

Chapter 5

Effect of dispersal limitation on small scale spatial structure of epiphytic bryophyte communities in a tropical lowland rain forest (Araracuara, Colombia)

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Abstract

Few studies explicitly study the spatial relationships of non-vascular epiphytes (bryophytes, algae and lichens) in tropical forests. We sampled epiphytic bryophytes on trunks of *Oenocarpus bataua*, and recorded the palm coordinates. Samples were taken at three heights (1 m, 3 m, 5 m). For each sample all species were identified and their dry mass was determined. The species assemblage of the samples tended to be more similar within palms than between palms. At the level of individual species, on the other hand, only 3 out of 42 species showed some form of spatial dependence, either on single palms or between palms. The biomass ratio of mosses to liverworts increased with increasing sampling height, as did the number of species. Total biomass showed no response to sampling height. Apparently, short distance dispersal is less important than long distance dispersal in determining the species composition of nonvascular epiphyte communities.

Resumen

Hay pocos estudios sobre las relaciones espaciales entre epífitas no-vasculares (briófitas, algas y líquenes) en bosques tropicales. Muestreamos briófitas epífitas en troncos de *Oenocarpus bataua* anotando las coordenadas de las palmas. Las muestras fueron colectadas a tres diferentes alturas (1 m, 3 m, 5 m). Cada muestra fue identificada hasta el nivel de especie y su peso seco fue determinado. La composición de especies en las muestras fue aún más similar en una palma que entre ellas. La proporción entre la biomasa de musgos y hepáticas incrementó con la altura en la muestra, asimismo como el número de especies. La biomasa de muestras total no mostró respuesta al incremento de altura en el tronco. Aparentemente, la dispersión a distancias cortas es menos importante que la dispersión a larga distancia en determinar la composición de especies de comunidades de epífitas no-vasculares.

Introduction

Epiphytic bryophytes and lichens are an important component of tropical forests, especially at higher elevations, both in terms of biodiversity and of ecosystem functioning (Gradstein *et al.* 1990). The ecosystem function may be divided in their role in rainfall interception (Pocs 1980, Veneklaas & van Ek 1990) and their capability of nutrient retention (Nadkarni 1986, Hofstede *et al.* 1993). Release of nutrients may affect nutrient cycling within forests (Coxson 1990). The possible impact of deforestation on cryptogams in the tropics is severe (Gradstein 1992a, b).

In many aspects of conservation ecology an understanding of plant dispersal is crucial. The sexual reproduction of bryophytes however, has proven to be complex and more work remains to be done before we fully understand their reproductive ecology (Mishler 1988). The evidence up to date is that most bryophyte species are dispersal limited, except for those species with a high reproductive effort as part of their life strategy (During 1992). Long distance dispersal up to hundreds of kilometers can occur, but these are uncommon events which are difficult to investigate (Van Zanten & Pócs 1981). Long distance dispersal usually depends on the production of spores, although the transport of vegetative propagules and bryophyte fragments by animals does also occur (Watson 1964). All sexual reproduction depends on the availability of free flowing water to transport the gametes (Mishler 1988). In the case of dioicous species this means that male and female plants have to be close together, since transport of gametes is likely to take place over just a few centimeters. It is possible however that for epiphytic bryophytes these distances are much larger given the availability of stem flow which may actively transport gametes over the space of a few meters.

Not only the production of spores is a rare event, but also the chances for successful establishment are small (During 1992). On top of this, many species show a marked response to local environmental conditions which are highly variable even within one host tree (Oldeman 1983). Many species specialize on certain positions within a tree (Cornelissen & ter Steege 1989) and this is determined by their ecological amplitude. On a finer scale, within the ecological amplitude of species, the structure of bryophyte communities is likely to be founder controlled (Schuster 1957, Rydin 1986, Wolf 1993). In a founder controlled community, the community structure is determined by colonization events alone without the involvement of other processes such as competition (Yodzis 1989). This means that the species to arrive first at a site, has the highest chance of remaining there which will exclude new arrivals. There is some evidence for competitive exclusion of bryophytes on trees (Barkman 1958), but to our knowledge no experimental work on this topic has been done with tropical species.

