

Chapter 6

Development of epiphytic bryophyte and lichen vegetation on plantation coffee trees

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Abstract

Using a coffee plantation as a model ecosystem, the present study focuses on the effects of time and dispersal distance on the species composition of epiphytic bryophyte and lichen communities. In a coffee plantation in Colombia, at 1700 m asl. an inventory of cryptogamic epiphytes was made in a four and eight year old plot, on a total of 68 coffee trees. We found an effect of plot age on the species richness and composition on trunks. As age increased, the proportion of macrolichens on the coffee stems increased markedly. Neighbouring trees had similar numbers of species, but different species composition. There was no consistent difference in these patterns between plot ages. On tree stems, the number of species on consecutive sample heights were more strongly correlated on the older trees. Apparently successful dispersal at short distance is not common. A preliminary comparison of the epiphytic flora in the coffee plantation with natural forests at similar altitude showed the coffee plantation to be relatively species poor with a total of 45 (morpho) species. Of the genera found in the coffee plantation 64% were shared with the natural forest. The proportion of the various groups of cryptogams (mosses, liverworts, macrolichens and crustose lichens) was similar in the oldest coffee stand to the forests we used for comparison.

Resumen

Utilizando un cafetal como ecosistema modelo, el presente estudio está enfocado sobre los efectos del tiempo y la distancia de dispersión en la estructura de comunidades de briófitas y líquenes. En un cafetal en Colombia a 1700 m de altura, se hizo un inventario de las epífitas cryptógramas en cafetales de cuatro y ocho años de antigüedad, sobre un total de 68 árboles. Encontramos un efecto de la edad de las parcelas sobre la riqueza de especies y la composición en los troncos. Con un incremento de la edad la proporción de macrolíquenes aumenta marcadamente. Los árboles vecinos mostraron cantidades comparables de especies pero una composición diferente. No había una diferencia consistente en estos patrones entre parcelas de diferentes edades. El número de especies en posiciones consecutivas sobre los troncos, estaba más fuertemente correlacionado en árboles viejos. Aparentemente el dispersión exitosa a distancias cortas no es común. Una comparación preliminar de la flora epífita en el cafetal, con un bosque natural a una

altura similar, mostró que el cafetal es relativamente pobre en especies con un total de 45 (morfo) especies. Los géneros encontrados en el cafetal (64%) también ocurren en el bosque natural. La proporción de varios grupos de cryptógramas (musgos, hepáticas, macrolíquenes y líquenes crustosos) eran similares en la parcela más vieja del cafetal y el bosque que usamos para la comparación.

Introduction

The development, or succession, of epiphytic bryophyte communities has been studied mostly using the age gradient along branch length (Fisher Stone 1989, van Leerdam *et al.* 1990) or stem thickness (Tewari *et al.* 1985) as a measure of the substrate age. However, this age gradient is difficult to separate from the microclimatic gradient which exists along the length of branches. The general trend of epiphyte colonization in montane rain forests is that outer branches are first colonized by fruticose lichens, followed by foliose lichens and bryophytes on the thicker branches (Wolf 1995). A study on the succession of epiphyllous lichens, however, showed that there was no identifiable time-dependent sequence of species (Rogers 1995).

To understand the processes behind the structure of epiphyte communities and to assess the threat of extinction of these species an understanding of their dispersal ecology is necessary (Gradstein 1992a). Nevertheless, the dispersal ecology of bryophytes has received scant attention (Mishler 1988). Many epiphytic bryophytes can persist for extended periods of time on isolated remnant trees, but the species richness on these trees is smaller than on trees in old growth forests (Sillett *et al.* 1995). In temperate forests some species of lichens are restricted to old growth forests not because of specific habitat requirements, but because of dispersal limitation (Sillett *et al.* 2000). For these lichens ensuring the availability of remnant trees in young managed forests and transplantation have been shown to be effective to ensure their development in young forests (Neillich & McCune 1997, Peck & McCune 1997, Sillett & McCune 1998). However, remnant trees may not be effective propagule sources for the recolonization of younger trees in the vicinity by all species of bryophytes and lichens. In the case of bryophytes, both the development of spores and the successful establishment are uncommon events for many species (During 1992), and small populations on few remnant trees are unlikely to ensure their viability in the long term. There is evidence that some bryophytes are dispersed by birds and other animals, but the extent to which this happens is unknown, especially for tropical species (Van Zanten & Pócs 1981).

