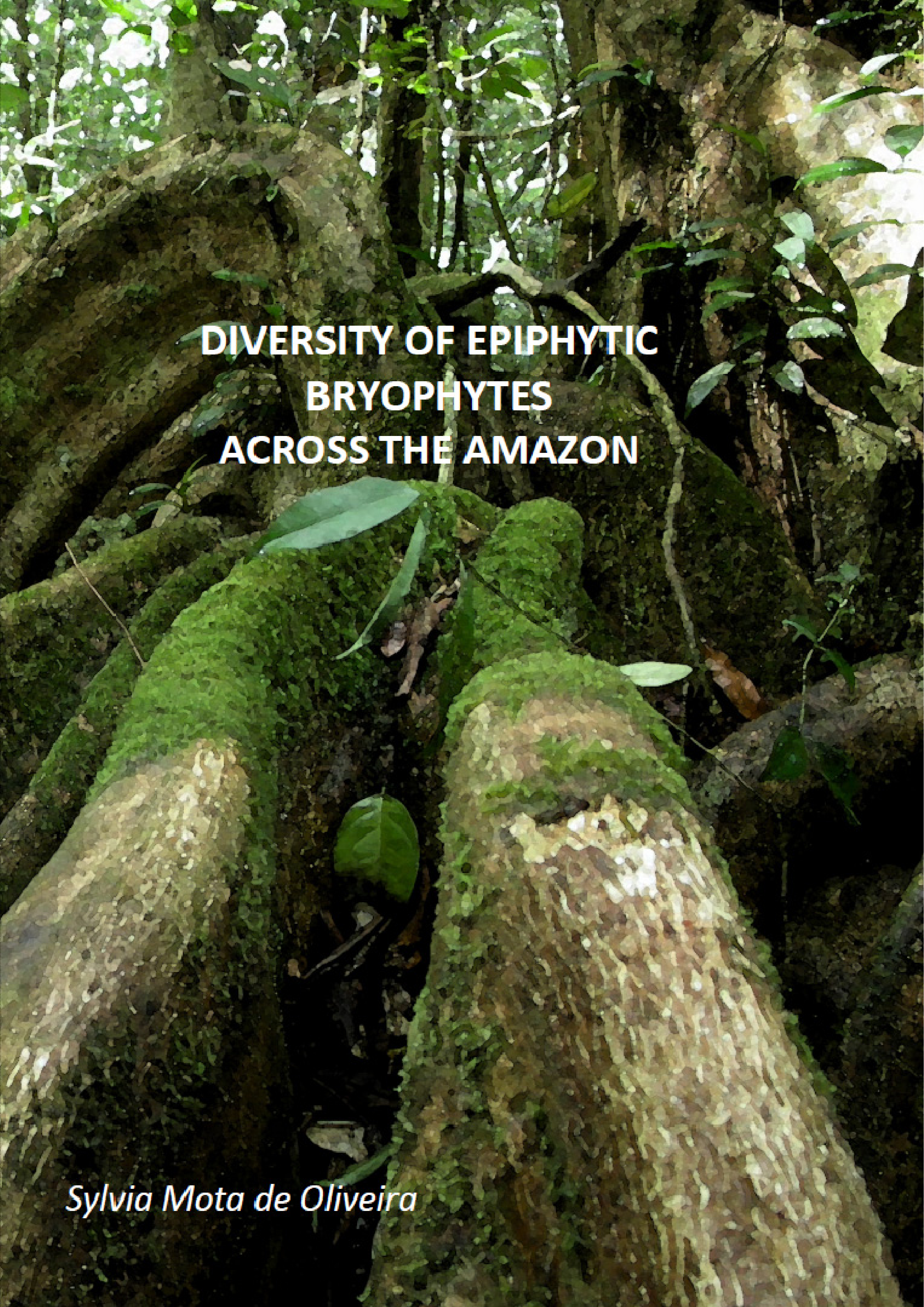


DIVERSITY OF EPIPHYTIC BRYOPHYTES ACROSS THE AMAZON

Sylvia Mota de Oliveira

DIVERSITY OF EPIPHYTIC BRYOPHYTES ACROSS THE AMAZON

Sylvia Mota de Oliveira

2010

The research for this thesis was carried out at the Ecology & Biodiversity Group of the Institute of Environmental Science, Utrecht University and funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Ministry of Education, Brazil

Sylvia Mota de Oliveira

Diversity of epiphytic bryophytes across the Amazon

ISBN: 978-90-393-53325
Keywords: Bryophyte, epiphyte, Amazon, Lejeuneaceae, diversity
Cover: *Pterocarpus officinalis*, photo by Hans ter Steege in Suriname
Printed by Ponsen & Looijen of GVO printers & designers B.V.
Designed by Carolinen Design Utrecht

DIVERSITY OF EPIPHYTIC BRYOPHYTES ACROSS THE AMAZON

DIVERSITEIT VAN EPIFYTISCHE BRYOPHYTEN IN DE AMAZONE

(met een samenvatting in het Nederlands)

DIVERSIDADE DE BRIÓFITAS EPÍFITAS NA AMAZÔNIA

(com resumo em Português)

Proefschrift

ter verkrijging van de graad van doctor aan de Universiteit Utrecht op
gezag van de rector magnificus, prof. dr. J.C. Stoof, ingevolge het besluit
van het college voor promoties in het openbaar te verdedigen op maandag
26 april 2010 des ochtends te 10.30 uur

door

Sylvia Mota de Oliveira

geboren op 7 september 1975 te Aracaju, Brazilië

Promotor: Prof. dr. M.J.A. Werger
Co-promotor: Dr. H. ter Steege

This thesis was accomplished with financial support from CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Ministry of Education, Brazil.

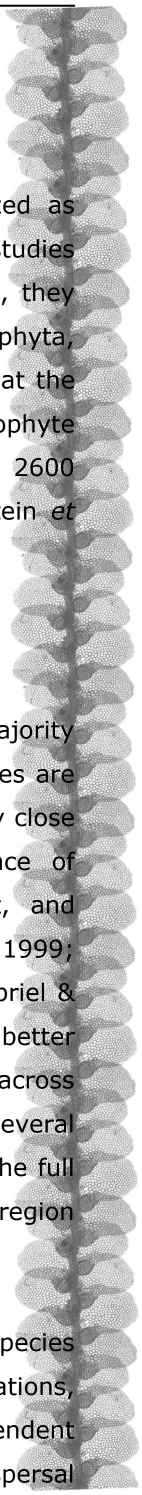
Dedico a Maria Vitoria, Daniel e Isabel, meus filhos

CONTENTS

1

1. Introduction

Bryophytes comprise around 18.000 species, commonly recognized as mosses, liverworts and hornworts. Based on phylogenetic studies supporting the hypothesis of a polyphyletic origin for these plants, they are now considered three distinct divisions of Plantae: Bryophyta, Marchantiophyta, and Anthocerophyta (Goffinet 2000). Here we treat the three divisions by the general denomination "bryophytes". Bryophyte species occurring in the Neotropics correspond to approximately 2600 Bryophyta, 1350 Marchantiophyta and 30 Anthocerophyta (Gradstein *et al.* 2001).



A short introduction in bryophyte ecology

The fact that bryophytes are non-vascular, and in their majority poikilohydric, means that hydration and other physiological processes are strongly affected by the physical and chemical conditions of the very close surroundings. The literature on this topic stresses the influence of microenvironmental features such as pH, substrate type, light, and relative humidity in species occurrence (Coley *et al.* 1993; Costa 1999; Holz *et al.* 2002; Szövényi *et al.* 2004; Wiklund & Rydin 2004; Gabriel & Bates 2005). Interestingly, local ecological variables may even be better predictors of bryophyte composition than regional variables across landscapes (Bacaro *et al.* 2008). Probably this happens because several ecological variables, relevant to bryophyte occurrence, will exhibit the full range within very short distances, no matter the extension of the region under study.

The environment, however, can only affect the occurrence of a species after successful dispersal has taken place. The alternation of generations, with a long lived and independent gametophyte, producing a dependent and frugal sporophyte, includes the possibility of two main dispersal mechanisms, sexual and asexual. Given the wide distributional range of bryophyte species compared to other plant groups, these mechanisms seem to lead to successful dispersal (Frahm 2008). Multiple events of long distance dispersal and fast colonization rates are documented (Young & Klay 1971; Miller & McDaniel 2004; Ah-Peng *et al.* 2007). In a very general view, asexual reproduction is assumed to be a short term solution for population growth and maintenance, while sexual reproduction brings long term advantages such as genetic variability and long distance dispersal, expanding the geographical and environmental range of the species (Longton 1992; Kimmerer 1994; but see also Pohjamo *et al.* 2006 for long distance dispersal of asexual propagules). Still, bryophytes do not grow in every suitable habitat patch. Evidence of dispersal limitation is often suggested in local scale studies (Kimmerer 2005; Zartman & Nascimento 2006), probably because here the effects of metapopulation dynamics – local extinction and recolonization – can be identified.

Most of the studies on bryophytes address only one of these two fundamental aspects – dispersal limitation / environmental limitation – of species occurrence. I believe that a better understanding of how exactly these processes shape community composition depends on investigating them together, and in terms of relative importance. And this is one of the goals of this thesis.

Bryology in the Amazon – description of the species records

The first collections of bryophytes in the Amazon are from expeditions of naturalists such as Karl von Martius and Richard Spruce, during the 19th century. At that time, the astonishing diversity of Lejeuneaceae was studied in detail by Spruce (1885), in one of the most important contributions to the knowledge of liverworts and hornworts in the Neotropics, *"Hepaticae Amazonicae et Andinae"*.

Bryophyte surveys in the lowland Amazon forest have taken place mostly in Brazil. In countries of the Amazonian-Andean arch, studies are concentrated in the species-rich montane and sub-montane bryoflora, leaving the lowlands poorly investigated. During the last 20 years, a few catalogues have been published for these countries, where specific records for the Amazon can be found. We give here an overview of the most recent and easily available literature. In Colombia, two catalogues (Uribe & Gradstein 1998; Pinzón *et al.* 2003) and one ecological study (Benavides *et al.* 2006) are the main contributions in terms of species list. From Bolivia, it is worth to mention the lists of mosses of Santa Cruz, published by Fuentes & Muñoz (2002), the *Catalogue of the Hepaticae and Anthocerotae of Bolivia* (Gradstein *et al.* 2003) and the ecological study of Acebey *et al.* (2003), which also brings species lists. The *Mosses of Amazonian Ecuador*, listed by Churchill (1994) and the *Hepaticas y Antoceros del Ecuador* (León-Yánez *et al.* 2006), which includes Amazonian material, are the main contributions for this country where I believe Amazonian bryophyte diversity may reach its peak! In Peru, checklists of liverworts and mosses recorded for the country (Menzel 1984; Menzel & Schultze-Motel 1992) include species sampled in Amazonian areas. In the northern contour of the Basin, many lists have been published for Guyana, Suriname and French Guiana (Florschütz-de Waard & Bekker 1987; Florschütz - de Waard 1990; Boggan *et al.* 1992; Buck 2003).

