

IS THE RESILIENCE OF EPIPHYTE ASSEMBLAGES TO HUMAN DISTURBANCE A FUNCTION OF LOCAL CLIMATE?

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Abstract. Field studies have shown a wide array of responses of vascular epiphyte diversity to human disturbance-assemblages of disturbed habitats range from largely unchanged to severely impoverished when compared with intact forest. This variability is not well understood. We explored the hypothesis that the relative impoverishment of disturbed-habitat epiphyte assemblages is a function of local climate, by analyzing the available literature on epiphyte diversity on isolated trees as a model system. We found that assemblages of moist and moderately seasonal areas experience considerably stronger impoverishment than those of aseasonally wet or distinctly dry areas. We argue that the integrity of the vertical microclimatic gradient is more crucial for the maintenance of epiphyte diversity in moderately seasonal forests than in distinctly dry or aseasonally wet forests.

Key words: diversity, fragmentation, isolated trees, land-use change, mesoclimate, species density, species richness, tropical forest, vascular epiphytes

INTRODUCTION

There is much discussion in conservation biology about the extent to which anthropogenic habitats can allow the persistence and migration of organisms living naturally in primary forest (Laurance 2006, Gardner *et al.* 2007). Tropical forests continue to be converted, degraded, and fragmented at a high rate, and the challenge of global climate change will require alterations in species migrations of unprecedented magnitude and rapidity (Bush 2002, Malhi & Phillips 2004). Understanding how alteration and fragmentation of their primary habitat affects organ-

isms is therefore critical for conservation (Gascon *et al.* 1999, Laurance 2006).

Case studies in secondary and degraded forests have yielded a wide range of responses of epiphyte diversity to habitat disturbance. While some studies have found vascular epiphyte assemblages significantly impoverished (Barthlott *et al.* 2001, Krömer & Gradstein 2003, Wolf 2005), others found them as diverse as those of undisturbed forests (Hietz-Seifert *et al.* 1996, Larrea & Werner 2010). The response to habitat alteration even varies greatly within single taxa. Bromeliads, for instance, were less species-rich in some secondary forests (Krömer & Gradstein 2003) but considerably more species-rich in others (Barthlott *et al.* 2001). This divergence of patterns, however, is unsurprising considering that non-primary forests differ greatly in age and struc-

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ture, and in their degree of structural differences from their various potential vegetations. Parameters of potential influence on epiphytes include type and degree of disturbance, host-tree age, vegetation structure (e.g. stand height, canopy openness) and resulting microclimate, substrate quality and quantity (e.g. availability of large horizontal limbs, humus and bryophyte mats), dispersal constraints, and local climate (mesoclimate). Many of these factors are difficult to quantify, and information on very few of them has been regularly provided, much less analyzed, in papers addressing the epiphyte assemblages of non-primary habitats. This circumstance has hampered comparisons, rendering land-use change effects poorly understood and unpredictable.

Isolated trees (hereafter termed “ITs”) scattered in anthropogenic land-use matrices constitute key-stone structures that offer refuge, enhance connectivity, and provide nuclei of regeneration for many groups of forest organisms (Manning *et al.* 2006, Zahawi & Augspurger 2006). Moreover, they offer an excellent model system for studying the effects human disturbance on epiphytes. ITs can be viewed as the “ultimate”, smallest possible forest fragment (Williams-Linera *et al.* 1995, Gove *et al.* 2009), being exposed to maximum edge effects and potentially constrained colonization. Unlike degraded or secondary forests, ITs do not differ between sites in the relative degree of their physical exposure, neither do they differ from undisturbed forest in important host parameters like age, surface area, or bark characteristics, unless biased in size or taxonomic composition.

