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Range size and climatic niche correlate with the vulnerability of epiphytes to human land use in the tropics

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ABSTRACT

Aim Range-restricted species account for a large proportion of global biodiversity, and many such species are highly threatened by deforestation and intensifying land use in the tropics. The effects of land use on the diversity of range-restricted species have rarely been studied and remain unknown for vascular epiphytes – diverse and important elements of tropical forests. This study analyses the vulnerability of range-restricted epiphyte species to human land use, compared to that of widespread species.

Location Western Ecuador (Chocó ecoregion): lowland rain forest (Bilsa, 0°21′ N 79°44′ W, 450–650 m a.s.l.) and Andean cloud forest (Otonga, 0°25′ S 79°01′ W, 1650–2250 m a.s.l.).

Methods The epiphytic vegetation of 220 study plots was surveyed. Distribution data based on herbarium specimens were compiled for all identified species in order to estimate their geographical and elevational ranges as well as the climatic conditions within the species' ranges. These range characteristics were compared for species found in contiguous primary forests, primary forest fragments, secondary forests, and for isolated remnant trees in pastures.

Results Of the 587 identified epiphyte species, 252 were endemic to the Chocó ecoregion (42.9%). Chocó endemics were not more strongly affected by human land use than non-endemics. However, small geographical ranges and narrow climatic niches were associated with higher vulnerability to habitat changes caused by land use. Epiphyte assemblages in young secondary forests had the lowest proportions of range-restricted species and were dominated by species with broad elevational ranges. Species in secondary forests occupied the broadest ranges of mean annual temperature and precipitation; species on isolated remnant trees at the lowland site inhabited on average warmer and drier geographical ranges than species in the primary forest.

Main conclusions Epiphyte species with restricted geographical distributions and narrow climatic tolerances are particularly vulnerable to human-induced habitat changes, but endemism to national or biogeographical entities alone is a poor indicator of vulnerability. Instead, narrower ecological niches correlate with lower plasticity towards changes in microclimatic habitat conditions. Besides a higher extinction risk due to their small range sizes, many range-restricted species might be threatened by their lower tolerance to the impacts of human land use.

Keywords

Biodiversity, cloud forest, deforestation, Ecuador, endemism, forest fragment, isolated remnant tree, primary forest, secondary forest, tropical rain forest.

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INTRODUCTION

Human land use is currently the most important threat to biodiversity (Pimm & Raven, 2000; Jetz *et al.*, 2007; Thuiller, 2007), especially in the tropics (Geist & Lambin, 2002; Foley *et al.*, 2005; van Vuuren *et al.*, 2006), where forests are disappearing at alarming rates (FAO, 2006). Range-restricted species are often particularly vulnerable to extinction (Lawton, 1993), and so endemism and geographical range sizes are a major focus for biogeography and conservation biology (Brown *et al.*, 1996; Davis *et al.*, 1997; Kier & Barthlott, 2001). High proportions of endemic species are an indicator of the biological uniqueness of an area (Williams *et al.*, 1996; Kier *et al.*, 2009). Continental-scale patterns of species richness are dominated by relatively few widespread species (Jetz & Rahbek, 2002; Lennon *et al.*, 2004; Kreft *et al.*, 2006). However, range-restricted species contribute considerably to overall biodiversity in the tropics (Gentry, 1986a; Stevens, 1989), especially in topographically complex areas (Hawkins & Diniz-Filho, 2006; Kreft *et al.*, 2006; Ruggiero & Hawkins, 2008).

The tropical rain forests of the northern Andes and the Chocó ecoregion constitute a globally important area of plant diversity and endemism (Myers *et al.*, 2000; Barthlott *et al.*, 2005). These forests are characterized by an extraordinarily high diversity and abundance of epiphytes (Gentry, 1986b; Gentry & Dodson, 1987a,b; Galeano *et al.*, 1998). Epiphytes make up 25% of all vascular plant species in Ecuador and 35% of the country's endemic species, for instance (Jørgensen & León-Yánez, 1999; Valencia *et al.*, 2000; Küper *et al.*, 2004). Epiphytes of the northern Andes and the Chocó are therefore a suitable model group with which to study the relationship between geographical range and vulnerability to land use in a biodiversity hotspot.

High rates of regional endemism may be linked to historical events such as mountain uplift or climatic oscillations, giving rise to the separation of populations and subsequent allopatric speciation (Cowling & Lombard, 2002; Orians & Groom, 2006). For many range-restricted species, this is probably the cause of their limited geographical distributions, but niche properties inherent to the ecology of the species themselves may also result in small ranges (Kruckeberg & Rabinowitz, 1985; Brown *et al.*, 1996; Kessler, 2002; Murray *et al.*, 2002; Pither, 2003). In general, epiphytes tend to have larger distributional ranges than closely related terrestrial species (Ibisch, 1996; Kessler, 2002). This is at least partly attributable to the higher capacity for long-distance dispersal among epiphytes (Kessler, 2002). However, restricted species ranges are also likely to be associated with narrower niche widths and lower ecological plasticity to habitat changes (Brown, 1995; Ibisch, 1996; Thuiller *et al.*, 2005).

To date, few studies have addressed the effect of human land use on the diversity of endemic plant species in a given area. Kessler (2001a) found maximum levels of endemism in habitats with intermediate levels of human disturbance. In this case, disturbance probably prevents the displacement of endemics by widespread and presumably more competitive species. However, competition is thought to play a comparatively minor role in epiphytic habitats (Nieder & Barthlott, 2001). Among terrestrial herbs, Lozada *et al.* (2008) found higher proportions of range-restricted species in less disturbed landscapes. This indicates a higher sensitivity of narrow-ranged species to human land use, at least for terrestrial plants. For epiphytes, however, the effects of anthropogenic habitat changes on range-restricted species remain unknown.

The present study analyses the relationship between geographical range size of epiphyte species and their sensitivity to habitat changes caused by human land use. Besides geographical range size, we also investigated the elevational distribution of epiphyte species and the climatic conditions within their ranges in order to relate the geographical ranges to ecological niche properties.

This study addresses three inter-related questions. (1) Are the epiphytes that are endemic to the Chocó ecoregion more sensitive to human land use than non-endemics? (2) Are epiphyte species with small range sizes more vulnerable to human land use than widespread ones? (3) Are epiphytes with narrow climatic niches more susceptible to anthropogenic habitat changes than more ecologically tolerant species?

