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Impact of forest conversion and climate change on bryophytes in the Tropics

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Abstract

The species-rich tropical rain forests are disappearing rapidly due to growing pressures on the natural resources. Land use changes and global warming have been identified as drivers of biodiversity changes in the Tropics. This paper explores the impact of forest conversion on epiphytic bryophyte diversity along four disturbance gradients in tropical montane rain forest areas, three in tropical America (Bolivia, Ecuador, Costa Rica) and one in Indonesia (Sulawesi). By comparing epiphytic bryophyte diversity and microclimate in fallows, secondary forests, cacao agroforests and on isolated trees, insight is obtained in the responses of the bryophytes to forest alteration and their ability to recover in the disturbed habitats. We recorded 60-80 bryophyte species on a limited number of whole trees in primary montane forests of tropical America, and 150 in an Indonesian montane forest. The high diversity in the Indonesian forest coincided with unusually high richness of trees and herbs, and underlines the importance of the Malesian region as a global biodiversity hotspot. It is estimated that up to 200 species of bryophytes may occur in one hectare of montane rain forest. Species losses following forest conversion varied from 30-60% in secondary forests, old fallows and on isolated trees, to 70-80% in young fallows and cacao agroforests. The latter systems are of lesser conservation importance for bryophytes than previously believed. Canopy closure and microclimate are identified as principal drivers of bryophyte diversity along the disturbance gradient. Lower air humidity and higher air temperatures in the disturbed habitats lead to reduced species richness, decreased species turnover, loss of shade epiphytes, shifts of epiphytic species towards lower relative heights on the trees and an increase of weedy, pantropical species. The results indicate that recovery of bryophyte diversity in the regenerating tropical rain forests is a slow process that may take a hundred years or more.

Because of their tight coupling to atmospherical conditions, epiphytes are predictably sensitive to global warming. The recent northward expansion of bryophytes and lichens in Europe is first evidence of the impact of climate change on epiphytes in temperate regions. In the Tropics, where long-term distributional records are lacking, the possible impact of global warming on epiphytic bryophytes has been studied by means of a translocation experiment in the Bolivian Andes. The results of the experiment confirm the sensitivity of epiphytic bryophytes to atmospheric changes and indicate that a 2.5 °C warming may rapidly affect the rich epiphyte bryophyte communities of the topical montane forest.

Zusammenfassung

Die stetig steigende Nachfrage nach natürlichen Rohstoffen führt zum rapiden Verlust der artenreichen Regenwälder der Tropen. Eingriffe in natürliche Lebensräume sowie die globale Erwärmung wurden als die primären Faktoren von Veränderungen innerhalb der tropischen Biodiversität erkannt. Dieser Beitrag beschreibt den Einfluss der forst- und landwirtschaftlichen Intensivierung auf die Diversität von epiphytischen Bryophyten entlang von vier

Störungsgradienten in tropischen Bergregenwäldern in Südamerika (Bolivien, Ecuador und Costa Rica) und Indonesien (Sulawesi). Vergleichende Betrachtungen der epiphytischen Moosdiversität und des Mikroklimas im Brachland, in Kakaoagroforsten, in Kakao-Waldgärten, an freistehenden Waldbäumen und in Sekundärwäldern verschiedener Altersgruppen geben Aufschluß über die Reaktion von Moosen auf die Umwandlung von Wäldern und die Regenerationsfähigkeit nach forstwirtschaftlichen Maßnahmen bzw. einer Entwaldung. Wir fanden 60-80 Bryophytenarten an 5-10 Bäumen in ungestörten, tropischen Bergregenwäldern Südamerikas und 150 Arten in indonesischen Primärwäldern. Letztere Größenordnung stimmt mit der ungewöhnlichen Baum- und Kräutervielfalt dieser Region überein und unterstreicht die Bedeutung der malesischen Region als hotspot globaler Biodiversität. Die Moosdiversität in einem Hektar ungestörten Bergregenwaldes wird auf 75-200 Arten geschätzt. Der Verlust von Waldarten variiert zwischen 30-60% in Sekundärwäldern, älteren Brachen und freistehenden Waldbäumen zu 70-80% in jungen Brachen und Agroforsten. Sowohl die Kronendachdichte als auch das Mikroklima konnten als die grundlegenden Faktoren, welche die Diversität der epiphytischen Moose entlang von Störungsgradienten beeinflussen, bestimmt werden. Die geringere Luftfeuchtigkeit und die höheren Temperaturen in gestörten Habitaten führen hier zu einer Abnahme des Artenreichtums, dem Verlust von Schattenarten, dem Herabwandern von epiphytischen Arten aus dem Kronenbereich zu niedrigeren relativen Höhen entlang des Baumes und der Zunahme von häufigen, wuchernden pantropischen Arten der epiphytischen Bryophyten. Diese Ergebnisse verdeutlichen den geringen Wert von Agroforsten für die Arterhaltung von epiphytischen Moosen aus Primärwäldern und den langsamen, Jahrhunderte umspannenden Prozeß der Wiederansiedelung von Waldarten in sekundären Tropenwäldern.

