

Diversity and Conservation of Epiphytes in a Changing Environment*

Peter Hietz

Institut für Botanik, Univ. f. Bodenkultur, Gregor-Mendel-Str. 33, A-1180 Vienna, Austria

Abstract: Epiphytes comprise about 10 % of the world's total vascular flora and in some humid tropical forests may be the most species-rich life form. Growing on trees, their fate is tied to that of their hosts and they are threatened by the loss of tropical forests. How many and which species are lost depends on the type and magnitude of disturbance and the type of vegetation that replaces the original forest, but very little is known about epiphyte diversity in other than primary forests. The available examples include isolated trees, secondary forests, orchards and coffee plantations. The studies suggest that the performance, survival and distribution of epiphytes in disturbed forests or secondary vegetation are influenced by stand density and microclimate, distance from seed source, tree size and sometimes tree species, type and history of disturbance, population dynamics of epiphytes and trees, and epiphyte physiology. Being sensitive to disturbance and microclimate, and because of their importance for tropical forest ecology, epiphytes may serve as indicators or guides for careful management. Such data are important to manage the landscape in tropical countries in a way that minimises negative effects on biodiversity.

INTRODUCTION

For many species of plants and animals the loss of their habitat represents the greatest threat to their survival (ref. 1). While there is considerably uncertainty about the extinction rate caused by human activities, it is generally acknowledged that species loss and the erosion of genetic diversity is highest in the tropics (ref. 2, 3). This is a result of high deforestation rates in many tropical countries (ref. 4) and the fact that tropical forests harbour more species of plants and animals than any other area of the world (ref. 1).

Great efforts have been made to conserve areas of natural vegetation and give them various degree of protection. This continues to be an important and urgent task, but it is clear that severe disturbance and destruction will not stop soon. It is therefore necessary to study not only diversity in pristine environments but also the impact of alternative uses and management practices on biodiversity to conserve as much as possible where disturbance and

*Invited lecture presented at the International Conference on Biodiversity and Bioresources: Conservation and Utilization, 23–27 November 1997, Phuket, Thailand. Other presentations are published in *Pure Appl. Chem.*, Vol. 70, No. 11, 1998.

deforestation cannot be prevented and, where possible, to improve the conservation value of areas already degraded.

Most research on the impact of habitat destruction in tropical areas has been done on vertebrates, particularly birds (ref. 5, 6, 7, 8). Birds are well-known and mobile organisms may immediately show the unsuitability of a disturbed habitat by leaving, whereas plants, unless directly killed, remain in place until they die or simply fail to reproduce. While concentrating on a few well-known groups has advantages, this leaves us with little information about the many other groups that are also, but perhaps differently affected. Among plants, vascular epiphytes, plants that grow on trees or shrubs without directly harming them, are the life form most restricted to and typical of humid tropical forests. Comprising about 30 000 species or 10% of the earth's total vascular flora (ref. 9), most are limited to tropical and subtropical forests, where they may be the most diverse life form in very humid formations (ref. 10, 11). The importance of epiphytes for tropical biodiversity is further multiplied by their providing substrate and food for many of the animals inhabiting tropical rainforest canopies, which may number millions of still undescribed species. The few studies available suggest that epiphytes are a vulnerable group and consequently represent a good indicator group of biodiversity that can be monitored to assess the effects of forest disturbance (ref. 12, 13). From the original forest covering practically the whole of Singapore, only 0.2 % or 200 ha remain today, plus about 5% of the area that can be described as natural or semi-natural vegetation. Because of the massive deforestation, 26 % of vascular plants found around the turn of the century are extinct in the territory today, and epiphytes disproportionately suffered a 62 % loss (ref. 12).

This paper presents a short overview of the effect of various human activities on epiphyte diversity in the humid tropics, including unpublished data of the author. Three different types of human impact on tropical forests will be discussed: Complete conversion of the original forest to some other arboreal vegetation such as secondary forests, timber plantations or orchards; fragmentation into smaller patches with deforested areas in between; and various degrees of disturbance, such as forestry operations. Two further potential factors, pollution and global climate change, will only be shortly discussed as there are practically no studies on their effect on vascular epiphytes.

