

Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador

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Received: 17 September 2007 / Accepted: 26 June 2008 / Published online: 16 July 2008
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Abstract The impact of human disturbance on colonisation dynamics of vascular epiphytes is poorly known. We studied abundance, diversity and floristic composition of epiphyte seedling establishing on isolated and adjacent forest trees in a tropical montane landscape. All vascular epiphytes were removed from plots on the trunk bases of *Piptocoma discolor*. Newly established epiphyte seedlings were recorded after 2 years, and their survival after another year. Seedling density, total richness at family and genus level, and the number of families and genera per plot were significantly reduced on isolated trees relative to forest trees. Seedling assemblages on trunks of forest trees were dominated by hygrophytic understorey ferns, those on isolated trees by xerotolerant canopy taxa. Colonisation probability on isolated trees was significantly higher for plots closer to forest but not for plots with greater canopy or bryophyte cover. Seedling mortality on isolated trees was significantly higher for mesophytic than for xerotolerant taxa. Our results show that altered recruitment can explain the long-term impoverishment of post-juvenile epiphyte assemblages on isolated remnant trees. We attribute these changes to a combination of dispersal constraints and the harsher microclimate documented by measurements of temperature and humidity. Although isolated trees in anthropogenic landscapes are considered key structures for the maintenance of forest biodiversity in many aspects, our results show that their value for the conservation of epiphytes can be limited. We suggest that abiotic seedling requirements will increasingly constitute a bottleneck for the persistence of vascular epiphytes in the face of ongoing habitat alteration and atmospheric warming.

Keywords Desiccation stress · Dispersal · Diversity · Human disturbance · Microclimate · Recruitment · Species richness · Tropical montane moist forest

Abbreviations

DBH Diameter at breast height
FDR False discovery rate
IT Isolated tree

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Introduction

Vascular epiphytes are a major element of tropical forest structure and biodiversity. They are characterised by traits that may reduce their resilience compared to terrestrial herbs: long generation cycles and sensitivity to atmospheric conditions. These traits are related to resource limitations (nutrients and water) that appear to characterise the epiphytic habitat (Benzing 1998; Zotz and Hietz 2001).

Not surprisingly, the majority of studies on vascular epiphyte assemblages have found pronounced adverse effects of habitat alteration, such as reduced diversity or floristic composition biased towards generalists and xerophytes (Barthlott et al. 2001; Krömer and Gradstein 2003; Flores-Palacios and García-Franco 2004; Hietz 2005; Werner et al. 2005). In addition to increased desiccation stress (Hietz 2005), community changes following disturbance have repeatedly been attributed to constrained dispersal (Wolf 2005; Cascante-Marín et al. 2006) and, in secondary forests recovering from clear-cutting, reduced quality of substrate available for colonisation (e.g. lack of bryophyte mats; Krömer and Gradstein 2003). The importance of dispersal constraints has been emphasised particularly in the ample literature on non-vascular epiphytes (Pharo and Zartman 2007). Where epiphyte assemblages survive initial disturbance, such as in moderately logged forest, forest fragments or on remnant trees, impoverishment should proceed gradually due to lowered survival of well-established plants or reduced establishment. The latter may be caused by limited diaspore rain or seedling performance.

Many studies have addressed the performance of different life-stages in trees (see e.g. Hubbell 2001), and the critical role of the early establishment phase for future community composition is well-established (Lieberman 1996). As with trees, epiphyte dispersal can be limiting and seedling mortality is high, suggesting that establishment also plays a critical role for epiphytes. Studies on early epiphyte life-stages incur particular difficulties, including minute and delicate diaspores, lack of keys to identify seedlings, destructive access, and extreme spatial heterogeneity of the epiphytic habitat. Our present understanding of early life-stages of vascular epiphytes and their role in population dynamics is largely based on few species of hemi-epiphytic figs, orchids, and bromeliads in intact forest or green-houses. Consequently, the mechanisms by which aspects of human disturbance affect epiphytes are unclear.

Isolated trees in an anthropogenic land use matrix (hereafter referred to as 'ITs') constitute keystone structures that offer refuge, enhance connectivity, and provide nuclei of regeneration (Janzen 1988; Wolf 2005; Manning et al. 2006; Zahawi and Augspurger 2006). Moreover, they offer an excellent model system for the studying of human disturbance effects on epiphytes, being exposed to multiple edge effects, constrained colonisation, and being easily replicable.