Detailed experimental studies of single species is probably the only way to fully understand the dispersal and population biology of bryophytes. However,

given the dearth of information available, a less narrow, explorative approach seems warranted. Inferences about the mechanisms behind the structure of epiphytic bryophyte communities, however, are usually confounded by the large number of variables that determine the successful reproduction and establishment of these species, especially in natural systems. Our approach was to limit the number of variables as much as possible by working with a single species of host tree and on a small scale.

The purpose of this study was to test to identify the effect of dispersal limitation on epiphytic bryophytes in a tropical lowland forest on the trunks of *Oenocarpus bataua* Martinus. This palm has the architectural model of Corner and has one single trunk which forms one to three new leaves each year (Echeverri 1993). By comparing similar patches (same host, comparable microclimate) we could test the effect of dispersal distance on the composition of bryophyte communities. High aggregation of species, for example, would indicate a high importance of local dispersal. Low aggregation of species, on the other hand, would indicate that either short distance dispersal is not the most important factor, or that other processes, such as competition determine the community structure.

Methods

Study area

Fieldwork was carried out in August 1999 in an undisturbed mature forest on a low terrace of the River Caquetá, near the community of Peña Roja (0°40'; 72°06', Amazonas, Colombia). The climate in the area is warm and humid, with an annual rainfall close to 3000 mm and the yearly average temperature of 27°C (Duivenvoorden & Lips 1993). The forest resembles the phytosociological association of *Oenocarpus bataua* and *Mauritia flexuosa* described by Duivenvoorden & Lips (1993). According to these authors, this palm community occurs on acid soils which are permanently saturated with water and have a relatively thin layer of organic material (10-50 cm deep).

Field methods

In the northern part of the banks of the River Caquetá, forty minutes from the community of Peña Roja, six *O. bataua* palms in each of two size classes (9-12 m and >12 m) were sampled at random out of 7 and 37 palms

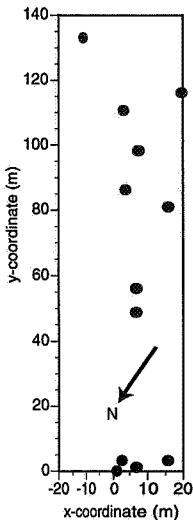


Figure 1. Map of the sampled palms. The arrow indicates the northern compass bearing.

Table 1. Pseudocode of the permutation tests. The variable *x* stands for the possible frequencies of the species in the plot (the number of times it occurred in the samples). These tests were implemented in MacPerl (5.20r4 available at www.cpan.org) and used the Fisher-Yates shuffle (Christiansen & Torkington 1998) to permute the arrays.

Crowding

for *x* = 2 - 20

 for *i* = 1 - 10000

 assign *x* occupied samples

 assign 36-*x* empty samples

 count nr. of occupied palms

Nearest conspecific neighbour

for *x* = 2 - 20

 for *i* = 1 - 10000

 assign *x* occupied samples

 assign 36-*x* empty samples

 calculate distance between conspecifics

 select smallest distance

respectively (Figure 1). These palms were found in an area roughly measuring 150 m x 20 m. The height of each palm trunk was measured with a 15 m long pole, with metric subdivisions or a clinometer, for taller trunks. Only those *O. bataua* palms taller than 9 m were included in the study, because palms with lower heights had sheaths of dead leaves that surrounded the trunk completely. This made it difficult to sample the epiphytes without damaging the palm. No effect of palm height was found and the palms were treated as one group in the analysis. Leaf scars on the trunks formed regular belts which we used as sample units.

At three heights, 1 m, 3 m and 5 m, the entire epiphyte vegetation on a belt was taken. The number of leaf scars up to the sampled belt was counted, and the width (cm) and exact height to the belt centre (cm) were measured. The taller belts, at 3 m and 5 m, were accessed using a ladder. All bryophytes were sampled for further identification in the Colombian National Herbarium (COL), were vouchers were also deposited (collection numbers M.P. Balcazar). Biomass estimates were based on these collections, which were sorted to species level, dried at 50°C and weighted on an analytical balance.

Statistical analysis

To map the species data, a Detrended Correspondence Analysis (DCA) was carried out using CANOCO (version 3.15 for PPC; Ter Braak 1988). DCA scores were preferred over a similarity index, because DCA scores reflect the position of the sample in relation to the whole dataset, whereas most similarity indices require a pairwise comparison of the samples (see also Legendre & Legendre 1998: 765).

