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Foliicolous lichens as model organisms to study tropical rainforest ecology: background, data, and protocols

Foliikole Flechten als Modellorgamismen für das Studium der ökologie tropischer Regenwälder: Hintergrund, Daten, und Protokolle

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Key words: Biodiversity, biofeedback mechanism, diffuse site factor, diversity maintenance, gap dynamics, intermediate disturbances, microclimatic zonation, Spacing mechanism.

Schlagwörter: Biodiversität, "Biofeedback"-Mechanismus, Lichteinfall, Aufrechterhaltung der Biodiversität, Lichtlückendynamik, mittlere Störungen, Mikroklimazonierung, "spacing"-Mechanismus.

Summary: Foliicolous lichens inhabit the surface of living leaves of vascular plants in tropical rainforests. Their potential use as models to study aspects of tropical rainforest ecology is demonstrated, and different protocols to work with foliicolous lichens are laid out. The main factor governing species composition of foliicolous lichens on individual leaves is relative light intensity, or diffuse site factor (DSF). Diffuse site factor preferences are known for more than 300 species, and logarithmically scaled DSF indices can be assigned to five categories: (1) = shaded understory (DSF = 0–2%), (2) transition towards clearings (DSF = 2–5%), (3) clearings (DSF = 5–13%), (4) transition towards canopy (DSF = 13–35%), (5) canopy (DSF = 35–100%). It is shown how these indices can be used to assess microclimatic zonation in tropical rainforests. Community and population structure of trees in tropical rainforests is influenced by gap dynamics, the creation of natural clearings through tree falls. The lower rainforest strata form a mosaic of a continuous shaded understory and discontinuous patches of partly exposed clearings, and two distinct foliicolous lichen communities can be found in these different environments: the shady un-

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derstory community and the light gap community. Species of the light gap community face difficulties in dispersing through the shaded understory into new clearings. High frequency of clearings in space and time (high gap dynamics), shifts lichen diaspore dispersal towards deterministic patterns, while low frequency causes stochastic patterns. It is shown how foliicolous lichen community structure can be assessed by means of an association of species test and how this can be used to model light gap dynamics. Tropical rainforests exhibit high species density. Different hypotheses have been developed to explain high species richness at community scale or below. Certain models address the phenomenon of coexistence in space and time of ecologically equivalent species with a high degree of niche overlap. The Janzen-Huston-Connell models predict spacing and intermediate disturbances to prevent succession from reaching a low diversity climax stage and instead to maintain a dynamic equilibrium at a high diversity stage. While this model is difficult to be tested on tree communities in long-term studies, foliicolous lichens show similar diversity patterns and, due to their short life cycles and their potential to be experimentally manipulated, can be used to test the Janzen-Huston-Connell model and alternative hypotheses concerning maintenance of diversity at the small scale.

Zusammenfassung: Foliikole Flechten wachsen auf der Oberfläche lebender Blätter von Gefässpflanzen in tropischen Regenwäldern. Mögliche Anwendungen als Modellorganismen für das Studium der ökologie tropischer Regenwälder werden aufgezeigt, zusammen mit unterschiedlichen Protokollen für das Arbeiten mit foliikolen Flechten. Die Artenzusammensetzung foliikoler Flechten auf einzelnen Blättern wird im wesentlichen durch den Lichteinfall reguliert, auch als "diffuse site factor" (DSF) bezeichnet. Lichteinfallpräferenzen sind für mehr als 300 foliikole Flechtenarten bekannt und logarithmisch unterteilte DSF-Zeigerwerte können in fünf Klassen unterteilt werden: (1) = beschattetes Unterholz (DSF = 0-2%), (2) übergang zu Lichtlücken (DSF = 2-5%), (3) Lichtlücken (DSF = 5-13%), (4) übergang zum Kronendach (DSF = 13-35%), (5) Kronendach (DSF = 35-100%). Die Anwendung dieser Zeigerwerte zur Analyse der Mikroklimazonierung in tropischen Regenwäldern wird aufgezeigt. Die Struktur von Baumgemeinschaften und Populationen in tropischen Regenwäldern steht unter dem Einfluss der Dynamik von Lichtlücken, welche durch den Fall von Bäumen verursacht wird. Unterholzschichten formen ein Mosaik aus zusammenhängenden, beschatteten Bereichen und zerstreuten Lichtlücken und zwei unterschiedliche foliikole Flechtengemeinschaften haben sich daran angepasst: die Unterholz- und die Lichtlückengemeinschaft. Arten der Lichtlückengemeinschaft müssen sich durch das beschattete Unterholz hin zu neuen Lichtlücken ausbreiten, was Probleme bereitet. Eine hohe räumliche und zeitliche Dichte von Lichtlücken begünstigt die Ausbreitung von Lichtlückenarten und führt zu eher deterministisch bestimmten Assoziationen in gegebenen Lichtlücken, wohingegen eine geringe Dichte eher stochastische Assoziationen erzeugt. Die Eignung des "association of species tests" zur Analyse solcher Gemeinschaften und der Modellierung der Lichtlückendynamik wird aufgezeigt. Tropische Regenwälder weisen eine hohe Artendichte auf. Unterschiedliche Hypothesen

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wurden entwickelt, um diese Artendichte zu erklären, und einige verweisen auf das Phänomen der räumlichen und zeitlichen Koexistenz ökologisch equivalenter Arten mit hoher Nischenüberlappung. Das Janzen-Huston-Connell-Modell geht davon aus, dass "spacing" und mittlere Störungen verhindern, dass die Sukzession einer Artengemeinschaft ein Klimazstadium geringer Diversität erreicht; anstelle dessen verweilt die Sukzession in einem dynamischen Gleichgewicht mit hoher Diversität. Dieses Modell ist an langlebigen Organismen wie Bäumen schwer zu testen, aber foliikole Flechten zeigen ähnliche Diversitätsmuster und können, aufgrund ihres kurzen Lebenszyklus und der Tatsache, dass sie experimentell leicht manipuliert werden können, dazu benutzt werden, das Janzen-Huston-Connell-Modell und alternative Hypothesen im Bereich der Biodiversitätsforschung zu testen.