MATERIALS AND METHODS

Study sites

Fieldwork was carried out at two study sites in north-western Ecuador about 120 km apart (Fig. 1): Bilsa and Otonga. Bilsa is situated in the lowlands of north-western Ecuador at elevations between 450 m and 650 m a.s.l (0°21′ N, 79°44′ W). Annual precipitation is between 2500 and 4000 mm, and mean annual temperature is between 23 °C and 25.5 °C (Clark, 1997; Clark *et al.*, 2006). High rainfall is complemented by relatively frequent fog cover, creating per-humid conditions (Parker & Carr, 1992; Clark, 1997) and promoting abundant epiphytic vegetation. The natural vegetation at Bilsa is dominated by non-flooded lowland rain forest with an average canopy height of between 30 and 35 m.

The second study site, Otonga, is located between 1650 and 2250 m a.s.l. on the western slopes of the Ecuadorian Andes (0°25′ S 79°01′ W). The area is characterized by a steep relief where minor landslides are common. Andean forests at this elevation receive moisture-laden winds from the Pacific Ocean, providing permanent high humidity and frequent cloud cover. According to data obtained between May 1996 and April 1997, the mean annual temperature at 2000 m a.s.l. is 15.6 °C (Nowicki, 2001). Annual precipitation during this period was 2584 mm. The natural vegetation consists of cloud forest with an average canopy height between 25 and 30 m. Due to the constantly high humidity, the abundance and diversity of epiphytes is high, especially in the primary cloud forest (Muñoz & Küper, 2001; Nowicki, 2001; Köster *et al.*, 2009).
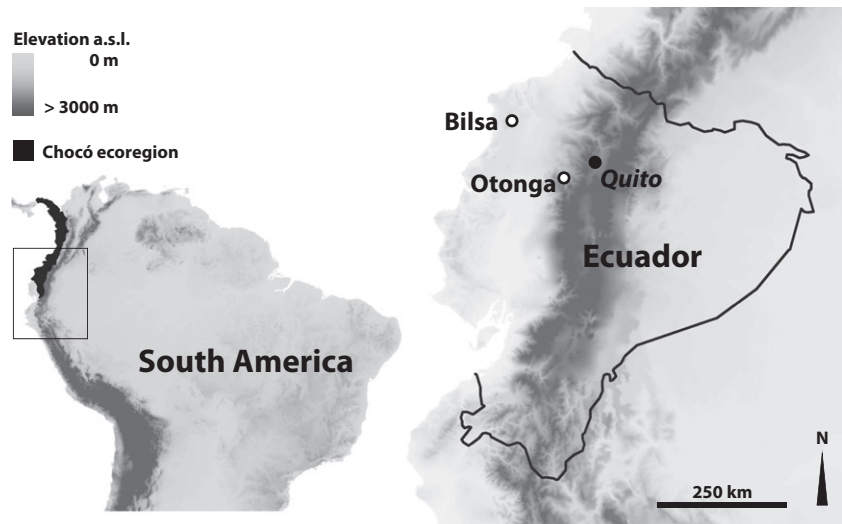
Figure 1 Location of the study sites Bilsa (450–650 m a.s.l.) and Otonga (1650–2250 m a.s.l.) in north-western Ecuador, the southernmost part of the Chocó ecoregion.

Both study sites have been colonized by settlers since the late 1960s and most of the forests have been converted into cattle pastures and sugar-cane plantations. However, considerable areas of both sites are still covered with primary forest (> 2000 ha at each study site) or have been re-covered by secondary forests. Most of the primary forests belong to the forest reserves of Bilsa and Otonga. Smaller fragments of primary forest of various sizes remain embedded in the farmland surrounding the reserves, and numerous trees were spared when the original forests were converted into pastures. Thus, the study sites represent mosaics of contiguous primary forest, primary forest fragments, secondary forest, and isolated remnant trees (IRTs) in pastures (see Figure S1 in Appendix S1, Supporting Information).

Field sampling

At each study site, 110 study plots were examined in natural and anthropogenic habitats: 25 plots in primary forests, 33 in forest fragments, 27 around IRTs in pastures, and 25 in secondary forests (Appendix S1, Tables S1–S2). These habitat types contain all the relevant epiphyte habitats at the two study sites. In this study, the term 'primary forest' is used for the large and contiguous old-growth forest tracts at each study site. The exact size of these areas is unknown due to a lack of updated aerial photographs, but it is well over 2000 ha at both sites. Forest fragments are defined as small to medium-sized remnant patches of the original forest embedded within agricultural land (0.3–23 ha). These forest patches are, however, subject to a certain degree of disturbance caused by the occasional extraction of timber and fuel wood. IRTs are also remnants of the original old-growth forest and were spared as single trees when the surrounding forest was converted into pastures. Finally, secondary forests are successional forests regenerating after complete clear-cutting (Guariguata & Ostertag, 2001). The structures and tree species compositions of these successional stages differ distinctly from primary forests and forest fragments (Guariguata et al., 1997).

The 33 forest fragment plots at Bilsa were established in seven fragments with areas between 0.4 and 23 ha, and at distances from the contiguous primary forest reserve between 321 and 1485 m. IRTs at Bilsa were found at distances from the next forest fragment of between 2 and 125 m. The IRTs grew in pastures which were about 6 years old ('young', 9 plots) or in pastures older than 10 years ('old', 18 plots). Secondary forests at Bilsa were about 12 years old ('young', 15 plots) or at least 20 years old ('old', 10 plots). At Otonga, the 33 forest fragment plots were established in 14 different fragments, with areas ranging from 0.3 to 13.5 ha and distances to the contiguous primary forest reserve between 20 and 2360 m. IRTs were located at distances to the next forest fragment between 11 and 195 m. Seven of the 27 IRTs were located in pastures cleared about 6 years ago ('young') and 20 in pastures older than 10 years ('old'). Secondary forests at Otonga were classified as about 10 years old ('young', 13 plots) or at least 24 years old ('old', 12 plots). The age of secondary forests and pastures in Otonga was determined by comparing the current vegetation cover to an aerial photograph taken in 1981 (Instituto Geográfico Militar del Ecuador, Quito) and by interviews with community members. For Bilsa, no aerial photographs were available; thus, data on pasture and secondary forest age follow the information given by landowners.

Study plots (modified after Gradstein et al., 2003) were each established around one main host tree that occupied the upper canopy with d.b.h. (diameter at breast height, i.e. 1.30 m) ≥ 25 cm and height ≥ 15 m that belonged to one of the common tree species within the study site. This main phorophyte was completely sampled for vascular epiphyte species using single-rope climbing techniques and/or binoculars (Perry & Williams, 1981; Dial & Tobin, 1994). The sampling included holoepiphytes and primary hemiepiphytes (Benzing, 1990), but not secondary hemiepiphytes, which were difficult to distinguish from vines and root creepers.