FOREST CONVERSION

As epiphytes depend on their host plants, usually trees, any conversion to a vegetation without trees will obviously result in a complete loss of epiphytes in the affected area. The diversity of epiphytes in oldgrowth forest is in part a result of the variety of sites available on single trees and in the whole forest canopy. Some species are adapted to the most humid and shady stem bases, others to exposed twigs and others require thick or rotten branches resulting in a partitioning of the available space and a more or less pronounced zonation within the tree (ref. 14, 15, 16, 17, 18). Additionally, many species may co-exist because tree- and branch-fall create a level of disturbance that prevents a few species from monopolising the available resources (ref. 19, 20). A less-structured secondary vegetation may not offer all of these microsites and the diverse disturbances in space and time and thus be unsuitable for some species.

I investigated epiphyte diversity in a plantation of alder (*Alnus acuminata*) in central Veracruz, Mexico, adjacent to an oldgrowth, possibly virgin cloud forest studied previously (ref. 18). The presence or absence of epiphyte species and their fertility were recorded on 36 trees, the same number as in the oldgrowth forest. Trees in the plantation were of more homogeneous size than in the oldgrowth, and the lack of any understory permitted much light to reach the ground. *Alnus acuminata* by itself does not appear to be an unsuitable host tree, as individuals in mixed stands carried about as many species of epiphytes as other trees of comparable size (ref. 21).

TABLE 1. Epiphyte Richness and Occurrence of Ecological Groups in an Oldgrowth Forest and an *Alnus* Plantation.

Figures in parentheses for the plantation are fertile species, all species in the oldgrowth forest were found with fertile individuals.

Epiphytic Species Living on:	Oldgrowth	Plantation
stem base	9	0 (0)
stem and thick branches	14	7 (3)
thick and thin branches	11	11 (7)
preference unclear	5	3 (1)
total	39	21 (11)

Twenty-one species of vascular epiphytes were registered on 36 trees of *Alnus* compared to 39 species in the oldgrowth forest (Table 1). While the number of species per tree was not significantly different from that of the oldgrowth forest when tree size measured as diameter at breast height (DBH) was accounted for (Fig. 1), species distributions and compositions were very distinct. In the plantation four common species were found on almost every tree, but most of the remaining species were rare. In the oldgrowth forest no species appeared as common and there was a more gradual decline in abundance (Fig. 2). As the plantation directly bordered the oldgrowth forest and no tree sampled was more than 100 m away, the plantation must have received a constant input of propagules and species may grow there that would not form viable populations in an isolated plantation of this structure. Indeed, only eleven of the 21 species had become fertile in the plantation, but every species in the oldgrowth forest was present with at least one fertile individual. The plantation completely lacked species that require the shaded and humid conditions prevalent close to the soil in mature and closed forests, and species generally found on large branches that accumulate organic matter and offer better rooting space and substrate were rare (Table 1). Only species thriving on thin and exposed branches were common.

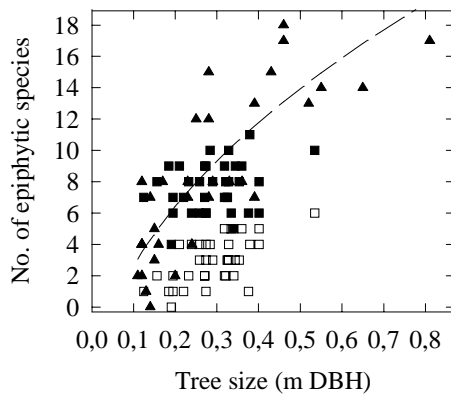


Fig. 1 Number of vascular epiphytes in an oldgrowth cloud forest ▲ and a plantation of *Alnus acuminata* (■ for fertile, □ for sterile plants). The broken line is a fitted function of the form $\text{No. spec} = a + b * \log \text{DBH}^2$ for the oldgrowth forest.

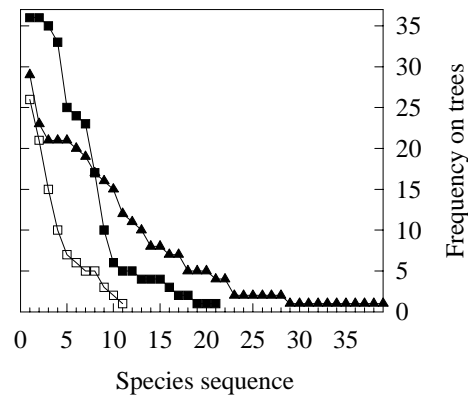


Fig. 2 Species sequence from the most common to the rarest, expressed as the number of trees a species was growing on. In both cases, 36 trees were sampled. Symbols as in Fig. 1.