Aufgrund ihrer engen Abhängigkeit von microklimatischen Bedingungen ihres Lebensraumes sind Epiphyten erwartungsgemäß empfindlich im Bezug auf die globale Erwärmung. Die jüngste nördliche Ausweitung der Verbreitungsgebiete von Moosen und Flechten Europas ist ein erster Beweis für den Einfluss des Klimawandels auf die Epiphyten der temperaten Zonen. Da Langzeitstudien zu deren Verbreitung innerhalb der Tropen fehlen, wurde der mögliche Einfluss von globaler Erwärmung auf epiphytische Bryophyten mittels eines Translokationsexperimentes in den bolivianischen Anden untersucht. Dieses bestätigt die Sensibilität von epiphytischen Moosen auf den Klimawechsel und zeigt, dass schon eine Erwärmung um 2.5°C einen maßgeblichen Einfluss auf die reichen, epiphytischen Bryophytengesellschaften der tropischen Regenwälder hat.

1. Introduction

Bryophytes are with ca. 15,000 species the second largest group of the land plants and are worldwide in distribution. More than half of the species (ca. 8,000) occur in the tropics, which harbor about five times more species than Europe and are the centre of diversity for many groups of bryophytes (FRAHM 2003). Much of this diversity is found in the tropical rain forests, especially in montane rain forests and cloud forests where thick epiphytic bryophyte mats may play an important role in the water balance and nutrient cycles of the forest (PÓCS 1980, NADKARNI 1984, HOFSTEDE et al. 1994; but see HÖLSCHER et al. 2004). The permanently humid microclimate in these forests favors the growth of the poikilohydric bryophytes, resulting in high species diversity and biomass. The increase of bryophyte abundance towards higher elevations and with increased humidity is one of the most striking features of bryophyte distribution in the tropics and serves to classify rain forests and cloud forests in different types (FRAHM & GRADSTEIN 1991, GRADSTEIN et al. in press). Bryophyte communities of the tropical rain forests have been described by KÜRSCHNER & PAROLLY (1999).

Most of the bryophytes within the rain forest are epiphytes; terrestrial species mainly occur in upper montane forests above 2000 m, where the forest soils are covered by a layer of humus favoring the growth of terrestrial bryophytes (GRADSTEIN & PÓCS 1989, HOLZ et al. 2002). Within the forest, epiphytic bryophytes are not evenly distributed but show distinctive distribution patterns which can be related to the microclimatic preferences of individual species (SILLETT & ANTOINE 2004, LÉON-VARGAS et al. 2006). Some occur exclusively in the moist, shaded understory of the forest, others are found only in the drier, outer portions of the tree crowns high above the ground; some species occur in both habitats. Following RICHARDS (1984), these ecological types are called „shade epiphytes“, „sun epiphytes“ and „generalists”, respectively. Shade epiphytes can often be recognized by their exposed habit (e.g., tufts, pendants, carpets), maximising exposure to light in the relatively poorly illuminated environment, while sun epiphytes are usually compact and prostrate to reduce water loss in the relatively dry, exposed outer canopy of the forest (MÄGDEFRAU 1982).

Community composition of epiphytic bryophytes in tropical forests is predominantly shaped by micro-environmental conditions, due to the excellent dispersal ability of bryophyte species (MOTA et al. 2009). The processes governing species composition of tropical bryophyte communities are very different from those of other tropical plant groups, which are mostly driven by dispersal, with the possible exception of ferns (CONDIT et al. 2002; TUOMISTO et al. 2003).

In most rain forests, more than 50% of the bryophyte species are restricted to the forest canopy. Therefore, study of bryophyte diversity and ecology of the tropical rain forest requires the use of special methods for access to the forest canopy. Many techniques have been described (MITCHELL et al. 2002); of these, tree climbing using the single rope technique has proven to be the most effective for epiphyte studies, allowing field work in many different locations at low costs (TER STEEGE & CORNELISSEN 1989). Bases on minimum area studies and species accumulation curves, GRADSTEIN et al. (2003) found that inventory of minimally 5 whole trees in one hectare may yield a representative sample of the epiphytic bryophyte flora of a homogeneous stand of forest. Trees should be standing well apart and differ in bark structure (smooth, rough) to optimize sampling results. In addition, treelets in the forest understory, which harbor a different bryophyte flora, should be sampled (SPORN et al. submitted).

