

DISTANCE, DYNAMICS, AND DIVERSITY IN TROPICAL RAINFORESTS: AN EXPERIMENTAL APPROACH USING FOLIICOLOUS LICHENS ON ARTIFICIAL LEAVES. I. GROWTH PERFORMANCE AND SUCCESSION

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Abstract. An experimental approach using artificial leaves was designed to test for the effect of niche fragmentation ('distance') and intermediate disturbances ('dynamics') on diversity patterns of foliicolous lichens. The long-term experiment was first surveyed after 36 months, with the observations being presented here. Foliicolous lichens grew well on the artificial leaves, and community parameters such as species richness, diversity, specific abundance, and successional patterns closely resemble those on natural leaves. As diaspore traps, the artificial leaves had a homogenizing effect, leading to a very uniform but rich foliicolous lichen flora, with a total of 109 species detected on 99 analyzed leaves and an average of 29 species per leaf on those leaves exposed for the entire period of 36 months. Almost all taxa that grew on natural leaves in the same environment were present on the artificial leaves, with the notable exception of those species of *Strigula* growing subcuticularly, which artificial substrata seem to exclude. At the selected scale, niche fragmentation, i.e., increased spatial distance between individual leaves, tended to increase diversity within the experimental set-ups (groups of five leaves each), probably due to enhanced stochastic effects by diaspore dispersal via small-scale rain splash. However, intermediate disturbances, simulated by individual leaf replacement within an experimental set-up, caused a decrease in diversity. This is explained by the fact that after 36 months, succession is still approaching a high-diversity phase, and any replacement of individual leaves in this stage with new, uncolonized leaves will naturally decrease diversity. Accepted 30 October 2001.

Key words: Diversity maintenance, niche fragmentation, intermediate disturbances, foliicolous lichens, Costa Rica, La Selva.

INTRODUCTION

A striking feature of tropical rainforests is their high small-scale diversity: while temperate forests contain less than 30 tree species per ha, up to 476 are found in tropical rainforests (Valencia *et al.* 1994, Dias Thomaz, pers. comm.). Many hypotheses focus on the origin of diversity (Vareschi 1980, Prance 1982, Loreau & Mouquet 1999, Levin & Muller-Landau 2000). Others address the mechanisms that maintain diver-

sity on a high level (Kubitzki 1985, Shmida & Wilson 1985, Linsenmair 1990, Wills *et al.* 1997, Hubbell *et al.* 1999), whose understanding is crucial for a sustainable management and conservation of tropical rainforests. High diversity increases interspecific competition, leading to outcompetition or reduced population sizes due to limitations imposed by the carrying capacity of the environment (Putman 1994, Hambright & Zohary 2000). Mechanisms that maintain high diversity should therefore either reduce competition or mitigate its effects. Accordingly, the corresponding hypotheses either focus on niche relations and specific interactions that reduce competition

by specific resource partitioning, or on the competitive effects between ecologically equivalent species (Hubbell 2001).

Foliicolous lichens, which grow on the surface of living leaves of vascular plants, are almost exclusive to tropical rainforests (Santesson 1952, Sérusiaux 1989, Lücking 2001a). Nearly 40% of more than 700 species known world-wide are pantropically or intercontinentally distributed (Lücking & Kalb 2001). Costa Rica, a small country of about 50 000 km², is home to almost 400 species, and there within a single spot at La Selva Biological Station, nearly 300 species coexist (Lücking 1999a, 2001b). More than 80 species have been found on a large palm leaf, and up to 49 on individual dicotyledonean leaves the size of a petri dish (Lücking & Matzer 2001). This high small-scale diversity, together with short life cycles and lack of distinct niche relations (Lücking 1998a, b; 1999b, c; Lücking & Bernecker-Lücking 2000) make foliicolous lichens excellent model organisms for studying mechanisms that maintain diversity in tropical rainforests.

Maintenance of high small-scale diversity within communities of ecologically equivalent species can be theoretically explained by the Connell-Huston model of intermediate disturbances (Connell 1978, Huston 1979, Hambright & Zohary 2000), and this also seems to apply to foliicolous lichens. Chronosequences of these organisms along subsequent leaves of a branch show an increase in diversity until a maximum on leaves of 24–36 months of age. After that, diversity decreases due to the increasing dominance of large, competitive taxa, and the theoretical climax stage of a true succession in an undisturbed, homogeneous environment would then be of low diversity (Lücking 1995).

However, leaves are regularly shed and replaced, which produces a mosaic of leaves of different ages, and these, consequently, support foliicolous lichen assemblies representing different successional stages with varying degrees of diversity. Within a group of leaves, continuous leaf renewal would thus prevent the reaching of an overall low-diversity climax stage and instead maintain overall high diversity (Lücking 1995). Spatial desynchronization of succession by intermediate disturbances is also expected to maintain high tree diversity in adjacent forest plots, e.g., through wind breaks or erosion, although proof of this is difficult to obtain due to the large time-scale involved (Hubbell *et al.* 1999). In foliicolous lichens, this mechanism could be further enhanced by the sto-

chastic effects of niche fragmentation, i.e., spatial isolation of comparable niche expressions, in this case the leaves, each of which represents a natural island.

Even if foliicolous lichens exhibit short life cycles, long-term patterns of undisturbed succession are difficult to observe since leaves are usually shed after 12–36 months, and only rarely retained for more than five years (Freiberg & Freiberg 1999). However, foliicolous lichens also grow on artificial substrata (Sipman 1994, Lücking 1998c), which can be exposed for periods that surpass the natural leaf lifetime and thus allow for the study of hypothetical long-term succession. Artificial leaves have already been used in experimental designs to test the effect of leaf shape on epiphyll cover (Monge-Nájera & Blanco 1995), but lichen species were not identified and questions relating to diversity were consequently not addressed.