A comparable study (ref. 22) in Costa Rica similarly found that the number of epiphytic bryophytes was lower on three trees of *Ficus* in an open pasture (71 species) than on three trees in a closed cloud forest (109 species) and that especially the species of the more humid inner crown were affected. It has been predicted that particularly shade species among bryophytes will be the most seriously affected by deforestation and disturbance, whereas the abundance of some lichens and "weedy" species that are rapid colonisers and growing on exposed locations may increase (ref. 23, 24)

Hickey (ref. 13) studied plant diversity in forests composed of rainforest trees and shrubs and an overstory of *Eucalyptus* in Tasmania. He compared oldgrowth (>110 years), forests burned by wildfire and forests logged and burned to prepare the soil for new growth. Burned and logged forests were 20 - 30 years old. The diversity of most plant groups was either unaffected or even higher in the younger forests because these included rainforest elements and species indicating disturbance. Only the group of epiphytic ferns (no other epiphytes were registered in these subtropical forests) was negatively affected and declined from an average of 5.5 species per 5 x 5 m plot in the oldgrowth forest to 3.2 species in the forests affected by wildfire and 1.5 species in the logged and burned forest. Several of the ferns belonged to the Hymenophyllaceae, a very drought sensitive group, which indicates that the lack of suitable humid microhabitats was among the reasons for this decline.

Secondary vegetation or plantations need not be of poor epiphyte diversity in all cases. When coffee is grown under shade and shade trees are old and not pruned, large trees may host a diverse epiphyte community. Of four coffee plantations studied in central Veracruz, two had young trees of the legume genus *Inga* as shade trees (with an average DBH of 0.20 and 0.17 m, respectively), one old individuals of *Inga* (DBH 0.31) and in the fourth the original forest trees (mostly oaks, DBH 0.28) were spared to provide shade and only the understory and part of the trees had been cleared to make way for coffee plants. On the young shade trees, epiphyte diversity was low, as in the plantation, and generally only species commonly found on small branches were present. In both coffee plantations with old shade trees the number of

epiphytes per tree and the total number of epiphytes per plot were about as high as in natural forests of the area (Fig. 3). Also in these cases there was some shift in species composition with a few species occurring close to the ground in the mature forests being absent or rare in the plantations.

Not all trees are equally suitable hosts for epiphytes. Though there appears to be very little host specificity of epiphytes (ref. 15, 25), some tree species are generally better hosts than others. Among the forest trees studied in central Veracruz, *Bursera simaruba* was generally a poor host because of its very smooth and defoliating bark and *Pinus* spp. were unsuitable for orchids and others with higher substrate requirements, possibly because of phenolic substances or resins (ref. 21). Often trees with a rough bark are preferred hosts. In a Puerto Rican watershed, 62.9% of trees that hosted orchids belonged to either *Guarea guidonia* or *Dacryodes excelsa*, and 80.2% of host trees were >16 cm DBH (ref. 25). It was therefore suggested that careful management of these two tree species may be crucial to the maintenance of orchid abundance and diversity in the area. Together with coffee shade trees, mango (*Mangifera indica*) is the most planted tree in central Veracruz. Contrary to the shade trees studied however, few epiphytes grew on mango trees (Fig. 3). One reason appears to be the very dense foliage concentrated in the outer crown, which allows too little light to reach the branches where epiphytes could grow. Additionally, mango bark is rich in tannins and phenolic compounds (ref. 26) that may inhibit germination or growth on its bark.