2. Impact of forest conversion

The species-rich tropical rain forests are disappearing rapidly due to growing pressures on the natural resources. Land use changes have been identified as the main current driver of biodiversity changes in the Tropics (SALA et al. 2000). Over 5 million hectares of pristine tropical forests are disturbed and transformed into agricultural land each year (ACHARD et al. 2002) and the majority of remaining tropical forests undergo frequent disturbance by human activities, such as timber extraction and agroforestry. The rapid conversion of the tropical rain forests poses the question as to the fate of the rich epiphyte communities of these forest (GRADSTEIN 1992). Can they survive in the degraded forests, in plantations or on remnant trees in pastures? Are they able to re-establish in the regenerating secondary forests and if so, how fast is their recovery?

We have studied the impact of forest conversion on epiphytic bryophyte diversity in different habitats along four different land use gradients in montane rain forest areas in tropical America and Indonesia (Table 1; Fig. 1): (1) Primary submontane rain forest and fallows (young, old) on the eastern slope of the Bolivian Andes in the “Yungas” of La Paz (600 m);

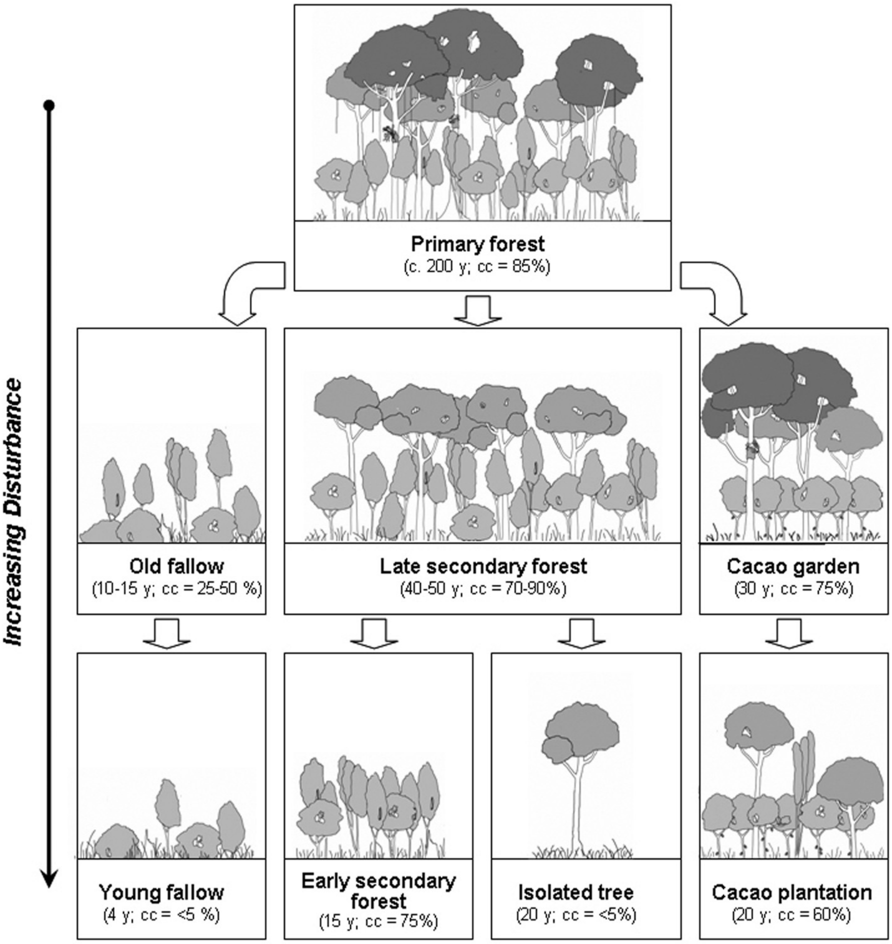

Figure 1: Disturbance gradients inventoried in this study. y, year (age of habitat); cc, canopy cover.

(2) Primary and secondary (young, old) upper montane rain forests dominated by *Quercus copeyensis* and *C. costaricensis* in the Cordillera de Talamanca, Costa Rica (2900 m); comprehensive descriptions of these oak forests were provided by KAPPELLE (1996, 2006); (3) Primary and old secondary montane rain forests and isolated trees in pastures in southern Ecuador near the "Estacion Biológica San Francisco" (1900 m), the fieldwork site of Research Units 816 of the German Research Foundation (BECK et al. 2008); and (4) Primary submontane rain forest and cacao agroforests (cacao gardens with natural shade trees, cacao plantations with planted shade trees) at the margins of Lore Lindu Park, Central Sulawesi, Indonesia (800-1100 m), the fieldwork site of the German-Indonesian research program "Stability of Rainforest Margins in Indonesia" (TSCHARNTKE et al. 2007).

