Araceae	75	10.7	44.0	34.7	6.7	4.0	-0.39	0.34	80	n.a.	leaf
<i>Catasetum viridiflavum</i>	Araceae	70	54.3	31.4	7.1	1.4	5.7	-0.76	0.69	21	25	stem
<i>Guzmania subcorymbosa</i>	Bromeliaceae	70	41.1	17.6	26.5	11.7	2.9	-0.57	0.79	40	n.a.	leaf
<i>Polystachya foliosa</i>	Orchidaceae	62	43.5	35.5	11.3	4.8	4.8	-0.63	0.92	17	25	leaf
<i>Anthrophytum lanceolatum</i>	Vittariaceae	61	27.9	31.1	27.9	11.5	1.6	-0.67	0.71	24	n.a.	leaf
<i>Lockhartia acuta</i>	Orchidaceae	58	17.5	36.8	33.3	7.0	5.2	-0.41	0.53	50	n.a.	stem
<i>Maxillaria discolor</i>	Orchidaceae	55	32.7	25.5	38.2	0.0	3.6	-0.76	0.56	15	n.a.	leaf
<i>Vittaria lineata</i>	Vittariaceae	54	70.4	9.3	9.3	5.6	5.6	-0.56	0.70	65	75	leaf
<i>Aspasia principissa</i>	Orchidaceae	53	54.7	17.0	13.2	7.5	7.5	-0.48	0.86	16	16	stem
<i>Masdevallia livingstoneana</i>	Orchidaceae	45	13.1	18.8	34.4	24.4	9.4	-0.04	0.02	17	13	leaf
<i>Anthurium clavigerum</i>	Araceae	44	20.5	45.5	22.7	9.1	2.3	-0.60	0.69	100	100	leaf
<i>Anthurium littorale</i>	Araceae	40	27.5	30.0	17.5	15.0	10.0	-0.27	0.90	31	38	leaf
<i>Epidendrum nocturnum</i>	Orchidaceae	38	23.7	50.0	7.9	10.5	7.9	-0.38	0.54	20	60	stem
<i>Epidendrum difforme</i>	Orchidaceae	36	25.7	34.3	31.4	5.7	2.9	-0.61	0.74	15	12	leaf
<i>Anthurium brownii</i>	Araceae	33	36.4	30.3	24.2	1.0	8.1	-0.64	0.46	75	66	leaf
<i>Trichocentrum capistratum</i>	Orchidaceae	31	25.8	54.8	3.2	12.9	3.2	-0.56	0.50	4	n.a.	leaf
<i>Pecluma pectinata</i>	Polypodiaceae	29	65.5	17.2	10.3	3.4	3.4	-0.74	0.93	65	60	leaf
<i>Stenospermatum angustifolium</i>	Araceae	22	54.5	22.7	18.2	0.0	4.5	-0.80	0.67	100	n.a.	stem
<i>Aechmea tillandsioides</i>	Bromeliaceae	19	5.6	33.3	38.9	11.1	11.1	0.03	0.00	70	120	leaf
<i>Notylia albida</i>	Orchidaceae	18	50.0	5.6	5.6	16.7	22.2	-0.05	0.01	9	15	leaf
<i>Dimerandra emarginata</i>	Orchidaceae	16	6.2	49.4	18.6	12.4	12.4	0.00	0.00	21	40	stem