Coffee (*Coffea arabica*) plantations can play an important role in species conservation. Especially the traditional Latin American practice to grow coffee under shade trees offers a diverse habitat to many species of birds (Greenberg *et al.* 1997, Petit *et al.* 1999), mammals (Gallina *et al.* 1996) and arthropods (Johnson

2000). There is an ongoing trend, however, to replace shade coffee with higher yielding varieties which require full exposure to sunlight (Rice and Ward 1996). This has led to a decrease in species diversity for arthropods and birds (Perfecto *et al.* 1996) and species diversity in general (Moguel and Toledo 1999). Observations in Papua New Guinea suggest that coffee plantations are also important refuges for bryophyte diversity (Norris 1990). Nevertheless, the impact of the conversion from shade to sun exposed coffee on bryophyte diversity has not been quantified yet but is likely to be severe.

Our interest in coffee plantations was not only fuelled by their role in species conservation. With a single host species and recorded plot history, these plantations offer a model ecosystem for epiphyte studies. Plantations, other than coffee, have been used to study distribution patterns of vascular epiphytes in the tropics (Madison 1979, Catling *et al.* 1986) but we are unaware of such studies of non-vascular epiphytes (in particular bryophytes and lichens). There are a number of advantages of studying non-vascular epiphyte distribution patterns in coffee plantations. The low stature of coffee trees offers easy access for sampling. Also, the microclimatic gradient is likely to be similar along the trunk of same-age trees. This allows for sampling across comparable sites on trees. Coffee trees have the Roux architectural model (Hallé *et al.* 1978) and do not show major physiognomical changes during their development that could influence comparisons across tree stands of different age classes.

The purpose of this study was to describe the development of the non-vascular epiphytic vegetation on coffee trees by comparing stands of different ages. Also, the effect of local dispersal on the spatial distribution of epiphytes was assessed. Finally, we made a preliminary comparison of the epiphytic species diversity in a coffee plantation to that of a natural forest at similar altitude.

Methods

Field work area

Coffee trees were sampled between July and August 1998 at Finca Los Micos between Santa Rosa de Cabal (Risaralda) and Chinchiná (Caldas) in the Central Cordillera of Colombia at 1700 m asl. It lies in the middle of an extensive coffee growing area named the Eje Cafetero. The total area is of 11 ha and the main coffee variety planted was Caturro, which was also the variety on which we sampled. This variety was grown at full sun exposure, so that we had comparable climatic conditions all through the sampled stands. Most coffee fields in the plantation were divided by rows of bananas. Virtually all agricultural land in the surrounding area was also used for coffee plantations.

One of the advantages of this farm in comparison to other farms that were visited in the area was the fact that the tops of the trees were not pruned. Although

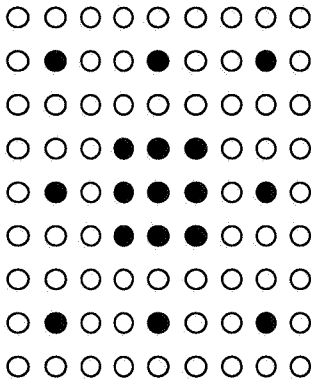


Figure 1. Schematic representation of the sampling design used in the studied coffee plantation. Actual distances between the trees are on average $1.39 \text{ m} \pm 0.06$ (s.d.) and 1.3 ± 0.1 in the top to bottom direction and 1.8 ± 0.1 and 2.1 ± 0.8 in the direction from left to right for the four and eight year old plots respectively

‘free growth’ of coffee trees makes manual harvesting more difficult, it is allowed to make the eradication of the coffee berry borer (*Hypothenemus hampei*) easier. Pruning induces more secondary and tertiary branching in the trees and this makes sampling more difficult and changes climatic conditions on the trunk.