In Brazil, inventories conducted by specialists started in the 1970’s (see review in Lisboa 1991) and a great number of them were carried out in Eastern Amazon, in the surroundings of Belém and Ilha do Marajó (Lisboa 1984, 1985; Lisboa 1994; Lisboa & Ilkiu-Borges 1997). Those include areas of terra firme forest, swamp and savannah woodlands. Inventories in Serra dos Carajás and scattered localities in the south of Pará set up the information available from the Amazonian southeastern contour (Ilkiu-Borges *et al.* 2004; Moraes & Lisboa 2005). In central Amazonia, inventories are concentrated in terra firme forests and campinarana sites up to approximately 100 km around Manaus (Lisboa 1976; Griffin III 1979; Zartman & Ilkiu-Borges 2007). Also areas of terra firme and savannah forest in the state of Roraima were sampled (Yano 1992; Santiago 1997). Additionally, species occurrences were published over the years as first records either for the region or for the federative states (Costa 2003; Santos & Lisboa 2003; Alvarenga *et al.* 2007), as lists of species in a particular taxon or biological group (Yano 1985; Lisboa 1993) and as new species descriptions (Zartman & Ackerman 2002). Comprehensive publications include a "*Catalog of Amazonian mosses*", based on bibliography, with 311 listed species (Churchill 1998) and "*The Hepaticae and Anthocerotae of Brasil*" (Gradstein & Costa 2003), with keys and descriptions, which is not specific for the Amazon but includes liverworts and hornworts recorded in the Brazilian Amazon.

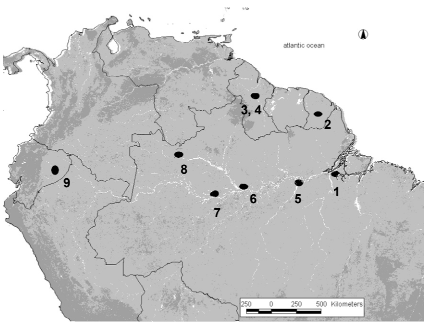
The data produced by these studies allowed a general description of the Amazonian bryoflora. It is estimated that 800 species occur in the region (Gradstein *et al.* 2001). They inhabit preferably bark and branches of trees, the surface of leaves and logs, and to a much lesser extent rocks and soil surfaces. The epiphytic habitat, corticolous in bryological terms, is the most common in number of species. One liverwort family – Lejeuneaceae - accounts for approximately 70% of all species recorded. Mosses are mainly represented by the families Calymperaceae, Leucobryaceae, Fissidentaceae, Pilotrichaceae and Sematophyllaceae.

The collections composing the reviewed literature, despite its informative value, lack a pre-established experimental design, which hampers its use for testing macroecological hypotheses. That is of course expected from inventories without an ecological goal. Unexpected, however, is the fact that hardly any of them explored the canopy. The importance of canopy sampling was already pointed out for more than a decade by Cornelissen & Gradstein (1990), when the authors observed that 50% of the listed species in a mountain forest in Guiana were restricted to the canopy. Recently, large scale biological projects established sampling protocols, a necessary step that became clear when conservation and governance policies needed robust scientific data from extensive regions such as the Amazon. Bryophytes are included as a target biological group in one of these large scale initiatives, PPBio, a Brazilian governmental project for biodiversity research. Surprisingly, the canopy is not mentioned in the standard protocol of bryophyte sampling of the project, which I suggest to be corrected as soon as possible. The concentration of the sampling effort in the understory certainly underestimates the bryoflora and diminishes the possibilities of ecological research.

Diversity across the basin – positioning bryophytes among current research hypotheses

Alpha and beta diversity patterns across the Amazon have been studied at different scales, from the entire basin to units as small as a few hectares. Biological processes explaining these patterns are obviously a function of the scale as well as of the group under study, which hampers generalizations. At large scale the main pattern of alpha diversity in the Amazon Basin seems relatively straightforward. Diversity of canopy trees increases from East to West and composition seem to be related with soil fertility and productivity (Phillips *et al.* 1994; ter Steege *et al.* 2006) and this East to West gradient is found in several other taxa studied (birds, amphibians, mammals). At regional and local scale the research focus is usually on beta diversity. Studies of beta diversity and turnover of species composition in plant communities have been concerned with two interacting processes: dispersal assembly and niche assembly. It is difficult, however, to separate their effects. Niche assembly, claimed when any relationship between environment and composition is consistent, was reported for trees and especially herbs and ferns (Tuomisto *et al.* 2003a; Drucker *et al.* 2008; Zuquim *et al.* 2009). It is frequently found more prominent than dispersal assembly patterns. On the other hand, environmental variables do not show the same range everywhere, which hampers the generality of the proposed relationships (Costa *et al.* 2005).

Few studies show dispersal overriding the main role of environment in community composition similarity (Condit *et al.* 2002). Very important to notice is that in most cases, dispersal assembly is tested only through the relationship between distance and composition, although it can also be driven by species relative abundance, without a clear spatial pattern. The assumption of a hierarchical framework such as metacommunity – local community dynamics can contribute to a better understanding of the role that is played by dispersal.



1. Caxiuana, Brazil
2. Saul, French Guyana (FG)
3. Mabura Mora, Guiana (MM)
4. Mabura Wallaba, Guiana (MW)
5. Floresta Nacional do Tapajos (TA)
6. Reserva Ducke, Brazil (RD)
7. Província petrolífera de Urucu, Brazil (UR)
8. Parque Nacional do Pico da Neblina, Brazil (SG)
9. Tiputini Biodiversity Station, Ecuador (EC)

Figure 1. Map of the study area, showing the sampling localities from East to West in the Amazon and Guiana Shield.

Lay out of this thesis

In order to reveal what are the general patterns in the ecology of epiphytic bryophytes in the Amazon, two aspects needed to be addressed: community structure and a large scale approach. The thesis presented here aims at taking the first steps along these lines.

In ***chapter two***, I conduct a first regional study of Amazonian bryophytes, studying species composition of communities in different height zones of trees from three forests in the Guianas. I test whether composition is mainly explained by height zone or by spatial distance. Do species maintain their preference for a given height zone across the region? Are there differences in species richness of different forests?

Additionally, I bring a list of all species with respective height zone(s), pointing out the ones considered indicator species.

In ***chapter three*** I present the first overall analysis of bryophyte alpha diversity in non-flooded forests of the Amazon, across nearly 3000 km. Surprisingly, the climatic gradients across the basin do not drive bryophyte richness. I take a hierarchical approach for the species composition of the local communities, firstly by testing the null hypothesis of local communities built as random samples of the metacommunity and secondly by using the Neutral Theory of Biogeography and Biodiversity (Hubbell 2001) as a first explanation for richness and species abundances in local communities. Can species disperse across the basin? Does abundance in the metacommunity drive occurrence and abundance of a given species in the local communities? Finally, I identify where community features cannot be explained by neutral theory and where other mechanisms influencing alpha diversity are still to be tested.

In ***chapter four*** I use the concept of the metacommunity and a hierarchical approach to address the relative roles of environment and dispersal in local community composition. Is height zone the main predictor of species composition at all localities and also across the basin? Do the relative roles of environment and dispersal on species composition change along the different height zones? And do the relative roles of environment and dispersal on species composition change from plot to locality to across locality scales?

In ***chapter five*** I select the most abundant terrestrial plant in the Amazon (!), the Lejeuneaceae *Cheilolejeunea rigidula*, in order to test dispersal across the basin based on molecular data. I compare the genetic distance of populations established in the same locality (maximum 5 km radius) with that of populations established in different localities. To which extent are populations of the same site and populations from different sites related? Does the metapopulation structure indicate panmixy or do I find distance decay in similarity? This chapter is excitingly related to the link 'metacommunity – local community' that we proposed in chapter 3.

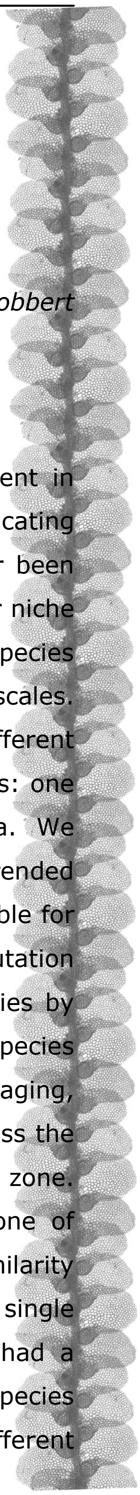
Finally, in ***chapter 6*** I discuss the predominant mechanisms at play in the species composition of epiphytic bryophyte communities in the Amazon, its relatedness with other plant groups already investigated, and a research agenda for future activities.

This thesis has two appendices. In **Appendix 1** a short resume of the floristics and microhabitat specialization of Amazonian epiphytic bryophytes is given. **Appendix 2** lists all species found in this study with their appropriate authorities.

2

2. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach

with Hans ter Steege, Johannes H. C. Cornelissen and S. Robbert Gradstein



ABSTRACT

Epiphytic bryophyte communities of tropical forests show a gradient in species composition from the base to the top of the host trees, indicating a strong role of niche assembly. This pattern, however, has never been tested at a regional scale. The aim of this study was to test whether niche assembly, rather than dispersal limitation, predominantly drives species composition of bryophyte communities across large spatial scales. Communities of epiphytic bryophytes were sampled from six different height zones of several trees in three lowland forests in the Guianas: one near Saul, French Guiana; and two near Mabura Hill, Guyana. We analysed the composition of these communities, using detrended correspondence analysis, in order to find the best explanatory variable for the variation in community composition. A multi-response permutation procedure was used to test the significance of grouping communities by height zone. We conducted an indicator species analysis to classify species as specialists or generalists and then tested, through weighted averaging, if specialists would indeed maintain their preferred height zone across the Guianas. Community composition was explained mainly by height zone. The similarity among communities inhabiting the same height zone of trees, across a distance of up to 640 km, was higher than the similarity among communities established along the vertical gradient of a single standing tree (30–50 m). More than half (57%) of the species had a preferred height zone, and the preference was consistent: species occupied roughly the same height zone on host trees in the different localities. Throughout the Guianas, epiphytic bryophyte communities are drawn from the same regional species pool, and their composition is shaped by micro-environmental conditions. The predominance of niche assembly over dispersal assembly rules is consistently found at both local and regional scales.