This paper reports the first results of a long-term experiment with artificial leaves to test the effects of niche fragmentation and intermediate disturbances on the diversity of foliicolous lichen communities in the understorey of a tropical rainforest. To demonstrate the general suitability of the experimental approach, we analyzed in detail the performance of foliicolous lichens on artificial leaves as compared to natural leaves.

MATERIAL AND METHODS

Experimental design. Artificial leaves with an ellipsoid shape 19 × 9 cm (average mesophyll leaf size, see Vareschi 1980) were cut out of green polyethylene lawn edging (WERGA FISKARS®, Austria, No. 202009) and fixed with coated flower wire to racks made of black plastic tubes, each rack containing five leaves (Fig. 1). The leaves of the Lauraceae *Ocotea atirrensis*, one of the phorophytes with the highest foliicolous lichen diversity at this and adjacent localities (Lücking 1995, 1998a), served hereby as a model regarding size and shape.

Two variables were considered in the experimental design. Niche fragmentation was simulated by the marginal distance between individual leaves: either 'narrow', with a distance of 2 cm, or 'wide', with a distance of 11 cm. These distances were chosen based on preliminary observations of foliicolous lichen distribution on compound leaves of the palm *Welfia georgii* at La Selva Biological Station, where 5–8 cm appeared to be a critical distance value in increasing beta-diversity between adjacent leaflets (Lücking, in prep.). Intermediate disturbances were simulated by regular exchange of individual leaves: in the 'per-

manent' design, all leaves were constantly exposed without replacement, whereas in the 'replaced' design, the first leaf was replaced by a new one after six months, and the next two adjacent leaves after 12 and 24 months respectively. Both variables were combined into four experimental set-ups (Fig. 2): narrow-permanent = NP, narrow-replaced = NR, wide-permanent = WP, wide-replaced = WR. Each set-up included five replicates, which resulted in a total of four set-ups \times 5 replicates (= 20 racks) \times 5 leaves = 100 leaves that were initially exposed, and a further $2 \times 5 \times 3 = 30$ leaves that were additionally exposed in the two 'replaced' setups.

Study area and experimental site. The experiment was installed at La Selva Biological Station, Costa Rica (Fig. 3A). The vegetation here consists of tropical lowland rainforest and swamp forest, with 4000 mm annual precipitation (Hartshorn & Hammel 1994, McDade *et al.* 1994). The foliicolous lichen flora of La Selva has been intensively studied with regard to

taxonomic composition, microsite preferences, and organismic interactions (Lücking 1999a, Lücking & Bernecker-Lücking 2000), and 293 species are currently known from the area (Lücking 1999a, 2001b).

The experimental site was established on the CCL trail at point 350 m, within a continuous area of old-growth primary forest (Fig. 3B). Four racks, one replicate of each experimental set-up, were grouped together within a distance of 1–2 m, and five replicate groups were placed at a distance of 4–12 m between each other within an area of 33 \times 14 m (Fig. 3C).

In order to provide for an environment as homogeneous as possible, the experimental site was chosen so as to represent the shady forest understory, with low-light conditions and constantly high relative air humidity. Microclimatic parameters (relative light intensity, atmospheric humidity) were determined during an initial period of six months (February to July 1997) by means of hemispherical photographs and evaporimeters (see Lücking 1998a, 1999a for methodological details). Hemispherical photographs in-



FIG 1. Rack with five artificial leaves in the rainforest understory.

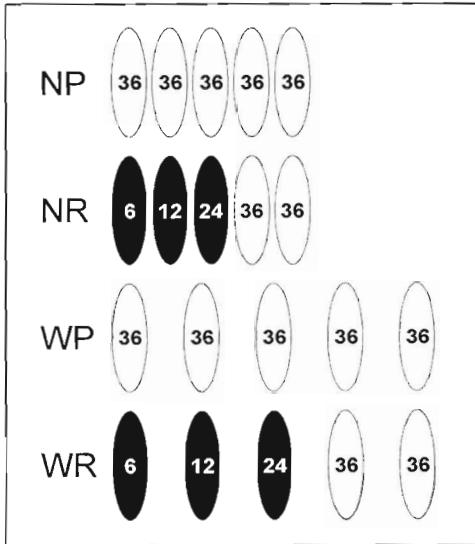


FIG 2. Comparison of four different experimental set-ups. White leaves = permanent, with time of exposure [months]; black leaves = replaced, with time of replacement [months].

icated 1–4% canopy opening depending on the replicate group, corresponding well to the shady forest understory (Chazdon & Fercher 1984, Lücking 1998a, 1999a). Monthly evaporation strongly correlated with precipitation ($r_{\text{Pearson}} = -0.85$, $P < 0.05$) and illumination data ($r_{\text{Pearson}} = 0.91$, $P < 0.05$) taken from the La Selva database (http://www.ots.ac.cr/rd-mcnfs/datasets/meteoro/ls_met/). Values varied between 1.6 and 21.1 mm/month, which also corresponds well to the shady forest understory (Hopkins 1965, Freiberg 1994). Monthly evaporation did not differ significantly between replicate groups (Fig. 4).

Foliicolous lichen inventory. Following regular replacement of individual leaves after 6, 12, and 24 months (August 1997, February 1998, February 1999), the experimental set-ups were completely surveyed after 36 months in February 2000. All leaves were individually detached from the racks, carefully studied in the laboratory using stereomicroscope and microscope, and immediately placed back onto the racks at the experimental site.