Lichens are prominent components of cool-temperate and tropical-montane ecosystems. Yet, evidence emerges that lichens exhibit their highest diversity in tropical rainforests (SIPMAN & HARRIS 1989; MONTFOORT & EK 1990; GRADSTEIN 1992; WOLF 1993; GRADSTEIN et al. 1996; APTROOT 1997a; APTROOT & SIPMAN 1997; KOMPOSCH & HAFELLNER 1999, 2000, 2002; SIPMAN & APTROOT 2001; COPPINS & WOLSELEY 2002). APROOT (1997b) recorded 173 lichen species on a tree in Papua New Guinea, and up to 80 foliicolous species where found on individual leaves in Costa Rica and Ecuador (LÜCKING 1995a; LÜCKING & MATZER 2001). The number of lichen species to occur in Costa Rica, within an area of 50,000 km^2, is estimated at 3,000 (LÜCKING et al. 2004). A tropical lichen workshop at Las Cruces Biological Station in Costa Rica revealed 450 species after a single day of collecting, and conservative estimates for the total number of lichen species at La Selva Biological Station reach 600 species, half of which are foliicolous taxa (LÜCKING 1999a, 2001a). This figure corresponds to 30% of the entire lichen flora of the British Islands (PURVIS et al. 1992), yet within an area of a few hectares.

Foliicolous lichens inhabit the surface of living leaves of vascular plants (SANTESSON 1952; SÉRUSIAUX 1977, 1989; LÜCKING 2001b). They are among the few groups of organisms essentially characteristic of the tropical rainforest in its proper sense, that is excluding upper montane forests and mixed tropical-subtropical or tropical-temperate forests. Contrary to most other lichens (ARMSTRONG 1988), foliicolous species exhibit short life cycles, producing their fruit bodies and vegetative propagules within few months after establishing a new thallus. Except for the genus *Strigula*, foliicolous lichens do not directly interact with the substrate and do not penetrate the leaf cuticle; they also grow easily on artificial substrata, such as glass and plastic (SIPMAN 1994; LÜCKING 1998a; SANDERS 2001, 2002; SANDERS & LÜCKING 2002; LÜCKING & BERNECKER-LÜCKING 2002, 2005).

The use of lichens as bioindicators has a long-standing tradition (GRINDON 1859; NYLANDER 1866). Most such studies and applications focus on the assessment of air quality and other types of pollution monitoring (VARESCHI

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1953; BRODO 1961; FERRY et al. 1973; HAWKSWORTH & ROSE 1976; RICHARDSON 1987; SEAWARD 1992, 1993; KRANNER et al. 2002; NIMIS et al. 2002; MONGE-NÁJERA et al. 2002). It is well-established that lichens specifically respond to various abiotic environmental factors, such as light and substrate pH, and corresponding indices have been established and published for many species (WIRTH 1992). Tropical rainforests face other type of problems, such as selective logging and partial or complete deforestation due to land use change (SHUKLA et al. 1990; HOUGHTON 1991; GROOMBRIDGE 1992; DAVIS 1993; RUDEL & HOROWITZ 1993; ROMERO 1999; COSTA & FOLEY 2000; VAJPEYI 2001; WOOD & PORRO 2002), and lichens have been used to monitor such changes (KANTVILAS & MINCHIN 1989; WOLSELEY 1991, 1997, 2002; WOLSELEY & AGUIRRE-HUDSON 1991, 1997; GALLOWAY 1992). A central question in their sustainable management is how biodiversity affects the structure and functioning of the forest, and how biodiversity can be maintained in managed forests (GOLDSMITH 1987; PIELOU 1993; STRONG 1997).

Patterns and processes such as tree community and population structure, gap dynamics, epiphyte biomass and diversity, and microsite differentiation play important roles in the functioning of tropical rainforests, but we are far from understanding these phenomena sufficiently enough to translate them into applications in rainforest management. Ecological studies in the past three decades have shown that foliicolous lichens relate to various of the aforementioned phenomena, and are therefore excellent model organisms to study aspects of tropical rainforest ecology, such as microclimatic zonation, gap dynamics, and biodiversity maintenance (LÜCKING 1995a, b, 1997, 1998b, c, 1999a, b, c, 2001b; LÜCKING & BERNECKER 2000, 2002, 2005; LÜCKING & MATZER 2001).

In this paper, the theoretical background concerning these aspects is revised, and evidence is given how foliicolous lichen ecology relates to these phenomena. Protocols are outlined how foliicolous lichens can be used as models to study aspects of microclimatic zonation, gap dynamics, and diversity maintenance in tropical rainforests.

Microclimatic zonation

Theoretical background

According to the gradient hypothesis (GAUCH 1982; PUTMAN 1994), species have an optimal performance response and a variational amplitude with regard to a given environmental factor. The total of all abiotic and biotic factors, and the specific response to them, confines the ecological niche of a species (GRINNELL 1917; HUTCHINSON 1957; Rickleffs 1997). The niche is thereby a multidimensional space, where each species can be represented by a point indicatding the overlayed position of the means of its optimal responses along each dimension. In practice, many environmental factors, in particular those of abiotic

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nature, are correlated, and therefore, aspects of the ecological niche can be displayed with a reduced number of dimensions, such as in PCA and CCA techniques (GAUCH 1982; PIELOU 1984; TER BRAAK 1986; JONGMAN et al. 1995). The occurrence of certain plants and plant-like organisms, such as lichens, within a given space-time occurrence of an ecological niche, is usually sufficiently well-explained by a small set of environmental factors. Among these are substrate characteristics and microclimatic parameters.