After 10–30 years of isolation in pastures, isolated remnant trees in Ecuador harboured post-seedling epiphyte assemblages that were substantially impoverished in terms of abundance and species richness, and strongly biased to canopy taxa (Werner et al. 2005; Nöske et al. 2008). The purpose of this study was to examine the role of establishment in such long-term community alterations at the same study site, using an experimental approach. Specifically, we examined: (1) if seedling establishment is reduced on ITs, (2) to what extent colonisation patterns mirror the biased floristic composition observed on ITs after prolonged isolation, and (3) potential factors for altered establishment.

Methods

Study site

Field work was done at 1800–2000 m a.s.l. in the surroundings of Estación Científica San Francisco (ECSF) near Podocarpus National Park in southeastern Ecuador (3° 58'S, 79° 04' W). The natural vegetation of slopes and ravines is moist montane forest with a canopy height of 15–25 m (Homeier et al. 2008). The area fosters a remarkably rich epiphytic and terrestrial flora (Homeier and Werner 2007; Lehnert et al. 2007).

Mean annual temperature at 1950 m is 15.5°C, mean annual precipitation is 2200 mm (Emck 2007). A moderate rainy season typically extends from March to July. On average, 1 month with <100 mm of rain occurs during the driest part of the year, from October to February (R. Rollenbeck, pers. comm.). Shorter dry spells of 1–2 weeks, typically induced by westerly foehn winds, occur more frequently (Emck 2007). Fog is uncommon at this elevation (Rollenbeck et al. [in press](#)).

Data collection

Sampling focused on the bases of tree trunks. Since trunk bases are a distinctive growth site and usually host only limited subsets of epiphyte communities, they are not representative of entire trees or even vegetation types. However, unlike tree crowns they offer easy non-destructive access and relatively homogenous growth conditions in terms of microclimate, substrate orientation and inclination, and availability of secondary substrates (e.g. non-vascular epiphytes, dead organic matter).

During December 2003–January 2004, we removed all vascular epiphytes from the trunk base of 93 individuals of *Piptocoma discolor* (Asteraceae), 48 isolated in pastures and 45 in adjacent enclosed forest.

Piptocoma discolor is locally common on slopes and in ravines of both forest and cleared pasture land. The species is characterised by fast growth (Homeier 2004) and its fissured, spongy bark apparently promotes the growth of epiphytic bryophytes and vascular plants. Root bases rarely extend beyond 0.2 m in height. All ITs had established in pastures, as evident from their architecture (short trunks, divaricated crowns).

Epiphytes were removed from cylindrical plots 0.5–2.25 m in trunk height, minimising substrate damage. Total plot area was 84.4 (ITs) and 90.4 m² (forest), respectively. Trees were revisited after 3–6 months to remove rare resprouting fragments of creeping plants that were overlooked during initial removal. After 2 years, all vascular epiphyte seedlings colonising these plots were recorded and identified. Accidental epiphytes, fern gametophytes and plants establishing in knotholes were omitted. Seedlings on ITs were marked with coated steel nails and their survival was recorded after 1 year.

Identification of seedlings was based on years-long local field experience. Young sporophytes of Vittariaceae and Dryopteridaceae (*Elaphoglossum*) species are easily confounded and we may have slightly overestimated the former. Seedlings of the closely related bromeliad genera *Tillandsia* and *Vriesea* are indistinguishable. Since they also share similar ecological requirements, we made no attempt to separate them (combined as '*Tillandsia*' in the following). For the same reasons, *Pecluma* and *Serpocaulon* (Polypodiaceae) were combined as '*Pecluma*'.

For each plot we recorded percentage cover of lichens and bryophytes, DBH, canopy openness, and, for IT plots, distance to enclosed forest. Canopy openness was measured with a spherical densiometer (Lemmon 1957), distance to forest by means of ArcGIS 9

(ESRI, Redlands, CA, USA.) and a geo-referenced aerial photograph. We logged air temperature and relative humidity at 2 m of height by sequentially running data loggers (Onset Hobo Pro, Pocasset, MA, USA) on pairs of ITs and forest trees ($n = 9$) during January 2004–March 2005. On average, logger pairs ran for 2 months ($62 \text{ days} \pm 26$). The months of November–March (2.4 ± 0.5 loggers/month) are overrepresented at the cost of April–October (1.1 ± 0.2).