In all locations we sampled epiphytic bryophytes on mature canopy trees, from the trunk base to the outer portions of the crown, by using the single rope tree climbing technique (TER STEEGE & CORNELISSEN 1988; MITCHELL et al. 2002). The number of trees sampled varied from (3)5-10 per habitat type and was uniform for each gradient, with one exception

(Table 1). Small plots were inventoried in different height zones (trunk base, trunk, lower canopy, middle canopy, outer canopy) on the trees following the protocol for representative sampling of epiphytic bryophytes in tropical rain forest (GRADSTEIN et al. 2003). In addition, we measured air humidity and air temperature at different heights in the forest and paid attention to the structure of the forest and tree characteristics (tree architecture, bark structure, etc.). Species identification was carried out using the *Guide to the Bryophytes of Tropical America* (GRADSTEIN et al. 2001) and other taxonomic literature.

Table 1. Description of study sites.

Country	Elevation	Habitat types studied	Nr. of trees sampled per habitat type	Reference
Bolivia	600 m	Primary forest, fallows (4, 10-15 y)	6(3)[1]	ACEBEY et al. 2003
Costa Rica	2900 m	Primary forest, secondary forests (15, 40 y)	5	HOLZ & GRADSTEIN 2005
Ecuador	1900 m	Primary forest, secondary forest (40 y), isolated trees	10	NÖSKE 2005 NÖSKE et al. 2008
Indonesia	800-1100 m	Primary forest, cacao gardens (30 y), cacao plantations (20 y)	8	ARYANTI et al. 2008 SPORN 2008 SPORN et al. 2009

[1] Three trees sampled in 4 y old fallow, six in other habitats.

Species richness in undisturbed rain forest. – Species richness of epiphytic bryophytes on canopy trees in undisturbed tropical rain forest was highest in Sulawesi, Indonesia, where 150 species were recorded on eight trees, in two hectares of submontane forest (Fig. 2D). This figure is the highest ever recorded on rain forest trees; in other study sites species richness varied between 60-80 species, on 5-10 trees (in 1-2 ha). A similarly high number as found in Indonesia has only been recorded in a montane cloud forest of Costa Rica (GRADSTEIN et al. 2001) where a slightly larger number of trees (10) were inventoried, in a larger area (4 ha). Since cloud forests are generally richer in epiphyte species than rain forests, the number of species recorded in the Costa Rican inventory was nearer to the average.

GRADSTEIN (2003) estimated that the total number of epiphytic bryophyte species in one hectare of tropical rain forest is about 40-120 in lowland forest and 75-150 in montane forest. These estimates also included species occurring on shrubs, rotten logs and soil, which add another 15-30% to the total bryophyte flora (HOLZ et al. 2002; SPORN et al. submitted). The data from Sulawesi therefore suggest that species richness in a hectare of montane rain forest may well be 200+ species. Interestingly, species richness of trees and terrestrial herbs in the rain forest of Sulawesi was also unusually high (KESSLER et al. 2005; CICUZZA et al. in press), underlining the importance of the Malesian region as a global biodiversity hotspot (MEYERS et al. 2000).

Species richness along the disturbance gradient. – In the majority of the study sites bryophyte species richness declined from primary forest towards the disturbed habitats (Fig. 2). Losses varied somewhat among different groups of bryophytes but were usually the same for mosses and liverworts except in the Bolivian fallows, where moss species richness declined more dramatically than that of liverworts (ACEBEY et al. 2003). Species losses were highest in the young, 4 y old fallows of Bolivia and the cacao agroforests of Indonesia, where species richness was reduced to about one third of that in the primary forest. The reduction correlated with the dryer microclimate of the disturbed habitats and the different vegetation structure, with a more open canopy and a predominance of fast-growing, smooth-barked trees with