While terrestrial plants chiefly depend on soil characteristics for their growth, epiphytes are more sensible to microclimatic parameters, due to their dependence on atmospheric input of nutrients and water (JOHANSSON 1974; PÓCS 1980; NADKARNI 1986; BENZING 1990; FRAHM & KÜRSCHNER 1992; WHITMORE 1998; LÜTTGE 1997; ZOTZ & HIETZ 2001). Microclimatic parameters are particularly important for atmospheric epiphytes that have little or no interaction with their substrate (BENZING 1980, 2000; GRIFFITHS & SMITH 1983; ZOTZ & HIETZ 2001). Besides certain vascular plants, such as bromeliads, orchids, and ferns, these include most bryophytes and lichens. Of particular interest for tropical rainforests are the foliicolous lichens, because of the almost complete absence of substrate interactions in these organisms, and because the occurrence of these lichens is an essentially tropical phenomenon (LÜCKING 2001b).

Foliicolous lichen data

Several studies investigated the response of foliicolous lichens to environmental parameters, including phorophyte leaf characteristics and microclimatic factors (NOWAK & WINKLER 1970, 1975; ROGERS & BARNES 1986; SÉRUSIAUX 1989; BARILLAS et al. 1993; COLEY et al. 1993; LÜCKING 1995a, b, 1998b, c, 1999a, b, c; CONRAN 1997; ANTHONY et al. 2002; HERRERA et al. 2004). Most studies agree in that there is no pronounced phorophyte specificity, except for subcuticular species in the genus *Strigula* and cases where phorophyte diversity is low, and that most species occur on a wide variety of different phorophyte types, including short-lived hairy and long-lived leathery leaves, palm leaves, and fern leaves, as well as artificial substrata such as plastic and glass (SIPMAN 1994; LÜCKING 1998a; SANDERS 2001, 2002; SANDERS & LÜCKING 2002; LÜCKING & BERNECKER-LÜCKING 2002, 2005). On the other hand, there is a significant correlation between the abundance of particular species and microclimatic parameters, such as illumination, temperature, humidity, evaporation, and wind speed. Illumination has been shown to be the single most important parameter explaining the composition of foliicolous lichen communities (LÜCKING 1998b, c, 1999c), probably because variation of light environments in tropical rainforests is much higher than that of other microclimatic parameters, because light is a minimum factor in tropical rainforest understories, where foliicolous lichens are most diverse, while potentially harmful to the photosynthetic apparatus in can-

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opy environments, and because there is usually a strong correlation between light and other parameters, such as temperature, humidity, and evaporation (CHAZDON & FETCHER 1984; KIRA & JODA 1989; FREIBERG 1996; CLARK et al. 1996).

The formation of three distinct foliicolous lichen communities in the rainforest understory, in natural clearings caused by fallen trees, and in the canopy is indicated in several papers on the subject (NOWAK & WINKLER 1970, 1975; LÜCKING 1995b, 1998c, 1999a, c; CÁCERES et al. 2000). These results seem to be surprising, since they contradict the distinct-preference gradient hypothesis, according to which species responses should distribute evenly along a single, continuous gradient to avoid competition, and no distinct communities should be formed. However, this is only true if all possible expressions of a given gradient occur at even frequency. If instead the gradient is expressed unevenly, with certain values more frequent than others, species tend to adapt their optimum responses to this pattern. For example, there are different rock types with certain pH values, and rock-dwelling lichen species mostly adapted to one type, but not to something in between, because 'inbetween' is rare or does not exist in nature (even if rock types with pH values ranging from 0 to 14 are theoretically possible). As a result, there are distinctive lichen communities on different rock types (WIRTH 1972; GILBERT & FOX 1986; BRODO et al. 2001).

Accordingly, in a tropical rainforests the light gradient is not evenly expressed: certain light environments are much more common than others, and apparently these correspond to the shady understory, natural clearings, and the canopy, with corresponding communities of foliicolous lichens (and other rainforest organisms, for that matter). Except for some taxa with wide amplitudes, most foliicolous lichen species can be assigned to one of these communities and receive a corresponding microsite index MI (LÜCKING 1997): shady understory community MI = 1, transition to clearings MI = 2, clearings MI = 3, transition to canopy MI = 4, and canopy MI = 5. If these indices are plotted against corresponding diffuse site factors (ANDERSON 1964), they show an exponential relationship:

$$DSF = 0.4 \times e^{MI},$$

where DSF = diffuse site factor and MI = microsite index. By using this formula, one can estimate the diffuse site factor for a given leaf by analyzing its foliicolous lichen community. Comparisons between measured values of DSF using electronic devices or hemispherical photographs and those estimated based on foliicolous lichen cover show a rather accurate relationship, with a deviation of 5–15% between the corresponding values (LÜCKING 1997), as long as the foliicolous lichen community on a given leaf is well-developed and sufficiently diverse (> 10 species) to minimize stochastic effects.

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One possible application is the reconstruction of microclimatic zones within tropical rainforests, such as a transect from the understory to the canopy or different zones within tree crowns. To test this, in a recent study we compared the distribution of foliicolous lichens on epiphyte leaves in tree crowns with long-term sensor measurements of different abiotic factors, such as temperature, humidity, and photon flux density (CARDELUS et al., in prep.). Under certain conditions (tree crown phenology, leaves with five or more foliicolous lichen species), we found a significant correlation between the microsite indices of the foliicolous lichen species and the light parameters (Fig. 1).