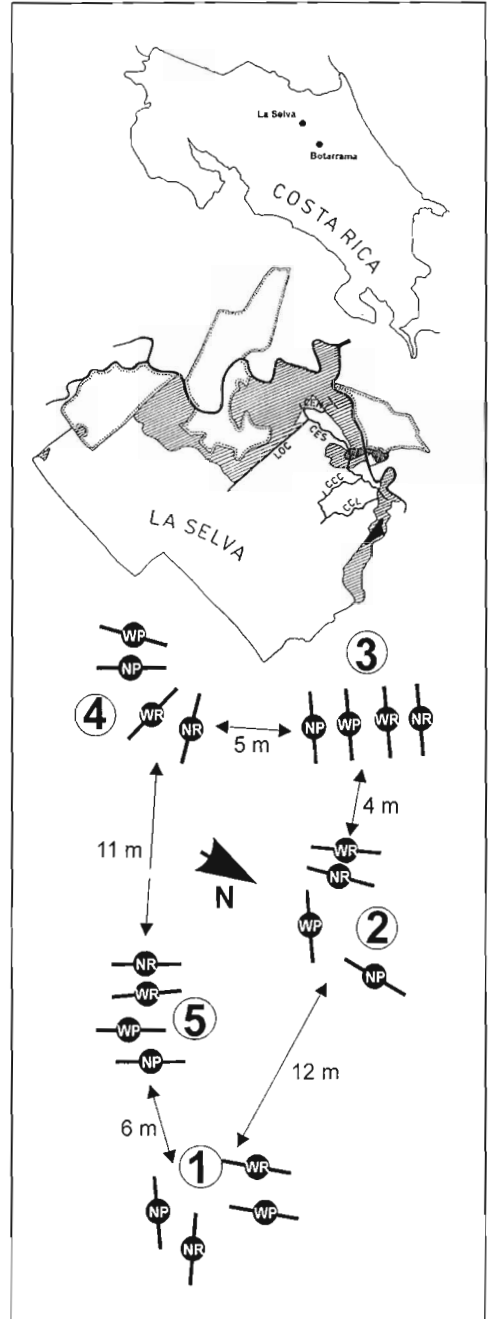


FIG 3. Ubication of the study area (top) and the experimental site (center), and map of the spatial arrangement of the experimental set-ups in five replicate groups (bottom).

Lichens present on the artificial leaf surfaces were determined using pertinent literature (see Farkas & Sipman 1997 for a survey). A cover index was used to estimate frequency of each species per leaf, with the categories rare (1–3 small individuals), moderately abundant (up to 10 small or a single large individual > 20 mm diam.), and dominant (more than 10 small or more than one single large individual). Each species present on a leaf was assigned a reproductive stage index RSI, depending on whether it was represented by sterile thalli [RSI = 1], or by individuals with asexual or vegetative [RSI = 2], young sexual [RSI = 3], or mature sexual reproductive structures [RSI = 4].

Together with the regularly replaced leaves, a total of 130 leaves was expected to be analyzed at this stage. However, due to the placement of the experiment in a natural environment, in order to ensure accessibility to foliicolous lichen diaspores, it was not possible to avoid partial mechanical damage to the experimental racks by branch or large leaf litter, which caused individual leaves to drop to the ground. In one case, an ant's nest had been built on the upper side of a leaf. Such leaves were excluded from the study, and hence 99 leaves out of a total of 130 were actually recovered after three years (Table 1).

TABLE 1. Expected and recovered artificial leaves after different exposure times.

Exposure [months]	Experimental set-up				Total expected	Total recovered
	NP	NR	WP	WR		
6	–	5	–	5	10	10
12	–	10	–	10	20	18
24	–	10	–	10	20	18
30	–	5	–	5	10	8
36	25	10	25	10	70	45

Assessment of growth performance. In order to assess the representativeness of the foliicolous lichen flora developed on the artificial leaves, comparison was made with 5 x 20 randomly sampled leaves of the mesophyll dicotyledonean type (see Vareschi 1980, Lücking 1998a, 1999a) within a distance of 15 m around each of the five replicate groups at the experimental site. In addition, the following data for comparison were taken from Lücking (1999a): 300 leaves samp-

led from 100 phorophytes dispersed over the whole study area (about one hectare), including all microsites, such as the shady understory, light gaps, and the canopy, plus two subsets of 60 leaves each of the mesophyll dicotyledonean and the palm type, sampled from 20 phorophytes dispersed over the study area but restricted to the shady understory.

The foliicolous lichen flora on artificial and natural leaves was compared using species composition and abundance (number of leaves with species present). Species composition between samples was compared by cluster analysis (weighted pair-group average) based on the similarity index of Sørensen (1948). Abundance values were correlated via the Pearson correlation coefficient. In a step-wise correlation, foliicolous lichen species were 'filtered' through specific indices reflecting their microsite preferences (Lücking 1997, 2001c). These microsite indices range from [1] to [5], with species preferring the shady understory, light gaps, or the exposed canopy, having index [1], [3], and [5] respectively, while [2] and [4] represent transitional species.

Preliminary analysis of experimental set-ups. Species richness and Shannon-Wiener index were taken as diversity measures. The Shannon-Wiener index was calculated as $SWI = \sum \ln(\text{cov}_i)$, with cov_i corresponding to the cover index of species i . Both species richness and Shannon-Wiener index were calculated for individual leaves and for each experimental set-up replicate. Potential effects of distance and dynamics on diversity were analyzed by means of two-way ANOVA.

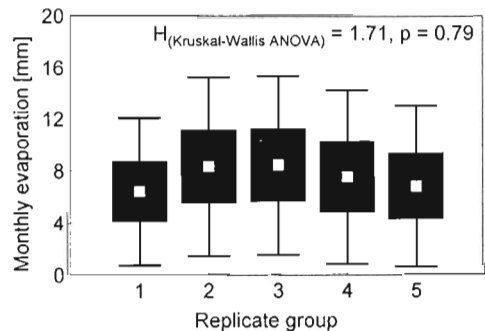


FIG 4. Monthly evaporation (indicating 6-month average) at each of the five replicate groups, compared by a Kruskal-Wallis ANOVA.