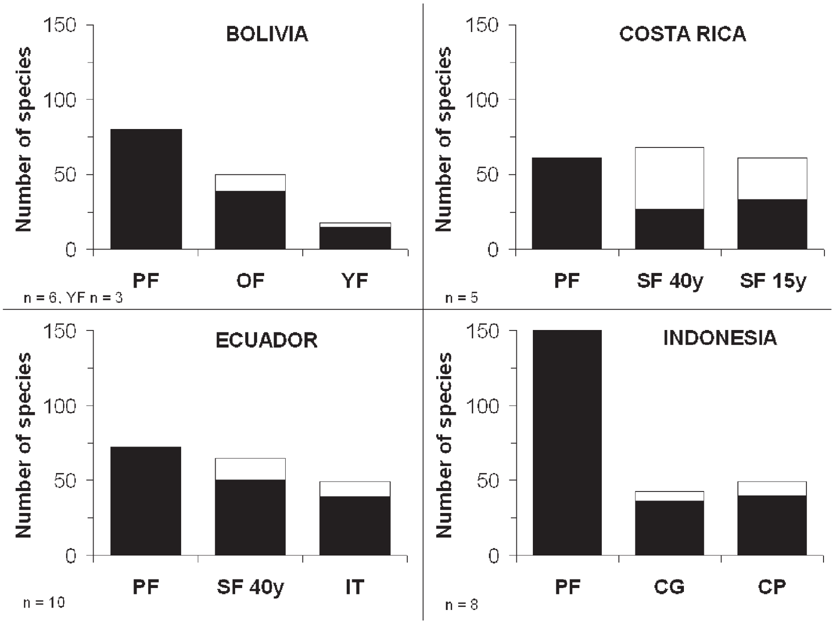

Figure 2: Species richness and turnover of epiphytic bryophytes in different habitats. Black: primary forest species. White: other species. CG, cacao garden; CP, cacao plantation; F, fallow; IT, isolated tree; OF, old (10-15 y) fallow; PF, primary forest; SF, secondary forest; YF, young (4 y) fallow. Note that in Bolivia only three trees were sampled in young fallows and six in old fallows and primary forest.

little-branched crowns and oblique (instead of horizontal) branches. This type of crown architecture and a smooth bark are unfavourable for the establishment of many epiphyte species. Species reduction was much greater in young fallows than in old, 10-15 y old fallows, where trees were larger and the vegetation more dense (but note that richness figures are somewhat biased by the lower number of trees sampled in young fallows).

In the agroforests we had expected more species in the cacao gardens with remnant forest trees than in the cacao plantations with planted shade trees; instead, plantations had slightly higher species numbers (Fig. 2). This was probably due to the presence of a rivulet, resulting in a somewhat moister microclimate and a more favorable environment for the establishment of epiphytic bryophytes (SPORN et al. 2009a).

In the Ecuadorian research site we recorded a 10% species decline in old secondary forest and a 32% decline on isolated, remnant forest trees in pastures. The relatively minor richness decline in the secondary forest was explained by the structure of the forest, which resembled that of the primary forest except for the lower canopy and the abundance of fast-growing, early successional tree species. The species decline on the isolated trees correlated with a significantly dryer microclimate on these trees and a breakdown of the vertical microclimatic gradient characteristic of the forest (NÖSKE 2005). The pasture trees had as many bryophyte species as cacao plantations of Indonesia and about twice as many as the submontane fallows of Bolivia. Species losses, however, were much less severe on isolated trees than in the two other habitat types (30% vs 65-70%), which underlines the importance of pasture trees for biodiversity conservation (GUEVARA et al. 1986). Interestingly, richness losses on isolated trees were similar (30%) to those reported for pasture trees in a montane cloud forest area of Costa Rica by SILLETT et al. (1995), but much lower than the figures (50-60%) of MERWIN et al. (2001) from the same area and of DREHWALD (2005) from the Andes of Ecuador and Peru. The data of DREHWALD were based on sampling of tree bases, those of MERWIN et al. on a general floristic survey including a random number of forest and pasture trees. The comparison illustrates the notion that different inventory methods may lead to different results and underlines the need for a standardized approach (WOLF et al. 2009).

As opposed to the other study sites we found no decline of epiphytic species richness in secondary oak forests of Costa Rica (HOLZ & GRADSTEIN 2005a). Richness in 15 y old secondary forest was similar to that in primary forest and 40 y old secondary forest had more species than primary forest (Fig. 2). An explanation for this unexpected finding was the dense canopy of the secondary forest, with 75% closure in primary and young secondary forest and 90% closure in the old secondary forest. The very dense canopy of the old secondary forest resulted in a more shaded environment than in the primary and early secondary forest and a permanently high atmospheric humidity. This should have enhanced the growth of the poikilohydric bryophyte species.

Species turnover along the disturbance gradient. – In all disturbed sites a significant loss of natural forest species occurred (Fig. 2). The loss was highest in cacao agroforests and very young fallows (75%), and somewhat less (30-60%) in secondary forests and on remnant trees. The low representation of forest bryophytes in the investigated cacao agroforest was unexpected and does not support the assumption that shaded cacao agroforests play an important role in the conservation of forest biodiversity (e.g., REITSMA et al., 2001; ANDERSSON & GRADSTEIN, 2005). Instead, our results indicate that the conservation importance of these agroforests for epiphytic bryophytes is limited.