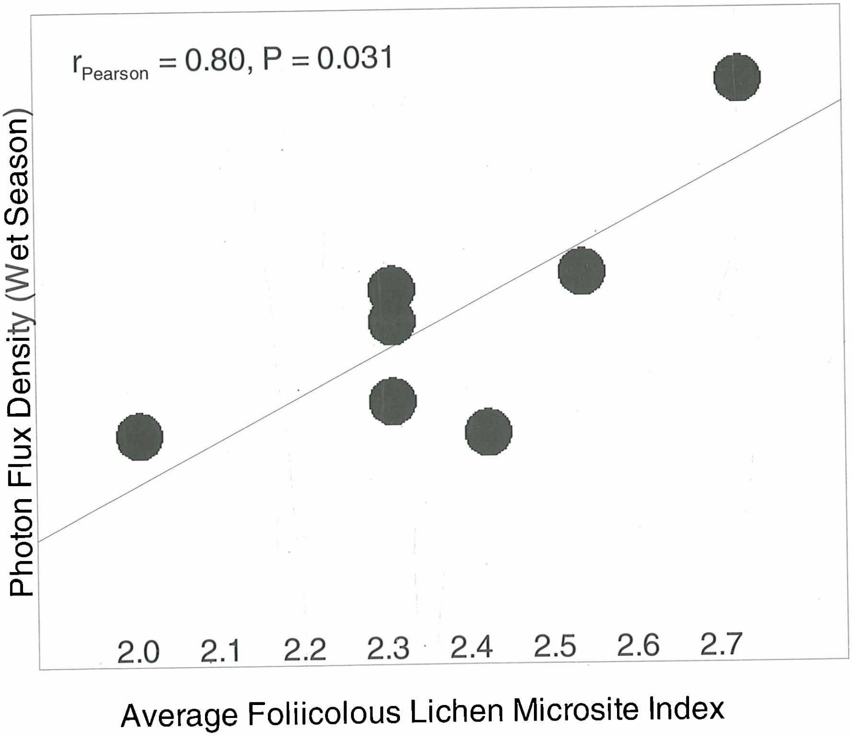

Figure 1: Linear correlation of foliicolous lichen microsite index values with photon flux density in the wet season in tree crowns at La Selva Biological Station, Costa Rica (after CARDELUS et al., in prep.).

Protocols using foliicolous lichens

A. Establishing diffuse site factor dependencies. Sampling sites corresponding to different strata (microsites) are preselected, to include the shady understory, clearings, and the canopy. For each sampling site, the diffuse site factor is determined, by using either hemispheric photographs or coordinated light measurements at the sampling point and a reference point outside the forest or above the canopy under diffuse conditions (cloud cover). Besides long-

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term sensor measurements, hemisphere photography is the most appropriate method, since it can be done at low costs and reproduces a snap-shot of the canopy structure, from which conclusions on long-term illumination patterns can be drawn. As a rule of thumb, the relative amount of canopy opening above a sampling point (0-100%) corresponds to the amount of light reaching the sampling point on average relative to the light reaching the exposed canopy.

Leaves are to be selected randomly from the main abiotic microsites within a tropical rainforest (LÜCKING 1997): understory (microsite index MI = 1: diffuse site factor DSI = 0-2%), transition towards clearings (2: 2-5%), clearings (3: 5-13%), transition towards canopy (4: 13-35%), and canopy (5: 35-100%). The first three can be sampled at ground level, within a height of 1-2 m, while special techniques, such as tree climbing or shooting leaves and branches from the canopy, are needed to sample canopy leaves. For statistically meaningful results, a total of about 100 leaves will be necessary, with more or less equal representation of the different microsites and their transitions. To avoid bias by other factors, only leaves of a certain phorophyte type, such as palms or mesophyllous lauroid leaves (*Lauraceae*, *Meliaceae*) should be collected.

Foliicolous lichens on each leaf are identified using pertinent literature (cf. FARKAS & SIPMAN 1997; LÜCKING 2007), and relative area cover RAC is estimated for each species on each leaf. This can be a rather crude approach, using for example five logarithmically scaled categories (0–5%, 5–10%, 10–20%, 20–50%, 50–100%). For each foliicolous lichen species, the microsite score MS is calculated using the following formula:

$$MS_s = 1 / AC_s \times \sum RAC_{si} \times MI_i,$$

where AC_s = total relative area cover of lichen species s across all leaves, RAC_{si} = relative area cover of lichen species s on leaf i, and MI_i = microsite index of leaf i. For example, if one collected 20 leaves each from the five microsite types, and a given lichen was absent from leaves with MI = 1, present with an average RAC of 10% on leaves with MI = 2, present with an average RAC of 20% on leaves with MI = 3, present with an average RAC of 5% on leaves with MI = 4, and absent from leaves with MI = 5, its microsite score MS would be $(20 \times 0 \times 1 + 20 \times 0.1 \times 2 + 20 \times 0.2 \times 3 + 20 \times 0.05 \times 4 + 20 \times 0 \times 5) / (20 \times 0 + 20 \times 0.1 + 20 \times 0.2 + 20 \times 0.05 + 20 \times 0) = 20 / 7 = 2.9$. The scores for each species are then correlated with the published microsite indices for those species, to identify possible deviations and outliers.

B. Microclimatic zonation. This protocol is a reciprocal application of the previous protocol. With the lichen data available for a given leaf, one can assess the microclimatic conditions and history of a given microsite where leaves with certain species compositions have been collected. For this protocol, it is neces-

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sary to randomly sample leaves within a transect from the understory to the canopy or spheric zones within a tree crown (following JOHANSSON 1974). Foliicolous lichens are then identified and their relative area cover is estimated as in protocol A. For each leaf, its microsite index MI is calculated as follows:

$$MI_l = 1/AC_l \times \sum RAC_{sl} \times MI_s,$$

where AC_l = total relative area cover of lichens on leaf l, RAC_{sl} = relative area cover of lichen species s on leaf l, and MI_s = microsite index of lichen s (from LÜCKING 1997, 2000). For example, one finds five lichen species on a leaf with RAC_i / MI_i as follows: 5% / 1, 20% / 1, 10% / 2, 10% / 3, 5% / 4. MI_L for the leaf would then be calculated as (0.05 × 1 + 0.2 × 1 + 0.1 × 2 + 0.1 × 3 + 0.05 × 4) / (0.05 + 0.2 + 0.1 + 0.1 + 0.05) = 0.95 / 0.5 = 1.9. The microsite index MI_l for each leaf can then be plotted graphically according to the spatial arrangement of the leaves along the transect or tree crown zones, in order to visualize diffuse site factor patterns.

To reduce noise and stochastic effects and to achieve statistically meaningful results, one should sample leaves with medium to high relative area cover (> 10%) and species richness (> 5 species, ideally > 10 species).

