DIVERSITY OF VASCULAR EPIPHYTES ON ISOLATED REMNANT TREES IN THE MONTANE FOREST BELT OF SOUTHERN ECUADOR

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Abstract. We studied the diversity of vascular epiphytes on isolated remnant trees of pastures in southern Ecuador. The objective of this study was to document the importance of remnant trees for the survival of vascular epiphytes following forest clearance. Twenty-one canopy trees (15 remnant trees, 6 forest trees) were divided into five zones following Johansson (1974) and climbed with the single rope technique. Recorded parameters include floristic composition, species richness, abundance, and spatial distribution of epiphytes. Bromeliaceae, Orchidaceae, Piperaceae and Polypodiaceae were relatively well represented on remnant trees in terms of species richness and abundance, whereas other families such as Dryopteridaceae, Ericaceae, Grammitidaceae or Hymenophyllaceae were poorly represented or absent. Diversity, species richness, and abundance of epiphytes were significantly lower on remnant trees compared with forest trees. Impoverishment was greatest on the stem base and in the outer crown, and least in the inner crown of the host trees. We postulate that microclimatic changes and increased drought stress following the isolation of the remnant trees resulted in lowered rates of establishment and survival of vascular epiphytes.

Resumen. Estudiamos la ecología y diversidad de epífitas vasculares en árboles remanentes aislados, en potreros en la estribación oriental de los Andes del Ecuador. El objetivo de este estudio fue documentar la importancia de los árboles remanentes en la sobrevivencia de plantas epífitas vasculares despues del clareo del bosque. Veintiún árboles de dosel (15 árboles remanentes y 6 árboles de bosque) fueron divididos en 5 zonas de acuerdo con Johansson (1974) y ascendidos mediante equipos de montañismo. Los parámetros colectados incluyen composición florística, riqueza de especies, abundancia y distribución espacial de epífitas. En arboles remanentes, las familias Bromeliaceae, Orchidaceae, Piperaceae y Polypodiaceae estuvieron relativamente bien representadas en cuanto a riqueza y abundacia de especies, mientras que miembros de otras familias como Dryopteridaceae, Ericaceae, Grammitidaceae ó Hymenophyllaceae demostraron una tendencia pronunciada a disminuir o desaparecer en cuanto a esas variables. La diversidad, la riqueza de especies y la abundancia de epífitas estuvieron significativamente más bajas en los arboles remanentes que en los arboles del bosque. El empobrecimiento relativo fue mucho más pronunciado en las bases del tronco y copas externas, y menor en las copas internas de los árboles. Los resultados indican una alteración del gradiente microclimático natural y un mayor estrés hídrico, resultando en menores tasas de establecimiento y supervivencia de las epífitas. *Accepted 17 March 2005.*

Key words: *deforestation, diversity, Ecuador, epiphytes, remnant trees, spatial distribution, tropical montane forest, tropical pastures.*

INTRODUCTION

Most studies on tropical forest fragmentation focus on forest fragments only, neglecting the characteristics of the surrounding habitats (Saunders *et al.* 1991). Consequently, it remains largely unknown how tropical forest organisms respond to habitat characteristics outside remnant fragments (Guevara 1995). Meanwhile, it has become increasingly apparent that under-

standing how species are affected by fragmentation requires information on their responses to all landscape components, including the forest-intervening matrices (Gascon *et al.* 1999).

This paper deals with vascular epiphyte assemblages on isolated remnant trees (IRTs) occurring in tropical pastures. Vascular epiphytes abound in tropical forests, especially in montane ones, and are often highly sensitive to anthropogenic disturbance (King & Chapman 1983, Hickey 1994, Turner *et al.* 1994, Barthlott *et al.* 2001, Krömer 2003, Krömer & Grad-

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stein 2003). However, knowledge of epiphyte assemblages on IRTs remains very poor.

Epiphytic vegetation provides important resources and habitat for a wealth of animals and microorganisms (Vance & Nadkarni 1990, Paoletti *et al.* 1991, Greeney 2001, Stuntz *et al.* 2002). These include insectivorous, nectarivorous and frugivorous vertebrates, especially bats and birds (Nadkarni & Matelson 1989, Castañeda 2001, Fleming *et al.* 2004). The latter play a key role in gene flow between forest fragments and regenerating forest patches on abandoned pastures and fields (McDonnell & Stiles 1983, Guevara *et al.* 1992). Generally birds and bats are reluctant to enter or cross open landscapes unless these areas offer significant reward (Charles-Dominique 1986, Nepstad *et al.* 1990, Githiru *et al.* 2002). Given suitable attractiveness, IRTs can stimulate movement of birds and bats across the forest border and function as catalysts for forest regeneration (Guevara *et al.* 1986, Janzen 1988, Cardoso da Silva *et al.* 1996, Duncan & Chapman 1999, Carrière *et al.* 2002a, 2002b).

The objective of this study was to describe the diversity and abundance of vascular epiphytes on IRTs. Specifically, we wanted to 1) document the effects of isolation on species composition, 2) determine possible causes of the structure and diversity of the vascular epiphyte assemblage on remnant trees, and 3) document the importance of remnant trees for the survival of vascular epiphytes following forest clearance.

STUDY AREA

The study was carried out in the valley of the Río San Francisco, southern Ecuador (3° 58' S, 79° 04' W), near the Estación Científica San Francisco (ECSF) at *ca.* 1800–2200 m elevation. The study area is situated within the Cordillera El Consuelo, forming part of the eastern range of the Ecuadorian Andes and bordering Podocarpus National Park. The region has been identified as a center of endemism and diversity for major groups of organisms such as birds, vascular plants or bryophytes (Fjeldså 1995, Borchsenius 1997, Navarrete 2000, Valencia *et al.* 2000, Parolly *et al.* 2004).

The relief is highly structured by deeply incised ravines, steep slopes of 20–55° inclination, and narrow ridge-tops. Landslides are very common and result in a complex mosaic of successional stages of vegetation. Soils are very heterogeneous but are generally shallow, highly acidic and very poor in basic cations

and effective cation exchange capacity (Schrumpf *et al.* 2001).

At 1950 m a.s.l. mean temperature is 15.5°C and average air humidity is 86%. Annual precipitation averages slightly above 2000 mm (Emck 2005). Rainfall seasonality is not very pronounced; differences between years exceed those within years (R. Rollenbeck, pers. comm.). April – June are generally the wettest months while September – February tend to be drier. Since the beginning of climate recording in 1998 periods without precipitation longer than one week have been recorded only during November – January. The San Francisco valley experiences slight lee- and föhn-effects (P. Emck, pers. comm.). Fog is uncommon throughout the year (pers. obs.).

Primary forests on the north-facing slopes are generally of low stature, with canopy height exceeding 15–20 m only in ravines. Physiognomic differences between ridges, slopes and ravines are large (Homeier *et al.* 2002). Forests on the south-facing slopes were largely converted to cattle pastures *ca.* 12–30 yrs prior to sampling, with loosely-spaced occurrence of isolated remnant trees (IRTs). However, two of the sampled IRTs were isolated as recently as 2 and 5 years prior to sampling (Appendix 1). *Cedrela montana* and *Tabebuia chrysantha* are the main remnant tree species, being preserved, at least temporarily, for their valuable timber. Trees surviving slash-and-burn clearance generally exhibit healthy growth. Forest regeneration is prevented by burning of pastures during dry periods (Hartig & Beck 2002). Remnant vegetation or secondary forest occurs in scattered patches, mostly in narrow bands along ravines.