The spatial pattern in the data was tested with two permutation tests (Manly 1991). In both cases, we determined the limits of a two sided 5% significance level based on 10,000 permutations of the arrangement of species presences over the samples. First we tested whether individual species co-occur more often on a single palm than expected from a random arrangement (crowding). As a test statistics we used the number of palms on which there was at least one occurrence of the species being tested (Table 1). In a second test, we calculated the sum of the distances to the nearest conspecific neighbour to test for spatial pattern (Besag & Diggle 1977) (Table 1). In both cases, and for each species, the values of the original data were compared to the limits generated by the permutation tests. Non-parametric Kruskal Wallis tests were performed to test for an effect of belt height on the moss/hepatic ratios, biomass, and number of species (JMP, version 3.2.2. SAS Institute Inc.).

Results

We found a total of 42 species of epiphytic bryophytes, belonging to 23 genera and 9 families (Table 1). The most speciose families of liverworts were the Lejeuneaceae with 11 genera and 13 species and Lepidoziaceae with 9 species. The Leucobryaceae with 2 genera and 6 species were the most speciose family of mosses (Figure 2). There were few species which had both a high frequency and a clear height preference. Sketching the results broadly, based on Figure 2), the mosses tended to be in the lower and middle tiers. Of the liverworts, only the Lejeuneaceae tended to be in the higher tiers, the Calypogeiaceae and Lepidoziaceae, like the mosses, tended to be in the lower and middle tiers.

The sample scores on the first axes of the DCA were mapped and show a larger range of the sample score values on separate palms than samples on the same palm (Figure 3). Since the palms were found in an area roughly resembling a 20 m x 140 m transect, the positions on the x axis in figure 3 follow their actual position closely. The advantage of using x+y on the x axis is that the three-dimensional spatial information can be shown in a two-dimensional graph (Rossi *et al.* 1992). This map also suggests that the species composition is more similar between some of the neighbouring palms than between palms at a larger distance. The gradient length of the DCA was high (6.9) indicating that the samples were well separated by the ordination. The fraction of variance explained by the first axis was relatively low however (9.6%). The latter suggests that there is no clear ecological gradient underlying the species data.

The spatial interpretation of the DCA was not corroborated by the pattern of individual species. On the level of individual species the occurrence of conspecific individuals was spatially independent (Figure 4 and Figure 5). Only three out of 42 species showed crowding on palms, *i.e.* they occurred more often on the same palm than expected from a random arrangement (see Figure 4). Also, only two species