Replacement of the forest bryophyte flora by non-forest taxa in the disturbed habitats was usually low and less than 25%, except in the secondary oak forests of Costa Rica where 45-60% of the species collected were not found in the primary forest (Fig. 2). Many of these had apparently migrated down-slope into the forest from the adjacent páramo vegetation, where they were common on twigs and branches of shrubs (HOLZ & GRADSTEIN 2005b). The same was seen in the diversity of the vascular plants (trees, shrubs, herbs), which had also increased in the secondary forest due to the establishment of páramo species in the forest (KAPPELLE et al. 1995).

Interestingly, 50-60% of the primary forest flora had already recovered in young (10-15 y old) secondary forest, but in old secondary forest recovery remained at 40-70%. The reason for the very uneven pace of the recovery process is unclear and needs further consideration. The different species compositions of the primary and old secondary forests support the notion that recovery of the flora of the primary forest is a very slow process (NADKARNI 2000). COSTA (1999) and HOLZ & GRADSTEIN (2005) estimated that full recovery may take at least 80-100 years, and possibly centuries when following a non-linear trend.

Shade epiphytes, sun epiphytes and generalists along the disturbance gradient. – It is usually assumed that the drought-intolerant shade epiphytes of the forest understory are more sensitive to disturbance and disruption of the forest canopy than the drought-tolerant sun epiphytes and generalists (e.g. COSTA 1999). The representation of shade epiphytes along the disturbance gradients is shown in Fig. 3. The figure shows a significant loss of shade epiphytes in fallows, agroforests and on isolated trees. All of these were habitats with a rather open, disrupted canopy and a relatively dry microclimate. No decline of shade epiphytes, however, occured in secondary forests with a closed canopy. The data are suggestive of the importance of an intact, closed canopy and permanently high atmospheric humidity for the conservation of the understory flora of the primary forest.

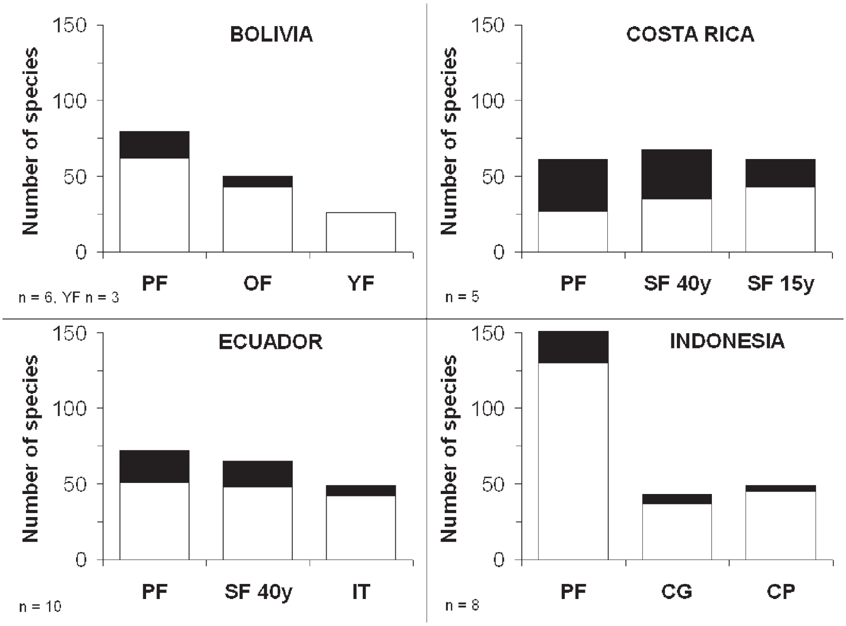

Figure 3: Richness of epiphyte types in different habitats. Black: shade epiphytes; white: sun epiphytes and generalists.

The importance of the microclimate has also been demonstrated in a comparison of the bryophyte diversity on understory treelets in submontane rain forest and on cacao trees in agroforests (SPORN et al. 2009a). The microclimate of the agroforests differed from that of the forest by higher air temperature and significantly lower air humidity during the afternoon. Species richness of bryophytes in the two habitats was similar, but species composition changed markedly from the natural forest to the cacao trees. The turnover towards the cacao trees was largely due to the loss of shade epiphytes and their replacement by sun epiphytes. In addition, a few species had established on the cacao trees that were not found in the forest. These were mostly weedy, pantropical species that are common in open, secondary habitats throughout the Tropics (SPORN et al. 2009b). In thus appeared that the loss of biodiversity in the agroforests was greater than the gain.