The farming technique employed was modern, with the use of herbicides, fungicides and biological control of coffee berry borer. However, the owner was conservative in the use of pest control, and relied in large part on manual herb control to reduce erosion and improve soil structure. Fumigation was directed at the leaves, and stems were unlikely to be much affected (J. Ruiz pers. comm.). There are some indications that bryophytes are resistant to some of the more common herbicides (Schenk 1997). The fact that many species of lichens have been found in the samples indicates that the fungicides were not general. We could not evaluate whether some species had reduced abundance as a result of spraying. Management, including the frequency of fumigation and chemicals used, was similar throughout the plantation.

Sampling methods

We sampled in two coffee stands of different ages, one four years old and the other eight years old. A two year old stand was available, but there were no epiphytes visibly present on the stems, except for some green algae, so that we did not include it in this study. In each stand, two plots were laid out which were at least 25 meters apart. The plots in the four year old stand are referred to as 4.1 and 4.2 respectively, similarly the plots in the eight year old stand are referred to as 8.1 and 8.2. In each plot a center tree was chosen and the surrounding trees were identified and numbered according to the design shown in Figure 1. The distance between the four and eight year old plot was approximately 100 m. This design was chosen so as to have similar frequencies of distance classes. On each tagged tree, the first sample

was taken on the main trunk (in those cases where more than one stem was present) between 20 cm and 40 cm, the second between 60 cm and 80 cm and a third between 100 cm and 120 cm.

To facilitate the collection of epiphytes and reduce damage to the tree, the sample area was thoroughly moistened before the whole sample was collected. Collections were deposited in the herbarium of the Universidad de Antioquia, Medellín (HUA). Some samples could only be identified to genus level and were separated into morphospecies.

Statistical analysis

We tested for an effect of distance on the number of species on each coffee tree with a spatial autocorrelation analysis based on Moran's *I*. This index is a measure of the spatial autocorrelation in a single variable, where positive autocorrelation translates into a positive value for Moran's *I* and vice versa. We also tested the effect of distance on the species compositions of the trees using Mantel correlograms tested with 9999 permutations (Legendre & Legendre 1998). These are correlograms for multivariate data based on the Mantel correlation coefficient. The computation of this coefficient is based on multivariate similarity or distance matrices and is particularly useful to describe the spatial structure of species assemblages. We used the version of the probabilistic coefficient of Raup and Crick as suggested by Legendre & Legendre (1998) to calculate the similarity matrices of the trees (9999 permutations). This coefficient is a measure of how close the arrangement of species over the samples is to a random assignment of species to the samples ("random sprinkling of species"). All distance classes were based on the Euclidean distances between trees. The species data was pooled before performing the spatial analyses so that individual trees were the sampling units.

Results

We found 45 species of epiphytic non-vascular epiphytes the plots sampled plots in the coffee plantation. A high proportion of the collections could only be identified to genus level and these were separated into 33 morphospecies. The species names, authors and their respective frequencies are shown in Table 1. The third tier in the four year old plot did not have any epiphytes. Few species showed a clear height preference on the coffee trees. *Fabronia ciliaris* had exceptionally low frequencies on the first tier of the four year old plots. However, in these plots there was a marked higher frequency of *Syrrhopodon sp.* on the highest tier. In general terms, most lichens show a preference for higher tiers, especially in the eight year old plots. This is not the case for the mosses and liverworts although there are some specific cases with slightly higher (e.g. *Frullania sp.* and *Omphalantus cf. filiformis*) or lower (e.g. *Sematophyllum subpinatum*) frequencies observed in the higher tiers.

Table 1. Species and morphospecies found in the plots. The species from the duplicates are grouped together for display in this table. The frequency of the species is expressed as an percentage of the number of times it occurred in a sample at each tier and the total number of samples taken of each tier (34). The heights of the tiers were 40 - 60 cm (1), 80 - 100 cm (2) and 120 -140 cm (3). No epiphytes were found on tier 3 in the four year old plots.