To also include epiphyte species confined to the lowermost forest stratum (Mehltreter et al., 2005; Krömer et al., 2007;

Zotz, 2007), an area of 20 m × 20 m around the main phorophyte was examined for the occurrence of additional species (Gradstein *et al.*, 2003). All epiphyte species occurring on trees with d.b.h. ≥ 10 cm up to a height of 2 m above the ground were recorded. To ensure comparability of IRTs in pastures, the 22 (Bilsa) or 25 (Otonga) trees with d.b.h. ≥ 10 cm closest to the IRTs were examined. This corresponds to the mean number of trees in the study plots of the primary forests.

The inventories for the entire study sites of Bilsa and Otonga were compiled, including epiphyte species found inside the 110 study plots at each site as well as species collected on fallen trees and along trails outside these plots.

Epiphyte identification

Specimens were identified by comparison with material at the herbarium of the Pontificia Universidad Católica del Ecuador (QCA) and the Herbario Nacional del Ecuador (QCNE), both in Quito. Identifications were checked by T.B. Croat (Araceae) and H. Navarrete (ferns). A complete set of specimen vouchers was deposited at QCA (Köster Nos 1–2382), with additional duplicates at the herbaria of Missouri Botanical Garden (MO), New York Botanical Garden (NY), and QCNE. Species names and family classification mostly follow the *Catalogue of the Vascular Plants of Ecuador* (Jørgensen & León-Yánez, 1999). They were amended according to the *Tropicos* database housed at the Missouri Botanical Garden (http://www.tropicos.org/) when indicated by recent taxonomic changes (Appendix S2).

Biogeographical data and analysis

For the biogeographical evaluation of the epiphyte communities, distribution data were compiled for all 587 species that could be reliably identified (84.3% of the 696 morphospecies present at both study sites; see Fig. 2 and Appendices S2–S3). In order to assign distributional ranges to all identified species, georeferenced collection localities for each species were gathered from herbarium specimen data provided online by *Tropicos* (Missouri Botanical Garden), the *AAU Herbarium Database* (University of Aarhus Herbarium), the *C.V. Starr Virtual Herbarium* (New York Botanical Garden), and the *Global Biodiversity Information Facility* (http://www.gbif.org/). Geographical coordinates and, where available, elevation information were extracted and checked for the Neotropical portion of species' ranges. The resulting database comprises more than 35,000 individual plant collections from the Neotropics. On average, 60.2 (± 94.8 SD) records per species were available, ranging from a single collection (for 46 species) to a maximum of 575 collections per species (Appendix S3). The frequency distribution of records per species was distinctly right-skewed, with most species represented by relatively few collections (median = 21).

Two approaches to measure endemism were applied in this study (cf. Petersen & Watson, 1998). First, as a discontinuous measure, species restricted to the Chocó ecoregion were classified as endemic. We defined this biogeographical entity in a broad sense, comprising the WWF ecoregions 'Chocó–Darién moist forest' and 'western Ecuador moist forest' as well as the western slopes of the Andes of Colombia and Ecuador (Fig. 1; Olson *et al.*, 2001). This included nine species occasionally also found on the eastern slopes of the north Ecuadorian Andes. But in spite of a few records in the eastern Andes, these species showed a distinct centre of distribution in the Chocó ecoregion and were restricted to the national territory of Ecuador (following Jørgensen & León-Yánez, 1999; Valencia *et al.*, 2000), and were therefore included as endemics in the analysis.

Second, as a continuous measure for endemism in a wider sense, the geographical range size in terms of the number of occupied 0.5° grid cells was determined for each species (cf. Kessler, 2001a). For this purpose, the georeferenced collection records were assigned to 0.5° grid cells using ArcGIS (ESRI, Redlands, CA, USA). These medium-sized grid cells allow for a trade-off between high accuracy and informative value regarding the size of the species ranges.

The estimated range sizes are nonetheless subject to a certain degree of bias due to factors such as varying data quality, collection intensity, georeferencing errors and incorrect voucher identification in herbaria. Range sizes of species represented by very few collections are probably mostly underestimated, but the ranges of many widespread species may also be underestimated due to extensive sampling gaps in the Brazilian part of the Amazon Basin, for example (cf. Fig. 2). In order to check for this effect of collection intensity on calculated range sizes, we compared the number of occupied 0.5° grid cells for each species with its overall latitudinal and longitudinal extent (as the square root of the product of the latitudinal extent and the longitudinal extent), a measure that is less susceptible to sampling gaps (cf. Gaston & Fuller, 2009). The strong positive correlation ($r^2 = 0.70$; $P < 0.001$) between both measures indicates that the number of 0.5° grid cells occupied by a species is indeed a suitable variable to estimate its range size. Apart from this, there is no reason why the assumed bias in calculating the range sizes should take effect differently amongst habitat types.

An endemism index was calculated as the reciprocal of the number of 0.5° grid cells occupied by a species, giving the highest values to the species with the smallest range sizes (Williams *et al.*, 1996; Kessler, 2001a; Müller *et al.*, 2003). For each of the 220 study plots, the values of this endemism index for all identified species found in the respective plot were summed to give a 'range-size rarity' for the plot. This metric combines endemism and species richness and allows for a higher weighting of narrow-ranged species (cf. Usher, 1986; Fjeldså & Rahbek, 1997; Kessler, 2001b; Kier & Barthlott, 2001; Kier *et al.*, 2009).