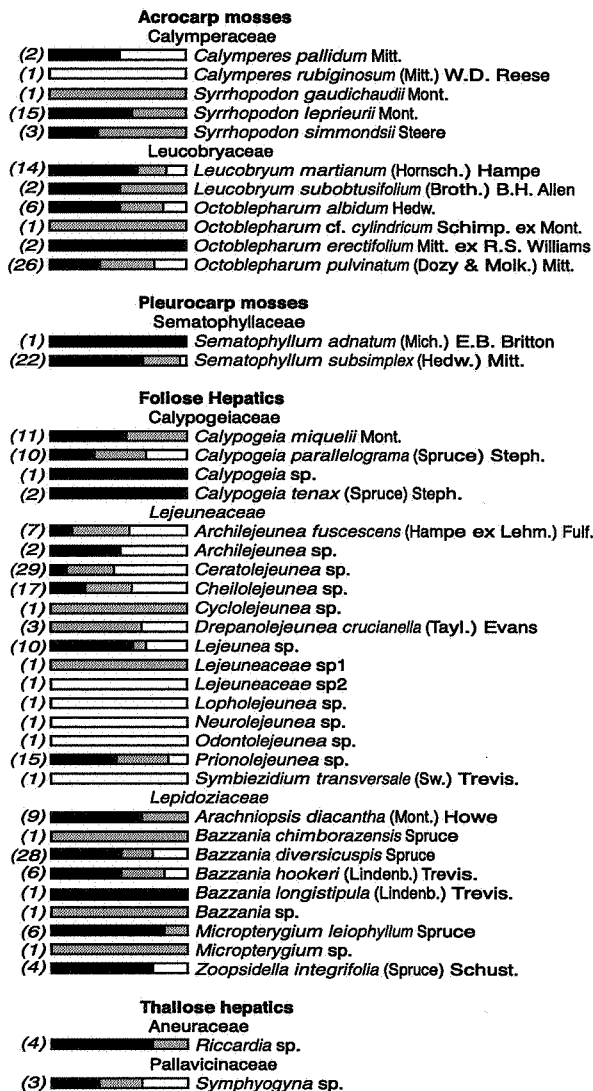


Figure 2. List of families (9), genera (23) and species (42) found on the palm species *Oenocarpus bataua* in the studied plot. The bars in front of the species names show the percentage of occupied samples found at the different heights: black (1 m), shaded (3 m) and blank (5 m). The number in front of the bar shows the total number of samples in which each species was found.

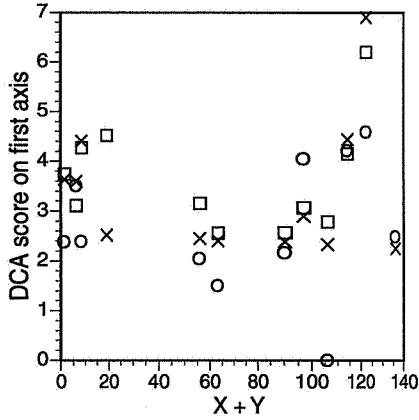


Figure 3. Map of the samples scores from a detrended correspondence analysis (DCA) the DCA scores based on the ln transformed biomass data. The open squares are the samples at 1 m height, the crosses those at 3 m, and the open circles those at 5 m height. See text for explanation of the x- axis.

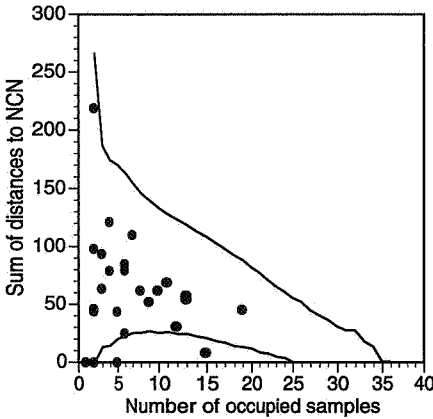


Figure 4. Nearest neighbour analysis of the samples. The lines show the upper and lower 2.5% limits based on 10000 permutations. Lying outside of the 2.5% lower limit are *Calypogeia parallelograma* and *Bazzania diversicuspis*.

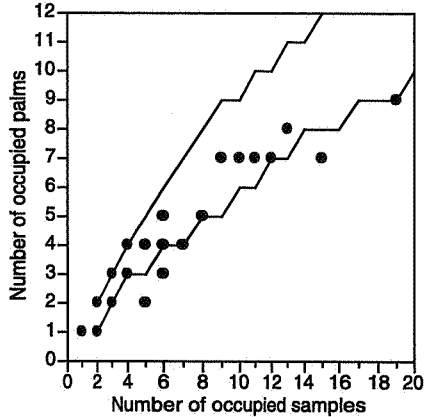


Figure 5. Permutation test of the crowding of species on single palm trunks. The lines show the upper and lower 2.5% limits based on 10000 permutations. Lying outside of the 2.5% lower limit are *Calypogeia parallelograma*, *Octoblepharum albidum* and *Bazzania diversicuspis*.

were spatially aggregated (Figure 5). Our overall interpretation of these two graphs is that there is no significant spatial pattern in the data of the individual species.

Sampling height had a significant effect on the moss/hepatic ratio and bryophyte cover (Table 2). Biomass however, did not respond to belt height. Species biomass was positively correlated with occurrence (Figure 6a). This was also found for the individual sampling heights (Figure 6a,b), with the exception of the samples at 7 m (Figure 6d). These correlations, however, were an artifact of the species which occurred only once. When these were removed from the dataset, no significant correlations were found per tier, although the overall data did show a significant correlation (Figure 6a).