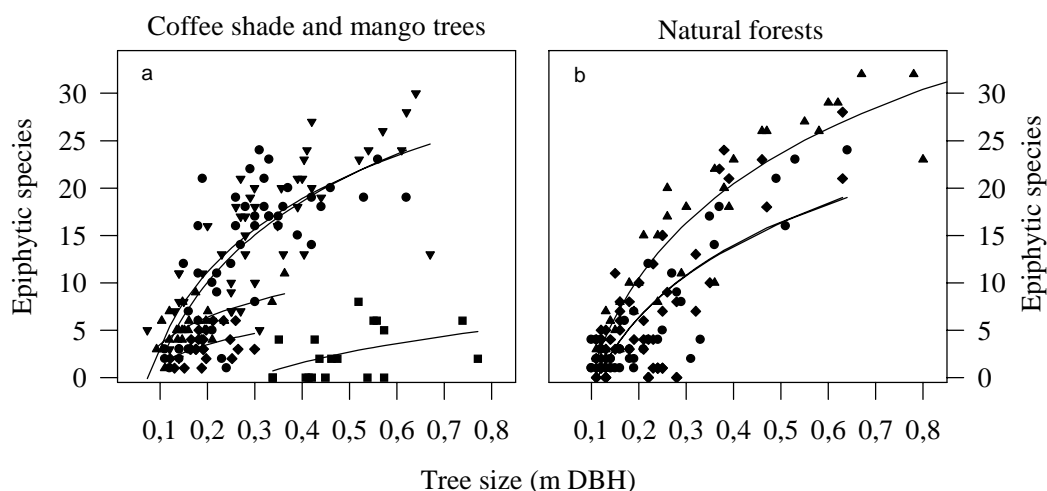


Fig. 3 a) Number of vascular epiphytes on shade trees in four coffee plantations (▲ old trees of *Inga*, ● old trees, mostly *Quercus*, remnants of the original forest; ■ and ▼ young trees of *Inga*) and on mango trees ■. b) For comparison epiphyte diversity in three old-growth forests in the area and at comparable altitudes (◆ 720 m, ● 1000 m, ▲ 1430 m) are shown. Data for Fig. 4b from ref. 21. Lines are fitted as in Fig. 1.

FOREST DISTURBANCE

Disturbance of original forests here means any operation that does not lead to a complete removal of the forest cover but affects some or all species concerned. Most forestry practices in tropical countries will fall into this category. The degree of disturbance varies widely from more than half of the tree cover removed, to the collection of inconspicuous non-timber species. To my knowledge no study has been published on the impact of forestry practices

other than clearcutting on epiphyte diversity in the tropics. However, some lessons can be drawn from studies on non-vascular epiphytes in temperate forests, which, together with factors discussed above, allow at least some predictions.

Diversity of epiphytic mosses and lichens was found to be significantly higher in oldgrowth boreal forests than in young managed forests (ref. 27, 28, 29). Interestingly, host tree species had a strong effect on the composition of the epiphyte community (ref. 30), a fact related to differences in bark chemistry of the hosts. Strong differences between host tree species, even of the same genus, in their communities of epiphytic cryptogams were also found in tropical rainforests (ref. 31), but evidence of host specificity or preference among vascular epiphytes is scarce. Some orchids significantly prefer one host over another (ref. 15) which may be related to bark chemistry inhibiting successful germination (ref. 32). In most cases the suitability of a host for vascular epiphytes appears to be related to its size, bark-roughness and branching patterns, affecting all or most species and there appears to be little true specificity. Probably the physiology of cryptogams and especially their mode of water uptake makes them more dependent on substrate chemistry than vascular plants, and orchids are indirectly affected through their obligate symbiosis with mycorrhizal fungi.

Not only the age of the trees in a forest but also the age and history of a stand may be important (ref. 29). Indeed some epiphytic lichens present in oldgrowth stands of British Columbia are thought to be relicts of more favourable climatic conditions when these species had a wider distribution (ref. 33). They are still present because of forest continuity over hundreds of years. Apart from tree and forest age, stand heterogeneity and the presence of gaps, trees with large-diameter lower branches, and oldgrowth remnant trees also foster epiphytic lichen diversity (ref. 34)

The degree and also the pattern of forest disturbance, together with the local climate, will determine the microclimate within the forest. Wherever disturbance increases forest openness, the locations close to the soil will become sunnier and drier, affecting especially epiphytes requiring high atmospheric humidity. This will influence other plants as well, but the negative effect is probably more severe for epiphytes, which cannot draw water from the soil.