METHODS

Fifteen IRTs in pasture on the north-facing slope of the San Francisco valley and 6 canopy trees at similar elevation in nearby primary forest on the south-facing slope were sampled.

Distances between IRTs and intact forest varied from approximately 100–500 m. Trees were selected randomly among accessible canopy trees of 30–50 cm diameter at breast height (DBH); forest trees 4–6 were sought for to avoid bias by host identity. Both subsamples have similar shares of trees from ridges, slopes and ravines.

Access to tree crowns was achieved using the single rope technique (Perry 1978). In a few cases specimens were gathered by employing a hooked pole or by cut-

TABLE 1. Floristic composition of epiphytes from the 6 forest trees (FTs) and 15 IRTs ordered by families.

| | Richness [no. species] | | | | | Abundance [no. stands] | | | | |
| | Total | | | Relative [%] | | Total | | | Relative [%] | |
	FTs	IRTs	Sum	FTs	IRTs	FTs	IRTs	Sum	FTs	IRTs
Alzateaceae	1	–	1	<1	–	1	–	1	<1	–
Araceae	6	2	8	3	3	7	4	11	<1	<1
Araliaceae	2	–	2		–	2	–	2	<1	–
Asclepiadaceae	1	–	1	<1	–	1	–	1	<1	–
Asteraceae	2	–	2	<1	–	4	–	4	<1	–
Bombacaceae	1	–	1	<1	–	1	–	1	<1	–
Bromeliaceae	23	13	25	10	19	502	374	876	10	24
Cactaceae	1	–	1	<1	–	1	–	1	<1	–
Clusiaceae	3	–	3	1	–	4	–	4	<1	–
Cunoniaceae	1	–	1	<1	–	2	–	2	<1	–
Cyclanthaceae	1	–	1	<1	–	5	–	5	<1	–
Dryopteridaceae	9	1	9	<1	1	190	1	191	4	<1
Ericaceae	13	1	13	6	1	84	1	85	2	<1
Gesneriaceae	1	–	1	<1	–	1	–	1	<1	–
Grammitidaceae	13	1	13	< 6	1	565	2	567	11	<1
Hydrangeaceae	1	–	1	<1	–	2	–	2	<1	–
Hymenophyllaceae	10	–	10	4	–	74	–	74	1	–
Lentibulariaceae	1	–	1	<1	–	592	–	592	12	–
Marcgraviaceae	2	–	2	<1	–	3	–	3	<1	–
Melastomataceae	5	–	5	2	–	7	–	7	<1	–
Moraceae	1	2	3	<1	3	1	3	4	<1	<1
Orchidaceae	105	31	120	47	46	2802	1004	3806	56	65
Piperaceae	10	7	12	4	10	52	24	76	1	2
Polypodiaceae	9	7	12	4	10	42	115	157	<1	8
Rubiaceae	1	–	1	<1	–	1	–	1	<1	–
Solanaceae	–	2	2	–	3	–	6	6	–	<1
Urticaceae	1	–	1	<1	–	2	–	2	<1	–
Vittariaceae	1	–	1	<1	–	26	–	26	<1	–
Total	225	67	253			4974	1534	6508		

ting off minor branches. Voucher specimens were deposited in AAU, ECSF, MO, SEL, QCA and QCNE.

Tree height, DBH, location, elevation, and time elapsed since isolation (age of clearing) were recorded. The latter was determined by interviewing land users. Epiphytes were sampled in each of 5 vertical tree zones following a zonation scheme slightly modified after Johansson (1974). Johansson-zone 1 (JZ 1) stretches from 0.25 m up to 3.0 m, JZ 2 from 3 m above ground to the first major ramification, JZ 3 comprises major branches > *ca.* 12 cm in diameter (inner crown), JZ 4 branches 12–5 cm in diameter (middle crown), and JZ 5 branches < 5 cm in diameter (outer crown). Surface areas of zones 3–5 are about equal.

Vascular epiphytes sampled included facultative and obligate holoepiphytes (*sensu* Benzing 1990), primary and secondary hemiepiphytes (Todzia 1986, Putz & Holbrook 1989), and accidental epiphytes (Benzing 1990). Non-hemiepiphytic climbers, hemiparasites and seedlings were excluded. Because of the common occurrence of clumped species, "stands" instead of individuals were recorded (stand = group of stems or plants spatially separated from another group of the same species by an area on the tree devoid

of epiphytes or occupied by another species; Sanford 1968). Covers of bryophytes, lichens and substrate accumulations >1 cm thick were estimated in steps of 5% in relation to tree surface. Substrate accumulations consisted of dead organic matter in various stages of decomposition ("crown humus"; Jenik 1973) and living bryophytes and lichens.

Statistical analysis was performed by two-tailed Mann-Whitney U-test and the Spearman rank-correlation test without transformations. Sørensen similarities between forest trees and IRTs were calculated for whole trees and Johansson-zones. Nonmetric multidimensional scaling (NMDS) was applied to the resulting matrices of similarity, here displayed as two-dimensional scatterplots.

RESULTS

Composition and diversity. A total of 6508 stands representing 253 species of vascular epiphytes (86 genera, 28 families) was recorded. The 6 sampled forest trees harbored 4974 stands of 225 species (80 genera, 27 families), the 15 sampled IRTs 1534 stands of 67 species (30 genera, 10 families). Bromeliaceae, Orchidaceae, Piperaceae and Polypodiaceae were best represented on remnant trees regarding species richness and abundance (Table 1). Abundance of Orchidaceae on IRTs was largely due to the succulent *Dryadella werneri*, constituting 73% of all orchids.

Compared with forest trees, species richness on IRTs was most strongly reduced in Dryopteridaceae (*Elaphoglossum*) (89%), Ericaceae (92%), Grammitidaceae (92%) and Hymenophyllaceae (100%), least in Bromeliaceae (44%), Piperaceae (30%) and Polypodiaceae (22%). Species with considerable abundance on IRTs included *Tillandsia complanata* and *Tillandsia tovariensis* (Bromeliaceae), *Dryadella werneri*, *Epidendrum stangeatum*, *Epidendrum* cf. *zosterifolium* and *Prosthechea grammatoglossa* (Orchidaceae), and *Pleopeltis macrocarpa* and *Polypodium remotum* (Polypodiaceae) (see Appendix 2).

The number of epiphyte stands on single trees varied greatly (Fig. 1). Forest trees held 55-2519 stands (mean 828.7; median 490.0), IRTs 3-872 stands (mean 102.3; median 47.0). Total abundance and species richness of epiphytes were significantly lower on IRTs, both on whole trees and in Johansson-zones, compared with forest trees (Table 2).