For all identified species, the elevational range and the centre of elevational distribution (following Kreft *et al.*, 2004) were calculated. The centre of elevational distribution weights the absolute elevational range as well as the mean elevation of collections for each species (Hengeveld & Haeck,
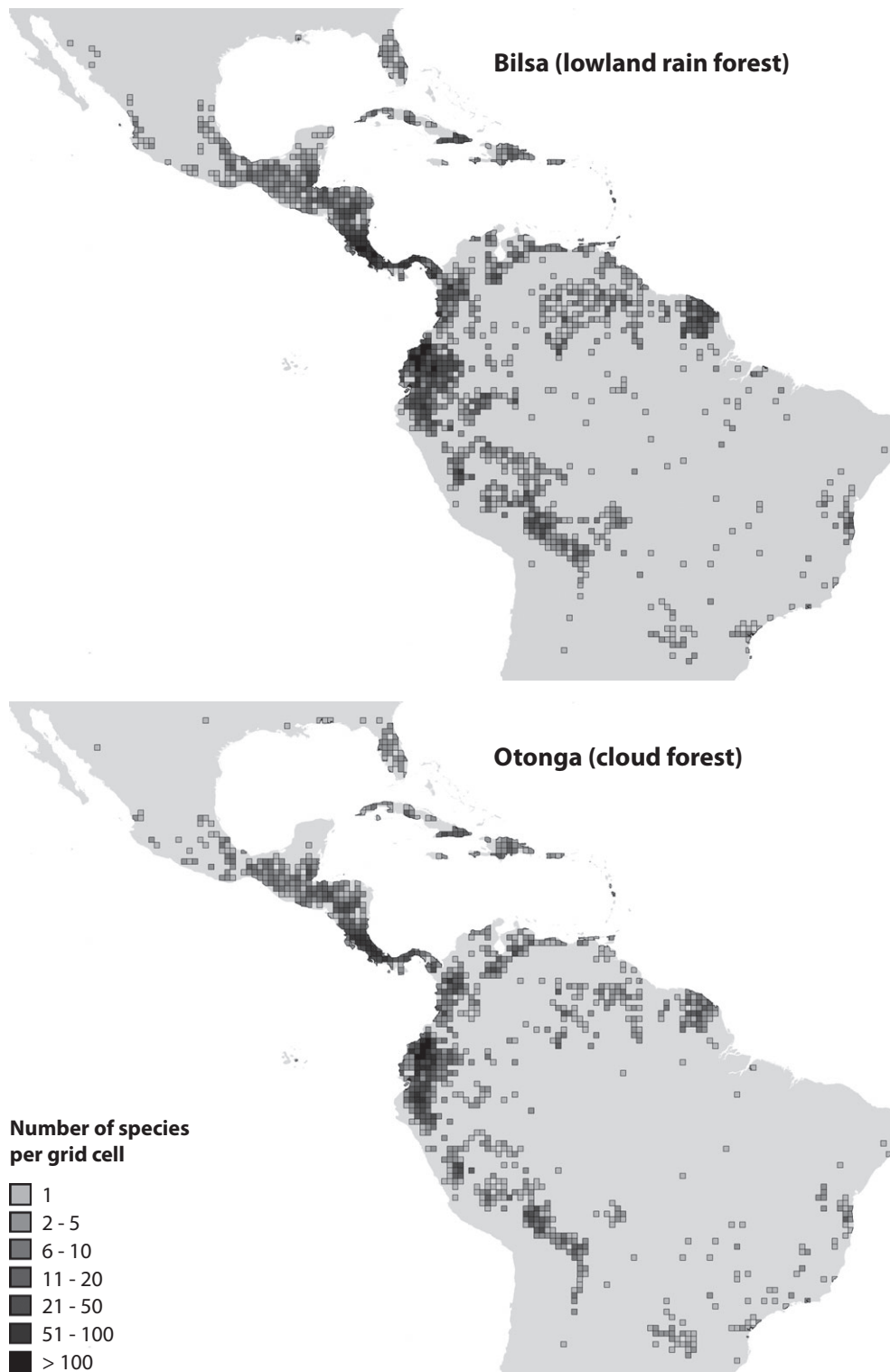
Figure 2 Neotropical distribution of epiphyte species found at the study sites of Bilsa (340 identified species) and Otonga (315 identified species). Grey-scale values of the 0.5° grid cells correspond to the number of species documented in the respective grid cells.

1982). For species with few collection records, minimum and maximum elevation were complemented with information provided by the *Catalogue of the Vascular Plants of Ecuador* (Jørgensen & León-Yánez, 1999). In order to avoid an

underestimation of rarely collected species not included in the catalogue, a minimum elevational range of 200 m for lowland species and 600 m for montane species was assumed according to the elevational ranges of the study sites them-

selves (cf. Ibisch *et al.*, 2002). Analogously to the endemism index, elevational range restriction was calculated as the reciprocal of the elevational range, resulting in high values for species with narrow elevational ranges.

To assess climatic conditions at the collection localities of the species, values of climatic variables for 10-arcminute grid cells were assigned to these record localities using ArcGIS. Mean annual temperature, precipitation, and number of wet days per year (with precipitation > 0.1 mm) were inferred from the global high-resolution climate data set CRU CL 2.0 (New *et al.*, 2002), and annual potential evapotranspiration (PET) was taken from data generated by the FAO (2004; calculated using the Penman–Monteith equation). For each species, the ranges of mean annual temperature and precipitation (i.e. the difference between the highest and the lowest values at the record localities of that species) were computed. Additionally, out of all record localities of a given species, the maximum values of annual PET and the minimum number of wet days per year were determined.

Values of the variables describing geographical and elevational ranges as well as climatic characteristics were calculated for each species and averaged for all species found in a study plot. For both study sites, the effect of habitat type on these biogeographical attributes of the epiphyte community was determined by performing analyses of variance (ANOVA). Where necessary, assumptions of normality and homogeneity of variance were ensured through log-transformation of the data. Pairwise differences between habitat types were detected using Tukey's honestly significant difference (HSD) tests. All statistical analyses were carried out with STATISTICA 7.0 (StatSoft, Tulsa, OK, USA).

RESULTS

The total numbers of epiphyte species were virtually identical at Bilsa (381) and Otonga (383), and they combined to a total of 696 species, revealing a substantial level of species turnover between sites. Of the 587 identified species at the two study sites, 252 (42.9%) were classified as endemics, i.e. they had documented distributions restricted to the Chocó ecoregion (Fig. 1; Appendices S2–S3). Of these 252 species, only 95 (37.7%) are listed in the Red List of Ecuador (Valencia *et al.*, 2000) as endemic to the country. At Bilsa, 141 of 340 identified species were classified as endemics (41.5%), of which 45 are given in the Red List. Endemism was similarly high at Otonga, with 130 of the 315 identified species (41.3%) being endemic according to the applied classification and 55 species included in the Red List.

Chocó endemics

A total of 220 Chocó endemics were found within the study plots at Bilsa and Otonga. Of the 122 endemic species in the 110 study plots at Bilsa, 12 were restricted to a single habitat type (six endemic species restricted to primary forest, two to forest fragments, three to IRTs, and one to secondary forests). Of these species, only *Anthurium lygrum* (found in 11 study plots) and *Pleurothallis claviculata* (5 study plots) were reasonably common, both exclusive to the primary forest. At Otonga, 18 of the 113 endemic species found in the 110 study plots were restricted to a single habitat type (six confined to primary forest, five to forest fragments and seven to IRTs). None of these species was found in more than three plots.