Keywords
Amazon, canopy, community assembly, dispersal, epiphytes, French Guiana, Guyana, liverworts, mosses.

Introduction

The turnover in species composition of plant communities in the Amazon forest has been attributed to two interacting processes: dispersal assembly and niche assembly (Condit et al., 2002; Phillips et al., 2003; Tuomisto et al., 2003a; McGill et al., 2006). Both processes can drive community composition, and, in our view, the relative importance of each process not only is a matter of scale, as is exhaustively argued, but also depends on the biology of the group under study. For instance, if most tropical tree species are generalists in terms of habitat preference (Hubbell, 2001, 2005), the turnover of species results from limitations in the ability to reach distant available spots, imposed by weight and other characteristics of the propagules (fruits, large seeds). The prediction of dispersal limitation driving the differences in similarity of tree communities was tested across the Western Amazon and Panama, with the distance between plots varying from 0.1 to 1400 km. Dispersal limitation explained most of the variation in tree community composition of plots separated by distances from 0.2 to 50 km in the Western Amazon (Condit et al., 2002). At the same spatial scale (across a 43-km-long transect), however, Tuomisto et al. (2003b) found patterns of niche assembly of communities of Melastomataceae and pteridophytes in the Western Amazon. Here, soil type was considered the main source of beta diversity in those plant groups, and dispersal limitation probably plays a lesser role than environment owing to the features of the propagules, since small seeds (Melastomataceae) and, especially, spores are more easily spread. A strong distance dependence of propagules is recorded for all plant groups. Smaller or lighter propagules such as the ones cited above, however, tend to show comparatively lower distance decay rates (Nekola & White, 1999). Therefore, one might argue that niche-based assembly rules determine community composition more prominently as dispersal limitation of species decreases. Bryophytes are an interesting group to investigate in this context, since they produce thousands of spores per capsule (see review in Glime, 2007); spores are extremely light and small (around 10–40 lm) and can easily become airborne and travel hundreds of metres (Miller & McDaniel 2004; Sundberg *et al.* 2006). Furthermore, this large number of propagules can be produced in one colony by many sporophytes, releasing spores throughout the whole year (Oliveira & Porto 2001). Miles & Longton (1992) showed that only 4.5–12.7% of the spores of two moss species could be trapped within a 2-m distance from the centre of the colony. Based on this and their geographical distribution patterns, bryophytes are generally considered to have the highest rates of dispersal, in terms of distance, compared with other taxonomic groups such as ferns and seed plants (van Zanten & Pócs 1981). We thus assume high dispersal ability in distance, and predict bryophyte communities to be consistently niche-assembled across large spatial scales.

It is challenging to investigate the bryophyte communities across the lowlands of the Amazon. The area has been poorly inventoried, and very few ecological studies have taken a regional approach (Florschütz-de Waard & Bekker 1987; Gradstein *et al.* 1990; Benavides *et al.* 2006). Published local-scale studies are mainly inventories based on understorey samples, with only a few exceptions (Lisboa 1976; Zartman 2003). Together these studies draw a general picture of the bryophytes in the Amazon, with species richness varying from 40 to 120 species per hectare, and low endemism rates (2.5–6%) (Gradstein et al., 2001a; Gradstein & Costa, 2003). The beta diversity of bryophytes across the region is considered to be low (Churchill 1998), although this has never been formally tested.

The epiphytic habitat is clearly the most important habitat for bryophytes in tropical forests, and epiphytic communities inhabit trees from the base to the outer branches of the canopy (Richards 1984). The microclimatic gradient that exists from understorey to canopy, with large differences in air temperature, relative humidity, quantity and quality of light, and CO2 concentration, is well documented (eg. Whitmore 1998; Lowman & Rinker 2004). Moreover, the ages, diameters, angles and bark textures of twigs, branches and trunks provide a range of conditions for bryophyte establishment along the vertical gradient. A clear species turnover in community composition along this gradient was recorded in Guyana (Cornelissen & ter Steege 1989). Apparently, in the Amazon forest, the majority of species inhabit a preferred height zone on the phorophyte, the canopy being more species-rich than the trunk (Gradstein *et al.* 2001b). Thus, based on the cited literature, there is already strong evidence for a predominant role of niche assembly at the local scale. At a regional scale, however, we may ask if the community composition of the different height zones is maintained over short and large distances, given the great dispersal potential of many bryophyte species (van Zanten & Pócs 1981). Specifically, we hypothesize that niche-assembly rules will prevail also at a regional scale in shaping epiphytic bryophyte community composition. Furthermore, we expect that species maintain their preferred height zone in the phorophyte across the region, a prerequisite for niche assembly. To test these hypotheses, we analysed the composition of bryophyte communities established along the vertical gradient on trees in three lowland forests on the Guiana Shield, separated by a maximum distance of 640 km.

Methods

The dataset originates from three studies undertaken by members of Utrecht University (Cornelissen & ter Steege 1989; Montfoort & Ek 1989; Bleij 1991). We compiled the majority of the data from the original reports, and added some extra data from the authors' original notebooks. Other data were recovered by re-examination of the collections deposited at the Nationaal Herbarium Nederland (NHN), Utrecht. Nomenclature of mosses is based on Gradstein et al. (2001a), and that of liverworts on Gradstein & Costa (2003), with updates.

Study areas

The studies were carried out in one forest in French Guiana and two in Guyana. These forests, being all lowland Amazonian forest, have similar (near sea-level) altitudes and temperatures. In French Guiana (FG), the study area was near Saul (3º37' N, 53º12' W), approximately 640 km from the localities in Guyana. In Guyana, we sampled two forests near Mabura Hill: Wallaba forest (MW), located at 5º20' N, 58º10' W; and Mora forest (MM), located approximately 20 km south-east of MW (5º13' N, 58º48' W). The forest around Saul, French Guiana, is a mixed forest with a canopy of 45 m; it is located on relatively dissected terrains of lateritic soils with a deep vertical drainage and has a total annual precipitation of around 2500 mm (Mori & Boom 1987). Wallaba forest and Mora forest, in Guyana, receive a total annual precipitation of around 2750 mm (Jetten 1994). Wallaba forest is dominated by *Eperua falcata* Aubl. and *E. grandiflora* (Aubl.) Benth.; it has a canopy of 30 m, and grows on excessively drained white sand soils – albic Arenosols. Mora forest, with a canopy of 50 m, is dominated by *Mora excelsa* Benth. and is subject to periodic flooding. The forest occupies the lowest grounds in broad strips along creeks, on dystric Fluvisols (Fanshawe 1952; ter Steege 2000).

Data collection

In total, 54 full-grown canopy trees were sampled. In French Guiana, the 28 phorophytes selected for sampling belonged to 20 distinct tree species and yielded 140 species of bryophytes. In Mabura Wallaba, two species of phorophytes were selected (*Eperua grandiflora* and *E. falcata*). A total of 11 individuals were sampled and 72 bryophyte species were recorded. In Mabura Mora forest all 15 phorophytes sampled were *Mora excelsa* and they yielded 67 species of bryophytes. Each tree was divided into six height zones, from the base up to 1 m (zone 1), via the lower and upper trunk (zones 2 and 3) to the crown (zones 4 and 5) and finally the outer sun-lit twigs (zone 6) (Cornelissen & ter Steege 1989). The height zones were used as a surrogate of the microclimatic gradient found from the canopy to the bottom of the forest. Therefore, their distances from the ground are relative to the height of the forest, in order to represent the best spacing of the gradient. The bryophyte communities were sampled by standardized procedures: bryophyte communities were sampled in plots of approximately 40 cm2. In each tree, one plot was placed in each height zone, to provide a total of six plots per tree. All sampled plots from FG and MW were deposited at the NHN. The relative abundances of species in the collections (plots) were estimated in a range from 1 to 5, using a logarithmic scale, in which the abundance values were estimated according to the percentage of coverage, as follows: 1 = 0.1–1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, and 5 = 50–100%. We checked at least one collection of each species recorded to FG and MW in order to match species identifications and we corrected synonyms for all three sites. The collections from MM were not available, so we excluded two doubtful species that each had only one record (Lejeunea species ‘A’ and Lejeunea species ‘B’). We also excluded 20 plots, owing to imprecise information in collectors’ notebooks, which could not be recovered through examination of the collections.

Data analysis

Plot ordination was carried out with detrended correspondence analysis (DCA), using abundance data. We calculated the explained variation (R^2) as the correlation between the matrix of distances in similarity between the plots, calculated as Euclidean distances, and the Euclidean distance between the plots in the ordination space. We then correlated the scores of the plots in the first axis of the ordination with their respective height zone, as this was the expected environmental gradient. The correlation was calculated using Spearman's rank correlation coefficient. Furthermore, a multi-response permutation procedure (MRPP) was carried out to calculate similarity among communities and to test if the similarities among communities in the a priori height-zone classification were significantly different from similarities among communities drawn at random. Indicator species analysis (ISA) was used to investigate the preference of species for each of the six height zones, in each locality separately. This method takes into account the relative abundance of a species in a particular group (here height zone) and the relative frequency of the species in this group. These two measures combined produce an indicator value (IV) that weighs the preference of a species for a particular group. Randomization procedures test for the significance of the indicator value obtained for each species. All analyses were carried out with PCORD 5 (McCune & Grace 2002). Finally, we conducted a direct gradient analysis (Jongman *et al.* 1987) in Microsoft Excel, calculating the 'weighted average height zone' for each specialist species in each locality separately. The calculation is based on the abundance and number of occurrences per zone. In order to verify whether those species considered specialists by the indicator species analysis in the localities separately maintained their preferences across the region, we correlated the 'weighted average height zone' of each species between the localities.

Results

The 304 plots yielded 155 species (see Table S1 in Supplementary material, this chapter, for a list of species and nomenclature) in 83 genera and 27 families of bryophytes. Lejeuneaceae (liverworts) was the most common family, with 62 species. The second and third most species-rich families were Macromitriaceae and Calymperaceae (mosses), with 11 and 10 species, respectively. The most common species was *Cheilolejeunea rigidula* (Mont.) R.M. Schust., which occurred in 60% of the plots, followed by *Ceratolejeunea cornuta* (Spruce) Stephani, *Lopholejeunea subfusca* (Nees) Schiffn. and *Cheilolejeunea adnata* (Kunze ex Lehm.) Grolle. The 12 most common species were liverworts. Among the mosses, *Zelometeorium patulum* (Hedw.) Manuel, *Octoblepharum albidum* Hedw. and *O. pulvinatum* (Dozy & Molk.) Mitt. were the most common species. The average number of species per plot was 11, ranging from 1 to 31.