In order to test whether differences between experimental set-ups are due to stochastic differences between, or high average diversity of, individual leaves, beta-diversity between leaves of a given set-up replicate was calculated as $BETA = [(s_{total} / s_0) - 1] / (n$

$- 1)$, where s_{total} = total number of species on n leaves, s_0 = average number of species per leaf, n = number of leaves.

All statistical calculations were performed with the program package STATISTICA 5.1™.

TABLE 2. Folii-colous lichen species and their abundance on 99 artificial leaves (n = number of leaves on which species was present).

Species	n	Species	n	Species	n
<i>Actinoplaca strigulacea</i>	1	<i>Echinoplaca epiphylla</i>	1	<i>Porina leptosperma</i>	36
<i>Anisomeridium foliicola</i>	53	<i>Echinoplaca leucotrichoides</i>	1	<i>Porina leptospermoides</i>	36
<i>Anisomeridium</i> sp.	6	<i>Echinoplaca verrucifera</i>	1	<i>Porina limbulata</i>	57
<i>Arthonia accolens</i>	41	<i>Eremothecella calamicola</i>	1	<i>Porina lucida</i>	7
<i>Arthonia aciniformis</i>	5	<i>Fellhanera fuscata</i>	4	<i>Porina mirabilis</i>	54
<i>Arthonia cyanea</i>	2	<i>Fellhanera naevia</i>	1	<i>Porina nitidula</i>	6
<i>Arthonia leptosperma</i>	70	<i>Fellhanera pilomarginata</i>	11	<i>Porina octomera</i>	2
<i>Arthonia mira</i>	5	<i>Fellhanera santessonii</i>	9	<i>Porina pseudoapplanata</i>	1
<i>Arthonia orbygniae</i>	6	<i>Gyalectidium filicinum</i>	63	<i>Porina radiata</i>	49
<i>Arthonia palmulacea</i>	34	<i>Gyalectidium imperfectum</i>	1	<i>Porina rubentior</i>	60
<i>Arthonia trilocularis</i>	8	<i>Gyalideopsis vulgaris</i>	4	<i>Porina rubescens</i>	3
<i>Aspidothelium papillicarpum</i>	4	<i>Lyomma ornata</i>	3	<i>Porina rubrosphaera</i>	25
<i>Aulaxina minuta</i>	57	<i>Lyomma palmae</i>	3	<i>Porina rufula</i>	53
<i>Bacidina defecta</i>	1	<i>Macentina perminuta</i>	2	<i>Porina subepiphylla</i>	1
<i>Bapalmuia lineata</i>	4	<i>Mazosia bambusae</i>	5	<i>Porina tetracerae</i>	43
<i>Bapalmuia palmularis</i>	30	<i>Mazosia dispersa</i>	8	<i>Porina tetramera</i>	31
<i>Byssolecania deplanata</i>	12	<i>Mazosia longispora</i>	2	<i>Porina vezdae</i>	1
<i>Byssolecania fumosonigricans</i>	5	<i>Mazosia melanophthalma</i>	46	<i>Psoroglaena</i> sp.	5
<i>Byssolecania hymenocarpa</i>	5	<i>Mazosia phyllosema</i>	66	<i>Sporopodium lepreurii</i>	28
<i>Byssoloma absconditum</i>	6	<i>Mazosia pilosa</i>	3	<i>Strigula obducta</i>	7
<i>Byssoloma aurantiacum</i>	3	<i>Mazosia rotula</i>	32	<i>Strigula phyllogena</i>	45
<i>Byssoloma leucoblepharum</i>	2	<i>Mazosia rubropunctata</i>	10	<i>Strigula platypoda</i>	3
<i>Byssoloma minutissimum</i>	32	<i>Microtheliopsis uleana</i>	26	<i>Tricharia hyalina</i>	5
<i>Calenia phyllogena</i>	5	<i>Phyllobathelium anomalum</i>	5	<i>Tricharia urceolata</i>	2
<i>Calopadia foliicola</i>	1	<i>Phyllobathelium firmum</i>	23	<i>Tricharia vainioi</i>	48
<i>Calopadia phyllogena</i>	2	<i>Phyllobathelium leguminosae</i>	5	<i>Trichothelium bipindense</i>	3
<i>Calopadia</i> sp. (campylidia)	12	<i>Phylloblastia amazonica</i>	60	<i>Trichothelium epiphyllum</i>	60
<i>Caprettia nyssaegenoides</i>	1	<i>Phyllophiale alba</i>	57	<i>Trichothelium juruensis</i>	1
<i>Chroodiscus australiensis</i>	1	<i>Phyllophiale fusca</i>	38	<i>Trichothelium minus</i>	27
<i>Chroodiscus coccineus</i>	2	<i>Phyllophiale viridis</i>	14	<i>Trichothelium minutum</i>	8
<i>Coenogonium dilucidum</i>	34	<i>Pocsia borhidii</i>	3	<i>Trichothelium pallescens</i>	2
<i>Coenogonium flavicans</i>	13	<i>Porina atropunctata</i>	51	<i>Trichothelium pallidesetum</i>	1
<i>Coenogonium isidiiferum</i>	1	<i>Porina</i> aff. <i>diaphana</i>	2	<i>Trichothelium porinoides</i>	6
<i>Coenogonium lisowskii</i>	33	<i>Porina epiphylla</i>	73	<i>Trichothelium sipmanii</i>	4
<i>Coenogonium siquirrensis</i>	16	<i>Porina fusca</i>	39	<i>Trichothelium ulei</i>	43
<i>Coenogonium subluteum</i>	19	<i>Porina guianensis</i>	56	<i>Woessia pseudohyphosphorifera</i>	3
		<i>Porina imitatrix</i>	7		