Out of 272 collections, only six were found with sporophytes from samples on three separate palms. Two palms had fertile individuals of *Sematophyllum subsimplex*. On one other palm fertile individuals of *Octoblepharum pulvinatum* and *Octoblepharum cf. cylindricum* were found (See Figure 2 for authorities of species names). Other reproductive structures (*i.e.* gemmae) were not tallied, as most of these are less conspicuous and finding them was too time consuming.

Discussion

Our results support the hypothesis that epiphytic bryophytes are dispersal limited in tropical forests. This is in accordance with previous studies which have shown that both the production of spores and successful establishment are relatively rare events (Mishler 1988, During 1992). The rarity of spore production was also indicated by the low number of sporophytes we found in our collection. We expected to find a larger similarity of the samples taken on single trunks (*i.e.* similarity within palms) as a result of vegetative propagation. Given the larger weight of both gemmae and plant fragments in comparison to spores, the former are less likely to be dispersed between palms. That we did not find such an effect is likely to be due to the low retention rates of branches and trunks for bryophyte fragments (Nadkarni *et al.* 2000). Colonization of trees by bryophytes may in fact be a rarer event than the ubiquity of plants suggests.

Table 2. Results of the Kruskal-Wallis tests of the effect of height on the named variables. The probabilities shown are before Bonferroni correction. Probabilities which were significant after a progressive Bonferroni correction are shown in bold. Biomass ratio refers to the ratio of moss and liverwort biomass in the samples.

Variable	Chi square	df	Probability
Biomass ratio	12.1748	2	0.0023
No. of species	9.1234	2	0.0104
Biomass	4.6966	2	0.0955
Cover	8.0399	2	0.0180

There were a few exceptions to the above. First, there was the slightly higher similarity of species assemblages on neighbouring trees as found in the DCA analysis. The second exception were the few species which showed significant spatial structuring in the permutation tests. The results from the DCA analysis could be due to a shared propagule source. There were few trees in the area we sampled, but any of these could have served as a potential propagule source. Other, older, palms could have had the same effect but our data do not allow this assumption to be tested.

The second exception is more interesting. *Octoblepharum albidum* was one of the species which occurred more often on a single palm trunk than expected from a random assignment of species (Figure 5) This species has been classified as a colonist with a high reproductive effort (Gradstein & Pocs 1989, Frey *et al.* 1995). The other species which had a significant spatial dependence on conspecifics

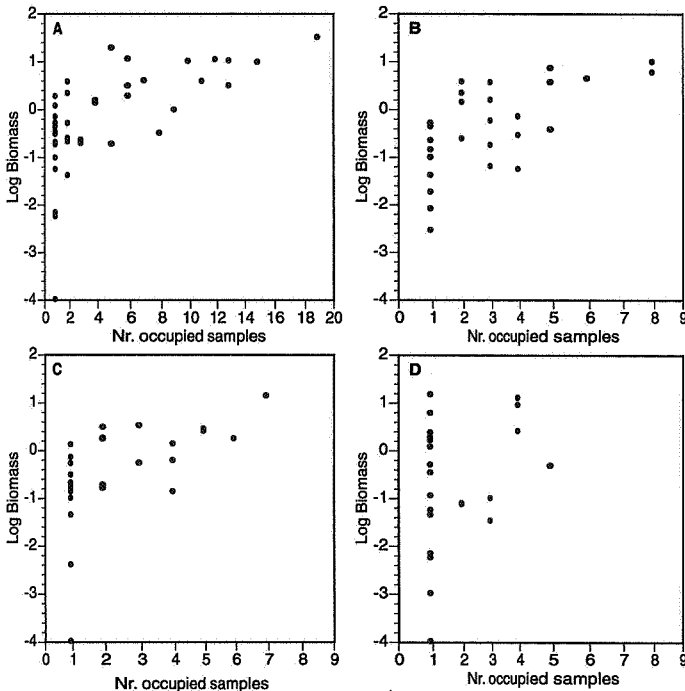


Figure 7. Relationship between species frequency and the log of their total biomass. Shown are a) all species across all heights, b) 1 m c) 3 m and d) 5 m. The correlations are highly significant ($P < 0.001$) for all plots except plot D when all data is included. When the species which occur only once are excluded, only Figure A is significant ($P < 0.001$).