Table 1. Number of species recorded per height zone in French Guyana, Mabura Mora and Mabura Wallaba forest, and in the three localities together; average similarity among plots per zone.

Height zone	**Number of species** **FG**	**MM**	**MW**	**Total**	**Similarity all plots**
1	57	20	14	70	0.21
2	51	43	25	77	0.12
3	62	35	27	82	0.13
4	95	43	38	110	0.2
5	83	46	29	98	0.26
6	81	34	38	92	0.31
Total	**140**	**67**	**72**	**155**	

The species richness in FG was the highest of the three localities (Table 1). We counted 51 species restricted to FG in this dataset. Since more trees were sampled in FG, we checked through species phorophyte curves and the average number of bryophyte species per phorophyte whether the higher richness was merely an artefact of the higher sampling effort. The species–phorophyte curves show that, for the same number of phorophytes in the three localities, FG still harbours more species (Fig. S1). Furthermore, confirming this result, the average number of species per tree in FG was 47, which was significantly higher (ANOVA; $F_{[2,\ 51]} = 26.2$; $P < 0.005$) than that in MW and MM forests (32 and 29, respectively). Canopy communities – plots on height zones 4, 5 and 6 – were significantly richer (ANOVA; $F_{[1,\ 302]} = 133.1$; $P < 0.005$) than understorey communities – plots on height zones 1, 2 and 3. In FG and MM, zones 4 and 5 yielded the highest number of species; in MW, zones 4 and 6 were the richest. Similarities among communities were highest in the canopy – zones 5 and 6 – followed by the lowest zone in the understorey – zone 1.

The DCA ordination of 291 plots (13 plots had fewer than three species and were excluded from this analysis) and 155 species resulted in two informative axes (k1 = 0.650, explained variation = 33%; k2 = 0.385, explained variation = 15%) for a total explained variation of 48% (Fig. 1).

The scores for the first axis of the DCA were significantly correlated with height zone for the entire dataset (Fig. 2) (Spearman's rank correlation: rs= 0.86, $P < 0.001$), which means that community species composition is explained mainly by the height zone on the phorophytes, at both the local and regional scale (Fig. 1a). Analyzing each locality separately, the highest correlation between DCA scores and height zone was recorded in MW forest ($R^2 = 0.87$, $P < 0.001$), followed by FG ($R^2 = 0.77$, $P < 0.001$)

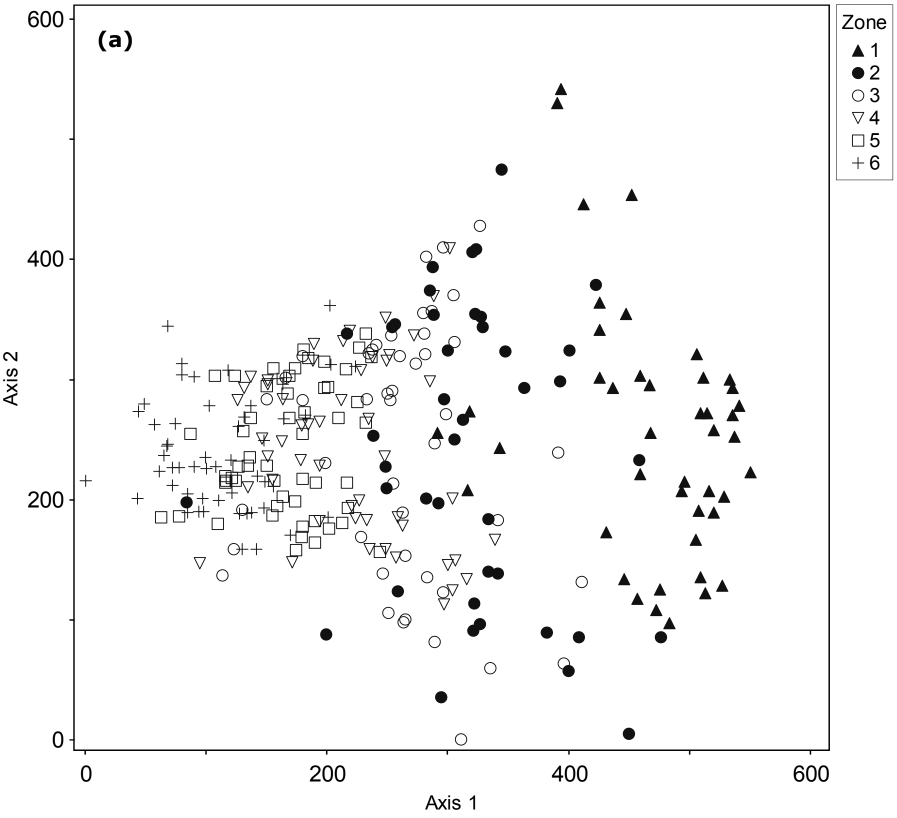
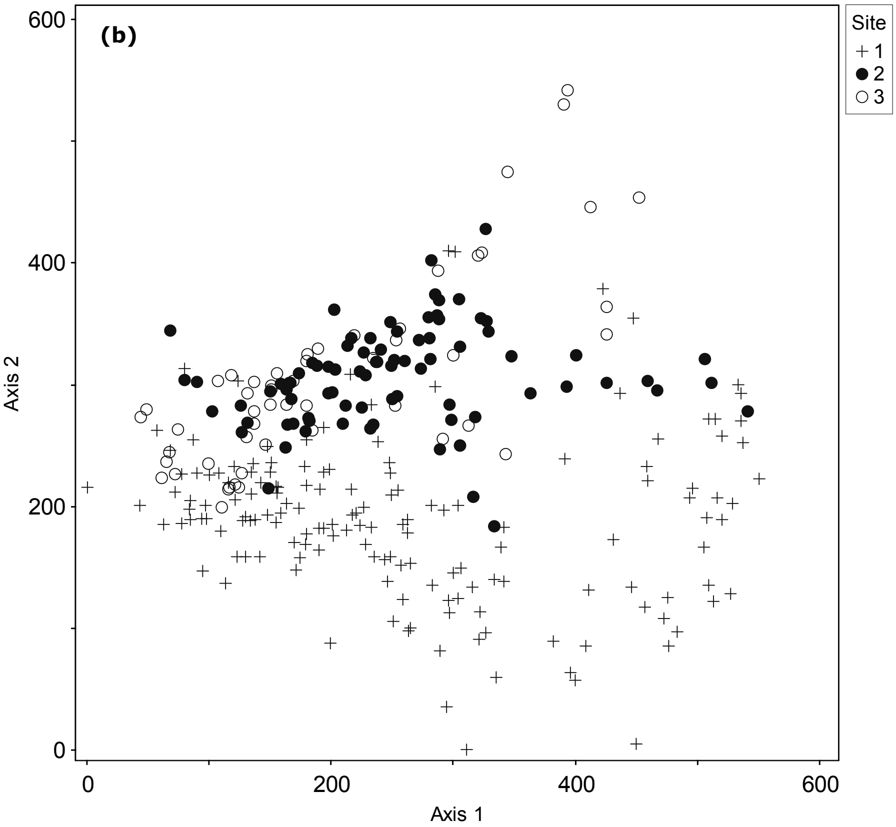


Figure 1. Ordination bi-plot of the DCA analysis of 291 plots and 155 species. Each point in the graph represents one sampling plot. The bi-plot is given twice with different labels for the sampling plots: **1a**. Symbols indicate the height zone of the plot (see legend). There is a clear gradient in zonation from plots in height zone 1, on the right, to plots in height zone 6, on the left. **1b** (next page). Symbols indicate the locality where the plot was sampled (1-French Guyana, 2-Mabura Mora, 3-Mabura Wallaba). The bi-plot clearly separates the FG plots in the bottom from the plots in Guyana (MW, MM) in the top of the graph.



and MM ($R^2 = 0.74$, $P < 0.001$). The second axis of the DCA separated the FG forest from the Guyanan localities (Fig. 1b). Finally, axis 3 separated the two Guyanan localities but contributed very little to explained variation. The significance of the contribution of height zone for the variation in community composition was confirmed by the multi-response permutation procedure ($A = 0.065$, $P < 0.001$).

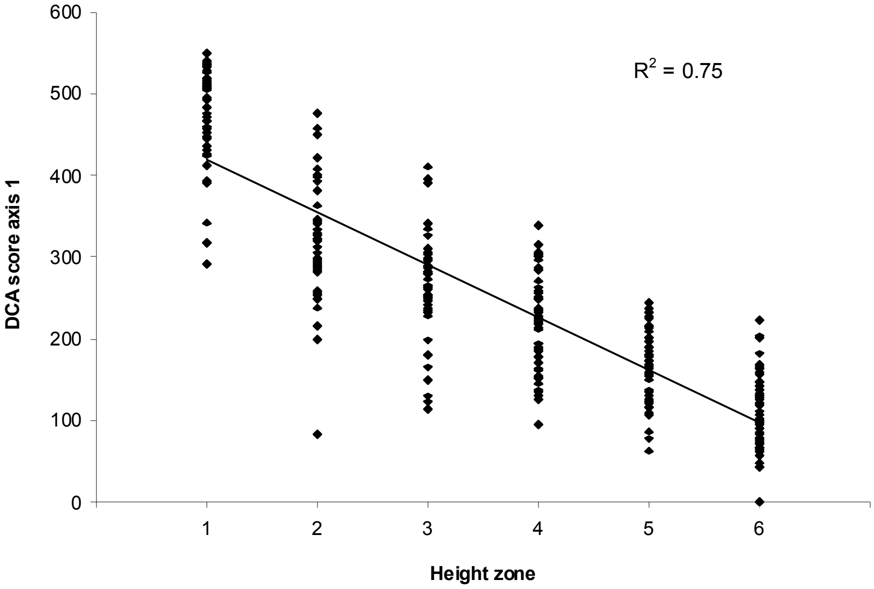


Figure 2. Correlation between the height zone and the score in the first DCA axis for each of the 291 plots in the analysis (Spearman's rank correlation). The best-fit line by linear regression is shown for illustrative purposes only.

Thirty-three species were found to be specialists by indicator species analysis in at least two localities. The majority of these were found to be specialist in all three localities. The weighted average height zone of these selected specialists was significantly and strongly correlated across sites, which means that species are consistent in their preferred height zone (Fig. 3). Because the preference for height zone is consistent across the region, it was reasonable to conduct a single indicator species analysis for the entire dataset. The result showed that in total 96 species (61% of all species) had a significant ($P < 0.005$) preference for one height zone. The strength of the preference is expressed by the indicator value, as explained in the Materials and Methods section (see Supplementary material). Interestingly, we found that 46% of the understorey specialists (zones 1, 2 and 3) were found in a single locality, whereas the canopy specialists (zones 5 and 6) were more widespread, with only 18% restricted to one locality.