Mean proportions of Chocó endemics per study plot differed significantly between habitat types at Bilsa (Fig. 3; ANOVA; $F_{5,104} = 9.58$, $P < 0.001$) but not at Otonga. Unexpectedly, young secondary forests at Bilsa had the highest proportion of endemics (47.7%) and were significantly different from all other habitat types except old secondary forests. The lowest proportion of endemics at Bilsa was found
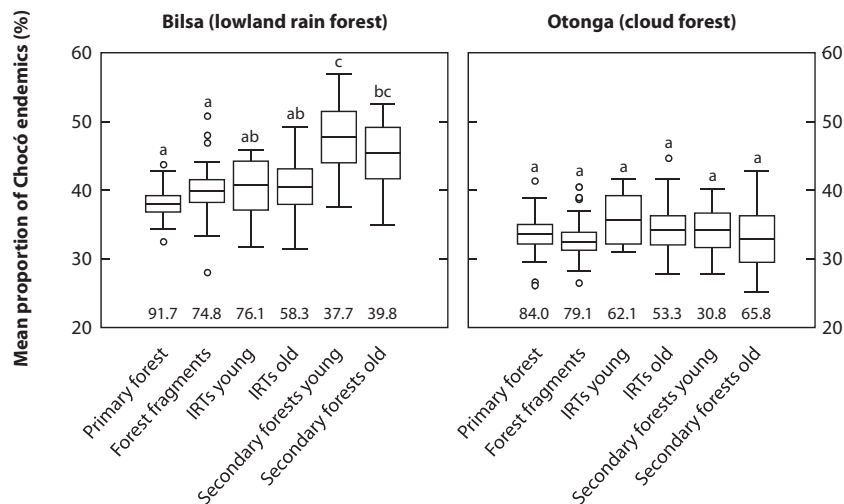
Figure 3 Box–whisker plots of mean proportion of Chocó endemic epiphytes per study plot for different habitat types at Bilsa and Otonga. Letters indicate differences significant at *P* < 0.05 (Tukey's HSD test). Boxes: 95% confidence intervals; whiskers: non-outlier ranges; circles: outliers; numbers beneath the box–whisker plots are mean species numbers per study plot; IRTs: isolated remnant trees.

in the primary forest (38.0%) and on IRTs in young pastures (39.9%). At Otonga, the proportion of endemics varied only slightly, from 32.4% in young secondary forests to 35.5% on IRTs in young pastures (ANOVA; $F_{5,104} = 0.95$, $P = 0.452$).

Geographical range size

Throughout the Neotropics, the species identified at Bilsa and Otonga were documented within a total of 1397 grid cells (Fig. 2). Species at Bilsa jointly occupied 1271 grid cells, averaging 38.9 (± 51.4 SD) grid cells per species. Species at Otonga occurred in 997 grid cells, with a mean of 27.0 (± 40.7 SD) grid cells per species. The species with the largest ranges were *Asplenium serratum* (290 grid cells), *Syngonium podophyllum* (267), *Ficus pertusa* (257) and *Blechnum occidentale* (253). In contrast, 47 species were documented from only a single grid cell.

Endemism indices per study plot were on average lower at Bilsa than at Otonga (Fig. 4a). They differed significantly between habitat types at both Bilsa (ANOVA; $F_{5,104} = 7.76$, $P < 0.001$) and Otonga ($F_{5,104} = 7.04$, $P < 0.001$). At both study sites, mean endemism indices were lowest in young secondary forests (0.08 at Bilsa and 0.11 at Otonga). While the highest values at Bilsa were found in the primary forest (0.12), the mean endemism index at Otonga was highest in old secondary forests (0.17). Mean range-size rarity per study plot was also lower at Bilsa (Fig. 4b; 6.55 ± 3.42 SD) than at Otonga (9.47 ± 3.51 SD). Again, mean range-size rarity differed significantly between habitat types at both Bilsa (ANOVA; $F_{5,104} = 24.5$, $P < 0.001$) and Otonga ($F_{5,104} = 23.0$, $P < 0.001$), with the lowest values in young secondary forests (3.1 and 3.2, respectively). Mean range-size rarity was highest in primary forest plots at both study sites (10.4 at Bilsa and 11.2 at Otonga). However, values for old secondary forests at Bilsa (3.5) equalled those of young secondary forests, while old secondary forests at Otonga (10.5) featured only slightly lower range-size rarity than primary forest.

Elevational distribution

As expected, species found at the lowland study site Bilsa had, on average, a much lower centre of elevational distribution (891 m a.s.l. ± 380 SD) than species from the montane site at Otonga (1686 m a.s.l. ± 488 SD). At both study sites, mean centres of elevational distribution per study plot differed significantly among habitat types (Fig. 4c; ANOVA; Bilsa: $F_{5,104} = 4.32$, $P = 0.001$; Otonga: $F_{5,104} = 10.03$, $P < 0.001$). At Bilsa, primary forest species had on average the highest centre of elevational distribution (937 m a.s.l.), whereas species found on IRTs in old pastures (874 m a.s.l.) and young secondary forests (889 m a.s.l.) showed the lowest elevational distribution. Young secondary forests at Otonga had also the lowest centres of elevational distribution (1625 m a.s.l.). Species found on IRTs in young pastures (1779 m a.s.l.) and in old secondary forests (1773 m a.s.l.) showed the highest elevational distribution.

Species found at Bilsa were confined to narrower elevational ranges than species from Otonga and therefore had a higher mean elevational range restriction value (Fig. 4d; 0.93 km^{-1} ± 0.97 SD compared to 0.71 km^{-1} ± 0.50 SD). Species in young secondary forests were least restricted in their elevational ranges and differed significantly from the more limited species in primary forests and forest fragments at Bilsa (ANOVA; $F_{5,104} = 4.21$, $P = 0.002$) as well as Otonga ($F_{5,104} = 9.56$, $P < 0.001$).