IRTs harbored 2-26 species (mean 10.5; median 10.0), forest trees 19-98 (mean 59.3; median 56.0) (Fig. 2). Diversity (Shannon, Simpson) was significantly lower on IRTs ($P < 0.001$, n = 21 and $P < 0.05$, n = 21 respectively; U-test). Species richness and abundance were correlated positively with covers of bryophytes and substrate accumulations, and negatively so with lichen cover (Table 3). Epiphyte assemblages on forest trees and IRTs were grouped as separate flor-
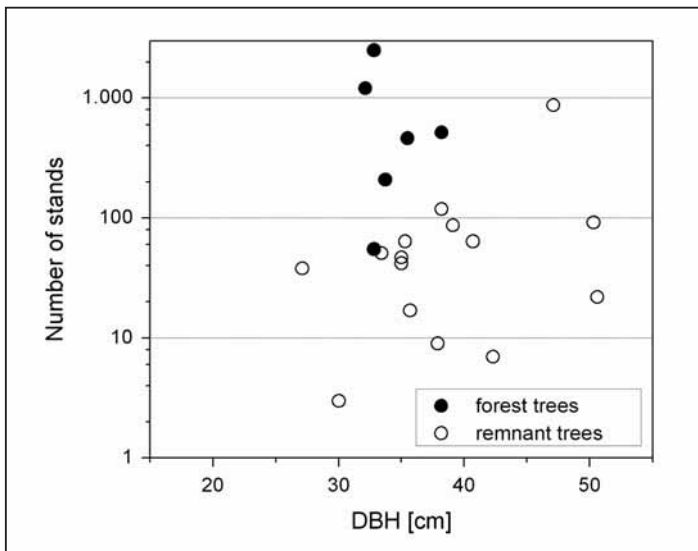

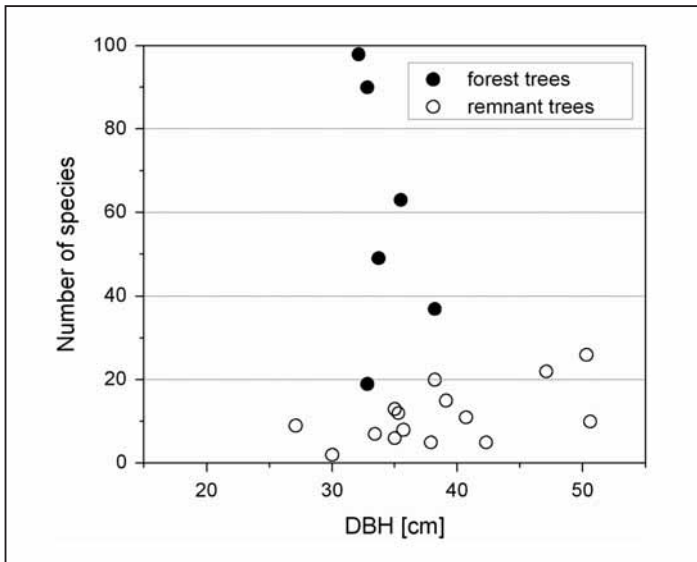FIG. 1. Abundance of epiphytes in relation to tree size (DBH).

FIG. 2. Epiphyte richness in relation to tree size (DBH).

istic units by NMDS (Fig. 3). The first dimension well reflects species richness with the poorest hosts (trees P4, P5 and P12) on the left and the richest trees (F1, F2 and F3) on the right of the graph.

Spatial distribution. Mean relative abundance was highest in JZ 4 and 5 on forest trees and in JZ 3 and 4 on IRTs (Fig. 4). Relative abundance and species richness on IRTs compared with forest trees were significantly lower in JZ 1 but higher in JZ 3 (Table 2). In addition, relative abundance on IRTs was significantly lower in JZ 5. Mean relative species richness on forest trees was highest in JZ 4, on IRTs in JZ 3 (Fig. 5). NMDS of the Johansson-zones based on assemblage structure clearly separated the two habitats (Fig. 6). Within each habitat, epiphyte assemblages of crown-zones (JZ 3-5) were grouped closely together, those of lower stems (JZ 1) were well isolated.

Upper stems (JZ 2) of forest trees, finally, were clearly distinct from crown-zones, whereas this zone showed great similarity to the crown in remnant trees.

DISCUSSION

Composition and diversity. Floristic composition of vascular epiphytes in the investigated forest shows close resemblance to other moist neotropical mid-elevation forests (e.g., Ibisch 1996, Ingram *et al.* 1996, Engwald 1999, Freiberg & Freiberg 2000, Krömer 2003, Krömer & Gradstein 2003) and species richness is very high (see also Bussmann 2001). In comparison, the epiphytic flora on IRTs in the study area is impoverished and monotonous. Bromeliaceae, Orchidaceae, Piperaceae, and Polypodiaceae, all being rich in drought-tolerant species, were relatively species-rich

TABLE 2. Species richness and abundance (absolute and relative respectively) along Johansson-zones. Forest trees vs. IRTs. Mann-Whitney U-test.

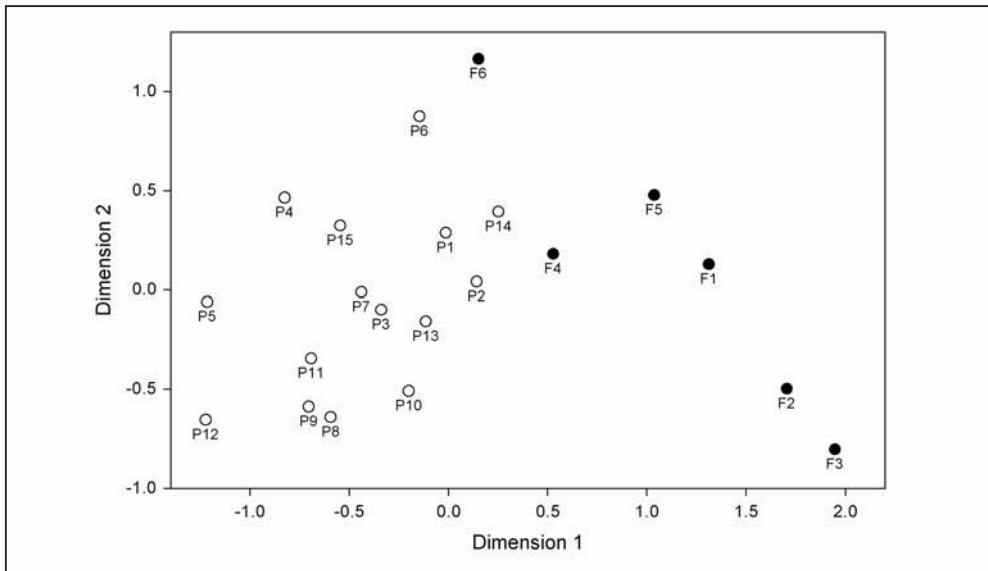|	JZ 1 (n = 21)	JZ 2 (n = 20)	JZ 3 (n = 21)	JZ 4 (n = 21)	JZ 5 (n = 21)	Totals (n = 21)
Species richness	p < 0.001	p < 0.01	p < 0.01	p < 0.01	p < 0.001	p < 0.01
Relative richness	p < 0.05	n.s.	p < 0.05	n.s.	n.s.	–
Abundance	p < 0.001	p < 0.01	p < 0.05	p < 0.05	p < 0.01	p < 0.01
Relative abundance	p < 0.05	n.s.	p < 0.05	n.s.	p < 0.05	–

FIG. 3. Nonmetric multidimensional scaling plot (first two dimensions) of epiphyte similarity based on Søren-sen index for entire host trees. Closed circles (F1-6) represent forest trees, open circles (P1-15) IRTs.

and abundant, whereas Ericaceae, Dryopteridaceae, Grammitidaceae and Hymenophyllaceae, all being common forest elements, were scarce or lacking on IRTs (Table 1). These findings agree with recent studies in Bolivia (Ibisch 1996, Krömer & Gradstein 2003). In a strongly seasonal montane forest in Bolivia (6–8 arid months), the epiphytic flora consisted of Bromeliaceae, Cactaceae, Orchidaceae, Piperaceae, and Polypodiaceae (Ibisch 1996). Krömer & Gradstein (2003) found that Piperaceae and Polypodiaceae were well represented in open fallows in moist sub-montane Bolivia (1500–2000 mm/an. precipitation; 2–3 arid months), while Bromeliaceae and Orchidaceae exhibited considerably reduced species richness compared with the primary forest. Dryopteridaceae (*Elaphoglossum*), Grammitidaceae, and Hymenophyllaceae were virtually lacking in the fallows.