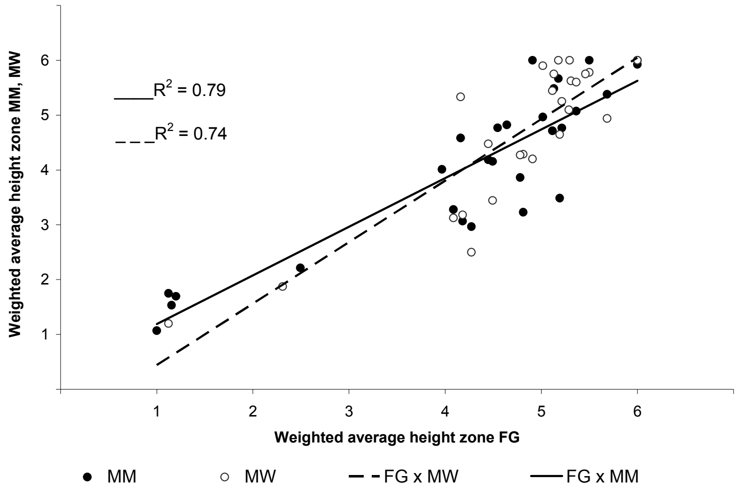


Figure 3. Correlation of the 'weighted average height zone' of species in FG with the 'weighted average height zone' in MM (dots, solid line, for species co-occurring in FG and MM) and MW (open squares, broken line, for species co-occurring in FG and MW).

Discussion

Across distant sites in the Guianas, epiphytic bryophyte communities show a clear vertical zonation. The turnover of species along the micro-environmental vertical gradient within a single standing tree (c. 30–50 m) is much stronger than the turnover across a geographical distance of 640 km. In fact, the variation in composition explained by DCA axis 1 (height zone) is more than twice that of axis 2 (distance). In our study, as hypothesized, individual species maintained their preferred height zone across localities, independent of forest type, soil type and phorophyte species. We take this as a strong indication of the predominance of niche-assembly rules. If dispersal assembly rules prevailed, the similarity between communities would be more strongly related to distance, through neutral processes (Hubbell 2001), than to zonation within the tree.

The turnover of species from tree base to top is probably best explained by microhabitat conditions. In general, temperature, light and wind velocity increase upwards along the vertical gradient, whereas age of substrate, roughness, nutrient stocks and humidity decrease. Similar vertical zonation is found in vascular epiphytes (Johansson 1974; ter Steege & Cornelissen 1989; Zotz & Vollrath 2003). How is the gradient of community composition established? The mechanism behind it still lacks strong support from physiological studies, but the influence of the microhabitat is clear: for instance, we found *Henicodium geniculatum* (Mitt.) W.R. Buck and *Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffner as specialists of height zone 6, whereas in Bolivia these two species are also restricted to the canopy of intact forest, but shift downwards in height zone in tree-fall areas, where light penetrates deeper (Acebey *et al.* 2003). Some species do require high light intensity, for example those in the highly pigmented genus *Frullania* (Glime 2007). *Frullania* species tolerate desiccation well compared with other species, as tested experimentally by Romero et al. (2006). In our study, *Frullania* inhabited the middle and outer canopy (zones 4, 5 and 6) and showed a preference for zone 6. At the other extreme, the preference for – or the limitation of species to – the understorey is probably the result of a low tolerance of desiccation and/or high light levels. Shade specialists tend to disappear from tree trunks of highly impacted forests (Costa 1999; Acebey *et al.* 2003) or have a decreased abundance as a function of forest fragmentation (Pereira Alvarenga & Pôrto 2007). Indeed, we found many of the species considered shade specialists (e.g. *Archilejeunea parviflora*, *Pilosium chlorophyllum*, *Octoblepharum pulvinatum*) as indicative species of height zone 1. The influence of micro-environment on the presence of species is confirmed by the high number of specialists in the dataset.

Despite the clear gradient in composition across the tree height zones and the high proportion of species with a preferred height zone, the similarity among communities in general, including within height zone, is low (12–31%). Similarity among communities can be affected by community structure, population dynamics of the different species, and epiphyte–host relationships. In terms of community structure, many species are present as singletons or doubletons, which is a pattern commonly found in other biological groups (see reviews in Rosenzweig 1995; Hubbell 2001). Therefore, part of the low similarity among communities is a consequence of community structure. Second, owing to temporal population dynamics (local extinction), species do not constantly occupy every suitable piece of habitat (Hutsemekers *et al.* 2008). The non-continuous nature of the substrate (tree trunks) imposes constraints to colonization, and hence, as in many patchy substrates, local dispersal limitation plays a role (Söderström 1989). Finally, host preference may have an influence on community composition through the preference of certain species for particular bark features (McCune *et al.* 2000; Szövényi *et al.* 2004). We assume that these three processes all negatively affect community similarity, leading to the low values reported above. The higher similarity among canopy communities, associated with a higher number of specialists and higher species richness, needs further investigation. At the species level, research has shown that dispersal strategy can be associated with spatial patterns of species richness (Löbel *et al.* 2009). At the community level, we assume that communities with higher dispersal rates show higher similarities. In this case, higher chances of dispersal in canopy communities, given the higher wind velocity favouring wind dispersal, could be an explanation for the increased similarity among these communities. In addition, the higher similarity in zone 1 compared with the other zones of the understorey – 2 and 3 – could be attributed to dispersal, if one considers that species inhabiting zone 1 are frequently found on logs, which would enhance chances of dispersal owing to higher substrate availability. In a montane rain forest of Costa Rica, the composition of communities in height zone 1 is indeed more similar to community composition in logs than that in any other zone (2–6) (Holz & Gradstein 2005).

The higher number of species recorded in French Guiana is partly a result of the higher number of phorophytes sampled. Despite this sampling effort bias, however, the bryoflora in FG is indeed the richest, as shown by the higher number of bryophyte species per tree and by the species–phorophyte curve. Interestingly, the species richness of vascular epiphytes is also higher in FG, when compared with MW and MM, a phenomenon related to a higher number of individuals of vascular epiphytes on the host trees in FG (ter Steege 2000). One could argue that the number of tree species of a site can influence bryophyte richness, since a higher number of tree species represents a wider array of bark features available. Given the high number of tree species in tropical forests, we believe that this is unlikely to happen here. Differences in tree species richness between tropical forests, as for instance between Saul and Guyana, are to a large extent the result of additional tree species with one individual. Such single tree individuals, even if they have a different bark, are so rare that they are unlikely to contribute significantly as a new source of bryophyte species. Gradstein (2006) proposed that the constant presence of fog in this area favours bryophyte growth. Explicitly, if water availability in FG is more constant than it is in the other sites, the chances of the successful establishment of propagules and bryophyte growth are higher, since external water is an important determinant for photosynthesis and growth (Proctor 2000; Leon-Vargas *et al.* 2006). In this case, as was also argued for vascular epiphytes (ter Steege 2000), higher numbers of individuals may lead to higher species richness. Based on the Checklist of the plants of the Guianas (Boggan 1996), we found that 75% of the species restricted to the FG dataset have been recorded somewhere else in Guyana or Suriname. Furthermore, there were hardly any species restricted to MW or MM (2 and 3, respectively), and we therefore conclude that these epiphytic communities are essentially part of the same regional species pool. The set of species present in MM and MW is just a smaller subset of that regional species pool than is FG's bryoflora.

Despite the fact that the debate concerning community assembly raised by the 'Neutral Theory of Biodiversity and Biogeography' has produced an interesting body of literature, most of the research has been theoretical

(Alonso & McKane 2004; McKane *et al.* 2004; Etienne & Alonso 2005; Zillio & Condit 2007). Only a few published papers deal with the role of dispersal and niche processes in the turnover of plant community composition based on original datasets. Compared with recent publications on the community assembly of vascular plants in the Amazon, we found a consistent and very particular pattern of turnover in community composition for epiphytic bryophytes. Canopy tree communities, for instance, do not correlate well with environmental factors. Most species are found to be habitat generalists (Pitman *et al.* 1999; Hubbell 2001), and the community composition has been interpreted by Condit et al. (2002) to be driven by dispersal limitation mainly at a scale of 0.2–50 km. Although Tuomisto et al. (2003a) have demonstrated that the community composition of ferns and Melastomataceae is determined more by environment, as we also verified for bryophytes, they found composition turnover related to distance at a scale of < 80 km as well. Epiphytic bryophytes clearly differ from all these groups by the presence of communities built from the same regional species pool over a large distance, with their local composition strongly driven by a micro-environmental gradient.

Acknowledgments

The authors are grateful to CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior / Brasil - for funding the first author; NHN - Nationaal Herbarium Nederland – Utrecht, for working space; to Bert Bleij and Dimitri Montfoort for making notebooks and data from the Guianas available; to Gijs Meijer and Chequita Bhikhi for support during the work with the Herbarium collections; to Marinus Werger and Heinjo During for discussions and comments on an earlier draft of the manuscript.

Supplementary material – ISA and species phorophyte curves

Table S1. Species found in the Guianan plots. The table shows species name and authority; indicator value (IV) given by indicator species analysis; number of records of the species in each height zone (1-6) for the total dataset. Height zones were established from the base up to 1 metre (zone 1), via the lower and upper trunk (zones 2 and 3) to the crown (zones 4-5) and finally the outer sun-lit twigs (zone 6). Indicator values were given only for significantly indicator species, ranging from 0 (no indication) to 100 (perfect indication). Species in bold are indicator species and numbers in bold refer to their preferred height zone.