RESULTS

Growth performance of foliicolous lichens on artificial leaves. The 99 leaves yielded a total of 109 species (Table 2), all typically foliicolous lichens representing 37% of the entire flora known from the study site. In their appearance, lichen thalli on artificial leaves did not differ from those growing on natural leaves (Fig. 5). The most abundant species (proportion of colonized leaves) were *Porina epiphylla* (74%), *Arthonia leptosperma* (71%), *Mazosia phyllosema* (67%), *Gyalactidium filicinum* (64%), *Phylloblastia amazonica*, *Porina rubentior*, *Trichothelium epiphyllum* (61% each), *Aulaxina minuta*, *Phyllophiale alba*, and *Porina limbulata* (58% each).

Species abundance on artificial leaves was strongly correlated with that on natural leaves (Table 3). Correlation was strongest when compared to understory phorophytes, independent of leaf type (palms vs. dicotyledoneans), and weakest when phorophytes of all microsite types were included. Correlation was stronger when phorophytes distributed over the whole study area were taken into account, compared with just those surrounding the experimental site. Indeed, the natural leaves sampled at the experimental site yielded 25 species not present on the artificial leaves, while the latter had 33 species not found on the surrounding natural leaves.

Step-wise correlation including the 100 phorophytes distributed over the study area, but selecting foliicolous lichen species with different microsite indices, gave the strongest correlation for index [1], i.e. species preferring the shady understory (Table 4). Of 65 species with microsite index [1], 52 are found at the experimental site and 48 on the artificial leaves. The 13 species with microsite index [1] which would be expected at, but are absent from the experimental site are mostly rare taxa, except for *Gyalidea epiphylla*, *Mazosia tenuissima*, *Strigula janeirensis*, and *Trichothelium annulatum*, so their absence can chiefly be explained by stochastic effects.

Of the 25 species present at the experimental site but not found on the artificial leaves, five are subcuticular *Strigula* species (*S. maculata*, *S. nemathora*, *S. nigrocarpa*, *S. smaragdula*, *S. subtilissima*).

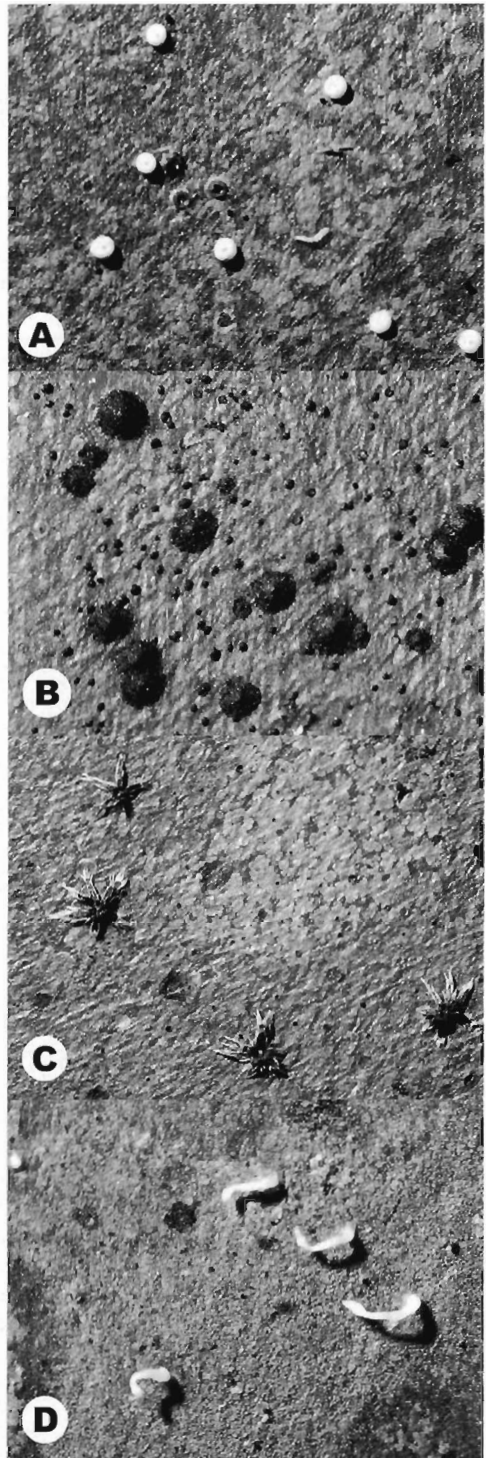


FIG 5. Selected lichen species growing on the artificial leaves, from top to bottom: *Aspidothelium papilliscarpum* Lücking, *Strigula phyllogena* (Müll. Arg.) R. C. Harris, *Trichothelium epiphyllum* Müll. Arg., and *Woessia pseudohyphophorifera* Sérus. & Lücking.

TABLE 3. Correlation of foliicolous lichen species abundance [number of leaves with presence of a given species] between artificial and natural leaves. 'Study area' includes phorophytes of all microsite types (understory, light gaps, canopy) distributed over the whole study area, while 'Understory' denotes subsets restricted to the shady understory. 'Experimental site' includes only phorophytes around the experimental site. n_L = number of phorophytes/leaves taken for the calculation of foliicolous lichen abundance (234 species in total). All correlations are highly significant at $P < 0.001$.