Data analysis

Because the number of taxonomic units increases nonlinearly with area, we downsized all plots to 1 m^2 prior to the analysis of taxa density (the number of taxa per plot). We did this by taking into account those plants growing on the lowest and highest 0.5 m^2 of each plot cylinder, in order to avoid bias of the resulting sub-samples from skewed vertical distribution patterns.

Analysis of taxa density at the genus level allowed us to classify plants as either hygrophytic, mesophytic or xerotolerant based on their vertical stratification in the local natural forest (Werner et al. 2005, F. Werner unpubl. data). At family level, several taxa locally are heterogeneous in this respect (Table 1). We applied individual-based rarefaction with 10,000 iterations to compare total species richness between treatments (Gotelli and Entsminger 2006).

Because parametric assumptions could not be matched, we analysed between-group differences of continuous variables through resampling using PC-Ord 4.25 (McCune and Mefford 1999). We used multi-response permutation procedure (MRPP; Mielke et al. 1982), one-factorial and on squared euclidean distance, applying a weighing factor ($C = n_i - 1 / \sum(n_i - 1)$) which results in a MRPP statistic equivalent to a two-sample t -test or one-way ANOVA F -test (Mielke et al. 1982). A , the chance-corrected within-group agreement, is a sample size-independent measure of 'effect-size'. When all items are identical within groups, then the observed $A = 1$ is the highest possible value for A . If heterogeneity within groups equals expectation by chance, then $A = 0$. If there is less agreement within groups than expected by chance, then $A < 0$.

Seedling densities on ITs were zero-truncated, so we used incidence data of 1 m^2 sub-plots to test for effects of canopy openness, distance to forest and bryophyte cover on epiphyte establishment. Data were analysed by means of a randomisation test (10,000 iterations), after separating IT plots into two equal-sized groups (higher and lower values of canopy openness, distance and bryophyte cover, respectively). Seedling mortality on ITs was analysed by means of the same randomisation procedure. Due to a low number of observations, we grouped seedling genera as either commonly ($>5\%$ of all epiphyte individuals) or uncommonly ($<0.5\%$) found as post-juveniles on local ITs (Werner et al. 2005) to test if seedling survivorship is coupled with abundance of post-juveniles.

Where appropriate, multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of $P < 0.05$ according to Benjamini and Hochberg (1995).

Results

Mean temperature was $16.4^\circ\text{C} \pm 0.8 \text{ SD}$ (ITs) and $15.3^\circ\text{C} \pm 0.6$ (forest), mean relative humidity was $87.6\% \pm 2.1$ and $96.3\% \pm 2.8$, respectively. Hourly means differed significantly ($P < 0.05$; Wilcoxon test) from 7:00 to 18:00 h (T_{mean}), and for the entire day (RH_{mean}), respectively. Differences in hourly means peaked at 10:00–11:00 a.m. (3.3°C) and 11:00–12:00 a.m. (19.8%; Fig. 1).

Table 1 Epiphyte seedling densities (individuals/m²) on forest trees (*n* = 45 plots) vs. isolated trees (ITs; *n* = 48)