Tropical rainforest dynamics

Theoretical background

Tropical rainforests are perceived as mature, slow-changing ecosystems with slow growth rates of their main structural components, the trees. Yet, they display intrisic dynamics which are the main reason for their importance as carbon sinks (ROTMANS & SWART 1991; DIXON et al. 1993, 1994). The main dynamic component is the turnover of trees, or gap dynamics (HARTSHORN 1980; HUBBELL & FOSTER 1986; DENSLOW & HARTSHORN 1994). When a tree falls and eventually decomposes, it provides space for other trees to grow up. Usually, there is a typical succession of early pioneer trees, followed by slower growing species, and eventually an canopy emergent will fill the gap. High gap dynamics result in very heterogeneous tree community and population structures, which is an important component of the biodiversity of tropical rainforests and allows many different organisms to coexist (HUBBELL et al. 1999). In selectively logged or secondary forests, one usually observes a loss of heterogeneity in community and population structure: in addition to loss of tree species, trees are younger on average and more similar in age, which implies that gap dynamics will be substantially reduced, and this affects the diversity of other rainforest organisms.

Foliicolous lichen data

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Tropical rainforests display three distinct foliicolous lichen communities in the shady understory, clearings, and the canopy (LÜCKING 1995b, 1998c, 1999a, c). In closed forests, the shady understory and the canopy form continuous layers and spaces, with no barriers for dispersal of organisms that prefer these microhabitats. Dispersal for organisms adapted to clearings is more difficult, because they have to cross the shady understory or traverse the more exposed canopy to reach another clearing. Trees and other ground-rooted plants solve these problems by relying on seedbanks, but epiphytes, and in particular lichens which do not produce seeds or comparable diaspores, have to disperse and establish immediately. Thus, a foliicolous lichen typical of the light gap community is faced with the difficulty to disperse between spatially discontinuous clearings through the shady understory, especially since foliicolous lichens chiefly disperse by rainsplash over short distances (LÜCKING 1995c; SÉRUSIAUX 1995). Most probably, light gap species disperse slowly across the shady understory on individual leaves that display light gap conditions.

Foliicolous lichen dispersal thus depends on gap dynamics and is more difficult if gaps are less frequent in space and time. A certain level of gap frequency will allow the gap community to establish more or less completely within a given gap, while less frequency will result in the establishment of mere community fragments, subject to a high level of stochasticity. This can be displayed by using an 'association of species' test, as done in several studies on foliicolous lichens (NOWAK & WINKLER 1970, 1975; BARILLAS et al. 1993; LÜCKING et al. 1998; LÜCKING 1999c; CÁCERES et al. 2000). Undisturbed tropical rainforest displays two distinct communities corresponding to the shady understory and natural clearings (Fig. 2A). An example of disturbed forests is Dois Irmãos, one of the many small remnants of the Atlantic Rainforest in northeastern Brazil, strongly affected by selective logging and secondary regrowth (CÁCERES et al. 2000). As a result, the structure of the forest is more homogeneous, with most trees being young and of similar age. Distinct light gaps are rare. Typical foliicolous light gap species still occur; yet they do not form a distinct community but are scattered throughout the association diagram (Fig. 2B).

Protocols using foliicolous lichens

C. Association of species test. This protocol requires stratified sampling within the understory and clearings. Both microsites are sampled along a transect at ground level, within a height of 1-2 m. Only corresponding microsites are sampled: understory sampling sites should display a diffuse site factor of 0-2%, while clearing sampling sites should display 5-13% (see Protocol A for details).

The 'association of species' test is based on the 'association test' or 'association of species' (GOODALL 1978; MCINTOSH 1978; GREIG-SMITH 1983) and

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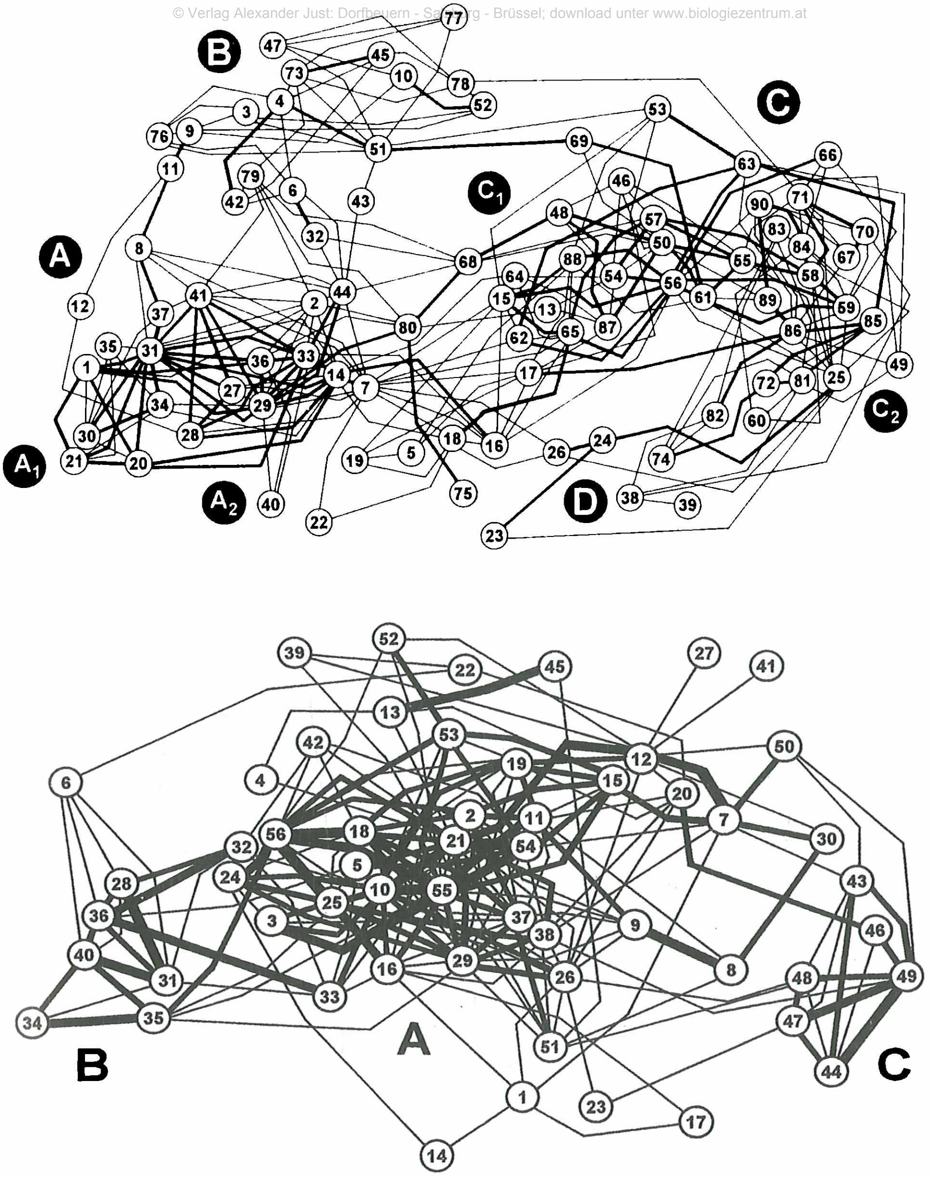