Epiphyte community changes following land-use change have often been attributed primarily to changes in microclimate (e.g. Barthlott *et al.* 2001, Hietz 2005, Nöske *et al.* 2008). Epiphytes are known for their high and fine-tuned humidity requirements, being linked more closely to the atmosphere than terrestrial biota (e.g. Kreft *et al.* 2004, Poltz & Zotz 2011). The relative degree to which epiphyte assemblages become species-poorer following disturbance may be linked to local climate. In aseasonally wet (perhumid) regions, epiphyte diversity on ITs may not be as strongly affected by desiccation stress as in areas of intermediate humidity, where a large share of the epiphytic flora depends on the maintenance of a mesic microclimate by intact forest canopies during dry periods. In various arid regions of the Neotropics we observed that ITs often harbor a relatively intact epiphytic flora. Because dry forest cano-

pies are usually low and open and cannot provide pronounced microclimatic buffering (Graham & Andrade 2004), it may be assumed that their epiphytes must be sufficiently well-adapted to persistent drought, even in situations of increased exposure such as experienced on ITs. To explore the hypothesis that the relative impoverishment of vascular epiphyte assemblages is a function of local climate, we compared studies on epiphyte diversity on ITs and mature forest trees at Neotropical sites.

METHODS

We screened the available literature on epiphyte diversity on ITs and, where needed, gathered additional information on site characteristics by contacting the respective authors. We restricted our survey to studies on vascular epiphyte assemblages that give species numbers for entire trees. To ensure consistency, several studies had to be excluded from analysis due to major differences in sampling area (Williams-Linera *et al.* 1995, Nkongmeneck *et al.* 2002), limited taxon sampling (Dunn 2000, Cascante-Marín *et al.* 2006), or the lack of a local baseline (e.g. Gonçalves & Waechter 2003, Poltz & Zotz 2011). Ultimately, seven studies allowed for meaningful comparisons and were included in our analysis (Hietz-Seifert *et al.* 1996, Flores-Palacios & García-Franco 2008, Nöske *et al.* 2008, Köster *et al.* 2009, Werner & Gradstein 2009, Larrea & Werner 2010, Köster *et al.* in press) (Table 1). To characterize the mesoclimate for each of the sites, we calculated an index of aridity, dividing monthly precipitation by monthly potential evapotranspiration (PET) (UNEP 1992). PET was calculated following the Thornthwaite method (Thornthwaite & Mather 1957) as:

$$PET_{Th} = 3.65 \times 10^{-4} d(t) I^{-1} [10T(t)]^a$$

where $d(t)$ is the total monthly daylight in hours, and $T(t)$ is the monthly mean temperature. The two variables I and a are empirically derived functions of mean annual temperature. Our analysis focused on species density, here defined as the number of species per host tree of comparable size. The “relative impoverishment” of ITs is given as the percentage of reduction in mean epiphyte species density on ITs relative to forest trees. For each of the studies we also calculated the qualitative Sørensen index as a measure of floristic similarity between forest and ITs from published species lists or unpublished own data using Estimate 8.2 (Colwell 2006). Polynomial regression was done with Xact 8 (Scilab, Hamburg, Germany).

TABLE 1. Site characteristics and vascular epiphyte diversity on isolated trees (ITs).

Study	Site	Region	Elevation [m]	Fog	Mean temp. [°C]	Precipit. [mm yr ⁻¹]	Aridity index	Canopy height [m]	Isolation of host trees [yr]	No. of host trees studied ^a	Effect of distance to forest ^b	Total species richness ^a	Relative impoverishment [%] ^b	Qual. Sørensen index
Flores-Palacios & García-Franco 2008	San Andrés Tlalnelhuayocan	E Mexico	1550	common	14.0	1650	2.07	30-45	85	88 ^c	n.s.	102 ^d	17 ^c	0.56
Hietz-Seifert <i>et al.</i> 1996	Los Tuxtlas	SE Mexico	100	rare	24.5	4700	3.41	30-35	28	165	**	83	20 ^d	0.74
Köster <i>et al.</i> in press	Bilsa	NW Ecuador	550	common	23.5	3100 ^e	2.80	30-35	5-15	52	n.s.	318	36	0.80
Köster <i>et al.</i> 2009	Otonga	NW Ecuador	2000	common	15.6	2550	3.07	25-30	5-25	52	n.s.	322	36	0.77
Larrea & Werner 2010	SierrAzul	NE Ecuador	2200	un-common	15.2	3500 ^e	4.40	25-35	6	90	–	155	3	0.68
Nöske <i>et al.</i> 2008	San Francisco	SE Ecuador	2000	un-common	15.6	2200	2.53	20	5-30	21	n.s. ^f	253	82	0.27
Werner & Gradstein 2009	Jerusalén	N Ecuador	2300	seas. common	16.9	530	0.60	5-8	not applicable	80	n.s.	8	4	0.77

^a values for entire study (forest trees and ITs combined).