Because of the limited water and nutrient supply, most epiphytes are growing slowly, with some notable exceptions such as epiphytes adapted to the high-disturbance habitat of small twigs (ref. 35). Preliminary studies on growth rates of bromeliads (Hietz P., unpublished) suggest that they take 10 - 20 years to mature and the epiphytic orchid *Dimerandra emarginata* (ref. 36) takes more than 30 years to reach full size. When logging operations remove all or most of the large trees, epiphytes that require large branches to root and / or with a long life cycle will also be affected. It has been suggested that hemiepiphytic figs (*Ficus* spp.), which are keystone species in many tropical rainforests (ref. 37), may be reduced over several logging cycles when the larger trees they grow on are repeatedly extracted (ref. 38). *Ficus* in South-east Asian dipterocarp forests require the high light conditions and suitable safe sites in the upper canopy for germination, and even then successful establishment is rare (ref. 39), which may make them susceptible to repeated disturbance.

FRAGMENTATION

The widespread deforestation in the tropics generally does not result in a straight frontier between virgin forest and deforested land, but human activities eat into the forest from many sides, usually starting from locations of easy access or high population pressure. This leads to a complex mosaic of virgin forest, parts disturbed or negatively affected by edge effects, secondary forests, and agricultural land, often resulting in patches of forest surrounded by deforested areas. The area negatively affected may thus be much larger than the area actually deforested. While total deforestation of the Brazilian Amazon basin between 1978 and 1988 was about 15 000 km² per year, the rate of habitat fragmentation and degradation, assuming an edge effect of 1 km, was about 38 000 km² (ref. 40). Plants in these forest fragments survive in the first place, but whether they may continue to do so depends on many factors.

Again, in contrast to studies on mammals and birds (ref. 41 and references therein), information on the survival of plants in such fragments is very scarce. Turner and co-workers (ref. 42) compared the flora of a 4 ha rainforest plot in Singapore's Botanical Garden with plants collected from that area around the turn of the century. From 448 species recorded about 100 years ago, only 220 or 49.1 % were still present in the 1990s. Epiphytes appeared more vulnerable than the average, but as only six species were present originally of which four had been lost, this may not be significant.

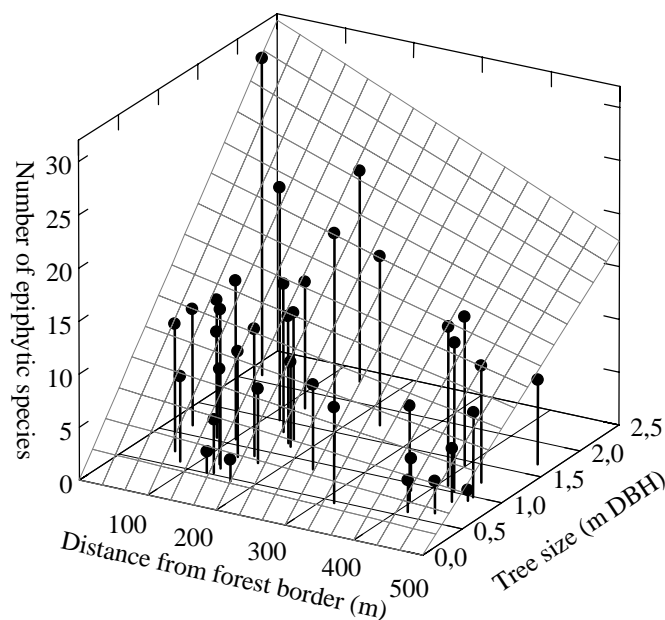


Fig. 4 Correlation between epiphyte species diversity on isolated remnant rainforest trees in a pasture with tree size (diameter at breast height) and distance of the isolated trees from the closed forest. Data from ref. 43. The mesh is a regression of the form $\text{No. species} = 4.079 * 12.5 * \text{km} + 9.151 * \text{DBH}$; $r^2 = 0.58$.

Another study (ref. 43) looked specifically for epiphytes in a much smaller spatial and time scale: Individual, isolated rainforest trees on a pasture that were spared when the forest was cut 28 years ago. The number of epiphytic species per tree was strongly correlated with tree size. Species living in the shady lower canopy were scarce or lacking, while others even profited from the higher light availability in the isolated crowns. Considering tree size, the

number of species was not or only little lower than in the primary forest, but the number of species per tree significantly declined with the distance of the isolated tree from the forest border (Fig. 4). This indicates that there was some, although not very much, decline on the isolated trees since the forest was cut 28 years ago, and that at least the trees closer to the forest received new diaspores, in any case more so than trees at a greater distance from the forest border.