Reduction of species diversity on IRTs was paralleled by reduced bryophyte cover, but correlated negatively with lichen cover, which was increased on

TABLE 3. Spearman rank-correlations between selected parameters (n = 21). None of the given parameters correlates with altitude, DBH, tree height or elapsed time since isolation.

	Species richness		Abundance		Shannon H'		Simpson D	
Species richness	–		0.936	**	0.765	**	– 0.412	
Abundance	0.936	**	–		0.567	**	– 0.237	
Shannon H'	0.785	**	0.860	**	–		– 0.823	**
Simpson D	0.692	**	0.682	**	– 0.823	**	–	
Bryophyte cover	0.605	**	0.651	**	0.270		– 0.015	
Lichen cover	– 0.534	*	– 0.545	*	– 0.211		0.047	
Substr. accum. cover	0.692	**	0.682	**	0.488	*	– 0.260	

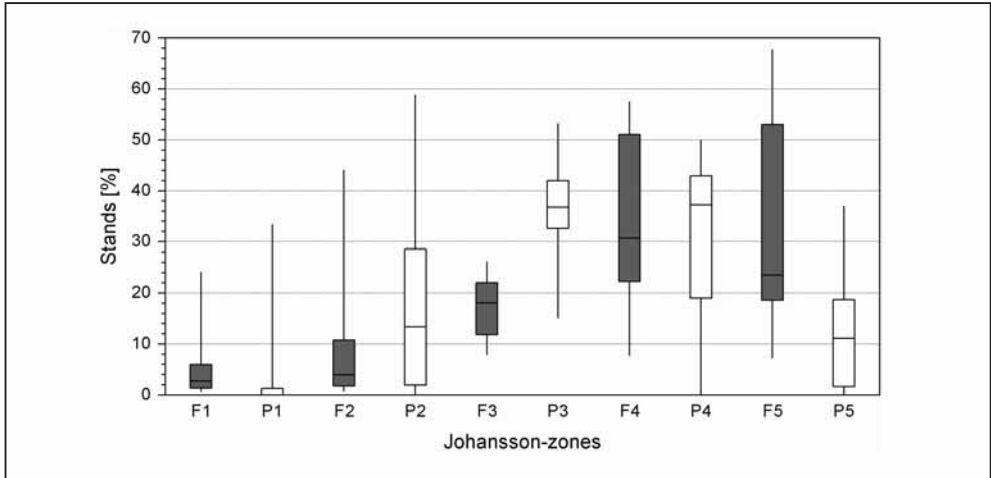*Significant at p < 0.05; ** significant at p < 0.01.

FIG. 4. Relative abundance (% of the hosts' stand numbers) recorded along the Johansson-zones: forest trees (gray) vs. IRTs (white).

IRTs. Decreased diversity and cover of epiphytic bryophytes in IRT crowns is related to increased evaporation and insulation, as has previously been documented by Sillett *et al.* (1995). Bryophyte cover tends to increase with humidity (Gradstein & Pócs 1989) while lichens avoid excessive humidity and shading (Sipman & Harris 1989, Gradstein 1992). Thus the observed patterns strongly suggest increased drought stress as the principal agent for the compositional shifts and general impoverishment in terms of species richness and abundance of assemblages on IRTs.

Numerous workers have noted the importance of humidity to epiphyte diversity (e.g., Gentry 1988, Ek *et al.* 1997, Kreft *et al.* 2004). Their extreme sensitivity to drought as a consequence of an aerial life style makes epiphytes important as prime indicators for
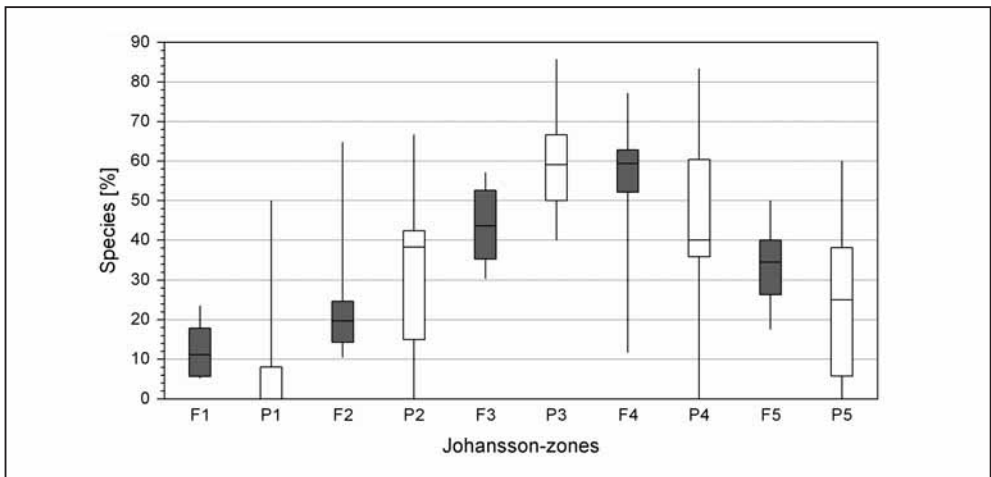