Species	4 year old plots		8 year old plots		
	Tier 1	Tier 2	Tier 1	Tier 2	Tier 3
Mosses					
<i>Brachythecium</i> sp.	8.8				
<i>Erythrodonium squarrosus</i> (Hampe) Paris			2.9		
<i>Fabronia ciliaris</i> (Bridel) Bridel	8.8	85	100	100	97
<i>Groutiella apiculata</i> (Hooker) H. Crum & Steere	2.9	8.8	18	12	15
<i>Pyrrhobryum spiniforme</i> (Hedwig) Mitten	2.9				
<i>Schoenobryum concavifolium</i> (Griffin) Gangulee	5.9	2.9	15	2.9	8.8
<i>Sematophyllum subpinatum</i> (Bridel) E. Britton	68	41	79	79	68
<i>Streptopogon calymperes</i> Muller Hal. Ex Geheeb			2.9		
<i>Syrrophodon</i> sp.	41	5.9	8.8	8.8	12
Liverworts					
<i>Aphanolejeunea</i> sp.	8.8	62	2.9	2.9	26
<i>Dicranolejeunea</i> sp.	2.9		2.94		
<i>Frullania</i> sp.	26	41	62	74	76
<i>Lejeunea</i> sp. 1	94	91	100	85	76
<i>Lejeunea</i> sp. 2	12	12	12	8.8	8.8
<i>Metzgeria</i> sp.	85	79	53	5.9	53
<i>Omphalantus</i> cf. <i>filiformis</i> (Swartz) Nees	21	38	24	47	50
<i>Plagiochila</i> sp.			5.9	2.9	
Macrolichens					
<i>Candelariella</i> sp.					8.8
<i>Dictyonema</i> sp.			2.9		
<i>Everniastrum</i> cf. <i>vexans</i> (Zahlbr.) Hale ex Sipman					2.9
<i>Everniastrum</i> sp.		2.9			
<i>Heterodermia</i> sp.					2.9
indet sp1			2.9	12	21
indet sp2	5.9	2.9	8.8	21	21
<i>Lobaria</i> cf. <i>peltigera</i> (Delise) Vainio				2.9	2.9
<i>Parmotrema</i> sp. 1	2.9				15
<i>Parmotrema</i> sp. 1			5.9		
<i>Physcia</i> sp. 1	21	35	8.8	21	44
<i>Physcia</i> sp. 2	2.9		2.9		2.9
<i>Physcia</i> sp. 3	8.8	8.8	5.9	15	2.9
<i>Physcia</i> sp. 4			2.9	2.9	
<i>Usnea</i> sp.					2.9
<i>Xanthoparmelia</i> sp. 1	18		15	2.9	23

Table 1. (continued)

<i>Xanthoparmelia</i> sp. 2		2.9		2.9	5.9
<i>Xanthoparmelia</i> sp. 3				2.9	
Crustose lichens					
<i>Caloplaca</i> sp.					2.9
<i>Chiodecton</i> sp.			2.9	12	2.9
<i>Cryptothecia</i> sp. 1	18	5.9	2.9		
<i>Cryptothecia</i> sp. 2		2.9	2.9	2.9	
<i>Dimerella</i> sp. 1	5.9	5.9			2.9
<i>Dimerella</i> sp. 2	5.9	18	2.9		5.9
<i>Graphina</i> sp.					2.9
<i>Graphis</i> sp.		2.9	5.9	5.9	8.8
<i>Lepraria</i> sp.		5.9	2.9	5.9	5.9
<i>Porina</i> sp.		8.8		5.9	

Comparisons between plots

There was a consistent increase of the number of species with an increase in plot age (Figure 2). Most of this increase could be attributed to a higher number of macrolichens in the 8 year old plots. The most common mosses on the four year old trees were *Fabronia ciliaris* and *Sematophyllum subpinatum* (Table 1). The most common liverworts were *Aphanolejeunea* sp., *Frullania* sp., *Lejeunea* sp1, *Metzgeria* sp., and *Omphalantus* cf. *filiformis*. All of these species, except *Aphanolejeunea* sp. were also common in the eight year old stand. Only three species were restricted to the four year old plots and these were all rare (*Brachythecium* sp., *Pyrrhobryum spiniforme*, and *Everniastrum* sp.). In comparison to the four year old plots, the older plots had 15 additional species: two mosses, one liverwort, 10 macrolichens and three crustose lichens (Table 1).