Climatic range characteristics

On average, species found at the lowland site Bilsa had narrower temperature ranges, higher maximum ambient energy (measured as PET) and broader precipitation ranges within their geographical distributions than species from Otonga, but virtually the same minimum number of wet days per year (Table 1). At Bilsa, young and old secondary forests harboured species with significantly broader ranges of mean annual temperature (ANOVA; $F_{5,104} = 7.06$, $P < 0.001$) and precipitation ($F_{5,104} = 6.52$, $P < 0.001$) than primary forest species. Together with species on IRTs in old pastures, they also tolerated significantly lower numbers of wet days per year within their geographical range than primary forest species ($F_{5,104} = 3.94$, $P = 0.003$). Maximum annual PET was on average highest within the ranges of species found on IRTs in old and young pastures ($F_{5,104} = 3.66$, $P = 0.004$), indicating a dominance of species adapted to higher ambient energy in these habitat types at Bilsa. In contrast, patterns at Otonga were more diffuse. Young secondary forests contained species with the broadest ranges of mean annual temperature (ANOVA; $F_{5,104} = 11.4$, $P < 0.001$) and precipitation ($F_{5,104} = 17.4$, $P < 0.001$) within their distribution. In addition, young secondary forest species experienced the lowest numbers of wet days per year throughout their range ($F_{5,104} = 9.40$, $P < 0.001$) and occurred in areas with the highest maximum PET ($F_{5,104} = 8.26$, $P < 0.001$). In contrast to species at Bilsa, species on IRTs at Otonga exhibited the narrowest temperature and precipitation ranges.

DISCUSSION

The epiphyte floras at Bilsa and Otonga are extremely species-rich and have high proportions of range-restricted species. More than 40% of the identified species were classified as endemics to the Chocó ecoregion, but only 16% are included in the Red List of endemic species of Ecuador (Valencia *et al.*, 2000). Although the concept of endemism is usually based either on natural geographical features or on human political boundaries (Petersen & Watson, 1998), it is evident that the former are more likely to bound areas defined by a particular biogeographical history and, thus, to harbour species equally confined to these areas (Brooks *et al.*, 2006). In contrast, endemism to a national territory is likely to be less significant for assessing the biological
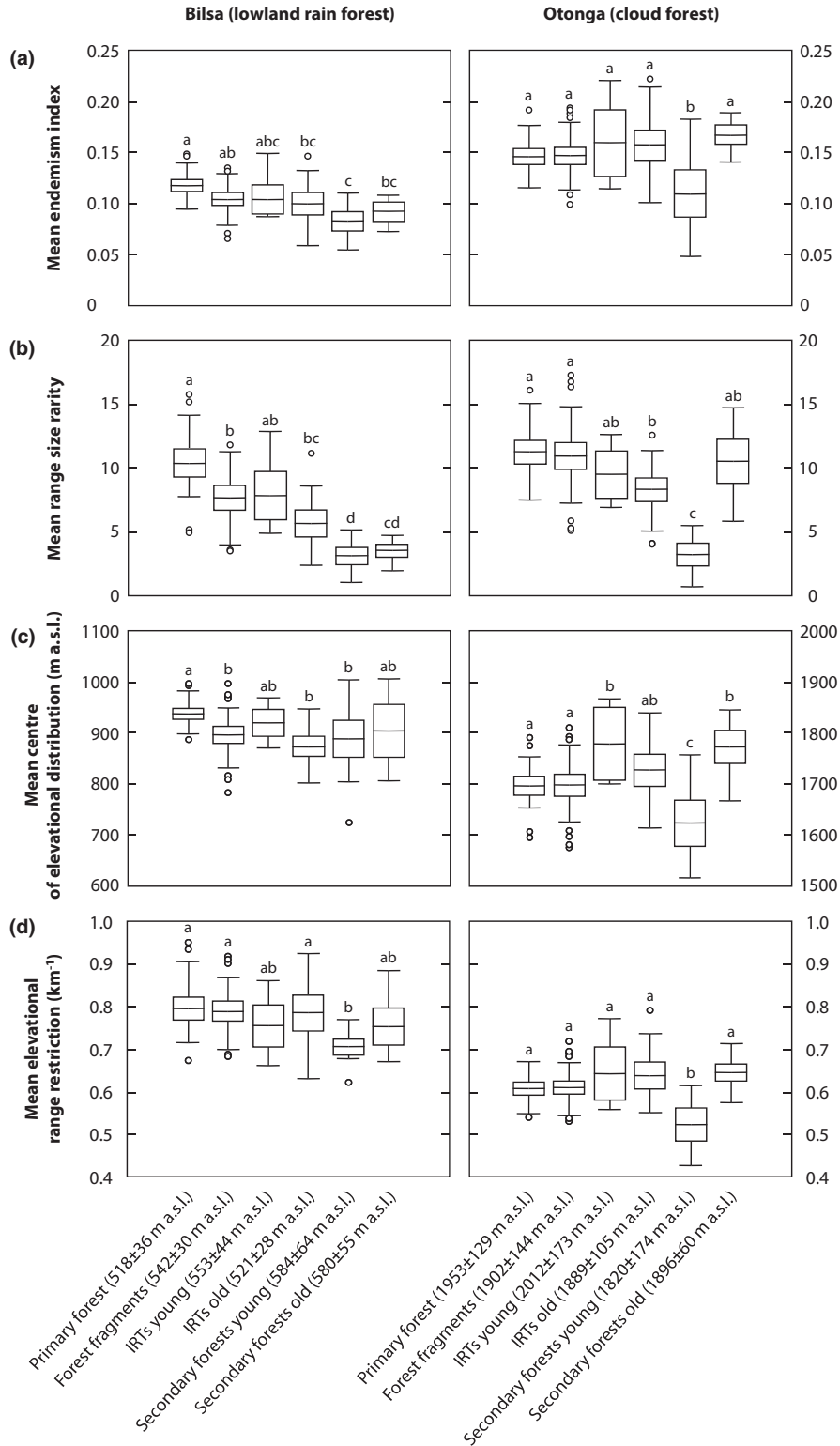
Figure 4 Box–whisker plots of (a) mean endemism index, (b) mean range-size rarity, (c) mean centres of elevational distribution, and (d) mean elevational range restriction for the epiphyte species found in study plots of different habitat types at Bilsa and Otonga. Endemism index is defined as the inverse number of 0.5° grid cells occupied by a species, averaged for all species found in a study plot. Range-size rarity is the sum of the endemism indices for all species found in a study plot and therefore represents a combination of endemism and species richness. The centre of elevational distribution (following Kreft *et al.*, 2004) weights the absolute elevational range as well as the mean elevation of collections for each species. Letters indicate differences significant at $P < 0.05$ (Tukey's HSD test). Boxes: 95% confidence intervals; whiskers: non-outlier ranges; circles: outliers; IRTs: isolated remnant trees. Note the different scaling of the centre of elevational distribution for the two study sites. Numbers following the habitat types give the elevation of the respective study plots (mean ± standard deviation).

uniqueness of species communities: this is supported by the low proportion of species endemic to Ecuador in our study.