A further phenomenon observed along the disturbance gradients was a significant vertical shift of epiphytic species towards lower relative heights on the trees in the disturbed habitats (Fig. 4). Indeed, the canopies of the early secondary forest were almost devoid of epiphytes, as is seen in many temperate forests. As shown by ACEBEY et al. (2003), the distribution shifts are reflective of the changed microclimatic conditions in the disturbed habitats. These authors showed that air humidity and temperatures at trunk bases in young secondary forest were similar to those at 25 m height in the primary forest. The drier and warmer microclimate, as well as higher light intensities in the understory of the secondary forest, may explain why sun epiphytes and generalist occur at low heights in these forests and why shade epiphytes are lacking or scarce.

The vertical distribution shifts of epiphyte species due to forest disturbance and microclimatic change have been little documented and deserve more attention. Study of this phenomenon may help improving our understanding of the niches of the epiphyte species, and the changes that may occur due to forest disturbance.

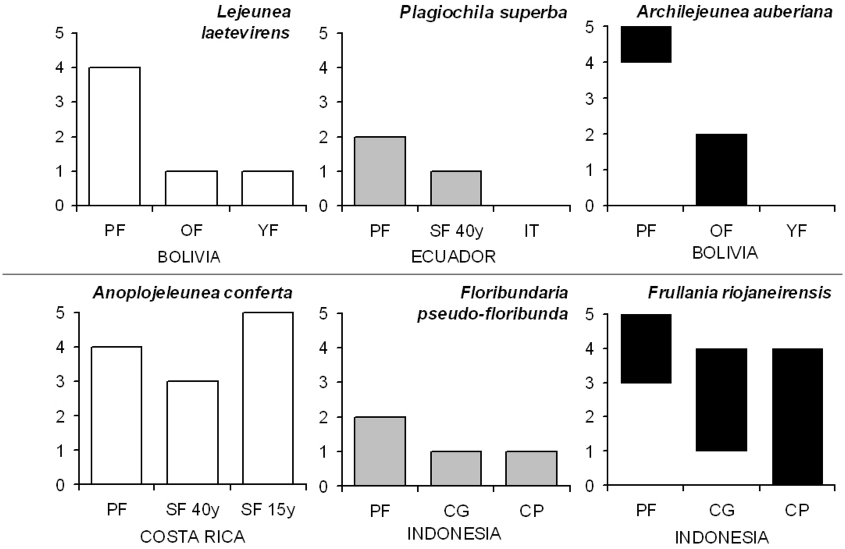

Figure 4: Vertical distribution of selected epiphytic bryophytes in different habitats. Black bars: sun epiphyte. Gray bars: shade epiphyte. White bars: generalists. Abbreviations as in Fig. 1. 1-5: height zones on the tree (1, trunk base; 2, trunk, 3 lower canopy; 4, middle canopy, 5 outer canopy).

Bryophyte species as disturbance indicators. Bryophytes are good ecological indicators and have frequently been used for monitoring air and water pollution, heavy metal contamination, and various other applications (FRAHM 1998). They are also sensitive indicators of tropical forest habitats (GRADSTEIN et al. 2001). Recently, first attempts have been made to identify bryophyte species that may be used as indicators of tropical forest disturbance (DREHWALD 2005; HOLZ & GRADSTEIN 2005; NÖSKE 2005). The study by DREHWALD focused on tree bases, the other two studies on whole trees. Moreover, the latter two studies used the method of DUFRENE & LEGENDRE (1997) for identification of indicator species, which includes statistical testing of species indicator values calculated based on abundance and faithfulness. Each study resulted in a different list of potential indicator species; *Plagiochila heterophylla* (undisturbed forest) and *Lejeunea flava* (disturbed forest) were the only species resolved as indicators in more than one study. The data indicate that usage of species of disturbance indicators may work only at the local or regional scale, and requires application of standard methodology. Also, some conceptual problems relative to disturbance indication by bryophyte species need to be considered (HOLZ & GRADSTEIN 2005). As argued by the latter authors, species distribution patterns do not necessarily reflect the type and amount of damage inflicted upon the forest. Instead, they are indicative of microclimatic and substrate conditions in the secondary microhabitat. Generalizations may therefore be misleading. We recommend that for the purpose of bioindication of forest disturbance, more work should be done on qualitative and quantitative comparisions of sun and shade epiphytes in different land use systems (see above). Because of their adaptation to different microclimatic conditions, these guilds might work well as sensitive ecological indicators of habitat changes.