	Forest	ITs	<i>A</i>	<i>P</i>	Ecol. req. ^a	Disp. mode ^b
	Mean ± SD	Mean ± SD				
Araceae	0.08 ± 0.23	– ± –	0.055	<0.01*	H-M	A
<i>Anthurium</i>	0.07 ± 0.20	– ± –	0.043	<0.05*	H-M	A
<i>Philodendron</i>	0.02 ± 0.13	– ± –	0.001	<0.5	H	A
Aspleniaceae (<i>Asplenium</i>)	1.90 ± 3.71	– ± –	0.112	<0.0001*	H	W
Blechnaceae (<i>Blechnum</i>)	0.01 ± 0.03	– ± –	0.001	<0.5	H	W
Bromeliaceae	0.03 ± 0.14	0.22 ± 0.45	0.061	<0.01	H-X	W
<i>Guzmania</i>	0.01 ± 0.05	– ± –	0.001	<0.5	H-M	W
<i>Tillandsia</i> ^c	0.03 ± 0.14	0.22 ± 0.45	0.067	<0.005*	M-X	W
Cyclanthaceae (indet.)	0.02 ± 0.11	– ± –	0.001	<0.5	H	A
Dryopteridaceae (<i>Elaphoglossum</i>)	0.36 ± 0.73	0.06 ± 0.24	0.065	<0.005*	H-M	W
Ericaceae (indet.)	0.01 ± 0.08	– ± –	0.001	<0.5	M	A
Grammitidaceae	0.06 ± 0.19	0.10 ± 0.27	–0.005	<0.5	H-M	W
<i>Melpomene</i>	0.03 ± 0.14	0.10 ± 0.27	0.014	<0.5	M	W
<i>Micropolypodium</i>	0.02 ± 0.11	– ± –	0.001	<0.5	H-M	W
<i>Alansmia</i>	0.01 ± 0.09	– ± –	0.001	<0.5	H	W
Hymenophyllaceae	0.31 ± 0.49	– ± –	0.169	<0.0001*	H-M	W
<i>Hymenophyllum</i>	0.16 ± 0.35	– ± –	0.086	<0.001*	H-M	W
<i>Trichomanes</i>	0.16 ± 0.38	– ± –	0.074	<0.005*	H	W
Orchidaceae	0.04 ± 0.15	– ± –	0.019	<0.1	H-X	W
<i>Dichaea</i>	0.03 ± 0.14	– ± –	0.012	<0.5	H	W
Indet.	0.01 ± 0.03	– ± –	0.001	<0.5	n.a.	W
Piperaceae (<i>Peperomia</i>)	0.29 ± 0.71	– ± –	0.072	<0.0001*	H-M	A
Polypodiaceae	0.69 ± 1.44	0.14 ± 0.34	0.057	<0.005*	H-X	W
<i>Campyloneurum</i>	0.01 ± 0.09	– ± –	0.001	<0.5	H-M	W
<i>Pecluma</i> ^d	0.65 ± 1.43	– ± –	0.090	<0.0001*	H	W
<i>Pleopeltis</i>	0.02 ± 0.13	0.14 ± 0.34	0.040	<0.05*	X	W
Urticaceae (<i>Pilea</i>)	0.02 ± 0.12	– ± –	0.012	<0.5	H	G
Vittariaceae	2.39 ± 5.51	– ± –	0.080	<0.0005*	H	W
<i>Polytaenia</i>	1.93 ± 5.04	– ± –	0.062	<0.0005*	H	W
<i>Radiovittaria</i>	0.06 ± 0.27	– ± –	0.020	<0.05*	H	W
<i>Vittaria</i>	0.39 ± 2.47	– ± –	0.002	<0.1	H	W

* Significant after FDR correction at *P* < 0.05

^a Ecological requirements: H = hygrophytic and shade-tolerant; M = mesophytic and moderately light-demanding; X = xerotolerant and light-demanding; classifications are based on vertical stratification patterns in local forest (Werner et al. 2005; F. Werner, unpubl. data)

^b Dispersal modes: W = wind-dispersed; A = animal-dispersed; G = gravity-dispersed

^c May include *Vriesea* spp

^d May include *Serpocaulon* spp

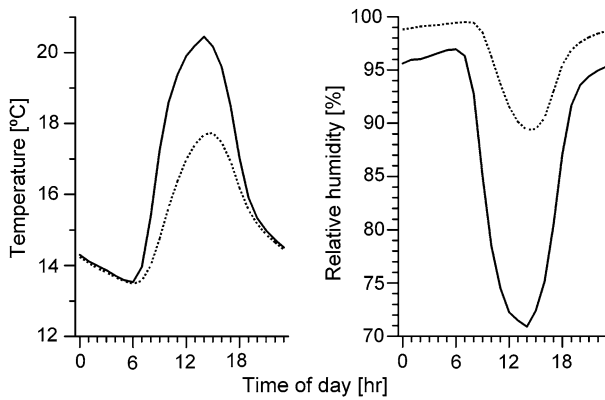


Fig. 1 Mean daily course of air temperature and relative humidity at 2 m height under the crowns of isolated trees (solid lines) and forest trees (stippled lines). Data are from 9 pairs of loggers sequentially set over the course of ca. 1 year

Lichen cover was significantly higher on the stem bases of ITs versus forest trees ($A = 0.703$, $P < 0.0001$), whereas bryophyte cover was lower ($A = 0.273$, $P < 0.0001$; Table 2).

Overall, the IT plots yielded 48 seedlings from 4 genera (bromeliads: *Tillandsia*; ferns: *Elaphoglossum*, *Melpomene*, *Pleopeltis*) in 4 families, the forest plots 533 seedlings from 24 genera in 13 families (Fig. 2; Table 1).