Chocó endemics

Chocó endemics were generally no more sensitive to anthropogenic habitat transformations than non-endemic species. On the contrary, secondary forests at Bilsa harboured even higher proportions of endemics than other habitat types (Fig. 3). This is probably due to the taxonomic composition of the epiphyte communities in secondary forests: especially in the lowland rain forest at Bilsa, they are dominated by Araceae, which exhibit extraordinarily high rates of endemism in the Chocó (T.B. Croat, Missouri Botanical Garden, pers. comm.). In any case, endemism to the Chocó ecoregion is not necessarily associated with lower ecological plasticity and therefore greater vulnerability to human-induced habitat changes. Species that are confined to a particular ecoregion due to its biogeographical history can in fact be highly plastic regarding their ecological requirements.

Geographical range size

In accordance with the higher floristic turnover between montane epiphyte floras compared to lowland floras (cf. Küper et al., 2004), epiphyte species found at the lowland site Bilsa had larger geographical ranges than at the Andean study site at Otonga. This also confirms the findings of Kessler (2001b), who found higher endemism of epiphytic bromeliads and ferns at higher elevations of the Bolivian Andes. The fact that this outcome is consistent with trends reported from other Neotropical studies suggests that our approach using occupied 0.5° grid cells and based on herbarium data is suitable for estimating range sizes, the potential biases discussed in the Materials and Methods notwithstanding.

Epiphytes with small range sizes were more sensitive to some forms of anthropogenic habitat transformation than widespread species. At least in young secondary forests, range-restricted species were under-represented (Fig. 4a). Range-size rarity – a variable combining the number and the geographical range sizes of the species in a study plot – was highest in the primary forests. It was lowest in young secondary forests, indicating their low capacity to maintain epiphyte diversity, especially of range-restricted species. This seems to contradict the proportions of Chocó endemics in this habitat. However, although endemism to the Chocó ecoregion is principally a consequence of the biogeographical history of this area (cf. Orians & Groom, 2006), restricted range sizes may also be an outcome of the narrow ecological niches of the species themselves (Kessler, 2002; Murray et al., 2002). This is in accordance with the higher proportions of range-restricted terrestrial herbs found in less disturbed landscapes by Lozada et al. (2008). It also points to an important difference between epiphytes and terrestrial plants: in plant communities characterized by high levels of interspecific competition, habitat disturbance induced by human land use

might favour competitively inferior species and might thus increase endemism (Kessler, 2001a). However, due to frequent natural disturbances within their habitat, epiphyte communities experience considerably lower levels of interspecific competition (Ibisch, 1996; Nieder & Barthlott, 2001). Thus, range-restricted epiphytes are not favoured by anthropogenic disturbance, and due to their narrower ecological tolerance they are even more vulnerable to habitat changes caused by human land use.

Elevational distribution

In line with the elevations of the study sites themselves, the epiphyte communities at Bilsa and Otonga are dominated by species with lowland and montane distributions, respectively. However, as in Amazonian rain forests near the Andes (Kreft et al., 2004), the average centre of elevational distribution of the species from Bilsa is distinctly higher than the study site itself. Due to the special climatic conditions at Bilsa, a considerable proportion of its flora consists of species with a predominant distribution in cloud forests (Parker & Carr, 1992; Clark, 1997). Many of these species at Bilsa probably grow at their ecological limits, requiring the perhumid habitat conditions found only in the interior of the primary forest, reflected by the higher mean elevational distribution of primary forest assemblages (Fig. 4c).

The patterns of mean elevational range restriction in different habitat types essentially reflect the patterns of geographical range size in terms of mean endemism index and range-size rarity. Again, young secondary forests are dominated by species with broader elevational ranges, indicating higher ecological tolerances. Young secondary forests appear to be less suitable for species with narrow ecological niches, probably due to the lack of several microhabitats that allow many habitat specialists to occur (Krömer & Gradstein, 2003).

In addition to greater ecological tolerances, dispersal limitations can be expected to play an important role in the ability of species to colonize secondary forests and, thus, to shape the composition of the epiphyte communities of these habitats. As also shown for early-successional woody vegetation in the Neotropics (Uhl, 1987), the importance of epiphytes dispersed by bats and other mammals was highest in the young secondary forests of our study (N. Köster, unpublished data). However, range sizes of Neotropical forest species tend to be largest for wind-dispersed species, intermediate for species with a characteristic bird dispersal syndrome, and smallest for apparently mammal-dispersed species (Gentry, 1983). Therefore, the higher small-scale dispersal ability of species in young secondary forests does not obviously account for their larger geographical range sizes and broader elevational ranges.

Climatic range characteristics

Epiphytes with narrower climatic niches were more vulnerable to anthropogenic habitat changes than more ecologically

Table 1 Mean values of climatic range characteristics for the epiphyte species found in study plots of different habitat types at Bilsa and Otonga in north-western Ecuador.

Habitat type	*n*	Range of mean annual temperature (°C)	Maximum PET (mm yr^{-1})	Range of mean annual precipitation (mm yr^{-1})	Minimum number of wet days per year
Bilsa					
Primary forest	25	11.97 ± 0.32 a	1453.0 ± 16.2 a	4017.3 ± 116.1 a	117.3 ± 3.5 a
Forest fragments	33	12.21 ± 0.52 a	1463.0 ± 23.6 ab	4121.0 ± 234.7 a	115.4 ± 4.6 ab
IRTs young	9	12.46 ± 0.39 ab	1472.6 ± 20.0 ab	4201.4 ± 213.4 ab	114.8 ± 3.3 ab
IRTs old	18	12.34 ± 0.64 ab	1480.1 ± 24.1 b	4221.3 ± 234.8 ab	112.2 ± 5.1 b
Secondary forests young	15	12.69 ± 0.75 b	1453.2 ± 33.2 a	4343.9 ± 342.5 b	112.7 ± 7.8 b
Secondary forests old	10	12.93 ± 0.30 b	1462.8 ± 22.2 ab	4406.6 ± 230.9 b	111.6 ± 3.7 b
Total	110	12.33 ± 0.59	1463.0 ± 24.8	4176.8 ± 257.7	114.5 ± 5.2
Otonga					
Primary forest	25	13.69 ± 0.55 ab	1421.3 ± 17.7 a	3570.5 ± 143.5 a	117.0 ± 3.1 a
Forest fragments	33	13.84 ± 0.65 b	1435.4 ± 22.1 a	3527.7 ± 199.8 a	114.4 ± 4.1 a
IRTs young	7	13.11 ± 0.57 ab	1416.6 ± 19.5 a	3242.2 ± 216.9 a	117.4 ± 4.6 a
IRTs old	20	13.17 ± 0.73 a	1427.8 ± 26.0 a	3232.0 ± 208.5 b	115.2 ± 5.3 a
Secondary forests young	13	14.91 ± 1.20 c	1467.4 ± 44.0 b	3868.1 ± 368.1 c	106.2 ± 9.5 b
Secondary forests old	12	13.47 ± 0.32 ab	1413.1 ± 17.8 a	3404.7 ± 127.6 ab	116.8 ± 2.9 a
Total	110	13.72 ± 0.85	1431.0 ± 28.8	3492.3 ± 280.9	114.6 ± 5.9