Only few species showed a marked change in frequency between plot ages. Increased frequency in the older plots was observed for *Fabronia ciliaris*, *Frullania* sp. and *Parmotrema* sp1. A decrease was observed for *Aphanolejeunea* sp., *Cryptothecia* sp1 and *Dimerella* sp2. The two four year old plots share fewer species with each other than the two eight year old plots, especially in the case of mosses and liverworts (Table 2). Plot 4.1 has a completely different set of crustose lichens than plot 8.1. The latter plot had a low number of crustose lichens so that it also had little overlap with the other plots. Plot 4.2 shared more species with the two eight year old plots than with the plot of the same age (Table 2).

The average heights of the coffee trees in the plots were 2.38 ± 0.16 m (s.d.) and 2.32 ± 0.16 in the four year old plots and 2.52 ± 0.19 and 2.48 ± 0.31 in the eight year old plots.

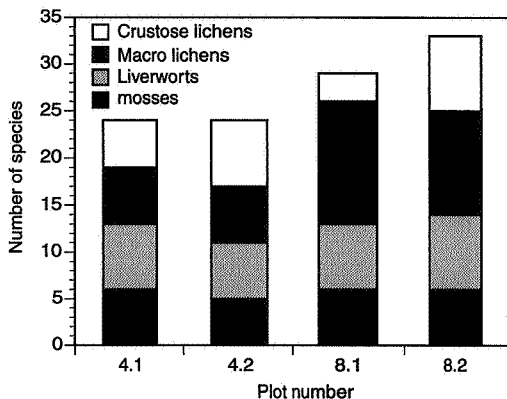


Figure 2. Number of morphospecies in each plot divided into taxonomic groups. The top white section of the bar are the crustose lichens, next in dark grey the macro lichens, light grey the liverworts and black the mosses.

Comparisons between trees

Species richness in plots 4.1 and 8.2 showed significant, positive, autocorrelation at short distances (Figure 3). This indicates that neighbouring trees have similar numbers of species. At intermediate distances these plots and plot 8.1 show negative autocorrelation. In other words, at distances between 5.4 m and 8.1 m (each lag is a 2.7 m wide distance class) trees have significantly different species numbers. The correlogram suggests a focal pattern characterized by peaks in species diversity (Figure 3).

The distance effect on species numbers was not reflected in the analogous analysis of the species composition between trees at different distances. A significant negative correlation was found for the similarity in species diversity at short distances in plots 4.1 and 8.2 (Fig 4). This suggests that trees standing close together were less similar in species composition than trees further apart.

Although we were not able to compare the species composition within trees (*i.e.* between height tiers), we could do so for the number of species on each tier. The correlation of species numbers from consecutive sampling heights were stronger in the older plots than in the younger (Figure 5), but this correlation was significant only between the top two tiers in plot 8.2.

Comparison with forest flora

We compared the species list to the species found by Wolf (1993) at 1500 and 1725 in a mature forest in the same region. The number of species found in forests at these altitudes was substantially higher (146) in comparison to the number found in this coffee plantation (45) (Figure 6). In a comparison at genus level, 22 (65%) of the

Table 2. Comparisons of species between plots. In the table, the percentage of shared species is shown expressed as a percentage of the total number of species occurring in either plot (total number shown between parentheses).

	4.1-4.2	4.1-8.1	4.1-8.2	4.2-8.1	4.2-8.2	8.1-8.2
Total	39 (31)	36 (36)	41 (37)	47 (36)	63 (35)	48 (42)
Moss	57 (7)	71 (7)	71 (7)	57 (7)	57 (7)	71 (7)
liverwort	57 (7)	50 (8)	63 (8)	86 (7)	75 (8)	88 (8)
Macrolichens	20 (10)	27 (15)	21 (14)	46 (13)	42 (12)	41 (17)
Crustose lichens	29 (7)	0 (6)	25 (8)	11 (9)	88 (8)	10 (10)

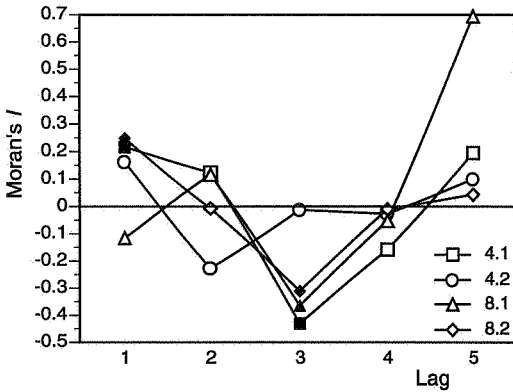


Figure 3. Correlograms based on Moran's I showing the autocorrelation of species richness on trunks. The lags are equidistant (2.7 m) and significant values of Moran's I after progressive Bonferroni correction are shown as black symbols.