Although forest seedlings were composed of anemochorous (91%), zoochorous (8%) and barochorous taxa (1%), seedlings on ITs comprised exclusively anemochorous taxa. The underrepresentation of zoochorous relative to anemochorous taxa on ITs was significant ($P < 0.0001$; randomisation test).

Density of seedlings was significantly smaller on ITs relative to forest trees ($A = 0.238$, $P < 0.0001$), averaging 0.51 seedlings per $m^2 \pm 0.72$ SD compared to 6.21 ± 7.21 on forest plots. The number of both families and genera encountered on $1 m^2$ sub-plots was also smaller, each measuring 0.40 ± 0.64 on ITs, whereas forest sub-plots harboured 1.69 ± 1.35 families and 1.73 ± 1.42 genera per m^2 , respectively. These differences were highly significant ($A = 0.274$, $P < 0.0001$ and $A = 0.269$, $P < 0.0001$, respectively).

Total richness in epiphyte families and genera was significantly lower on ITs. Richness of the forest sample rarefied to the size of the IT sample (48 individuals) was 7.92 ± 1.22

Table 2 Characteristics of plots on forest trees ($n = 45$) and isolated trees (ITs; $n = 48$)

	Forest	ITs	A	P
	Mean \pm SD	Mean \pm SD		
Host DBH (cm)	37.88 \pm 13.49	34.18 \pm 12.34	0.010	0.172
Plot size (m^2)	2.01 \pm 0.74	1.76 \pm 0.60	0.023	0.074
Canopy openness (%)	17.03 \pm 4.47	68.08 \pm 15.65	0.828	<0.0001
Distance to forest (m)	–	189 \pm 117	–	–
Lichen cover (%)	9.03 \pm 8.32	47.50 \pm 15.45	0.703	<0.0001
Bryophyte cover (%)	38.94 \pm 20.63	17.55 \pm 13.40	0.273	<0.0001

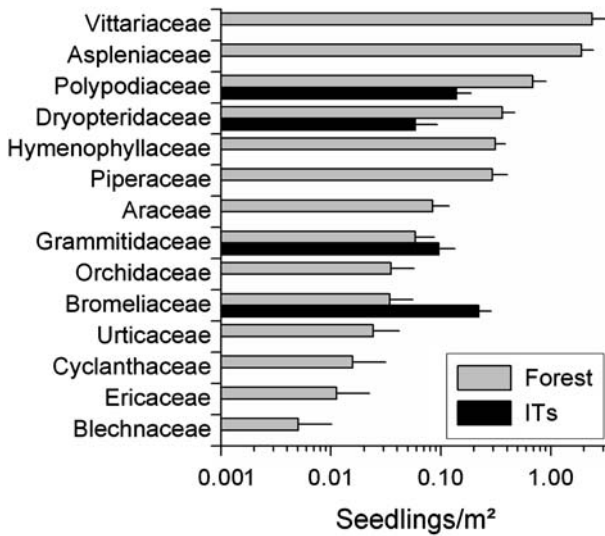


Fig. 2 Density of epiphyte seedlings on isolated trees (ITs) and in forest after 24 months of colonisation (means and standard errors)

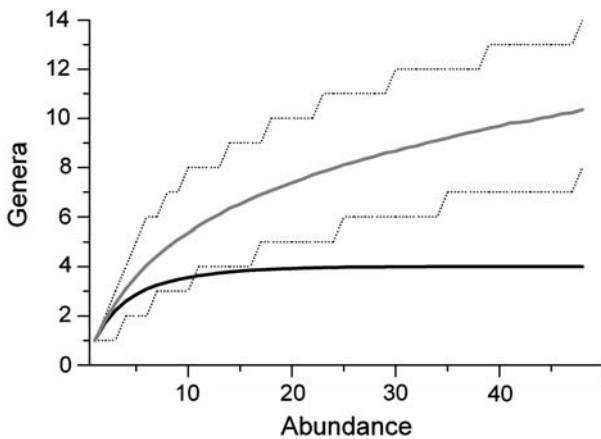


Fig. 3 Individual-based rarefaction (10,000 iterations) of generic richness in the forest (grey line) and on isolated trees (black line). Dotted lines reflect the respective 95% confidence intervals for the forest sample as determined from the 0.025 and 0.975 frequency values in the simulated data

families (95% CI = 6–10 families) and 10.35 ± 1.54 genera (95% CI = 8–14 genera) (Fig. 3).