Concluding remarks. – Our studies in Bolivia, Costa Rica, Ecuador and Indonesia are first data on the impact of forest conversion on bryophytes in the Tropics. They need to be consolidated by further fieldwork, and by field and greenhouse experiments. Canopy closure and microclimate appear to be the main drivers of epiphytic bryophyte diversity. The data support the notion that maintainance of canopy cover is crucial to the conservation of tropical rain forest biodiversity (STEFFAN-DEWENTER et al. 2007). In addition, tree characteristics (architecture, bark structure) play a role. Evidence is also arising that bryophytes are more sensitive to disturbance than other groups of epiphytes. A comparison of epiphytic bryophyte and lichen diversity along the disturbance gradient in southern Ecuador (Fig. 1) showed that about 40% of the bryophyte species occurred with high fidelity in only one of the three habitat types, as compared with only 10% of lichen species (NÖSKE et al. 2008). And in arid forest areas of northern Ecuador, where microclimatic conditions in open, disturbed habitats and dense, natural forest are rather similar, WERNER & GRADSTEIN (2008) found no decline of vascular epiphyte diversity towards the open, disturbed habitats. Bryophyte diversity, however, significantly declined, in spite of the negligent microclimatic changes along the disturbance gradient. These data are highly suggestive of the sensitivity of epiphytic bryophytes to forest disturbance.

3. Impact of global warming

Global warming has been identified as a major driver of biodiversity changes (SALA et al. 2000) and is worldwide gaining in importance. LOVEJOY & HANNAH (2005) proposed that global warming impacts biological organisms in four different ways: (1) by changes in the local abundance of species; (2) by changes in community structure; (3) by habitat shifts, with species moving towards habitats with cooler microclimates; and (4) by range shifts, with species moving towards higher latitudes or elevations. However, most of the evidence for climate change effects on biodiversity is derived from modelling or from observations on the behavior of animal taxa (birds, butterflies, amphibia, etc.). Empirical studies on plants are still scarce and only very few deal with epiphytes, in spite of their predicted sensitivity to global warming (ZOTZ & BADER 2008).

The first empirical data on the impact of global warming on non-vascular epiphytes are coming from work in Europe. Based on analysis of historical herbarium records, FRAHM & KLAUS (1997, 2001) found that 32 subtropical bryophyte species had extended their ranges several hundred kilometres east- and north-eastwards into Central Europe during the 20th century. These range extensions correlated with an increase of the mean winter temperature by ca. 1.5 °C. In The Netherlands, VAN HERK et al. (2002) observed significant shifts in the geographical ranges of epiphytic lichens based on a monitoring of the lichen flora in permanent plots during almost twenty five years. During the first fifteen years, significant floristic changes occurred in relation to changes in air pollution levels. In later years, however, when changes in air pollution levels became insignificant, major range shifts occurred which correlated significantly with a measured rise in air temperature. A significant increase in the frequency of warm-temperate species was observed, and a significant decrease of cold-temperate ones. Moreover, several tropical species were newly detected in the country. The recent expansion of tropical and warm-temperate bryophytes and lichens in Europe is striking first evidence of the possible impact of global warming on epiphytes.

In the Tropics, an assessment of the possible impact of global warming on epiphytic bryophytes is hampered by lack of long-term distribution records and monitoring. Nevertheless, first evidence is now arising from transplantation experiments. In the high Andes of Bolivia, JÁCOME et al. (2009) carried out a translocation experiment on whole epiphytic bryophyte communities. Branches of one meter length covered by dense mats of epiphytic bryophytes were cut at 3000 m and moved to a warmer climate downslope, to 2700 m (1.5°C increase) and to 2500 m (2.5°C increase). On each branch the cover of individual bryophyte species at the beginning of the experiment, and after one and two years, was recorded. Relocated branches at 3000 m served as controls. After two years, epiphyte communities of branches translocated to 2500 m had changed more strongly than those at 2700 m and 3000 m, both in terms of community composition as well as in community structure. The changes occurred gradually and communities translocated to 2700 m did not differ significantly from the communities at other elevations. The experiment showed that exposure to air temperature increases of 2.5 °C have a measurable effect on the structure of epiphyte bryophyte communities of tropical montane forest within two years.

The results of the translocation experiment in Bolivia confirm the sensitivity of epiphytic bryophytes to atmospheric changes and predict that changes in the climatic regimes of tropical montane forests will rapidly affect the rich epiphyte bryophyte communities. The data indicate that the response of these epiphyte communities to global warming will not be abrupt but will take place in a gradual manner. JÁCOME et al. (2009) therefore suggested that essential ecosystem functions of the epiphytic bryophyte communities of the study site, such as nutrient cycling and water retention, would not be seriously affected by the predicted global warming. Nevertheless, the conclusions should be appreciated with care since responses detected over short-time periods may not necessarily reflect long-term effects on biodiversity (HOLLISTER et al. 2005). Monitoring of community responses over longer periods of time is necessary to ascertain the effects of global warming on tropical bryophytes.

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