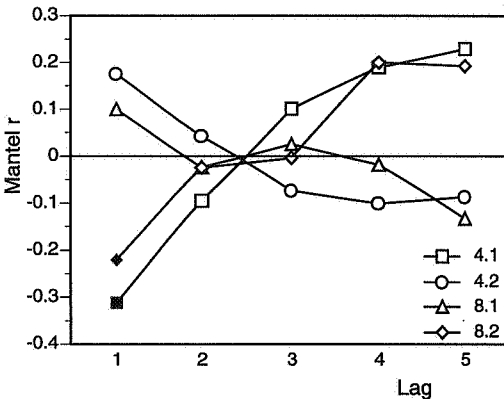


Figure 4. Mantel correlograms of the species similarity based on the Raup & Crick probabilistic coefficient. Black symbols indicate a significant value of Mantel's r after progressive Bonferroni correction. The lags are equidistant (2.7 m).

genera found in the coffee plantation were also found by Wolf (1993) at similar altitude, 6 (18%) at higher altitude, 1 (3%) at lower altitude. Four species found on coffee stems were not found or distinguished by Wolf at any altitude, namely *Aphanolejeunea* sp. (liverwort), *Fabronia ciliaris* (moss), *Lepraria* sp. (crustose lichen) and *Xantoparmelia* spp. (macrolichen).

The proportion of the four taxonomic groups changes with plot age, and becomes more similar to that of the old growth forest. This change is almost entirely attributable to the higher incidence of lichens in the older plots.

Discussion

Effect of stand age

The diversity of epiphytic bryophytes has been found to increase with plot age in rain forests, whereby the species richness increases due to permanence of the

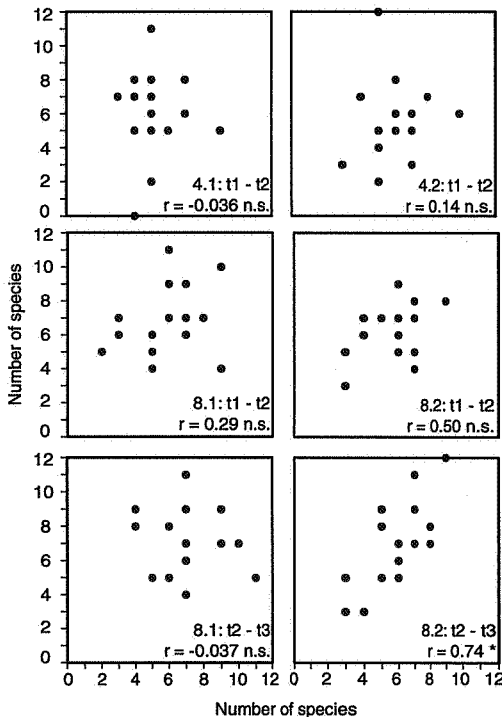


Figure 5. Scatter plots of species diversity on consecutive sampling heights. Inside the plot frame the plot number and the tier numbers are shown. Also the correlation coefficient and significance are shown. Correlation coefficients significant at the $P < 0.05$ level after standard bonferroni correction are marked with an asterisk (*).

pioneers and the colonisation by additional species at later successional stages (Equihua and Gradstein 1995). In the succession of epiphytic bryophytes, allogenic factors such as the increased diversity in microsites due to tree growth are probably more important than competitive displacement, although the latter also plays a role (Fisher Stone 1989). In our study, most common species in the four year old plots were also present in the older plots, with the exception of *Aphanolejeunea* sp. Unlike the results of studies that use branch length as a proxy for substrate age (Tewari *et al.* 1985, Fisher Stone 1989, Wolf 1995), lichens are not the first group to colonize these coffee stems. Instead, the most efficient colonizers of the younger stems were mosses and liverworts.