FIG. 5. Relative species richness (% of the hosts' total species richness) recorded along the Johansson-zones on forest trees (gray) vs. IRTs (white).
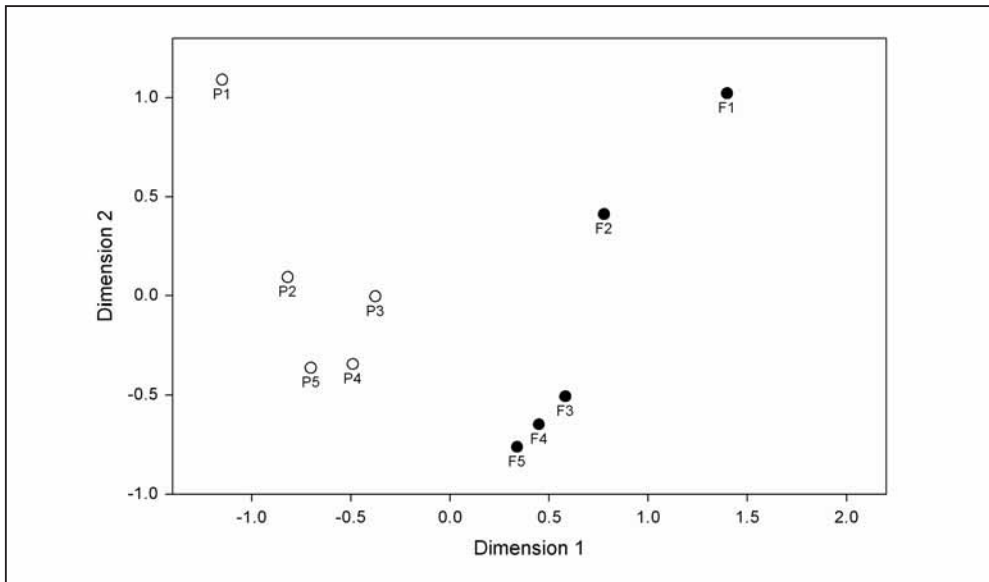
FIG. 6. Nonmetric multidimensional scaling plot (first two dimensions) of epiphyte similarity based on Søren-sen index for the five Johansson-zones. Closed circles (F1-5) represent the pooled respective Johansson-zones of forest trees, open circles (P1-5) those of IRTs.

mesoclimates and climate change (Richter 1991, Lugo & Scatena 1992, Nadkarni 1992, Benzing 1998, Richter 2003). One of the most striking patterns shown by epiphytes is the large decrease in both numbers of species and individuals in drier habitats (Gentry & Dodson 1987). When transplanted to warmer and drier conditions, epiphytes responded with higher leaf mortality, lower leaf production and reduced longevity (Nadkarni & Solano 2002).

Flores-Palacios & García-Franco (2004) reported similar impoverishment of epiphyte assemblages after isolation in montane Mexico. The site is moderately moist and experiences a distinct dry season (1650 mm/an. precipitation with 7 dry months).

Decreased diversity on IRTs is not a general trend though. In moist areas of lowland southern Mexico and lower montane northern Ecuador, species richness on IRTs was similar to that on forest trees (Larrea 1995, Hietz-Seifert *et al.* 1996), although floristic composition was more uniform on IRTs than on forest trees in at least one of these studies (Larrea 1995). Both sites show high precipitation and little seasonality with > 4000 mm/an. precipitation and the two driest months with ca. 100 mm, and ca. 3500 mm/an.

and no arid months respectively (P. Hietz and H. Greeney, pers. comm.). We suggest that in aseasonal, perhumid climates impoverishment of epiphyte vegetation on IRTs compared with nearby forest is less severe than in moderately seasonal climates such as the present study area. In areas with perhumid climates high air humidity may be maintained in open habitats following deforestation, allowing for high epiphyte species richness on IRTs, even though considerable turnover may follow isolation. Under slightly seasonal conditions with moderate levels of drought stress, however, species richness of epiphytes is high only in the forest, where high air humidity is maintained under the closed canopy. Opening up of the canopy in these areas leads to significant changes in the air humidity regime (Werner, unpubl. data) and subsequent impoverishment in abundance and diversity of epiphytes. Interestingly, in arid regions where total annual precipitation is low and epiphyte diversity limited, epiphyte assemblages on IRTs are often relatively unchanged compared with the forest (Werner, pers. obs.). It thus appears that loss of diversity on IRTs in tropical regions is most severe in areas with a moderately seasonal climate. However, fog appears

disproportionately beneficial for epiphytes on IRTs, complicating the interpretation of precipitation effects wherever it occurs regularly.

Vertical distribution. Vertical stratification of epiphytes on forest trees in relation to changes in microclimatic conditions along the tree has often been described (e.g., Johansson 1974, Sudgen & Robbins 1979, Kelly 1985, ter Steege & Cornelissen 1989). Data on remnant trees are very scarce, however. On IRTs in Mexico branches with diameters less than 5 cm were only sparsely colonized by vascular epiphytes (Hietz-Seifert *et al.* 1996). A similar pattern was found in this study (Fig. 4; Table 2). Inner crowns of IRTs in the study area, however, were significantly richer in terms of relative species richness and abundance than inner crowns of forest trees). The uneven distribution of species diversity in IRT crowns may reflect reduced rates of successful colonization after isolation.

Nadkarni (1992) reported paucity of epiphytes on trunk bases (JZ 1) of IRTs in Costa Rica. In our study low species richness in JZ 1 was also evident and was paralleled by a decline in covers of lichens and bryophytes. Microclimatic changes are likely to be greatest close to the ground, but the disproportionate and general impoverishment of the trunk bases (even concerning lichens) may also be related to fire. Indeed, Robertson & Platt (2001) reported direct fire damage to epiphytes up to 1 m above ground.

Concluding remarks. The comparison between the vascular epiphyte flora on IRTs and forest trees showed that numerous taxa decrease in abundance or vanish after isolation. Many of these are typically drought-intolerant, hygrophilous taxa, such as Dryopteridaceae, Grammitidaceae and Hymenophyllaceae. These taxa are partly replaced, if at all, by drought-tolerant, heliophilous species such as *Tillandsia complanata* and *Prosthechea grammatoglossa* (Appendix 2). The most species-rich and diverse IRT sampled in this study had been isolated as recently as 2 years prior to sampling and carried many dead epiphytes, especially pleurothallidinid orchids (Appendix 1, IRT 6).

When isolated from neighboring vegetation, forest trees have higher probabilities of dying than when in the forest interior due to their exposure to adverse environmental conditions (Lovejoy *et al.* 1986, Lawton & Putz 1988, Kapos *et al.* 1997). These conditions include higher wind speeds, mean and maximum temperatures, vapor pressure deficit and solar radiation (compare also reviews by Murcia 1995, Holl 1999). In Panama, edge-interior ratio of trees that died after edges were created was 14:1 (Williams-Linera 1990) and mid-term mortality peaks were found associated with drought events (Laurance *et al.* 2001). We propose that the same mechanism will affect epiphytes on IRTs.

Guevara *et al.* (1998) proposed that IRTs function as "stepping stones" for native fauna and "safe sites" for flora, and function as a structurally discontinuous canopy. Our study suggests that IRTs might be "safe sites" for epiphytes at the most in perhumid and arid climates. Here, epiphytic vegetation on IRTs appears to be less reduced compared with the forest than in areas with a moderately seasonal climate. It has further been suggested that diversity and composition of epiphytic vegetation on IRTs depend on diaspore influx from adjacent forest vegetation and, consequently, on distance to these forests (Wolf 1995, Hietz-Seifert *et al.* 1996, Zimmerman *et al.* 2000, Nkongmeneck *et al.* 2002).

In conclusion, we propose that changed epiphyte assemblages on IRTs, compared with those on forest trees, are to a large extent explained by the altered microclimatic conditions on IRTs and their adverse effects on rates of establishment and survival. Reduced availability of suitable niches may further affect epiphyte diversity on IRTs (Sillett *et al.* 1995, Barthlott *et al.* 2001). The observed assemblage changes seem to parallel those along the edges of remnant forests. More detailed studies on the epiphyte assemblages of IRTs and along forest edges are necessary to arrive at a better understanding of the unique structure of these assemblages and the processes determining their development.