Artificial leaves	Study area dicoryledonean and palm leaves ($n_L = 100/300$)	Understory dicoryledonean and palm leaves ($n_L = 40/120$)	Understory dicoryledonean leaves ($n_L = 20/60$)	Experimental site dicoryledonean leaves ($n_L = 20/100$)
6–36 months ($n_L = 99$)	0.58	0.81	0.80	0.73
36 months ($n_L = 45$)	0.53	0.78	0.77	0.72

Two further taxa abundant on natural leaves but absent from artificial ones were *Badimia dimidiata* and *Bapalmuia nigrescens*. On the other hand, some species common on artificial leaves were not found on the surrounding natural leaves, such as *Arthonia trilocularis*, *Fellbanera santessonii*, *Mazasia bambusae*, *Povrina lucida*, *P. nitidula*, *Tricharia hyalina*, *Trichothelium minutum*, and *T. porinoides*. Most of these are rare taxa, so their absence on the sampled natural leaves might also be due to stochastic effects.

Based on their foliicolous lichen species composition, the five experimental replicates cluster together in a group that includes natural leaves from phorophytes surrounding replicate 2, but separate from other natural leaves sampled at the experimental site (Fig. 6).

Chronosequences of foliicolous lichens on artificial leaves. Species richness continuously increased with time of exposure ('leaf age'), approaching a sigmoidal curve but still with a strong linear relationship (Fig. 7A). No visible flora had developed after six months,

and after 12 months the number of species per leaf remained below 10. Average species richness on leaves exposed for 36 months amounted to 29.2, with individual leaves having up to 39 species. Foliiicolous lichen cover index was linearly correlated with time of exposure (Fig. 7B), while average reproductive stage index RSI leveled off after 24 months, well-approximated by a logarithmic relationship (Fig. 7C).

A total of 32 species was found on leaves with 12 months exposure time, the following being significantly more abundant compared to their abundance on all leaves: *Coenogonium subluteum* (factor 4.3), *Phyllophiale viridis* (3.0), *Gyalectidium filicinum* (2.1), *Phylloblastia amazonica* (1.8), *Povrina mirabilis* (1.7), and *Phyllophiale alba* (1.6). After 12 months, the average RSI approximated 2.0, i.e., species were chiefly represented by individuals with asexual or vegetative reproduction, such as *Arthonia leptosperma* and *Coenogonium flavicans* with pycnidia, and *Coenogonium isidiiferum*, *Phylloblastia amazonica*, *Phyllophiale alba*, *Phyllophiale fusca*, and *Phyllophiale viridis* with their characteristic isidia. Only three species, *Coenogonium*

TABLE 4. Microsite index-dependent stepwise correlation of foliicolous lichen species abundance between artificial and natural leaves. Species are successively excluded according to their microsite indices (Lücking 1997, 2001c). n_s = number of foliicolous lichen species retained in the calculation, from a total of 234. All correlations are highly significant at $P < 0.001$.

Artificial leaves	Index [1]-[5] ($n_s = 219$)	Index [1]-[4] ($n_s = 203$)	Index [1]-[3] ($n_s = 183$)	Index [1]-[2] ($n_s = 137$)	Index [1] ($n_s = 65$)
6-36 months ($n_L = 99$)	0.57	0.57	0.60	0.66	0.79
36 months ($n_L = 45$)	0.53	0.51	0.55	0.63	0.74

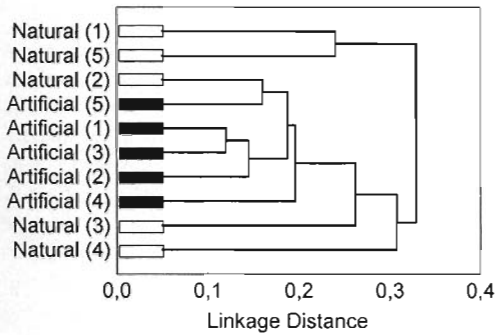


FIG 6. Clustering of artificial leaf replicate groups and adjacent natural leaves according to their lichen species composition.

subluteum, *Macentina perminuta*, and *Porina tetramera*, produced individuals with mature sexual fruit bodies after such a short exposure time.

Preliminary assessment of effects of distance and dynamics on diversity. No significant differences were found between species richness and Shannon-Wiener index as diversity measures (Pearson's correlation: $r = 0.98$, $P < 0.001$). Both were highest in the 'wide permanent' set-up and lowest in the 'narrow replaced' set-up (Table 5). Increasing the distance between adjacent leaves from 2 to 11 cm resulted in an strong increase of average species richness by 24.5% (from 42.0 to 52.3 per replicate) in the 'permanent' set-up and by 12.9% (from 40.2 to 45.5 per replicate) in the

TABEL 5. Follicolous lichen species richness (top rows) and Shannon-Wiener index (bottom rows) determined on replicates of artificial leaves belonging to different experimental set-ups.

Set-up	Replicate					Ø
	1	2	3	4	5	
NP	54	—	—	—	30	42.0
NR	39	47	34	—	41	40.3
WP	60	36	66	—	47	52.3
WR	48	46	41	—	47	45.5
NP	3.73	—	—	—	3.19	3.46
NR	3.44	3.62	3.26	—	3.44	3.44
WP	3.79	3.29	3.90	—	3.57	3.64
WR	3.66	3.62	3.46	—	3.62	3.59