ITs further differed substantially in seedling composition from forest trees. The xero-tolerant genera *Pleopeltis* and *Tillandsia* were significantly more abundant on IT plots than on forest plots, whereas numerous hygrophytic and mesophytic taxa were significantly less abundant (Table 1). For instance, the fern families *Aspleniaceae* and *Vittariaceae* which dominated forest plots were entirely absent from ITs.

Seedling density on IT plots was negatively related to distance to forest and canopy openness, and positively related to bryophyte cover (Fig. 4). The likelihood of colonisation

Fig. 4 Effects of distance to forest, canopy openness and bryophyte cover on seedling densities on isolated trees (means and standard errors). Bars reflect the seedling density on each 24 plots of higher or lower predictor values, respectively, with ranges and means as follows: distance to forest low: 10–129 m (mean 92), high: 132–432 (287); canopy openness low: 22–72% (57), high: 72–92 (79); bryophyte cover low: 3–13% (7.4), high: 15–58 (28). Note that the shown data was standardised to 1 m² plot size and binarised prior to significance testing

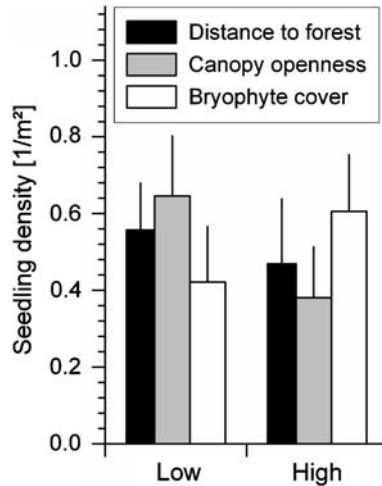


Table 3 Establishment and mortality of seedlings, and the representation of their respective (sub-)adult stages on isolated trees (ITs)

Genus	Seedlings		Post-juveniles ^a	
	<i>n</i>	Mortality (%/a)	Rel. abundance on ITs (% of ind.)	Abundance ratio ITs/forest trees
<i>Elaphoglossum</i>	5	60.0	0.13	0.0002
<i>Melpomene</i>	9	33.3	0.25	0.0001
<i>Pleopeltis</i> ^b	15	6.7	7.0 ^b	1.10
<i>Tillandsia</i> ^c	19	26.3	46.6	0.34

^a Calculated from Werner et al. (2005) after exclusion of one outlier species (*Dryadella wernerii*)

^b Note: abundant creepers tend to be underestimated by the 'stand' concept employed by Werner et al. (2005)

^c Including *Vriesea* spp

(1 m² sub-plots) differed significantly regarding distance to forest ($P = 0.026$), but not for canopy openness or bryophyte cover ($P = 0.086$ and $P = 0.230$, respectively).

During the third year of study, seedling mortality on ITs averaged 25%. Seedlings of genera that are commonly found in post-seedling stages on ITs suffered significantly lower mortality than seedlings of genera that are uncommon ($P = 0.040$). Among the former genera (*Pleopeltis* and *Tillandsia*) only 18% of plants died, whereas the latter genera (*Elaphoglossum* and *Melpomene*) exhibited 43% of mortality (Table 3).

Discussion

Post-juvenile assemblages of vascular epiphytes on remnant trees at our site are substantially less abundant (by 85%) and diverse (80% of species per tree) 10–30 years after their isolation in pastures (Werner et al. 2005). This impoverishment strongly affects mesophytic and hygrophytic species, whereas xerotolerant canopy taxa remain relatively well-represented. The compositional skew of post-juvenile assemblages was mirrored by the

patterns of seedling establishment we observed on ITs after 2 years. Seedlings of mesophytic and hygrophytic taxa were restricted to few individuals in the genera *Elaphoglossum* and *Melpomene*, whereas the great majority of seedlings were from the xerotolerant genera *Pleopeltis* and *Tillandsia* (Fig. 2).

Seedlings of animal-dispersed taxa were relatively scarce even in forest plots, reflecting the domination of the local epiphyte flora by wind-dispersed taxa (Homeier and Werner 2007; Lehnert et al. 2007). Moreover, endozoochorous seeds have a low probability for attaching to near-vertical surfaces such as trunks. The absence of animal-dispersed taxa from ITs intuitively suggests stronger dispersal constraints in zoochory versus anemochory. However, since animal-dispersed taxa locally share relatively high humidity requirements (Werner et al. 2005; F. Werner, unpubl. data), increased desiccation stress on ITs (Fig. 1) may cause a similar pattern.