^b “Effect of distance to forest” is marked by asterisks where epiphyte species numbers on ITs drop with increasing distance from closed forest. “Relative impoverishment” is the reduction in mean epiphyte species density (species per tree) on ITs relative to forest trees; asterisks mark significant differences in species density between habitat types. Significance levels: * $p < 0.05$, ** $p < 0.01$, n.s. = not significant. See original publications for details on statistical analyses.

^c excluding two forest plots where mean tree size was substantially smaller than in ITs. Species density values controlled for taxonomic identity of host trees at the same site: 0.61 (*Quercus* spp., inner crowns only; Flores-Palacios & García-Franco 2004); 0.87 (*Liquidambar macrophylla*, entire trees taken at 0.3 m dbh; Flores-Palacios & García-Franco 2006).

^d deduced from the linear regression equations (species no. vs. dbh at dbh = 0.5 m) given by Hietz-Seifert *et al.* 1996.

^e pers. comm. L. Carrasco (Bilsa) and H.F. Greeney (SierrAzul) respectively.

^f from Werner 2008.

RESULTS AND DISCUSSION

We found that responses of vascular epiphyte assemblages on ITs differed widely between studies (Fig. 1). In two aseasonally wet areas of SE Mexico and NE Ecuador, species density on isolated trees was not significantly reduced relative to forest trees of similar size (Hietz-Seifert *et al.* 1996, Larrea & Werner 2010). In contrast, at two moist study sites in NW Ecuador with a moderately pronounced dry season but frequent fogs throughout the year, epiphyte diversity was distinctly lower on ITs compared with forest trees. Both at Bilsa (Köster *et al.* in press) and Otonga (Köster *et al.* 2009), species density on ITs was 36% lower. At a slightly seasonal moist forest in SE Ecuador, species density on ITs was over 80% lower (Nöske *et al.* 2008, Werner 2008). This species-rich site regularly experiences short but pronounced dry spells induced by foehn winds (Emck 2007). ITs at an even more seasonal and drier site in eastern Mexico showed a moderate decline in species density (Flores-Palacios & García-Franco 2008). Finally, in a perarid forest area in northern Ecuador with annual

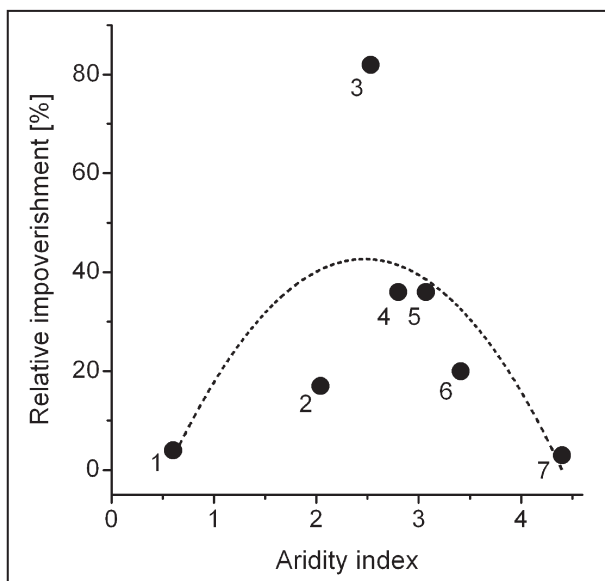


FIG. 1. The relationship between humidity (given as an index of aridity) and the relative impoverishment in mean epiphyte species density (species number per tree) on isolated trees (ITs) relative to trees in intact forest. Case studies: (1) Werner & Gradstein 2009; (2) Flores-Palacios & García-Franco 2008; (3) Nöske *et al.* 2008; (4) Köster *et al.* in press; (5) Köster *et al.* 2009; (6) Hietz-Seifert *et al.* 1996; (7) Larrea & Werner 2010. The stippled line reflects 2nd-degree polynomial fit ($y = -0.11x^2 + 0.57x - 0.27$; $r^2 = 0.48$, $p = 0.13$).

rainfall of 530 mm, species density on ITs was similar to adjacent forest (Werner & Gradstein 2009).