Species	**IV**	**1**	**2**	**3**	**4**	**5**	**6**
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiff.			1	1	4	1	4
Acroporium pungens (Hedw.) Broth.				5	3	4	1
Archilejeunea auberiana (Mont.) A. Evans							2
***Archilejeunea fuscescens* (Hampe & Lehm.) Fulford**	10.2		**18**	18	15	12	3
***Archilejeunea parviflora* (Nees.) Schiffn.**	6.4	**3**					
Bazzania cuneistipula (Gottsche, Lindenb. & Nees) Trevis.				1			
Bazzania hookeri (Lindenb.) Trevis.			3	4	3	3	
Bryopteris filicina (Sw.) Nees						1	
***Callicostella pallida* (Hornsch.) Angström**	11.6	**7**	2			1	
***Callicostella rufescens* (Mitt.) A. Jaeger**	4.3	**2**					
***Calymperes afzelli* Sw.**	7.4	**10**	3	6	8	2	
Calymperes erosum Müll. Hal.		3	11	13	14	10	2
***Calymperes lonchophyllum* Schwaegr.**	13.9	**19**	16	9	4	1	1
Calymperes platyloma Mitt.			2	2			
***Ceratolejeunea coarina* (Gottsche) Schiff.**	5	1	**5**	1	1	3	2
Ceratolejeunea confusa R.M.Schust.				1	4	2	3
***Ceratolejeunea cornuta* (Spruce) Stephani**	18.1		13	19	**38**	30	27
***Ceratolejeunea cubensis* (Mont.) Schiff.**	11.3		2	6	5	**14**	9
***Ceratolejeunea guianensis* (Nees & Mont.) Stephani**	13		9	18	**22**	20	9
***Cheilolejeunea adnata* (Kunze ex Lehm.) Grolle**	15.7	2	14	11	17	**28**	16
Cheilolejeunea clausa (Nees & Mont.) R.M.Schust.			1	1	2	2	1
***Cheilolejeunea holostipa* (Spruce) Grolle & R.L. Zhu**	10.6	2	4	10	**19**	19	14

Species	**IV**	**1**	**2**	**3**	**4**	**5**	**6**
Cheilolejeunea rigidula **(Mont.) R.M.Schust.**	21.1	3	21	29	**50**	50	47
Cheilolejeunea trifaria **(Reinw., Blume & Nees) Mizut.**	17.3		6	11	27	**30**	15
Chryso-hypnum diminutivum (Hampe) W.R. Buck		2		1			
Colura cylindrica **Herz.**	19.4					1	**11**
Colura tortifolia (Nees & Mont.) Steph.					1		1
Crossomitrium patrisiae (Brid.) Müll. Hal.		2	1		2	1	4
Cyclolejeunea convexistipa (Lehm. & Lindenb.) Evans		4	2		2	2	1
Cylindrocolea planifolia (Stephani) R.M. Schust.					1	1	1
Cyrtohypnum involvens **(Hedw.) W.R.Buck & H.A. Crum**	24.5	**16**	4	2	3		
Diplasiolejeunea cavifolia **Steph.**	33.4				1	1	**20**
Diplasiolejeunea cobrensis **Gottsche ex Stephani**	9.3						**5**
Diplasiolejeunea pellucida **(C.F.W. Meissn. ex Spreng.) Schiffn.**	28.6					1	**16**
Diplasiolejeunea rudolphiana **Steph.**	55.6						**31**
Drepanolejeunea fragilis **Bischl.**	35.5	1	3	2	4	15	**33**
Fissidens guianensis **Mont.**	46.4	**25**	2		2		
Fissidens inaequalis Mitt.		1					
Fissidens radicans **Mont.**	5.8		1	3	**6**	1	
Fissidens weirii **Mitt.**	14.9	**7**					
Fissidens zollingeri Mont.		1					
Frullania apiculata **(Reinw., Blume & Nees) Nees**	19.5		2	3	8	20	**24**
Frullania caulisequa **(Nees) Nees**	30.9			3	20	30	**41**
Frullania gibbosa **Nees**	4.8			1	1	2	**5**
Frullania kunzei **(Lehm. & Lindenb.) Lehm. & Lindenb.**	27.3			1	1	4	**21**
Frullania patens Lindenb.				1	3		
Frullania nodulosa **(Reinw., Nees & Blume) Gottsche et al.**	19.3				7	12	**20**
Frullania riojaneirensis **(Raddi) Spruce**	24.1					1	**14**
Frullanoides liebmanniana **(Lindenb. & Gottsche) Slageren**	7.6				2	4	**8**
Glossadelphus truncatulus (Müll. Hal.) M. Fleisch.		1					
Groutiella apiculata **(Hook.) Crum & Steere**	7.1			1	3	**7**	3
Groutiella obtusa **(Mitt.) Florsch.**	14.3				5	**17**	13
Groutiella tomentosa (Hornsch.) Wijk.& Marg.		1	2			8	8
Haplolejeunea cucullata **(Steph.) Grolle**	6.4	**5**					
Harpalejeunea oxyphylla (Nees & Mont.) Steph.			2		6	7	1

Species	**IV**	**1**	**2**	**3**	**4**	**5**	**6**
***Harpalejeunea stricta* (Lindenb. & Gottsche) Steph.**	13.5			1	2	7	**13**
Harpalejeunea tridens (Besch. & Spruce) Steph.					1		
***Henicodium geniculatum* (Mitt.) W.R. Buck**	24.1				2	15	**24**
Holomitrium arboreum Mitt.				1	4	6	2
Isopterygium tenerum (Sw.) Mitt.		6	2	2	6	5	2
Jaegerina scariosa (Lorentz) Arzeni				1	1	1	1
***Lejeunea longifissa* Steph.**	5		1		**3**		
Lejeunea cerina (Lehm. & Lindenb.) Gottsche et al.		8	4	5	6	2	3
***Lejeunea flava* (Sw.) Nees**	4.6				2	1	**4**
***Lejeunea laetevirens* Nees & Mont.**	11.7	1	6	7	8	18	**20**
Lejeunea phyllobola Nees & Mont.		4	9	10	6	2	
Lejeunea reflexistipula (Lehm. & Lindenb.) Gottsche et al.				1	3	2	1
Lejeunea sp. 02				1			
***Lepidolejeunea involuta* (Gottsche) Grolle**	3.6	2	**4**		1	1	1
***Lepidopilum polytrichoides* (Hedw.) Brid.**	4.3	**2**					
***Lepidopilum scabrisetum* (Schwägr.) Steere**	9.8	**6**	2	2			
Lepidopilum surinamense Müll. Hal.			1				
***Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffner**	20.5		1		2	9	**19**
Leptoscyphus porphyrius (Nees) Grolle				1	1	2	
***Leucobryum martianum* (Hornsch.) Hampe ex Müll. Hal.**	10.5	**10**	5	1	1		
***Leucolejeunea unciloba* (Lindenb.) A. Evans**	9.3				1	2	**7**
Leucoloma cruegerianum (Müll. Hal.) A. Jaeger		3	2	1	1		
***Leucomium strumosum* (Hornsch.) Mitt.**	38.5	**23**	4		1		
***Leucophanes molleri* Müll. Hal.**	8.5	**4**					
***Lophocolea bidentata* (L.) Dumort.**	9.6	**5**	1				
***Lophocolea liebmanniana* Gottsche**	7.9	**6**	1	1	1	2	1
***Lophocolea martiana* Nees**	4.3	**2**					
Lopholejeunea eulopha (Tayl.) Schiffn.			1		3	1	1
***Lopholejeunea subfusca* (Nees) Schiffn.**	37.7		1	4	15	28	**43**
Macrocolura sagittispula (Spruce) R.M.Schust.		1	2	1	5	8	
Macromitrium cirrosum (Hedw.) Brid.					5	5	2
Macromitrium leprieurii Mont.					1		
Macromitrium pellucidum Mitt.					8	8	8
***Macromitrium podocarpi* Müll. Hal.**	7.8			1	**8**	5	4

Species	**IV**	**1**	**2**	**3**	**4**	**5**	**6**
***Macromitrium punctatum* (Hook & Grev.) Brid.**	15.2				3	**15**	10
Marchesinia brachiata (Sw.) Schiffn.					1	1	
Mastigolejeunea auriculata (Wils.) Schiffn.			6	12	15	19	13
***Meiothecium urceolatum* (Schawaegr.) Mitt.**	23					2	**14**
***Metalejeunea cucullata* (Reinw et al.) Grolle**	5.2				1	**5**	2
Meteorium nigrescens (Sw. ex Hedw.) Dozy & Molk.					1	1	
Metzgeria decipiens Schiff.						1	1
***Microlejeunea acutifolia* Stephani**	7	1	1	3	**9**	7	4
***Microlejeunea epiphylla* Bischl.**	13.5		1		5	1	**12**
***Mniomalia viridis* (Mitt.) Müll. Hal.**	8		3	7	**10**	4	1
Neckeropsis undulata (Hedw.) Reichdt.		8	2	7	6	1	3
Neurolejeunea breutelii (Gott.) Evans				3	8	6	3
***Neurolejeunea seminervis* (Spruce) Schiffn.**	11.9				**17**	12	4
***Octoblepharum albidum* Hedw.**	14.4		6	14	**21**	17	5
Octoblepharum cocuiense Mitt.		9	4	1			
***Octoblepharum pulvinatum* (Dozy & Molk.) Mitt.**	15.4	**24**	16	10	13	1	
Octoblepharum stramineum Mitt.				1	2	1	1
Odontolejeunea lunulata (Weber) Schiffn.					1		2
Odontoschisma falcifolium Stephani			3	2	1	1	2
***Orthostichopsis tetragona* (Sw. ex Hedw.) Broth.**	12.1		1	6	**18**	17	12
Phyllodrepanium falcifolium (Schwägr.) Crosby		1					
***Pictolejeunea picta* (Gottsche ex Stephani) Grolle**	16	**16**	3	1	1		
***Pilosium chlorophyllum* (Hornsch.) C. Mull.**	22.7	**13**	1				
Pilotrichum bipinnatum (Schwägr.) Brid.		1					
Pilotrichum evanescens (Müll. Hal.) Crosby					1		1
Pireella pohlii (Schwaegr.) Card.			2	2	2		
Plagiochila disticha (Lehm. & Lindenb.) Lindenb.		6	5	7	7	9	5
***Plagiochila laetevirens* Lindenb.**	45.3	**38**	15	3	1	1	
***Plagiochila montagnei* Nees**	9.1	1	3	3	10	11	**14**
***Plagiochila patentissima* Lindenb.**	4.3	**2**					
***Plagiochila subplana* Lindenb.**	12		7	**18**	20	3	
Porotrichum substriatum (Hampe) Mitt.		1	5	4	9	9	1
Prionolejeunea denticulata (Web.) Schiff.		1					
***Pycnolejeunea contigua* (Nees) Grolle**	17.1		1		2	8	**16**