The rain of wind-dispersed diaspores should decrease geometrically with growing distance from the source (Madison 1979). Our data revealed a significant effect of distance to forest on seedling establishment, which shows that diaspore rain was reduced on ITs. However, the effect of distances to forest on IT seedling densities was rather small (Fig. 4). Forest vegetation is not necessarily the sole source of diaspores for IT assemblages, as reproductive adults especially in the genera *Pleopeltis* and *Tillandsia* also occur on ITs (Table 3; Werner et al. 2005). By adding to the diaspore rain from forest sources, such plants may dilute the effects of dispersal constraints. However, while diaspores originating from ITs may have weakened the relationship between total seedling density and distance to forest, they cannot explain the scarcity of hygrophyte seedlings on ITs. Since the studied ITs formed regrowth, their entire epiphytic flora (including reproducing adults) must have established in isolation, subjected to the same establishment constraints as seedlings in our study.

We found that hygrophytic understorey specialists characterised seedling assemblages of forest plots (e.g. *Asplenium*, *Pecluma*, Vittariaceae spp.) but were entirely absent from ITs (Table 2). Instead, IT seedling assemblages were strongly predominated by xerotolerant taxa that were poorly represented in the forest understorey, despite of their common occurrence in the forest canopy (Werner et al. 2005). A corresponding paucity in understorey taxa has been reported from ITs and disturbed forests elsewhere (Barthlott et al. 2001; Krömer and Gradstein 2003; Flores-Palacios and García-Franco 2004, 2008; Hietz 2005), and cannot be explained easily by other factors than microclimatic changes (Fig. 1).

ITs can be viewed as forest fragments that are exposed to multiple edge effects, including increased light levels, wind velocity, temperature, and reduced air humidity (Laurance 2004). The resulting harsher microclimate strongly affects many organisms, including epiphytic lichens and bryophytes (Moen and Jonsson 2003; Hylander 2005). In our study, however, IT plots exposed to higher light levels (greater canopy openness) did not show a significantly lower probability of colonisation. This may be related to the great stochasticity inherent to establishment dynamics throughout (Hubbell 2001; Laskurain et al. 2004), coupled with an unexpectedly low number of observations (only 48 seedlings in 21 of 48 plots). Moreover, canopy openness is not an ideal measure of exposure. Although canopy openness is a good proxy for wind penetration, air humidity and temperature in forest understorey, these parameters are presumably little influenced by canopy properties of solitary trees. Canopy openness thus reflects only one of several major components of physical edge effects that affect water budgets in plants. The measured differences in canopy openness between IT plots may further be of negligible relevance for epiphytes that already perceive even the most shaded IT plots as exceedingly exposed.

Light levels, temperature and relative humidity were greatly altered around IT trunk bases (Fig. 1; Table 2), to the point of closely resembling conditions in the upper forest canopy (F. Werner and C. Gehrig, unpubl. data). Upper canopy conditions on IT trunk bases were mirrored by abundance patterns of non-vascular epiphytes. Lichens, most of which are sensitive to excessive humidity, flourished, whereas bryophytes, which favour constant humidity (Nöske et al. 2008), exhibited low covers (Table 2). Regardless of diaspore influxes, it seems most unlikely that seedlings of vascular understory epiphytes may establish successfully in such a harsh, canopy-like environment. Hietz and Briones (1998, 2001) showed that vertical stratification of (adult) epiphytic ferns closely reflects exposure tolerance, being correlated with a wealth of morphological and physiological traits that influence rates of uncontrolled water loss. Zotz and co-workers could further demonstrate that water relations are strongly influenced by the surface-volume ratio and hence plant size in vascular epiphytes (Zotz et al. 2001; Zotz and Hietz 2001).

Mortality rates on ITs were remarkably low (25% on average), despite an unusually dry year of 2006 (R. Rollenbeck, pers. comm.). Much higher mortality rates—particularly due to drought—have been found in early epiphyte seedlings elsewhere (Benzing 1978; Larson 1992; Laman 1995; Tremblay 1997; Zotz 1998; Castro Hernández et al. 1999; Hietz et al. 2002; Zotz et al. 2005). Moreover, seedling mortality declines drastically with age (Castro Hernández et al. 1999; Mondragón et al. 1999; Hietz et al. 2002; Zotz et al. 2005), suggesting that many of the seedlings recorded after 2 years had already passed an intense phase of selection.