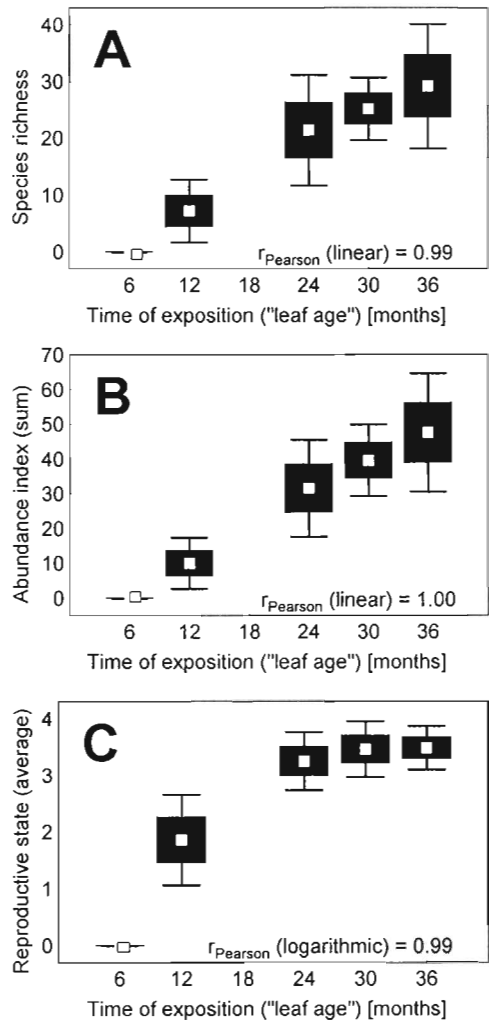


FIG 7. Relation between lichen species richness, abundance index, and reproductive state and time of exposure of the artificial leaves, and magnitude of correlation for linear and logarithmic approximation models.

'replaced' set-up. However, these differences are neither statistically significant in the ANOVA (Fig. 8), nor when 'wide' set-up combinations are compared to 'narrow' set-up combinations (Kruskal-Wallis H-test: $P = 0.13$ for species richness and $P = 0.12$ for Shannon-Wiener index).

Although average species richness per replicate (= five leaves combined) was higher in the 'wide per-

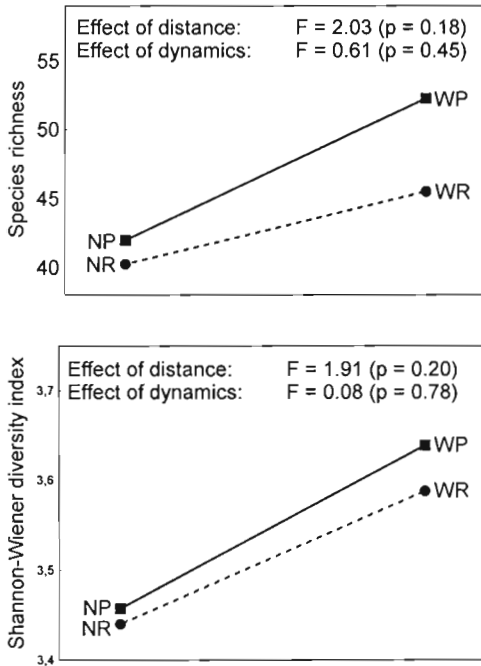


FIG 8. Effects of distance and dynamics on lichen species richness and Shannon-Wiener diversity index, as tested by an ANOVA.

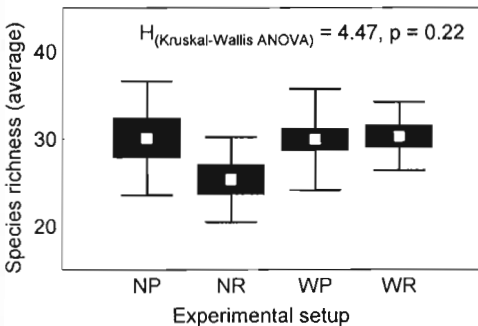


FIG 9. Comparison of lichen species richness on artificial leaves with an exposure of 36 months, between the four different experimental set-ups, tested by a Kruskal-Wallis ANOVA.

permanent' (52.3) compared with the 'narrow permanent' set-ups (42.0), that of individual leaves was not significantly different (Fig. 9). In fact, it was practically the same in the 'narrow permanent' (range = 19–38, average = 30.1) and the 'wide permanent' set-up (range = 21–39, average = 30.0). Accordingly, the 'wide permanent' set-up showed a slightly higher beta-diversity (range = 0.14–0.22, average = 0.18) than the 'narrow permanent' set-up (range = 0.11–0.17, average = 0.14), but this difference is not statistically significant due to the small number of observations (Kruskal-Wallis H-test: $H = 0.86, P = 0.35$).

Comparing the 'permanent' and the 'replaced' set-up combinations, the latter showed slightly lower values for both species richness (42.0 vs. 40.3 and 52.3 vs. 45.5, respectively) and Shannon-Wiener index. In both cases, the differences are not statistically significant (Kruskal-Wallis H-test: $P = 0.36$ for species richness and $P = 0.52$ for Shannon-Wiener index). Thus, instead of an expected increase in diversity, a decrease was observed when regularly replacing individual leaves within a replicate.

DISCUSSION

Growth performance and chronosequences of foliicolous lichens on artificial leaves. The foliicolous lichen flora that developed on artificial leaves reflects rather well the communities found on natural leaves, both in terms of species composition and abundance. The only exceptions are subcuticular species of the genus *Strigula*, which obviously cannot grow on artificial substrata. Species richness on those artificial leaves exposed for 36 months, ranging from 19 to 39 (average 29 species), was essentially the same as on natural leaves of about the same size found at the same or adjacent localities. Lücking (1995) reported up to 38 species on leaves of the Lauraceae *Ocotea atirrensis*, which were used as the primary model to design the artificial leaves in this experiment. Even up to 49 species were recently cited from similar-sized leaves found in Costa Rica and Amazonian Ecuador (Lücking & Matzer 2001), but such values are certainly exceptional and possibly due to the growth of such leaves under conditions intermediate between the shady understory and light gaps, where two specifically different associations occur (Lücking 1999c). It can thus be assumed that the artificial substrate does not negatively affect the diversity of foliicolous lichens to be expected on natural leaves of the same size and under the same microclimatic conditions.