This simplified system highlights important factors controlling the survival and diversity of epiphytes in isolated fragments. The size of the fragment determines the number of plants surviving in the first place, but also the degree to which a fragment will differ from the closed forest and thus its suitability in the long run. The distance from the closed forest and other fragments as well as the pattern of fragmentation (large strips or compact areas, for instance, ref. 40) determine the possible exchange of diaspores and pollen and thus the degree to which subpopulations in single fragments are isolated. For animal pollinated or dispersed plants, the mobility of the pollen or diaspore vector and its ability to cross unforested spaces also affect colonisation rates and genetic exchange between subpopulations, which are crucial factors for metapopulation survival in a fragmented landscape. The abundance of euglossine bees, which are important pollinators for some orchids and many other rainforest plants, strongly declined with fragment size (closed forest, 100 ha, 10 ha, 1 ha and open vegetation) in an Amazonian rainforest area (ref. 44). As the diaspores of epiphytes have to be transported in and between tree crowns and falling to the soil usually means death, most have very mobile seeds (ref. 9), a fact that may allow them to travel more easily between fragments than plants with heavy seeds.

While slow growth and long population cycles are a disadvantage when the rate of disturbance is substantially increased, they increase the survival at least in the mid-term in fragmented forests or after a singular disturbance. If plants do not die from the changed conditions, small populations can survive for extended periods even if the number of individuals is not sufficient to form a viable population over many generations. Even single plants can continue producing seeds for decades, which may eventually lead to the colonisation of secondary forests or plantations growing between fragments of oldgrowth forest. Single remnant trees have been shown to be potential nuclei for the reforestation of abandoned pastures or fields, as they attract birds from the forest that deposit seeds of forest plants and lead to an intense regrowth beneath the spared trees (ref. 45) and host epiphytes long after the forest had been cleared (ref. 43).

POLLUTION

The effect of pollution on natural plant communities in the tropics has received little if any attention, but, as dramatically demonstrated by the smog covering large areas of South-east Asia in 1997, should no longer be ignored. Many non-vascular epiphytes are known to be highly sensitive to atmospheric pollution and lichens have long been used as indicators of air quality (ref. 46). Deriving most of their nutrients directly or indirectly from the atmosphere and without the buffering capacity the soil provides for ground-rooted plants, vascular epiphytes are also likely to suffer from atmospheric pollution. Epiphytic species of *Tillandsia* are sensitive to lead pollution (ref. 47) and have been suggested as bioindicators for air quality assessment (ref. 48, 49)

GLOBAL CLIMATE CHANGE

There is a broad scientific consent that human change of land-use patterns and atmospheric trace gases will lead to a significant global climate change and has probably already done so. While the global climate has changed many times in the past, the change associated with a predicted doubling of atmospheric CO₂ will be faster than previous ones. Many species and whole vegetation types may not be able to migrate fast enough following their suitable climate (ref. 50). With mobile diaspores and shorter generations than trees, epiphytes may be better adapted to migrate with shifting climate zones than many tropical trees. On the other hand, most climate models predict increasing seasonality of precipitation in areas now covered by rainforests (ref. 51), which would reduce the perhumid area with the highest diversity of epiphytes.

Independent from eventual changes in temperature or precipitation, an increase in atmospheric CO₂ has a fertilising effect on plants and has been, although cautiously, related with a doubling of rainforest turnover rates in the past four decades (ref. 52, 53). This is likely to result in a decrease in diversity in tropical forests (ref. 54). Not all species of epiphytes will be equally able to cope with increasing turnover and shorter life cycles of their host trees and at least the species composition of epiphytes and plants in general can be expected to change.

CONCLUSIONS AND RECOMMENDATIONS

Being restricted to tropical forests and by definition growing on trees or shrubs, epiphytes are automatically vanishing with the loss of rainforests. As they are highly sensible to climatic conditions and often of slow growth, they appear in many cases to be even more vulnerable than other plants. This makes them suitable indicators of changes in local climate, forest structure and ecosystem health, which may also affect other species or ecosystem processes.