Figure 2: Association of species diagrams of foliicolous lichens from an undisturbed rainforest in Braulio Carrillo National Park, Costa Rica (after LÜCKING 1999c) and from an Atlantica rainforest remnant in NE Brazil (after CÁCERES et al. 2000). Thick arrow indicates the intact light gap association in A, thin arrows the dispersed light gap species in B.

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should not be confused with the 'association analysis' which groups samples rather than species (COETZEE & WERGER 1975; GAUCH 1982; GREIG-SMITH 1983). The test is based on the idea that species which frequently are found close together, but do not have mutualistic or parasitic interactions, do so because they have similar ecological preferences. The test is well-suited for non-vascular cryptogams, i.e. lichens and bryophytes, because of their small thalli and mostly two-dimensional communities (NOWAK & WINKLER 1970, 1975; KÖHLE & WINKLER 1973; SEIDEL 1975; BARILLAS et al. 1993; LÜCKING 1999c).

In order to apply the association of species test, one has to select samples of a size small enough to provide more or less homogeneous environmental conditions, but large enough to include a sufficiently high number of individuals, and thus potentially high diversity. Foliicolous lichens are an ideal group of organisms for the test to be applied, since medium-sized leaves (mesophyll size class according to VARESCHI 1980) provide natural islands for which rather homogeneous conditions can be assumed, and which support a relatively high number of species (up to 50) and individuals (usually more than 100; LÜCKING & MATZER 2001).

The idea of the test is to compare the observed frequency of joint occurrence of a given pair of species within a sample with the expected frequency based on the abundance of each species. If the observed frequency is significantly higher than expected, one would assume that the two species share similar ecological preferences. This corresponds to a simple Chi Square test, where the χ^2 value is a relative measure of the strength of the 'association' between two species, i.e. the deviation of their observed versus expected joint occurrence. However, since the χ^2 value and its corresponding significance level depends on the number of observations, χ^2 values cannot be directly compared between different studies. Instead, LÜCKING (1994, 1999c) demonstrated that there is a linear relationship between the values of χ^2 to be expected and the number of samples analysed and therefore proposed a standardized value:

$$\chi^2_{\text{stand}} = \chi^2 / n,$$

where n = number of samples, in order to estimate the strength of an 'association', or overlap in ecological preferences, between two species. The same author also showed that very common and very rare species cannot display high association values, which corresponds to the fact that such species are common because they have wide ecological amplitudes, or are too rare to display statistically meaningful patterns. Also, the behaviour of the χ^2 distribution implies that most observed 'associations' will be positive, and negative 'associations' (species that occur together less frequently than expected) are rare.

The most straightforward way to visualize 'associations' between species is a plexus diagram (NOWAK & WINKLER 1970, 1975; KÖHLE & WINKLER 1973;

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SEIDEL 1975; MCINTOSH 1978; BARILLAS et al. 1993; LÜCKING 1999c). The standardized χ^2_{stand} values are compiled in a similarity matrix and the matrix is displayed two-dimensionally by means of multidimensional scaling. This mixed classification/ordination technique (now partially implemented in PC-ORD 5.03) arranges species that frequently occur together as groups of points which are connected by lines whose thickness corresponds to the χ^2_{stand} values (LÜCKING 1999c; CÁCERES et al. 2000).

A simple protocol would then include sampling of, for example, n = 100 leaves (ideally half from the shady understory and half from clearings), identifying each foliicolous lichen species on each leaf, calculate the abundance of each lichen species (number of leaves on which species is present), calculate the observed and expected joint occurrences of each species pair (for example, for two species with abundance values of 50 each, the expected number of joint occurrences would be 25, while the observed number could range between 0 and 50), calculate the corresponding matrix of standardized χ^2_{stand} values, transform the matrix into a two-dimensional scatterplot by means of multidimensional scaling, and construct the plexus diagram by adding lines that highlight high χ^2_{stand} values between species pairs.

The structure of the plexus diagram is then used to draw conclusions about the forest structure and dynamics. If there are two distinct associations that represent shady understory and light gap species, then one can assume that there is a certain tree demography and gap dynamics at work that allows both associations to develop more or less completely. If there is no distinct light gap association, and the light gap species are instead scattered over the plexus diagram, then gap dynamics is supposed to be strongly reduced, usually because of the absence of sufficiently old trees. On the other hand, a distinct light gap association in combination with a dissolved understory association would indicate a high level of disturbance and disruption of the otherwise continuous understory layer.

Diversity maintenance and ecologically equivalent species: the Janzen-Huston-Connell approach

Theoretical Background

Ecological theory postulates that species that co-exist in space and time reduce competition by using resources in different ways (GAUSE 1930). In a given space-time occurrence, the number of ecologically equivalent species, inhabiting the same ecological niche and using the same resources, should be one, because ecologically equivalent species should outcompete each other. Thus, ecological equivalence is not expected to substantially contribute to within-community diversity. Instead, diversity is supposed to be chiefly maintained by niche differentiation and mutually dependent interactions between species us-

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ing different resources (RICKLEFFS 1997). However, although there are never two species that occupy exactly the same ecological niche, there might be considerable niche overlap between species even within the same community, to the extent that they can be considered ecologically equivalent. Studies also show that there are communities in which a high number of ecologically equivalent species co-exist in space and time, and in which ecological equivalence does significantly contribute to diversity.