We have found little information about the ecology of the species in our samples. *F. ciliaris* is a common species with a wide geographical range (Buck 1983). This species is associated with areas of human activity such as cities and farms (Churchil & Linares 1995). *S. subpinnatum* also has a widespread distribution and is common in Colombia between 300 m and 2500 m asl. (Churchill & Linares 1995). Both species were common in all sampled plots (Table 1). In the older plots, the vegetative growth of *S. subpinnatum* is probably the cause of the lower frequency of *Aphanolejeunea* sp. on the lower tier in the four year old plots and in all tiers in the older plot. *Aphanolejeunea* sp. is very small (width less than 1 mm) and usually epiphyllous (Lücking 1995). It may have been competitively excluded by larger species such as the much larger *S. subpinnatum*. Apart from the effect on

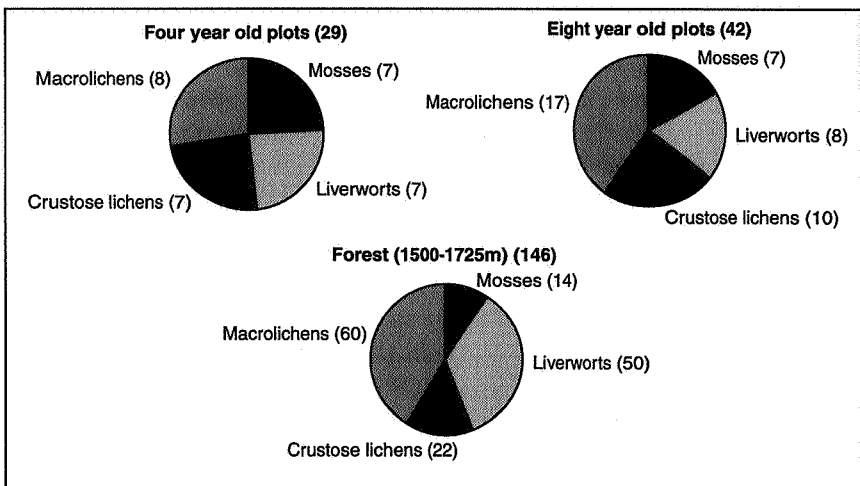


Figure 6. Pie charts comparing the proportions of the taxonomic groups between the two ages of coffee trees and a natural forest at the same altitude (data Wolf 1993). Between parentheses the total number of species and morphospecies found is shown.

this species, the overall role played by competitive displacement in these epiphytic bryophyte communities was probably small.

It is difficult to discuss the ecological requirements of the common liverworts on the basis of only genus names. *Frullania*, *Lejeunea*, and *Metzgeria* belong to taxonomically complex families which adds to the scarcity of information about their ecology. For tropical lichens a similar lack of information is prevalent. The increase of the number of species, however, was mainly due to an increase in the number of macrolichens. There are two possible explanations for this. Thalli of some of the species present in the eight year old plot may have been present in the younger but too small to be visible. A more likely explanation, however, is that most species of lichens are dispersal limited, as has been shown for other lichen species in temperate areas (Peck & McCune 1997). With few propagules available for colonization, the chance of successful establishment on a coffee tree is low. This chance is a function of time and with increased tree age, the chance of receiving a propagule also increases. Thus, the additional species in older plots was probably not the result of additional habitat available for colonization, either in quantity or quality, but a result of the longer period of exposure to the regional species pool. This may also explain why many, but not all, of the rare species were found in the older plot.

Another indication that the time available for colonization determines the presence of species is that the four year old plots share less species than the older plots (Table 2). Apparently there is no given sequence of species which colonize young trees first and then older trees. Instead there is a random draw from the regional species pool. The fact that the two year old plots did not have any epiphytes yet is another indication that the chance of settlement in each time unit is small. Again the lichens were the group that shared the least amount of species, even between plots of the same age (Table 2).