As some examples have shown there is considerable scope of conserving epiphyte diversity in an agricultural landscape or managed forests though some loss will inevitably occur if the microclimate of the forest interior is changed. Large forest trees carry the bulk of epiphyte diversity and biomass because of their size, the variety of microsites and because they have been available for enough time for slow-growing epiphytes to complete their life cycles. Avoiding the unnecessary damage of trees and saving large trees also of commercial species as seed sources for future generations of trees and people is also in the long term economic interest of forest managers and owners. A few additional measures such as conserving pockets of completely undisturbed forest where the microclimate of the forest interior is maintained and perhaps paying attention to tree species that are particularly good hosts for some or all epiphytes will conserve most or all species at very little additional costs. These and similar measures will also help to maintain the diversity of birds (ref. 55) and other species. If forests are cleared for whatever reason, even individual isolated remnant trees are much better than no trees and may form nuclei for the recolonisation in a secondary forest.

Tree size and age is also crucial in orchards or tree plantations. The tradition of growing coffee under old shade trees is probably an important reason for the relatively good conservation of many epiphytes in densely populated central Veracruz. Also the diversity of mammals (ref. 56) and insects (ref. 57, 58, 59) was found to be much higher in such coffee

plantations than in cultures without shade, and shade trees provide a range of other ecological services for coffee growers and society (ref. 60).

REFERENCES

- 1 UNEP. *Global Biodiversity Assessment*. Cambridge Univ. Press, Cambridge (1995).
- 2 N. Myers. In *Biodiversity* (E. O. Wilson and F. M. Peters, eds.), pp. 28-35. National Acad. Press, Washington (1988).
- 3 T. C. Whitmore and J. A. Sayer (eds.). *Tropical Deforestation and Species Extinction*. Chapman and Hall, London (1992).
- 4 FAO. *Forest Resources Assessment, 1990: Tropical Countries*. FAO Forestry Paper 112, FAO, Rome (1993).
- 5 A. G. Johns. *Biol. Cons.* **31**, 355-375 (1985).
- 6 A. G. Johns. *Biol. Cons.* **75**, 3-10 (1996).
- 7 J. M. Thiollay. *Cons. Biol.* **6**, 47-63 (1992).
- 8 M. Jullien and J. M. Thiollay. *J. Biogeogr.* **23**, 7-25 (1996).
- 9 M. Madison. *Selbyana* **2**, 1-13 (1977).
- 10 A. H. Gentry and C. H. Dodson. *Biotropica* **19**, 149-156 (1987).
- 11 A. H. Gentry and C. H. Dodson. *Ann. Missouri Bot. Gard.* **74**, 205-233 (1987).
- 12 I. M. Turner, H. T. W. Tan, Y. C. Wee, A. Bin Ibrahim, P. T. Chew, R. T. Corlett. *Cons. Biol.* **8**, 705-712 (1994).
- 13 J. E. Hickey. *Aust. J. Bot.* **42**, 383-404 (1994).
- 14 D. L. Kelly. *J. Biogeogr.* **12**, 223-241 (1985).
- 15 H. ter Steege and J. H. C. Cornelissen. *Biotropica* **21**, 331-339 (1989).
- 16 A. van Leerdam, R. J. Zagt and E. J. Veneklaas. *Vegetatio* **87**, 59-71 (1990).
- 17 J. K. Zimmerman and I. C. Olmsted. *Biotropica* **24**, 402-407 (1992).
- 18 P. Hietz and U. Hietz-Seifert. *J. Veg. Sci.* **6**, 719-728 (1995).
- 19 J. H. Connell. *Science* **199**, 1302-1310 (1978).
- 20 D. H. Benzing. *Vascular epiphytes*. Cambridge Univ. Press, Cambridge (1990).
- 21 P. Hietz and U. Hietz-Seifert. *J. Veg. Sci.* **6**, 487-498 (1995).
- 22 S. C. Sillett, S. R. Gradstein and D. Griffin III. *The Bryologist* **98**, 251-260 (1995).
- 23 S. R. Gradstein. In *Bryophytes and Lichens in a Changing Environment* (J. W. Bates and A. M. Farmer, eds.), pp. 234-258. Clarendon Press, Oxford (1992).
- 24 S. R. Gradstein. *Tropical Bryology* **6**, 83-93 (1992).
- 25 L. E. Migenis and J. D. Ackerman. *J. Trop. Ecol.* **9**, 231-240 (1993).
- 26 R. Hegnauer. *Chemotaxonomie der Pflanzen*. Vol. 3. Birkhäuser Verlag, Basel (1964).
- 27 M. Kuusinen. *Ann. Bot. Fenn.* **31**, 77-92 (1994).
- 28 M. Kuusinen. *Ann. Bot. Fenn.* **31**, 245-260 (1994).
- 29 M. Kuusinen. *Biol. Cons.* **75**, 43-49 (1996).
- 30 M. Kuusinen. *Lichenologist* **28**, 443-463 (1996).
- 31 J. H. C. Cornelissen and H. ter Steege. *J. Trop. Ecol.* **5**, 131-150 (1989).
- 32 J. K. Frei and C. H. Dodson. *Bull. Torrey Bot. Club* **99**, 301-307 (1972).
- 33 T. Goward. *Acta Bot. Fenn.* **150**, 31-38 (1994).
- 34 P. N. Neitlich and B. McCune. *Cons. Biol.* **11**, 172-182 (1997).
- 35 M. W. Chase. *Selbyana* **10**, 24-30 (1987).
- 36 G. Zotz. *Selbyana* **16**, 150-154 (1995).
- 37 F. R. Lambert and A. G. Marshall A.G. *J. Ecol.* **79**, 793-809 (1991).
- 38 L. Yueh Kwong and P. Ashton. *Trends Ecology Evolution* **5**, 395 (1990).
- 39 T. G. Laman. *Ecology* **76**, 2617-2626 (1995).
- 40 D. Skole and C. Tucker. *Science* **260**, 1905-1909 (1993).
- 41 I. M. Turner. *J. Appl. Ecol.* **33**, 200-209 (1996).
- 42 I. M. Turner, K. S. Chua, J. S. Y Ong, B. C. Soong and H. T. W. Tan. *Cons. Biol.* **10**, 1229-1244 (1995).
- 43 U. Hietz-Seifert, P. Hietz and S. Guevara. *Biol. Cons.* **75**, 103-111 (1996).
- 44 T. E. Lovejoy, R. O. Bierregaard Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart and M. B. Hays. In *Conservation Biology*.