In tropical rainforests, it is not rare to find more than 200 species of trees within a single hectare, and up to almost 500 species have been reported from Ecuador and Brazil (GENTRY 1990; VALENCIA et al. 1994; SPICHINGER et al. 1996; HUBBELL et al. 1999; THOMAZ & RABELLO, pers. comm. 2000). How can so many species co-exists in space and time? Why is the effect of outcompetition absent in these communities? Certainly only part of the diversity can be explained by niche differentiation: different tree species growing on a mosaic of different soils, or with different pollination and dispersal syndroms. For many species, a more or less high degree of niche overlap and ecological equivalence must be assumed. It is also obvious that small fractions of a given community, as they are represented by one-hectare plots for trees, seem to carry a large part of the diversity of the entire community. Diversity patterns and community structure is repeated in community fragments, or in other words: the community structure is fractal and carries a high level of entropy, that is maximum dispersion of individuals of the same species.

The theoretical models that best seem to explain these phenomena are the Janzen-Connell model, or Janzen's spacing mechanism, which postulates that individuals of the same species tend to disperse within space (JANZEN 1970; BECKER et al. 1985; ARMSTRONG 1989; SCHUP 1992; BURKEY 1994), and the Huston-Connell model of intermediate disturbances (CONNELL 1978; HUSTON 1979). In that model, one assumes an unoccupied space-time occurrence of a given ecological niche (such as a clearing within a forest). At the beginning of succession, during the pioneer stage, different species that fit the niche (fast growing pioneer trees) start to fill the space-time occurrence randomly, as long as space is available. During this phase, species richness will increase with each random addition of a species during succession. Once the space-time occurrence is occupied, individuals and species will compete, and the diversity curve levels off. Expansion of one individual is only possible at the cost of another one disappearing. Outcompetition will eventually eliminate individuals of a given species, and the diversity curve will reverse into negative: the number of species will drop. Assuming that no species is equal to another in its competitive capacity, in the climax stage only the most competitive species will occupy the space-time-occurrence of this particular niche, and diversity is zero.

The Huston-Connell model of intermediate disturbances postulates that there are stochastic, non species-specific events that randomly disturb the de-

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velopment of individuals, and hence affect the course of succession. If these events are strong enough to knock out individuals but not as strong as to affect the entire community ('intermediate'), they slow down the outcompetition process, and the time-course of the succession will be prolonged: the maximum diversity stage will be reached later, and so will the zero diversity climax stage. A higher average diversity will be observed over the course of time. The more frequent these intermediate disturbances, the higher the probability that they knock out competitive individuals. A certain level of disturbances would then maintain succession close to the diversity maximum stage.

While this model is straightforward in its predictions and easy to visualize in computer simulations, its verification on tree communities is rather difficult, because even in the most dynamic forests, turnover cycles of trees usually far extent the life of individual researchers. The application of the Huston-Connell model is therefore limited. Foliicolous lichens, on the other hand, have very short-life cycles, but show diversity patterns comparable to those of trees (LÜCKING & MATZER 2001). In addition, by growing on living leaves, foliicolous lichens provide the ideal model to study the dynamics of space-time occurrences of ecological niches, because: an individual leaf comes closer to anything else in representing a space-time-occurrence of an ecological niche; it is isolated in space and has a well-defined beginning and ending; for all we know at present, niche differentiation among foliicolous lichens growing on the same leaf is low, and these lichens can therefore be considered ecologically equivalent; leaves provide an ideal model to assess succession based on time; and leaves can be considered either on an individual basis, with disturbances affecting individual lichen thalli, such as mechanical damage through rain, being intermediate, or they can be viewed as part of a larger foliicolous community, the phyllosphere, with the shedding of an entire leaf representing the intermediate disturbance

Foliicolous lichen data

Few studies have addressed the development of foliicolous lichen communities on individual leaves with time. In general, these seem to follow a 'tolerance' type of succession, i.e. species establish themselves based on the time they need to colonize and establish themselves, rather than the community already present on the leaf (SCHELL & WINKLER 1981; CONRAN & ROGERS 1983; HARTMANN 1993; ROGERS et al. 1994; LÜCKING 1995a, 2001b; SCHUBERT 1997). Plotting species richness or diversity indices over time indicates that a diversity maximum is reached usually somewhere between 24 and 36 months after the leaf was formed, and then in most cases a slight decrease in the number of species is observed, before the leaves are shedd (LÜCKING 1995a). Incidentally, average leafspan in tropical rainforests is between 12 and 36 months, with few plants producing leaves that can reach five or more *(Lauraceae)* and even ten or

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more years (some palms; CHABOT & HICKS 1982; LÜCKING 1998b). On such leaves, one can observe the settlement of lichens that are not typically foliicolous, but rather corticolous, such as *Leptogium* species. These lichens grow to much larger sizes and outcompete the typically foliicolous species, eventually reducing the number of species. However, even on leaves which are several years old, the decrease of diversity is usually not pronounced, and a theoretical climax stage of a single species as postulated above is never observed. Whether this is because small-scale individual disturbances are at work or whether the leaves just don't get old enough, is unknown.

Fortunately, one can take advantage of the fact that foliicolous lichens also grow on artificial substrata, and that way surpass the problem of limited leaf age (fig. 3 in annex). In a pilot experiment, LÜCKING & BERNECKER-LÜCKING (2002) exposed a set of 100 artificial leaves, to test for the effects on dymamics and spatial isolation on diversity maintenance. They found that spatial arrangement affected diversity patterns, but the time frame of three years was too short to assess the effect on temporal dynamics on foliicolous lichen diversity patterns.