In spite of the limited number of studies available for this analysis, the data suggests that, as predicted, the response of vascular epiphyte assemblages to disturbance does indeed vary systematically with mesoclimate. A strong, significant decrease in species density on ITs was observed only in the studies with intermediate humidity conditions, whereas both the aseasonally wet and distinctly arid sites were little affected (Fig. 1, Table 1). Thus a continuous supply of moisture at perhumid sites appears to facilitate suitable growth conditions for a large number of epiphyte species on ITs, even though post-disturbance turnover in species composition may be considerable (e.g. Larrea & Werner 2010; compare also Sørensen indices in Table 1). In contrast, much lower species numbers were found under moderately moist, slightly seasonal conditions, where many taxa depend on the protection by an intact canopy during periods of drought. Where the forest canopy is opened up, vapor pressure deficits increase strongly during dry spells (e.g. Laurance 2004), which may result in high mortality among resident moist forest epiphytes (Werner 2011). In dry forests, where the vertical microclimate gradient is poorly developed even in intact stands (Graham & Andrade 2004), disturbance appears to result in relatively low declines in species numbers. We suggest that the effective adaptations to drought which are essential for dry forest epiphytes promote their persistence on ITs. This notion is supported by the paucity of epiphytic understory specialists recorded for tropical dry forests. In coastal Ecuador, for instance, Gentry & Dodson (1987) found 41 species of understory specialists among vascular epiphytes in a wet forest, but none in a seasonal, semi-deciduous moist forest. A corresponding pattern has been found by Hietz & Hietz-Seifert (1995a, b) in montane eastern Mexico. However, the most fragile, shade- or moisture-demanding taxa of any local community are unlikely to flourish in the multiple edge environment of ITs (e.g. Poltz & Zotz 2011), and the β -diversity of IT assemblages tends to be reduced (Flores-Palacios & García-Franco 2004, 2008; Hietz 2005, Larrea & Werner 2010; but see also Köster *et al.* 2009).

Factors other than mesoclimate cannot readily explain the observed hump-shaped pattern of species impoverishment (Fig. 1). Differences in host-tree size between habitat types were controlled for by restricting sampling to a certain range of stem diameter at breast height (dbh), or accounted for by regressing species numbers against dbh (Hietz-Seifert *et al.*

1996) in all studies included in our comparison. Tree species may vary widely in their quality as epiphyte hosts (e.g. Reyes-García *et al.* 2008, Köster *et al.* in press). However, host-tree species composition was controlled for in all but two studies where large numbers of trees were randomly selected (Hietz-Seifert *et al.* 1996, Flores-Palacios & García-Franco 2008). At the latter site at least, epiphyte diversity patterns remained similar when controlling for host-tree species identity (Flores-Palacios & García-Franco 2004, 2006; Table 1), suggesting that host-tree identity was not a major source of variability. ITs which established themselves after forest clearance may be expected to be poorer in epiphytes than remnant ITs, because their flora depends more strongly on colonization from distant sources. However, species density on ITs was unchanged at the only site where ITs were regrowth (Jerusalén; Werner & Gradstein 2009). Time since isolation of ITs, matrix quality (pasture in all cases), or distance to forest as a proxy of dispersal limitations are also possible predictors, but neither showed a relationship with differences in relative impoverishment between the compared studies. Distance to forest had significantly adverse effects on species density in one study (Hietz-Seifert *et al.* 1996) out of six for which this correlation was analyzed (Table 1).

In conclusion, our results support the notion of a general relationship between mesoclimate and disturbance effects on species density in vascular epiphytes. Maximum impoverishment may be expected in moist areas prone to short dry spells, as at the study site of Nöske *et al.* (2008). At this site, more than 50% of well-established vascular epiphyte individuals tagged in lower forest strata died within one year of their host trees being isolated in a fresh clearing (Werner 2011).

Our paper shows that the fate of epiphytes in anthropogenic tropical habitats remains insufficiently understood. The hypothesis of a hump-shaped relationship between mesoclimate and epiphyte species losses still awaits rigid testing, for which the number of comparable studies presently is very low. Clearly, several factors other than climate (e.g. dispersal limitations) can be important local determinants of epiphyte assemblages in man-made landscapes (Cascante-Marín *et al.* 2006, Werner & Gradstein 2008) and will need to be considered in future studies. Advances in this field of research will have important applications in conservation planning and management, as well as in the prediction of global climate change effects on the diversity and functionality of tropical epiphyte communities.

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