Climatic variables refer to the values for all occupied grid cells within the Neotropical range of each species, averaged for all species of a study plot and for all study plots of a habitat type. Numbers given are averages ± standard deviation. Letters indicate differences significant at $P < 0.05$ (Tukey's HSD test). *n*: sample size; PET: potential evapotranspiration using the Penman-Monteith equation; IRTs: isolated remnant trees.

tolerant species. The geographical range and climatic requirements of a given species are tightly connected (Brown, 1995; Pither, 2003). However, the realized climatic niche space of a species describes its ecological tolerances much more directly than mere geographical range size. Epiphytes in particular depend strongly on sufficient and continuous water supply (Kreft *et al.*, 2004). The ecological tolerance to climatic conditions was on average highest in secondary forests, with species also having lower numbers of wet days combined with higher ambient energy (measured as PET) throughout their geographical ranges (Table 1). Epiphytes in young secondary forests at the montane site Otonga had mean PET maxima as high as at the lowland site Bilsa. Thus, the influence of microclimatic differences between habitat types can even exceed that of differences in local climate. The broader ecological niches of epiphytes in secondary forests point to a filtering of species due to the less favourable microclimatic conditions compared to primary forests, as proposed by Krömer & Gradstein (2003). In secondary forests, epiphytes are mainly represented by early successional species that are able to establish before canopy soil and epiphytic bryophyte cover have developed (Krömer & Gradstein, 2003). These early colonizer species need to have an especially high ecological tolerance, because climatic fluctuations are not compensated by canopy soil or epiphytic mosses and liverworts (Nadkarni, 1984; Freiberg, 1997; Zotz & Vollrath, 2003). This microclimatic plasticity of secondary forest epiphytes is also reflected in the macro-scale association of the species with climate.

IRTs in pastures are likely to exhibit the strongest differences from primary forests in microclimate (Werner *et al.*, 2005; Werner & Gradstein, 2008). Accordingly, epiphyte communities of IRTs at the lowland site Bilsa were distinctly shaped by microclimatic constraints due to higher temperatures and lower humidity outside the closed forest: species on IRTs at Bilsa had the highest PET maxima within their overall geographical ranges, a pattern that was reflected by a high proportion of drought-tolerant species in this habitat type (N. Köster, unpublished data). In the cloud forest area of Otonga, the microclimatic constraints on IRTs are, in contrast, buffered by the generally high humidity, with fog occurring daily from midday onwards.

Implications for conservation

Epiphyte species with restricted geographical distributions and narrow climatic tolerances are particularly vulnerable to human land use. In addition to higher extinction risks due to their small range sizes, many endemic epiphytes might also be threatened by lower ecological plasticity towards the impacts of land use. However, applying the concept of endemism for assessing the conservation value of biological communities must be done cautiously, and only after careful selection of the area of reference. Especially in cases like the Chocó ecoregion, which crosses national boundaries, endemism to a national territory (as applied for setting conservation priorities in, e.g. Plantlife International, 2004) is of little significance concerning the biological uniqueness of an area (cf. Brooks *et al.*, 2006), but even a biogeographical entity like the Chocó might be circumscribed too broadly to express the singularity of its biota. The rain forests of western Ecuador exhibit high numbers of endemic species, which are in some cases restricted to extraordinarily small areas (Dodson & Gentry, 1991). The range-restricted epiphytes of this area are more vulnerable to anthropogenic

habitat transformation than widespread species. However, the vulnerability to human land use is associated with low ecological plasticity and small geographical ranges and not necessarily with endemism to the Chocó ecoregion.

Microclimate acts as an important ecological filter shaping the species composition of epiphytes in anthropenically transformed habitats (Köster *et al.*, 2009; Werner & Gradstein, 2009). Epiphyte assemblages of IRTs and secondary forests are therefore not a random sample of the natural species pool in primary forests. Many species with narrow ecological niches are likely to disappear in anthropenically transformed landscapes. This is reflected by the macroclimatic and geographical distribution patterns of epiphyte communities in different habitat types. Vulnerability assessments based on microhabitat requirements for individual species are extremely time-consuming for species-rich communities. However, taking the potential bias discussed in the Materials and Methods into account, the climatic variability within the geographical range of a given species might provide valuable indications of its ecological plasticity towards habitat changes and, thus, of its vulnerability to human land use.

The disproportionate loss of range-restricted species in anthropenic habitats is evidence of the great importance of protected areas for epiphyte conservation. Geographical species ranges are largely shaped by macroclimate, but local species occurrence is, at least in part, determined by microclimatic habitat conditions. Many rare epiphyte species depend on the perhumid microclimate of intact primary forests, and the buffering effects of large primary forest areas will be even more important under future climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Maps of the study areas at Bilsa and Otonga, and details of the 110 plots at each study site.

Appendix S2 Range sizes and climatic niches of the 587 identified epiphyte species from Bilsa and Otonga.

Appendix S3 Distribution maps of the 587 identified epiphyte species from Bilsa and Otonga.

BIOSKETCH

Nils Köster is scientific curator of the tropical and subtropical living collections at the Botanic Garden and Botanical Museum Berlin-Dahlem, Freie Universität Berlin. He is interested in the taxonomy and systematics of Neotropical Araceae, and in the diversity, biogeography, and ecology of Neotropical epiphytes. He did his doctorate in the former Epiphyte Project Group at the University of Bonn, headed by Wilhelm Barthlott and the late Jürgen Nieder. This manuscript is part of Nils Köster's dissertation, which investigates tropical epiphyte diversity under human impact by comparison of primary forests, secondary forests, and forest fragments in Ecuador. The biogeographical analyses of this project were conducted in collaboration with Holger Kreft, now professor at the University of Göttingen.

Author contributions: J.N. and W.B. conceived the initial ideas of the study; N.K. designed the research and collected the data; H.K. and N.K. analysed the data; N.K. wrote the paper.

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