ACKNOWLEDGMENTS

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APPENDIX 1. Host tree characteristics. Forest trees (FT) and isolated remnant trees (IRT).

No.	Host species	DBH [cm]	Height [m]	Altitude [m]	Years isolated	Species of epiphytes	Stands of epiphytes	Shannon H' log10	Simpson D
FT 1	*Tapirira guianensis*	35.5	17.3	1810	–	63	463	1.40	0.07
FT 2	*Alzatea verticillata*	32.1	16.3	2030	–	98	1209	1.28	0.12
FT 3	*Alchornea pearcii*	32.8	12.0	2230	–	90	2519	1.32	0.08
FT 4	*Tabebuia chrysantha*	38.2	19.5	1890	–	37	517	0.68	0.49
FT 5	*Tabebuia chrysantha*	33.7	20.1	1950	–	49	209	1.42	0.06
FT 6	*Cedrela montana*	32.8	17.2	1930	–	19	55	1.10	0.09
IRT 1	*Tabebuia chrysantha*	47.1	19.2	1860	30	22	872	0.42	0.65
IRT 2	*Cedrela montana*	39.1	13.7	1870	30	15	87	0.92	0.15
IRT 3	*Juglans neotropica*	27.1	13.2	1940	5	9	38	0.66	0.31
IRT 4	*Juglans neotropica*	35.0	17.2	2010	15	6	42	0.62	0.28
IRT 5	*Tabebuia chrysantha*	33.4	9.8	2060	12	5	9	0.62	0.19
IRT 6	*Tabebuia chrysantha*	50.3	16.4	2050	2	26	92	1.21	0.08
IRT 7	*Tabebuia chrysantha*	50.6	16.7	2050	12	10	22	0.90	0.12
IRT 8	*Cedrela montana*	42.3	14.5	2050	12	5	7	0.67	0.10
IRT 9	*Tabebuia chrysantha*	35.3	18.3	2130	14	12	64	0.67	0.30
IRT 10	*Tabebuia chrysantha*	40.7	22.2	2080	14	11	64	0.74	0.24
IRT 11	*Tabebuia chrysantha*	33.4	14.5	2130	14	7	51	0.63	0.27
IRT 12	*Juglans neotropica*	30.0	12.1	2040	14	2	3	0.28	0.33
IRT 13	*Piptocoma discolor*	35.0	8.0	2040	13	13	47	0.76	0.31
IRT 14	*Heisteria* sp. nov.	38.2	21.1	1840	30	20	119	1.10	0.11
IRT 15	*Beilschmiedia costaricensis*	35.7	18.8	1840	30	8	17	0.81	0.13

APPENDIX 2. Species list. Abbrevations of life forms include "AE" for accidental epiphytes, "E" for facultative and obligate holoepiphytes, "PH" for primary hemiepiphytes and "SH" for secondary hemiepiphytes.

	Life form	Stands FTs	IRTs	Frequencies FTs	IRTs
ALZATEACEAE					
Alzatea verticillata Ruiz & Pav.	PH	1	0	1	0
ARACEAE					
Anthurium dombeyanum Brogn.	E	0	2	0	1
Anthurium grubbii Croat	E	1	0	1	0
Anthurium scandens (Aubl.) Engl.	E	0	2	0	1
Anthurium cutucuense Madison vel aff.	SH	1	0	1	0
Philodendron ceronii Croat	SH	1	0	1	0
Philodendron sp. nov. 1	SH	1	0	1	0
Philodendron sp. nov. 2	SH	2	0	2	0
Stenospermation sp. nov.	E	1	0	1	0
ARALIACEAE					
Schefflera cf. *pentandra* (Ruiz & Pav.) Harms	PH	1	0	1	0
Schefflera sp.	PH	1	0	1	0

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
ASCLEPIADACEAE					
Matelea sp.	AE	1	0	1	0
ASTERACEAE					
Baccharis cf.	AE	1	0	1	0
Pentacalia cf. *moronensis* H. Rob. & Cuatrecas.	SH	3	0	1	0
BOMBACACEAE					
Spirotheca cf.	PH	1	0	1	0
BROMELIACEAE					
Guzmania coriostachya (Griseb.) Mez	E	3	0	1	0
Guzmania killipiani L.B. Sm.	E	3	0	1	0
Guzmania morreniana (Linden Hortus) Mez	E	3	0	1	0
Pitcairnea riparia Mez	SH	3	0	1	0
Racinaea dielsii (Harms) H. Luther	E	1	0	1	0
Racinaea euryelytra J.R. Grant	E	4	1	3	1
Racinaea monticola (Mez & Sodiro) M.A. Spencer & L.B. Sm.	E	21	1	2	1
Racinaea schumanniana (Wittm.) J.R. Grant	E	10	0	3	0
Racinaea tetrantha (Ruiz & Pav.) M.A. Spencer & L.B. Sm.	E	6	0	1	0
Racinaea undulifolia (Mez) H. Luther	E	9	0	2	0
Tillandsia barbeyana Wittm.	E	77	45	5	8
Tillandsia barthlottii Rauh	E	91	26	3	8
Tillandsia biflora Ruiz & Pav.	E	4	11	3	4
Tillandsia complanata Benth.	E	24	121	5	14
Tillandsia confinis var. *caudata* L.B. Sm.	E	2	0	1	0
Tillandsia fendleri Griseb.	E	3	5	3	4
Tillandsia laminata L.B. Sm.	E	28	0	2	0
Tillandsia naundorffiae Rauh & Barthlott	E	98	10	6	5
Tillandsia stenoura Harms	E	0	1	0	1
Tillandsia tovariensis Mez	E	30	102	5	12
Vriesea appendiculata (L.B. Sm.) L.B. Sm.	E	73	47	4	11
Vriesea fragrans (André) L.B. Sm.	E	5	0	1	0
Vriesea incurva (Griseb.) Read	E	0	3	0	3
Vriesea lutherii J.M. Manzanares & W. Till	E	2	0	1	0
Vriesea tequendamae (André) L.B. Sm.	E	2	1	1	1
CACTACEAE					
Rhipsalis riocampanensis J.E. Madsen & Z. Aguirre	E	1	0	1	0
CLUSIACEAE					
Clusia cf. *alata* Triana & Planch.	PH	1	0	1	0
Clusia cf. *ducuoides* Engl.	PH	1	0	1	0
Clusia sp.	PH	2	0	2	0
CUNONIACEAE					
Weinmannia pubescens Kunth	AE	2	0	1	0
CYCLANTHACEAE					
Asplundia sp.	SH	5	0	2	0