Species	**IV**	**1**	**2**	**3**	**4**	**5**	**6**
Pycnolejeunea macroloba (Mont.) Schiffn.		1	8	13	21	21	9
Pycnolejeunea sp01 (blank)			1				
Racopilum tomentosum **(Hedw.) Brid.**	8.5	**4**					
Radula flaccida **Lindenb. & Gott.**	6.2	3	**5**				
Radula husnotii **Castle**	4.3	**2**					
Radula javanica Stephani		10	15	14	19	12	5
Radula kegelii **Gottsche**	4.3	**2**					
Rectolejeunea flagelliformis **A. Evans**	33.2		4	4	10	18	**37**
Rhacopilopsis trinitensis **(Müll. Hal.) E. Britton & Dixon**	10.8	1		2	**10**	4	1
Schiffneriolejeunea amazonica Gradst.							1
Schlotheimia rugifolia **(Hook.) Schwaegr.**	8.4				1	**7**	2
Schlotheimia torquata (Hedw.) Brid.					1		
Sematophyllum subpinnatum **(Brid.) Britt.**	13.9			1	3	**15**	7
Sematophyllum subsimplex **(Hedw.) Mitt.**	10.5	11	8	**15**	5	2	
Stictolejeunea squamata **(Willd.) Schiffner**	8.7	5	5	**14**	13	7	3
Symbiezidium barbiflorum **(Lindenb. & Gott.) Evans**	19.9	1	8	7	14	22	**31**
Symbiezidium transversale var. *hookerianum* (Gottsche) Gradst. & van Beek			5	5	7	15	17
Syrrhopodon cryptocarpus Dozy & Molk.				1	2		
Syrrhopodon incompletus **Schwaegr. var.** ***incompletus***	5.8	**7**	5	1	5		
Syrrhopodon ligulatus Mont.		1	2	3	3	3	2
Syrrhopodon parasiticus **Brid.**	28.6			5	11	15	**32**
Syrrhopodon simmondsii Steere		1	1	3	2		1
Taxithelium planum **(Brid.) Mitt.**	46	**32**	7		2		
Taxithelium pluripunctatum **(Renauld & Cardot) W.R.Buck**	4.3	**2**					
Thysananthus amazonicus **(Spruce) Schiffn.**	17.2			1	8	22	**24**
Trichosteleum papillosum **(Hornsch.) A. Jaeger**	7.8		**12**	7	9	11	5
Vesicularia vesicularis **(Schwägr.) Broth.**	23.4	**11**					
Xylolejeunea crenata (Spruce) Stephani		1					
Zelometeorium patulum **(Hedw.) Manuel**	14.3	1	4	7	**21**	20	12

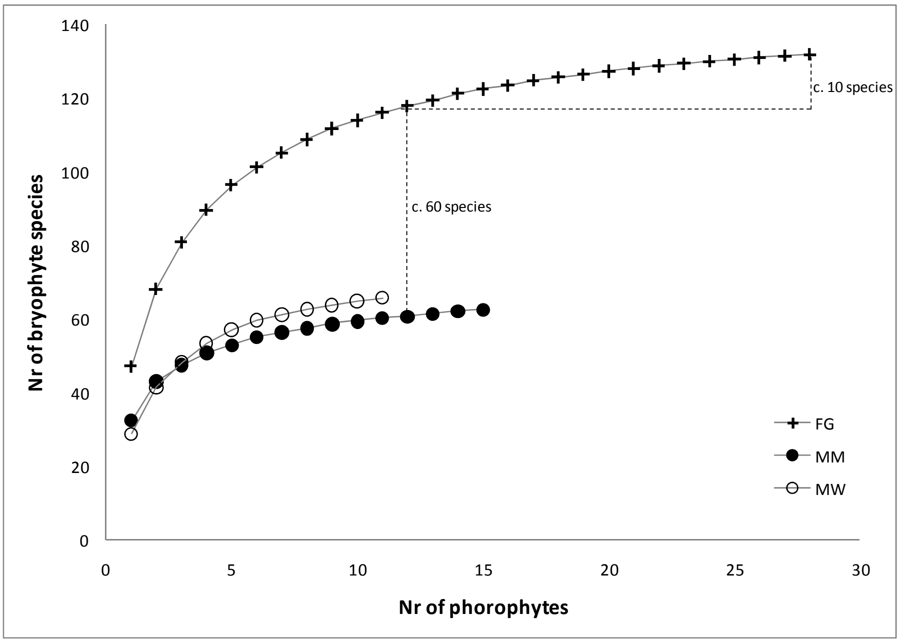


Figure S1. Species phorophyte curves for three sites in the Guianas. Curves were constructed with Ecosim* based on 1000 randomisations of the data. Standard Error at 10 trees for all curves is less than 10 species. The difference in richness between trees of the sites is large. At 12 trees the cumulative number of bryophyte species is around 60 for Mabura Wallaba (MW) and Mabura Mora (MM) and almost 120 for Saul, French Guiana (FG). The sampling effect, sampling many more trees in FG (28 vs 11 for MW and 15 for MM) only adds another 10 species.

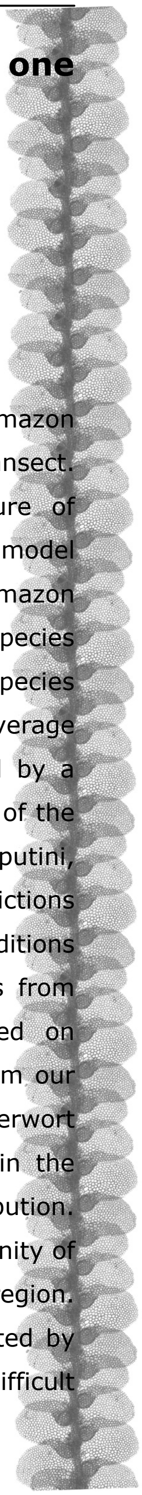
* Gotelli, N.J. & Entsminger G.L. 2001 EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

Epiphytes in the lower canopy of *Eperua grandiflora*, Mabura, Guyana

3

3. Diversity of Amazonian bryophytes in one basin-wide metacommunity

with Hans ter Steege



Abstract

We present the first view of bryophyte diversity for the entire Amazon based on a new dataset, from nine localities along an East-West transect. We asked whether local richness and local community structure of epiphytic bryophytes are consistent with the predictions of a neutral model and whether epiphytic bryophytes show a diversity gradient in the Amazon related to either environmental gradient or geographical distance. Species richness did not follow the predominant climatic gradients and species composition did not show a spatial pattern. Localities showed an average richness of 64 species and species relative abundances explained by a neutral model, with a detectable effect of dispersal limitation (most of the recruitment in a locality is originated within locality). One site (Tiputini, Ecuador) had a species richness that was inconsistent with the predictions of a neutral model. We argue that local high relative humidity conditions at this site enhance the rate of establishment success of species from another substrate, and therefore the number of species. Based on simulations of a neutral model with parameterization estimated from our dataset we drew a number of predictions, among which the liverwort *Cheilolejeunea rigidula* being the most common terrestrial plant in the Amazon, due to its very high local abundance and widespread distribution. We conclude that the entire Amazon comprises a single metacommunity of epiphytic bryophytes, with species able to disperse across the region. Because the occurrence of rare bryophyte species is poorly predicted by macroenvironmental variables, the risk of extinction is exceedingly difficult to assess, and runs along with the loss of forest habitat.

Introduction

The Amazon basin is, with over six million km^2, the largest tropical forest region in the world. Basin-wide, macroecological research across the area has focused on alpha- and beta-diversity of trees (Terborgh & Andresen 1998; ter Steege *et al.* 2003; ter Steege *et al.* 2006; Stropp *et al.* 2009), on phylogeography of vertebrates as amphibians (Santos *et al.* 2009) and birds (Rahbek & Graves 2001), and on regional studies within the ongoing debate about balancing dispersal and niche processes (Pitman *et al.* 2001; Condit *et al.* 2002; Ruokolainen *et al.* 2007). In general, these studies suggest relationships between species composition and diversity and the environment, although the ecological mechanisms invoked have not accounted for a common and strong explanation of the variation seen in communities. The assumption that a high level of complexity is the fundamental driver of biodiversity (e.g. complex interspecific interactions, or feedbacks between species and environment) frequently takes place before a proper test of how much could be explained if none of the biological processes were relevant (Gotelli 2001; McGill *et al.* 2006). A priori identification of how much can be explained by a null model in a biological system should be a first step to evaluate the real role of ecological mechanisms.

The Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001) provided a new framework for studies on alpha diversity, specifically concerning the first level of complexity commented above. In the last decade, the neutral theory instigated many ecological studies, by proposing to test patterns of diversity predicted by the neutral theory against empirical data. The theory assumes saturated landscapes and functional equivalence among all individuals of all species. Through random death and recruitment of individuals and an immigration rate at which individuals can be recruited from a metacommunity, this model usually reproduces the same species abundance distributions curves that ecologists record for their plants. Accepting hypotheses, however, goes beyond fitting species abundance distributions curves, as pointed out by McGill et al. (2006). In a review of the literature concerned with testing neutral theory, the author suggests that estimating parameters and simulating the mechanics proposed by the model to compare real and simulated data is an interesting fitting test. Likewise, testing predictions of the model with different biological groups is useful to verify its generality.

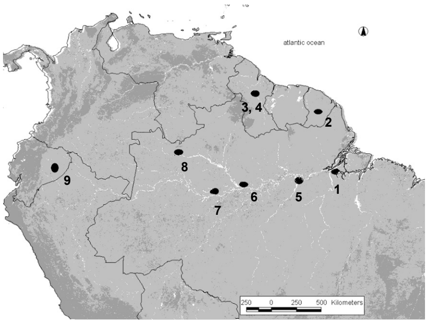
Compared to recent macroecological research in the Amazon, the study of bryophyte diversity lacks two components: a detailed study of community structure, and a large scale perspective. Community structure is essential for testing diversity hypotheses and comparing local communities. There is a considerable amount of inventories and records for bryophytes published for the region (Lisboa 1984, 1985; Lisboa & Yano 1987; Yano & Lisboa 1988; Yano 1992; Lisboa & Maciel 1994; Churchill 1998; Lisboa *et al.* 1999; Fuentes & Muñoz 2002; da Costa 2003; Pinzón *et al.* 2003; Ilkiu-Borges & Lisboa 2004a, b; Ilkiu-Borges *et al.* 2004; Yano & Camara 2004; Moraes & Lisboa 2005), but due to the non-systematic nature of the sampling procedures used in these publications, and the lack of information on community structure, a comprehensive assessment of diversity across the Amazon could not be carried out at this time. Ecological studies are scant and mainly deal with local hypotheses (Cornelissen & ter Steege 1989; Acebey *et al.* 2003; Zartman 2003) (Florschütz-de Waard & Bekker 1987; Benavides *et al.* 2006).