Protocols using foliicolous lichens ·

D. True succession. This protocol takes advantages of the fact that foliicolous lichen communities can be readily analyzed using imaging techniques. One initially marks a set of recently produced leaves (20-100) that have no lichen cover but grow on phorophytes that do support a high foliicolous lichen diversity. Every month, all marked leaves are photographed in the same position, using a digital camera. To obtain meaningful results, leaves have to be left exposed and photographed for at least 6-12 months, until pioneer lichen species start to produce reproductive organs. To cover a possible diversity maximum stage, the observation period has to be extended to at least 36 and up to 60 months. During such a prolonged period, it is likely that some of the initially marked leaves will be destroyed by natural forces; therefore it is recommende to initially select a relatively high number of leaves to account for such losses.

After the observation period is concluded, 10-20 successional series are selected for closer study, and the corresponding leaves are sampled for lichen identification purposes; the remaining leaves should be left exposed for further studies. With some experience, or the assistance of an experienced taxonomist, it is possible to identify most of the lichen thalli to species level by just screening the images, while in case of doubt, one would make an identification on the sampled material. For each image of a successional series, one records three parameters: species richness, total relative area cover (see Protocol A), and Shannon-Wiener diversity index. These values are then plotted against the monthly time intervals, to display temporal changes in the three parameters.

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E. Chronosequences. While the aforementioned protocol accurately documents the succession of individual communities, it requires long observation periods with continuous access of the researcher to the study site. To overcome this problem, one can use chronosequences of subsequent leaves along branches to simulate succession (SCHELL & WINKLER 1981; LÜCKING 1995a, 2001b). While this method is very time-effective, it has two shortcomings: the age of individual leaves is estimated rather than determined with certainty, and it introduces space as an additional variable, with each leaf having its individual history. Nevertheless, these errors can be buffered by averaging over a set of branches, and this method gives a rather good fit of the actual succession.

Branches are selected from phorophyte species known to have rather long-lived leaves, such as *Lauraceae* and palms (LÜCKING 1998b). One selects branches which have a complete set of 7-15 leaves from the youngest to the oldest. Ideally, leaves are alternate and more or less aequidistant to each other. Branches should not have older sections covered by branches overneath, because this would introduce microclimatic differences as well.

To estimate leaf age, the youngest leaf of each branch is marked. One has to come back regularly for about three months until the next leaf has been formed and shows the same stage as the previously marked leaf. The time span between these two observations is the estimate of age difference between subsequent leaves. This is a rather crude approximation and depends on additional factors such as seasonality, although averaging over several branches of the same phorophyte species usually gives a relatively good estimate. Once the leaves of a given branch are collected, one proceeds as in Protocol D to analyze the chronosequences and display the results.

F. Stochasticity and spacing. Effects of stochasticity and spacing can be addressed by studying supposedly identical fragments of the same community. Opposite leaves or leaflets of composed leaves (palms, *Meliaceae)* provide an ideal model to do so. For example, in sufficiently small, composed leaves which had their leaflets all produced at the same time, all leaflets should be covered by identical foliicolous lichen communities. The dissimilarity between such leaflets is then an indication of stochastic effects taking place. Sets of leaflets or partitions of leaves can also be used to study spacing patterns. In strongly dispersed communities, one would assume that community fragments carry a substantial part of the overall diversity, while in aggregated communities, the opposite would be the case.

The protocols work by comparing species composition of foliicolous lichens communities between leaves or leaflets, using similarity values such as the Sørensen index. This index has certain advantages over Euklidean distance and similar indices, since it only takes into account the joint presence, but not the joint absence, of a given species on two leaves or leaflets, to calculate the similarity value (LÜCKING 1998c). There are many ways of applying this method

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to the problem of stochasticity. For example, in a series of leaflets on a pinnate palm leaf, are two adjacent leaflets more similar to each other than two leaflets that have another or several leaflets in between them? Is there a distance-related pattern of the behaviour of similarity values? Starting from a given leaflet, do similarity values vary randomly or do they decrease and level off with increasing distance of leaflets?

To study spacing, one ideally works with larger leaves that are divided hierarchically into sections. The foliicolous lichen species composition of each of the smallest sections is determined (see Protocol A), and that of larger inclusive sections calculated. Sections at different levels are then compared to each other by calculating their similarity values, and to the higher level sections. If there is a high amount of spacing, then small sections should be rather similar to each other, or at least the similarity values should not display spatial structure across the leaf surface, and small sections should also be rather similar to the entire leaf, i.e. carrying a significant portion of its diversity. If, however, the dispersal pattern is more aggregate, then similarity values between small sections and between small and large sections should be low, and small sections should also have low diversity indices compared to larger sections and the entire leaf.

G. Experimental approaches using artificial leaves. The aforementioned protocols have the disadvantage that they use living leaves as study objects and hence introduce additional factors that cannot be controlled by the researcher and have to be mitigated by studying a larger number of objects. Fortunately, foliicolous lichens also grow on artificial substrata, such as glass and plastic surfaces. Once the often tricky problem of their exposure is solved, these substrata can be manipulated in almost any desired way, while providing constant conditions as to substrate characteristics themselves.

Three substrata have been successfully used to replace natural leaves for the observation and manipulation of foliicolous lichens communities: glass microscope slides (WINKLER 1967), artificial plastic leaves (e.g. MONGE-NÁJERA & BLANCO 1995; LÜCKING & BERNECKER-LÜCKING 2002, 2005), and transparent plastic cover slips (SANDERS 2001, 2002; SANDERS & LÜCKING 2002). Glass microscope slides have the advantage that they can be directly observed under a microscope. The easiest way to expose them is to fix them to a tape that is expanded between two trees or plastic poles (LÜCKING & BERNECKER-LÜCKING 2002, 2005). Artificial plastic leaves can be cut from any suitable plastic material into desired sizes and shapes. They are easily fixed to plastic tube racks using non-corrosive plastic-coated garden wire through holes in the center of each leaf (LÜCKING & BERNECKER-LÜCKING 2002, 2005). Transparent plastic cover slips, which can also be observed under the microscope, are simply fixed to fine and sturdy plastic net (SANDERS 2001, 2002; SANDERS & LÜCKING 2002); due to their light weight, they can even be exposed directly over natural leaves.

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Annex

Fig. 3 on page VI.

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