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
DRYOPTERIDACEAE					
Elaphoglossum latifolium (Sw.) J. Sm.	E	3	0	1	0
Elaphoglossum oleandropsis (Sodiro) Christ	E	94	1	4	1
Elaphoglossum cf. *craspedotum* Copel.	AE	1	0	1	0
Elaphoglossum cf. *cuspidatum* (Willd.) T. Moore	E	1	0	1	0
Elaphoglossum cf. *muscosum* (Sw.) T. Moore	E	4	0	3	0
Elaphoglossum cf. *pachyphyllum* (Kunze) C. Chr.	E	1	0	1	0
Elaphoglossum cf. *rimbachii* (Sodiro) H. Christ	E	79	0	4	0
Elaphoglossum sp. 1	E	6	0	2	0
Elaphoglossum sp. 2	E	1	0	1	0
ERICACEAE					
Cavendishia isernii Sleumer vel aff.	SH	1	0	1	0
Cavendishia cf.	E	1	0	1	0
Ceratostema loranthifolium Benth. vel aff.	E	1	0	1	0
Disterigma pentandrum S.F. Blake	E	21	0	2	0
Macleania mollis A.C. Sm.	E	26	0	2	0
Macleania hirtifolia (Benth.) A.C. Sm. vel aff.	E	1	0	1	0
Oreanthes cf. *hypogaeus* (A.C. Sm.) Luteyn	SH	1	0	1	0
Cavendishia cf. *bracteata* (Ruiz & Pav. ex. J. St.-Hil.) Hoerold	SH	1	0	1	0
Psammisia sp.	E	1	0	1	0
Semiramisia speciosa (Benth.) Klotzsch	E	1	0	1	0
Sphyrospermum cordifolium Benth.	E	11	1	2	1
Sphyrospermum sp.	E	17	0	3	0
Thibaudia vel aff.	E	1	0	1	0
GESNERIACEAE					
Columnea sp.	SH	1	0	1	0
GRAMMITIDACEAE					
Ceradenia melanopus (Grev. & Hook.) Bishop	E	4	0	1	0
Cochlidium serrulatim (Sw.) L.E. Bishop vel aff.	E	1	0	1	0
Enterosora sp.	E	1	0	1	0
Grammitis paramicola L.E. Bishop	E	11	0	1	0
Lellingeria subsessilis (Baker) A.R. Sm. & R.C. Moran	E	1	0	1	0
Melpomene anfractuosa (Kl.) A.R. Sm. & R.C. Moran	E	1	0	1	0
Melpomene cf. *pilosissima* (Mart. & Gal.) A.R. Sm.& R.C. Moran	E	1	0	1	0
Melpomene firma (J. Sm.) A.R. Sm. & R.C. Moran	E	20	0	1	0
Melpomene flabelliformis (Poiret) A.R. Sm. & R.C. Moran	E	488	0	4	0
Melpomene xiphopteroides (Liebm.) A.R. Sm. & R.C. Moran	E	29	2	2	1
Terpsichore pichinchae (Sodiro) A.R. Sm.	E	1	0	1	0
Terpsichore sp.	E	5	0	2	0
Zygophlebia matthewsii (Kunze ex. Mett) L.E. Bishop	E	2	0	1	0
HYDRANGEACEAE					
Hydrangea sp.	SH	2	0	1	0

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
HYMENOPHYLLACEAE					
Hymenophyllum fucoides var. *fucoides* (Sw.) Sw.	E	11	0	2	0
Hymenophyllum lindenii Hooker	E	4	0	1	0
Hymenophyllum myriocarpum Hook.	E	13	0	2	0
Hymenophyllum plumosum Kaulf.	E	1	0	1	0
Hymenophyllum ruizianum (Kl.) Kunze	E	1	0	1	0
Hymenophyllum trichophyllum Kunth	E	5	0	1	0
Hymenophyllum undulatum (Sw.) Sw.	E	36	0	2	0
Hymenophyllum sp.	E	1	0	1	0
Trichomanes hymenoides Hedw.	E	1	0	1	0
Trichomanes lucens Sw.	E	1	0	1	0
LENTIBULARIACEAE					
Utricularia jamesoniana Oliver	E	592	0	3	0
MARCGRAVIACEAE					
Marcgravia sp. nov.	SH	2	0	1	0
Ruyschia sp. nov.	SH	1	0	1	0
MELASTOMATACEAE					
Blakea vel aff. 1	E	2	0	1	0
Blakea vel aff. 2	SH	2	0	1	0
Blakea subpanduriforme Cotton & Matezki	SH	1	0	1	0
Blakea sp.	SH	1	0	1	0
Clidemia sp.	SH	1	0	1	0
MORACEAE					
Ficus krukovii Standl.	PH	1	0	1	0
Ficus sp. 1	PH	0	2	0	2
Ficus sp. 2	PH	0	1	0	1
ORCHIDACEAE					
Barbosella cucullata (Lindl.) Schltr.	E	3	0	2	0
Cochlioda rosea (Lindl.) Benth.	E	0	1	0	1
Cranichis sp.	E	24	0	1	0
Cryptocentrum cf. *lehmanni* (Rchb. f.) Garay	E	183	0	2	0
Cyrtochilum sp.	E	36	0	1	0
Dryadella werneri Luer	E	396	735	2	2
Elleanthus bifarius Garay	E	4	0	2	0
Elleanthus blatteus Garay	E	1	0	1	0
Elleanthus robustus (Rchb. f.) Rchb. f.	E	7	0	2	0
Epidendrum gracilimum Rchb. f. & Warsz.	E	343	0	2	0
Epidendrum loxense F. Lehm. & Kraenzl.	E	1	0	1	0
Epidendrum repens Cogn.	E	4	0	1	0
Epidendrum sophronitoides F. Lehm. & Kraenzl.	E	5	0	2	0
Epidendrum stangeatum Rchb. f.	E	3	17	1	4
Epidendrum cf. *zosterifolium* F. Lehm. & Kraenzl.	E	19	108	3	10
Epidendrum cf. *coryophorum* (Kunth.) Rchb. f.	E	80	13	3	3

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
Epidendrum mancum Lindl.	E	2	0	1	0
Epidendrum sp. 1	E	6	0	1	0
Epidendrum sp. 2	E	0	1	0	1
Epidendrum sp. 3	E	1	0	1	0
Epidendrum sp. 4	E	0	5	0	4
Epidendrum cf.	E	0	2	0	1
Fernandezia subbiflora Ruiz & Pav.	E	42	0	1	0
Kefersteinia sp.	E	0	3	0	1
Lepanthes wageneri Rchb. f.	E	71	6	4	1
Lepanthopsis acuminata Ames	E	9	0	1	0
Lepanthopsis floripecten (Rchb. f.) Ames	E	134	0	1	0
Lycaste ciliata (Ruiz & Pav.) Lindl. & Rchb. f.	E	1	1	1	1
Masdevallia bangii Schlchtr.	E	1	0	1	0
Masdevallia bicolor Poepp. & Endl.	E	2	0	2	0
Masdevallia persicina Luer	E	3	0	1	0
Maxillaria acuminata Lindl.	E	24	0	5	0
Maxillaria aggregata Enders	E	30	0	3	0
Maxillaria brevifolia (Lindl.) Rchb. f.	E	8	0	2	0
Maxillaria cryptobulbon Carnevali & A.T. Atwood	E	2	0	2	0
Maxillaria imbricata Barb. Rodriguez	E	25	0	2	0
Maxillaria jenishiana (Rchb. f.) C. Schweinf.	E	4	0	2	0
Maxillaria mapiriensis (Kraenzl.) L.O. Williams	E	43	0	3	0
Maxillaria notylioglossa Rchb. f.	E	5	0	1	0
Maxillaria ochroleuca Lodd. ex. Lindl.	E	6	0	1	0
Maxillaria polyphylla Rchb. f.	E	10	0	2	0
Maxillaria rufescens Lindl.	E	19	4	3	1
Maxillaria stenophylla Rchb.f.	E	3	0	1	0
Maxillaria cf. *pulla* Linden & Rchb. f.	E	14	0	1	0
Maxillaria cf. *xantholeuca* Schlchtr.	E	5	0	1	0
Maxillaria calantha Schlchtr. vel aff.	E	5	0	2	0
Maxillaria notylioglossa Rchb. f. vel aff.	E	1	0	1	0
Maxillaria sp.	E	1	0	1	0
Myoxanthus affinis (Lindl.) Luer	E	1	0	1	0
Myoxanthus ceratothallis Luer	E	1	0	1	0
Myoxanthus uxorius Luer	E	3	0	1	0
Myoxanthus sp.	E	1	0	1	0
Odontoglossum sp.	E	0	10	0	1
Oncidium sp. 1	E	25	3	1	1
Oncidium sp. 2	E	114	0	2	0
Pityphyllum pinoides Sweet	E	88	0	2	0
Pleurothallis crocodiliceps Rchb. f.	E	4	0	2	0
Pleurothallis decurrens Poepp. & Endl.	E	0	5	0	2
Pleurothallis galeata Lindl.	E	8	0	1	0