As expected from the placement of the experimental site in the forest understory, the artificial leaves discriminate in favor of species with microsite index [1]. On the other hand, there is no discrimination between species that naturally prefer palm or dicotyledonean type leaves (Lücking 1999a). This might be due to the undulating 'topography' of the artificial leaves caused by the prefabricated shape of the polyethylene material, which could have a similar effect as the parallel venation of palm leaves. The latter is assumed to produce differences in water retention after rainfall (Lücking 1998a, b).

The minutely rough surface structure of the artificial leaves seems to have a filtering effect on the foliicolous lichen flora, leading to a very homogeneous species composition, as indicated by the clustering of the experimental replicates independent of their spatial proximity to natural leaves at the experimental site. Obviously, substrate type (artificial *vs.* natural) is more selective than small-scale spatial relationships. This effect may also explain the strong correlation of foliicolous lichen species abundance between artificial and natural leaves of phorophytes distributed over the study area compared with those concentrated at the experimental site. Provided that every leaf acts as a diaspore trap for foliicolous lichens, and the diaspore composition depends on the species pool within effective distance, slight differences in phorophyte features will lead to slight differences in foliicolous lichen composition. In the natural environment, such differences are difficult to detect since they are overlaid by the multiple effects of other environmental factors (Monge-Nájera 1989, Lücking 1998a, b), but on artificial leaves they become visible.

Chronosequences of foliicolous lichens on artificial leaves are quite comparable to those found on natural leaves, provided that the environmental conditions are similar. In a study in Braulio Carrillo National Park near La Selva Biological Station, Hartmann (1993) found that freshly produced leaves of *Cyclanthus bipartitus* (Cyclanthaceae), as well as the plastic tape markers on the leaf surface, showed initial colonization with *Coenogonium* (= *Dimerella*), *Phyllophiale*, and *Tricharia* species after 4–7 months. Thus, the typical 'pioneer' species, i.e., the first colonizers on young leaves, are the same on natural and artificial substrata (Hartmann 1993, Lücking 1998b).

Artificial leaves even show the same phenomenon as natural leaves in that the youngest leaves are not visibly colonized until an age of approximately six months. This might be due to changing leaf

characteristics that prevent young, less protected leaves from colonization. However, the present observations on artificial leaves, which naturally do not change with 'age', rather support the hypothesis that young leaves are first covered by an invisible layer of fungal hyphae and algal colonies, which provide the necessary preconditions for colonization by lichenized fungi (Lücking 1998a, Sanders 2001). Thus, contrary to the assumption that epiphyll colonization follows a pseudosuccession of the 'tolerance' model (Rogers *et al.* 1994, Schubert 1997), a true 'Clementian' succession might in fact take place when epiphylls are considered as a whole.

Chronosequences of the natural leaves of 139 phorophytes studied at the Botarrama trail, another site close to La Selva Biological Station, showed exactly the same patterns of diversity, with a maximum being reached after 24–36 months (Lücking 1995, and in prep.). This means that foliicolous lichens on artificial leaves behave as on natural leaves, an important precondition for the validity of hypotheses derived from experimental approaches.

Effects of distance and dynamics on diversity. Dynamics simulated by the replacement of individual leaves had no positive effect on overall diversity. After 36 months, succession of the foliicolous lichen flora still approaches the maximum diversity phase, which implies that replacement with young, uncolonized leaves cannot result in an increase of diversity. From individual observations with up to 10-year-old palm and cycad leaves in Costa Rica, we assume that diversity on individual leaves might significantly decrease only after 60–120 months, since only then do competitive species, or facultatively foliicolous lichens, begin to dominate, forming very large thalli (Kiew 1982, Lücking, unpubl. observ.). Thus, only then can leaf replacement lead to an increase in overall diversity, but whether this holds true is to be tested in the second phase of the ongoing experiment.

Distance between individual leaves did affect diversity, increasing average species richness per replicate by up to 24.5%. A higher number of experimental set-ups using larger distances, and a higher number of replicates per set-up, would be necessary to test for potential maximum increase in diversity and meaningful statistical significance. Still, it is notable that the higher diversity observed in the 'wide' experimental set-ups was due to a higher beta-diversity between adjacent leaves, and not the result of a higher average alpha-diversity on individual leaves.

No experimental data are yet available, but field observations, together with the morphology of reproductive organs (disc-shaped isidia, hyphophores and campylidia with filiform conidia), indicate that foliicolous lichen diaspores are chiefly dispersed by rainwater, either running water or via a splash mechanism (Sérusiaux 1995). The latter has been experimentally tested in other plants and fungi (Brodie 1951, MacDonald & McCartney 1988) and shown to be effective within short distances of 0–70 cm. Since foliicolous lichen diaspores are dispersed in masses rather than individually, daughter colonies develop within a small area that presumably reflects the splash diameter. Leaves within the splash diameter are thus more likely to develop a similar foliicolous lichen flora from the same dispersal event than those more distant from each other. Furthermore, secondary colonization by rapidly developing species onto surrounding areas, leading to a homogenization of the foliicolous lichen flora, is less likely as the distance between adjacent leaves increases.

Thus, stochastic differences between adjacent leaves, reflected in their beta-diversity, increase with distance, and consequently, similar average or alpha-diversity results in higher overall or gamma-diversity. It therefore seems that niche fragmentation, i.e., spatial dispersion of corresponding niches, would positively affect diversity. This is also seen in the large compound leaves of the palm *Welfia georgii*, where distances above 5–8 cm between individual leaflets increase beta-diversity, but this increase levels off at about 30–50 cm distance (Lücking, in prep.). Further observations on compound leaves, as well as further experiments with artificial leaves, should establish the minimum distance where such effects begin to operate, the optimum distance where a maximum is reached, and the maximum distance where no further increase is possible due to saturation effects, and how these distances relate to splash diameters caused by raindrops in the forest understory.

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