(*Calypogeia parallelogramma* and *Bazzania diversicuspis*) were not included in the abovementioned classification by Frey et al. (1995). However, two out of three of the *Bazzania*'s they included were found to be perennial stayers with high reproductive effort, and possibly this was also the case for the *B. diversicuspis* in our study. Of these species only *O. albidum* was found with sporophytes in our collections, albeit only once.

One caveat that should be kept in mind when interpreting our results is that an environmental gradient is likely to exist along the palm trunks. The main reason to limit our sampling to 5 m above the soil was to limit the effect of a possible environmental gradient, but nevertheless there are some indications that such a gradient did exist. This was not immediately evident from the values for total biomass as this was not correlated with belt height (Table 2). There was however a decrease in total cover (Table 2) which was attributable to the small size of the species occurring at the highest belts, many of which were Lejeuneaceae. The number of species increased with belt height and this was also due to an increase in smaller sized species. The best indication for an environmental gradient, however, was the change in the ratio between mosses and liverworts. Proportionally more liverworts were present at the highest belt in comparison to the lowest. Unfortunately, we were not able to measure temperature and humidity at each sampled position on the palm trunks. Nevertheless we think that this change in the ratio of liverworts and mosses reflects the decrease in humidity from the forest floor. A different interpretation of the shift in the importance of mosses versus liverworts is given by Gradstein *et al.* (1989). They relate high liverwort species richness and cover to wet conditions at altitudes between 1200 and 3800 m a.s.l. Florschütz-de waard & Bekker (1987) on the other hand did not find consistent changes in the ratio of the number of species of mosses and liverworts, and they associate the occurrence of mosses with the environmental conditions closer to the forest floor. The latter authors suggest that liverworts have the highest adaptability to different habitats, especially the Lejeuneaceae. Their interpretation is consistent with the results in our study.

The existence of an environmental gradient means that our interpretation of the results from Figure 5 should include the fact that some species did not occur multiple times on the same trunk as a result of the constraints imposed on them by their ecological amplitude. Next to dispersal limitation, the availability of suitable patches is an obvious constraint for the settlement and development of epiphytic bryophytes.

The ecological constraint for settlement may not have been such an important factor in our study as the above suggests. We base this on the relationship between biomass and number of occupied samples of the species. The overall response of species biomass to occupancy was positive, showing an increase in

biomass with an increase in the number of occupied samples (Figure 6a). However, this relationship was not found for each belt height separately (Figure 6b,c,d). This was the result of a lack of preference of most species to any given belt height. This resulted in a high amount of singletons (species occurring only in one sample) at each belt height, so that the correlations were not significant as soon as these singletons were left out.

We chose a small scale for this study to test if any effect of distance on the distribution of epiphytes could be found. However, to understand the mechanisms behind the distribution that we have described, a theoretical model will probably be more helpful than field data alone. Computational models may make up for the difficulty of designing effective field experiments which monitor the colonization by epiphytes (VanDunné & Wolf 2001). Such a model should incorporate the following considerations which are play a role in determining the structure of communities of epiphytic bryophytes. First, the size of the species pool, and the ecological amplitude of each species. Second, a time step in the availability of spores reflecting the time from settlement to sporulation, which may be different for each species (During 1979). Third, although we did not find a measurable effect of vegetative propagation, this is bound to play an important role. Competitive exclusion of species, on the other hand, may not be necessary to incorporate. Even though there is evidence for competition on trees (Barkman 1958) and in chalk grassland communities (Van der Hoeve & During 1997) the role of competition in the development of epiphytic communities remains to be shown.

Conclusions

To assess the effects of the unabated degradation and fragmentation of tropical forests, and to design and implement sustainable harvesting practices, the development of the epiphytic vegetation needs to be understood. This study offers another indication that dispersal is one of the constraints for epiphyte settlement. In temperate forests, there is some evidence that dispersal limitation restricts some species of lichens to old growth forests (Sillett *et al.* 2000). and we give further evidence that this is also the case for bryophytes in tropical forests. Theoretical models may be the best tool to further understand the mechanisms behind epiphyte colonization and the constraints acting on it. Field studies on the other hand, could help disentangle the distinction between micro-site and recruitment limitation of epiphytes.

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