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
Pleurothallis lilijae Foldats	E	1	0	1	0
Pleurothallis palateensis Luer	E	3	0	1	0
Pleurothallis peroniocephala Luer	E	3	0	2	0
Pleurothallis rabei Foldats	E	21	3	3	1
Pleurothallis rubens Lindl.	E	26	0	4	0
Pleurothallis talpinaria Rchb. f.	E	1	0	1	0
Pleurothallis xanthochlora Rchb. f.	E	4	0	1	0
Pleurothallis cf. *bivalvis* Lindl.	E	18	0	6	0
Pleurothallis cf. *erinacea* Rchb. f.	E	0	1	0	1
Pleurothallis sp. 1	E	1	0	1	0
Pleurothallis sp. 2	E	27	0	3	0
Pleurothallis sp. 3	E	5	0	1	0
Pleurothallis sp. 4	E	1	0	1	0
Pleurothallis sp. 5	E	1	0	1	0
Pleurothallis sp. 6	E	2	0	1	0
Pleurothallis sp. 7	E	1	0	1	0
Pleurothallis sp. 8	E	1	0	1	0
Pleurothallis cf. sp. 1	E	1	0	1	0
Pleurothallis cf. sp. 2	E	0	1	0	1
Pleurothallis cf. sp. 3	E	9	0	1	0
Pleurothallis cf. sp. 4	E	13	3	1	1
Pleurothallis cf. sp. 5	E	1	0	1	0
Pleurothallis cf. sp. 6	E	1	0	1	0
Pleurothallis cf. sp. 7	E	0	1	0	1
Polystachya stenophylla Schltr.	E	17	0	3	0
Prosthechea grammatoglossa (Rchb. f.) W.E. Higgins	E	4	43	2	5
Prosthechea pulchra Dodson & Higgins	E	1	0	1	0
Prosthechea vespa (Vell.) W.E. Higgins	E	11	0	2	0
Prosthechea cf. *hartwegii* (Lindl.) W.E. Higgins	E	11	0	1	0
Psilochilus mollis Garay	AE	1	0	1	0
Scaphyglottis bicornis (Lindl.) Garay	E	24	0	1	0
Scaphyglottis punctulata (Rchb. f.) C. Schweinf.	E	27	1	3	1
Sobralia candida Poepp. & Endl.	E	1	0	1	0
Sobralia cf. *croecea* Poepp. & Endl.	E	1	0	1	0
Stelis floriani Luer	E	1	0	1	0
Stelis sp. 1	E	1	0	1	0
Stelis sp. 2	E	16	2	2	1
Stelis sp. 3	E	1	0	1	0
Stelis sp. 4	E	4	0	2	0
Stelis sp. 5	E	1	0	1	0
Stelis sp. 6	E	12	3	2	2
Stelis sp. 7	E	0	1	0	1

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
Stelis sp. 8	E	0	1	0	1
Stelis sp. 9	E	0	1	0	1
Stelis sp. 10	E	0	7	0	1
Stelis sp. 11	E	4	0	1	0
Stelis sp. 12	E	8	6	1	1
Stelis sp. 13	E	1	0	1	0
Stelis sp. 14	E	1	0	1	0
Stelis sp. 15	E	252	0	1	0
Stelis sp. 16	E	17	0	1	0
Stelis sp. 17	E	350	0	1	0
Stelis sp. 18	E	2	0	1	0
Stelis cf. 1	E	8	0	2	0
Stelis cf. 2	E	2	0	1	0
Trichopilia fragrans (Lindl.) Rchb. f.	E	0	14	0	1
Trichosalpinx berlineri Luer	E	13	2	2	2
Trichosalpinx intricata (Lindl.) Luer	E	1	0	1	0
Trichosalpinx robledorum Luer & Escobar	E	1	0	1	0
Trichosalpinx werneri Luer	E	17	0	1	0
Trichosalpinx sp.	E	19	0	2	0
PIPERACEAE					
Peperomia ceroderma Yunck.	E	0	1	0	1
Peperomia ciliaris C.DC.	E	1	0	1	0
Peperomia hartwegiana Miq.	E	6	11	3	4
Peperomia tetraphylla (G. Forst.) Hook. & Arn.	E	11	5	3	2
Peperomia tovariana C.DC.	E	10	0	2	0
Peperomia vulcanicula vel aff.	E	5	3	2	1
Peperomia sp. 1	E	1	1	1	1
Peperomia sp. 2	E	0	1	0	1
Peperomia sp. 3	E	1	2	1	1
Peperomia sp. 4	E	2	0	1	0
Peperomia sp. 5	E	14	0	1	0
Piper sp.	SH	1	0	1	0
POLYPODIACEAE					
Campyloneuron amphostemon (Kunze ex. Klotzsch) Fée	E	1	1	2	1
Campyloneuron angustifolium (Sw.) Fée	E	0	5	0	3
Niphidium amocarpos (Kunze) Lellinger	E	0	1	0	1
Niphidium cf. *crassifolium* (L.) Lellinger	E	1	0	1	0
Pecluma eurybasis (C.Chr.) M.G. Price	E	2	0	1	0
Pleopeltis macrocarpa (Bory ex.Willd.) Kaulf.	E	21	55	3	7
Pleopeltis percussa (Cav.) Hook & Grev.	E	0	1	0	1
Polypodium fraxinifolium Jacq.	E	1	0	1	0
Polypodium levigatum Cav.	E	1	0	1	0

Appendix 2 continued

	Life form	Stands		Frequencies	
		FTs	IRTs	FTs	IRTs
Polypodium remotum Desv.	E	11	48	4	4
Polypodium sessilifolium Desv.	E	3	4	1	2
Polypodium loriceum L.	E	1	0	1	0
RUBIACEAE					
Palicourea cf.	AE	1	0	1	0
SOLANACEAE					
Solanum sp.	SH	0	2	0	2
Trianea sp.	E	0	4	0	2
URTICACEAE					
Pilea sp.	AE	2	0	1	0
VITTARIACEAE					
Vittaria stipitata Kunze	E	26	0	3	0