- The Science of Scarcity* (M. E. Soulé ed.), pp. 257-285. Sinauer Assoc. Inc., Sunderland, Massachusetts (1986).
- 45 S. Guevara, S. E. Purata and E. Van der Maarel. *Vegetatio* **66**, 77-84 (1986).
 - 46 M. S. Baddeley and D. L. Hawksworth (eds.) *Air Pollution and Lichens*. The Athlone Press, London (1973).
 - 47 J. D. Martinez, M. Nathany and V. Dharmarjan. *Nature* **233**, 564-565 (1971).
 - 48 T. Strehl and E. A. Lobo. *Aquilo Ser. Bot.* **27**, 19-27 (1989).
 - 49 D. H. Benzing, J. Arditti, L. P. Nyman, P. J. Temple and J. P. Bennet. *Environm. Exp. Bot.* **32**, 25-32 (1992).
 - 50 R. L. Peters. In *Global Warming and Biological Diversity* (R. L. Peters and T. E. Lovejoy eds.), pp. 15-30. Yale Univ. Press, New Haven (1992).
 - 51 S. H. Schneider, L. Mearns and P. H. Gleick. In *Global Warming and Biological Diversity* (R. L. Peters and T. E. Lovejoy eds.), pp. 38-55. Yale Univ. Press, New Haven (1992).
 - 52 O. L. Phillips and A. H. Gentry. *Science* **263**, 954-958 (1994)
 - 53 O. L. Phillips. *Eniron. Cons.* **23**, 235-248 (1996).
 - 54 S. L. Pimm and A. M. Sugden. *Science* **263**, 933-934 (1994).
 - 55 Johns A. D. In *Tropical Deforestation and Species Extinction* (T. C. Whitmore and J. A. Sayer eds.), pp. 15-53. Chapman and Hall, London (1992).
 - 56 S. Gallina, S. Mandujano and A. Gonzalez-Romero. *Agrofor. Syst.* **33**, 13-27 (1996).
 - 57 D. Nestel, F. Dickschen, M. A. Altieri. *Biodiv. Conserv.* **2**, 70-78 (1993).
 - 58 I. Perfecto and R. Snelling. *Ecol. Appl.* **5**, 1084-1097 (1995).
 - 59 I. Perfecto, J. Vandermeer, P. Hanson and V. Cartín. *Biodiv. Cons.* **6**, 935-945 (1997).
 - 60 D. Nestel D. *Ecol. Econom.* **15**, 165-178 (1995).