Tree growth is likely to have changed the microclimatic gradient along the trunks to some extent, especially because in cases where secondary trunks were formed. We failed to reliably measure these differences. The base of the trunk appeared to offer darker conditions with a higher relative humidity in the older plots than in younger plots. At the height of the highest samples these differences were minimal. Few species were restricted to a specific height on the trunk and there is this may be the result of a high level of niche overlap.

All in all, the process of epiphytic succession on these coffee trees had a probabilistic rather than a sequential character, as was also found for epiphyllous lichens (Rogers 1995). In this context, the repeated occurrence of species assemblages is a measure for the effectiveness of dispersal (Wilson *et al.* 1996). This will be further discussed below.

Effect of local dispersal

Two main factors that may limit successful plant recruitment are seed and microsite limitation (Eriksson & Ehrlén 1992). Nevertheless, recruitment limitation has not received the attention it deserves in plant ecology (Hurt & Pacala 1995). In epiphyte ecology, much emphasis has been put on the availability and quality of substrate, while only recently the importance of dispersal limitation has been recognized (Peck & McCune 1997; Sillet *et al.* 2000).

In this study we were not able to differentiate between an effect of dispersal limitation and a limitation in establishment as the most important factor determining the species composition of epiphyte communities. Neighbours of trees with a high number of species also had many species but this pattern was not consistent and not related to plot age (Figure 3). This neighbourhood effect is unlikely to reflect an effect of local dispersal. If it did, the similarities between trees would have shown a positive correlation (Figure 4). A number of factors may have influenced these patterns. Bark characteristics, for instance, can change as trees age (Studlar 1982). There is also a possible allelopathic effect of lichens on bryophytes (Frahm *et al.* 2000; Wirth *et al.* 1999). Furthermore small differences in the ability to retain propagules caused by bark roughness or already present vegetation can influence distribution patterns (Nadkarni *et al.* 2000). Other authors have attributed differences in epiphyte vegetation between neighbouring trees to differences in the nutritional status of the bark (Gausla *et al.* 1998). These bark conditions can be affected by the soil characteristics in which the host trees are rooted (Gustafsson & Eriksson 1995). Such differences are not expected in our study, because all trees received equal amounts of fertilizer dampening any effect of irregularities in soil nutritional status. Finally, differences in microclimate could have played a role despite our efforts to exclude them by working in a plantation.

We are unable to conclude that the tighter correlation between the number of species on consecutive tiers on older trees could be due to dispersal within stems. We did expect this, however, because short distances and the available water to disperse gametes, spores and vegetative propagules are advantageous to dispersal.

With the caveats mentioned above, we tentatively conclude that long distance dispersal from the regional species pool plays a more important role in determining the species composition of cryptogams on these coffee trunks than short distance dispersal. Peck & McCune (1997) report an effect of dispersal limitation at distances < 35 m. Our data suggest the possibility that even at much smaller distances (< 2.5 m), the effect of dispersal limitation can be observed.

Comparison to natural forest

The comparison to the data from Wolf (1993) is in many ways preliminary. If the objective of this study had been only to make an accurate comparison to the

diversity of natural forests, the replication in the study should have been over a number different plantations within this altitude range. Nevertheless, given the lack of information on this subject (Gradstein 1992b) this initial comparison seemed warranted. Although Hyvönen *et al.* (1987) found that the diversity of bryophytes in disturbed areas was sometimes higher than in natural forests, the number of species in the sampled coffee plantation was markedly lower than in forests at similar altitude (Figure 6). The development of the vegetation tended towards a proportion of taxonomic groups that was similar to the natural forest (Figure 6). If the rotation periods of standing trees is reduced many lichens species may not persist in coffee plantations. A deleterious effect of short rotation cycles on lichen diversity has also been found in temperate managed forests (Dettki & Esseen 1998)

Concluding remarks

Further studies are needed to fully understand the dispersal ecology of non-vascular epiphytes. Plantation studies offer a useful model vegetation for detailed studies of the distribution patterns of epiphytes and can yield results in the short term. However, long term experiments are needed to fully understand the mechanisms behind the observed patterns. The role of agro-ecosystems in the conservation of species diversity is also an important topic for future research. Some urgency is warranted with the latter as traditional farming systems, which have a relatively high non-crop species diversity, are converted to intensified forms of agriculture.

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