Diverging survival rates add further support to the notion that seedling assemblages were shaped by mortality. The genera *Pleopeltis* and *Tillandsia* exhibited lower mortality than the genera *Melpomene* and *Elaphoglossum*. Adults of the former genera locally abound on ITs, where adults of the latter genera are rarely found (Table 3), suggesting that seedling mortality differs between epiphyte taxa according to their predisposition for life under high levels of exposure. This conclusion implicates that diverging rates of seedling mortality (filtering) shape the composition of post-juvenile assemblages. The fact that post-juvenile stages of *Melpomene* and *Elaphoglossum* favour growth sites with higher moisture levels than *Pleopeltis* and *Tillandsia* further suggests that the tolerance of seedlings to drought is a major predictor of seedling mortality. For instance, *Pleopeltis macrocarpa*, a desiccation-tolerant fern that regionally extends into perarid montane forest (Werner and Gradstein in press), accounted for almost a third of all seedlings recorded on ITs and showed the highest survival rate at our site (Table 3). Thus, our results strongly suggest that both decreased diaspore rain and drought-related seedling mortality reduce seedling densities on ITs, and that increased physical exposure rather than properties of diaspore rain shape the floristic composition of IT seedling assemblages.

Caution should be exercised in extrapolating our results to entire trees. In relation to forest, trunk bases of ITs experience a more strongly altered microclimate than their crowns (Werner and Gehrig unpubl. data). Moreover, they essentially lack important microsites such as near-horizontal surfaces, humus accumulations or crotches. Hence, epiphyte seedling establishment on ITs may be less altered in the canopy than on trunk bases.

The study of establishment limitations is a key for the understanding of current and future patterns of epiphyte diversity. Drought inflicts a major challenge for adults of many epiphyte species (e.g. Zotz and Tyree 1996; Benzing 1998), and seedlings are even more drought-sensitive (Zotz et al. 2001). Desiccation stress increases with structural forest disturbance and—in most regions—with atmospheric warming (Laurance 2004; Malhi and

Phillips 2004). Thus, abiotic seedling requirements may increasingly constitute a bottleneck for the persistence of epiphyte populations.

Many if not most vascular epiphyte species require 1–2 decades to reach maturity (Larson 1992; Benzing 1998; Zotz 1998; Hietz et al. 2002; Schmidt and Zotz 2002). As many of them cannot be identified in immature state, classic ecological inventories will invariably record consequences of changing land use and climate only with considerable time lag. Even experimental approaches with post-seedling life stages (e.g. Nadkarni and Solano 2002) can only provide limited insight in this regard, since they do not take into account seedling requirements and may therefore underestimate the sensitivity of species. Thus, a better understanding of seedling requirements and performance is needed to construct meaningful climate envelopes, and predict the development of epiphyte communities after habitat modification and with global climate change.

Conclusions

With exception of a few hardy canopy taxa, we found that rates of establishment of vascular epiphytes on ITs were much smaller than on corresponding forest trees. Thus, altered recruitment is apt to explain the dramatic and non-random impoverishment of post-juvenile epiphyte assemblages on remnant trees, which is locally observed after prolonged isolation in pastures (Werner et al. 2005; Nöske et al. 2008). Although isolated trees in anthropogenic landscapes are considered key structures for the maintenance of forest biodiversity in many aspects (Manning et al. 2006), our results suggest that their value for the conservation of epiphytes can be very limited.

Although we found evidence for seedling establishment on ITs being constrained by dispersal, the results imply additional establishment limitations. Patterns of floristic seedling composition and mortality suggest substantial influence of increased desiccation stress on IT seedling assemblages, which may greatly exceed the influence of dispersal constraints (compare Snäll et al. 2003). Disentangling the roles of these diversity drivers in complex anthropogenic landscapes poses methodological difficulties that may have led to an overestimation of the role of dispersal limitation in epiphytes (Pharo and Zartman 2007; Werth et al. 2007). Given that establishment constraints are a key for the prediction of future epiphyte communities, further studies on this matter will yield critical new insights.

Acknowledgments We thank F. Lauer and M. Kühnlein for their help with ArcGIS data processing, C. Gehrig for microclimate data analysis, and N. M. Nadkarni, M. Kessler and two anonymous reviewers for most helpful comments on earlier versions of the manuscript. We acknowledge the generous support by the German Academic Exchange Service (DAAD), the German Research Foundation (DFG), and Idea Wild. This is publication no. 199 of the Yanayacu Natural History Research Group.

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