Here, we present the first consistent analysis of bryophyte diversity for the entire Amazon region, and a new dataset for testing theory. A balanced and systematic sampling of epiphytic bryophytes across nearly 3000 km in the Amazon, allowed us to explore both alpha- and beta-diversity of these plants. In this paper we focus solely on patterns of alpha-diversity. We conducted our analysis in a step-wise process, 1) by testing the null hypothesis of local communities built as random samples of the metacommunity, 2) by using neutral theory as a first explanation for richness and species abundances in local communities and 3) by identifying where community features can be explained by neutral theory and where other mechanisms influencing alpha diversity are still to be tested. The fundamental questions raised here are: are local richness and community structure of Amazonian epiphytic bryophytes consistent with the predictions of a neutral model across the region, do epiphytic bryophytes show a diversity gradient in the Amazon, and if so, is it related to environmental gradient or geographical distance?

Methods

Study area

In order to sample communities of epiphytic bryophytes, we selected nine localities across the Amazon basin, along an East-West transect as presented in Figure 1:



1. Caxiuana, Brazil
2. Saul, French Guyana (FG)
3. Mabura Mora, Guiana (MM)
4. Mabura Wallaba, Guiana (MW)
5. Floresta Nacional do Tapajos (TA)
6. Reserva Ducke, Brazil (RD)
7. Província petrolífera de Urucu, Brazil (UR)
8. Parque Nacional do Pico da Neblina, Brazil (SG)
9. Tiputini Biodiversity Station, Ecuador (EC)

Figure 1. Map of the study area, showing the sampling localities from East to West in the Amazon forest.

Sampling procedure

At each locality, epiphytic bryophyte communities were sampled from the bottom to the top of eight selected canopy trees growing on a non-flooded plateau (terra firme forest). The trees were divided into height zones, used as a surrogate for the microclimatic gradient found from the bottom to the canopy of the forest. The height zones were established as follows: from the base up to 1.5 metre (zone 1), via the lower and upper trunk (zones 2 and 3) to the base of the crown (zone 4) and finally the outer sun-lit twigs (zone 6) (for details see Mota de Oliveira et al. 2009). The bryophyte communities were bulked samples of 4 patches of approximately 10 cm^2 per height zone. The material from the sites Saul (FG), Mabura Mora (MM) and Mabura Wallaba (MW) was collected in more trees and it also comprised samples taken from the middle crown (zone 5). In order to balance the sampling strategy, we used a sub-set of the data of these three sites, which consisted of eight randomly chosen trees per locality and five height zones (zones 1 to 4 and zone 6).

The specimens present in the samples were identified using identification keys, monographs (Reese 1993; Gradstein 1994; Dauphin 2003) and available floras (Gradstein *et al.* 2001; Gradstein & Costa 2003). Each bulk sample was considered a 'plot' and consisted of a species list. We considered the use of an abundance measure inappropriate, due to the impossibility of separating individuals for most of the species and due to the variation in plant size. To quantify community structure per locality, we used frequency as a surrogate of abundance, summing the number of plots in which each species was recorded. This value ranged from 1 to 40, the maximum possible frequency in a site.

Data analysis

The diversity of the sites was compared through species richness. First we tested the null hypothesis that local communities are random draws of the metacommunity. The metacommunity data was generated from the sum of all occurrences of all species in the dataset (Hubbell 2001; Jabot et al. 2008). It was first used to draw random local communities to test the null hypothesis. We then used the same metacommunity to simulate neutral dynamics driving the composition of the local communities, through a simulation algorithm written in Matlab (Supplementary material, this chapter). We calculated the parameter *m*, defined as immigration rate, using the freeware Tetame (Chave & Jabot 2006), which estimates the neutral parameters based on maximum likelihood (Etienne 2005).

Conceptually, m varies from 0 to 1 and represents the proportion of individuals being recruited in the local community from the metacommunity by immigration. The results obtained in the modeled communities, such as richness, percentage of local communities in which each species is recorded, maximum and average abundance, and the frequency distribution of Sørensen similarities between local communities were compared to field data. For the latter, we compared the Sørensen similarity of the nine sites (38 single comparisons) with 1000 similarities of the hypothetical communities (1 with 2, 2 with 3, 3 with 4 … 1000 with 1). We assessed the difference between the distributions with MCAnova (Ecosim) for the mean and Chi-square for the distribution.

In order to evaluate if species richness was influenced by climatic factors, we correlated richness values with climatic data obtained from TRMM - Tropical Rainfall Measuring Mission (Hijmans et al. 2005).

Finally, we tested the relationship between species composition and distance using a Mantel test (Legendre 1998). The Mantel test evaluates the null hypothesis of no relationship between two dissimilarity (distance) matrices. Floristic dissimilarity was firstly calculated for each pair of sites (Relative Sørensen), to be correlated with their geographical distance, and secondly for each pair of trees, and again correlated with the geographical distance of the sites, but now including zero distance for trees on the same locality.

Results

We listed 263 bryophyte species on a total of 72 phorophytes in nine localities across the Amazon. Species richness of the localities varied from 51 in Reserva Ducke - Brazil, Central Amazon, to 128 in Tiputini - Ecuador, Western Amazon (Table 1). Species richness peaked in two out of the nine localities: Tiputini, in Ecuador, and Saül, in French Guiana. The other localities, in Guyana, Eastern and Central Amazon, showed an

Table 1. Total number of species (S), total number of records (N), the calculated *m* in Tetame (*m*), Fisher's alpha (Fɑ), number of singletons (Sing), average number of species per plot (SPP), percentage of species restricted to each site (RE), and percentage of epiphylls in each site (EP). In the bottom row, totals are given for S and N, while average is given for the other columns.

Site	**S**	**N**	***m***	**Fɑ**	**Sing**	**SPP**	**RE (%)**	**EP (%)**
CX	61	236	0.21	26.7	20	6	13.1	8.2
EC	127	700	0.16	47.0	31	17	37.8	16.5
FG	102	514	0.22	39.9	26	14	14.7	9.8
MM	63	434	0.11	18.7	14	12	1.6	7.9
MW	74	335	0.19	26.4	20	9	6.8	9.5
RD	51	199	0.19	22.2	21	5	13.7	7.8
SG	65	183	0.26	36.0	33	5	16.9	10.8
TA	63	234	0.26	28.3	27	6	9.5	7.9
UR	70	229	0.27	34.4	30	6	14.3	5.7
	263	3064	0.21	30.5	24.7	9	14.2	9.4

average richness of 64 species. On average, nine species were recorded per plot, ranging from 5-6 species in Eastern and Central Amazon to 17 species per plot in Ecuador.

The species belonged to 29 families. The most common families in number of records were Lejeuneaceae (55%), Calymperaceae (9%), Leucobryaceae (6%) and Sematophyllaceae (5%), and these were the only families recorded in all localities. The most common species was *Cheilolejeunea rigidula*, followed by *Ceratolejeunea cornuta*, *Octoblepharum pulvinatum*, *Octoblepharum albidum*, *Archilejeunea fuscecens, Sematophyllum subsimplex, Lopholejeunea subfusca* and *Symbiezidium barbiflorum*. These eight species together accounted for 21% of the records in the metacommunity. Most sites had at least one locally abundant species, which was not listed among the twenty five most abundant in the metacommunity. This was the case with, for instance, *Ceratolejeunea minuta* in Caxiuanã, *Archilejeunea crispistipula* and

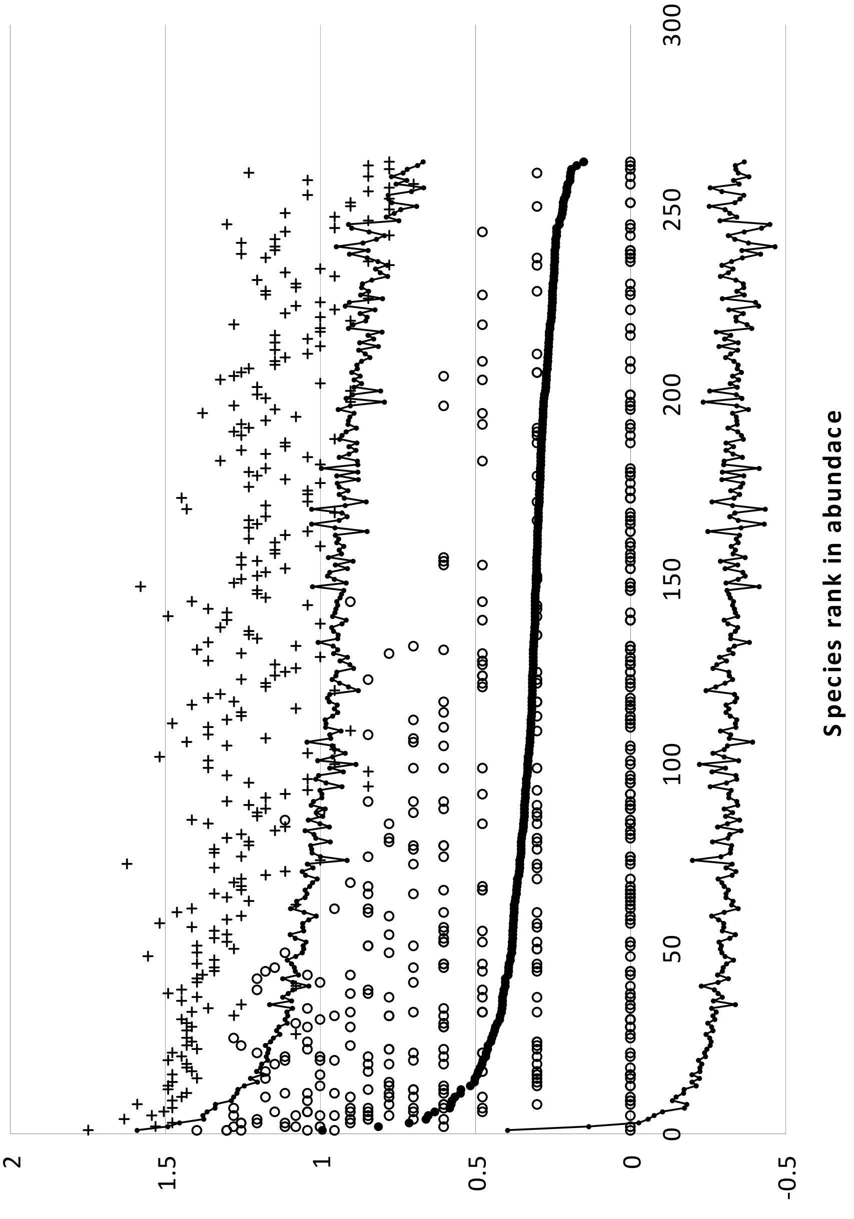


Figure 2. Log transformed species abundances (thick black line); 95% confidence interval (thin lines below and above) and maximum abundance predicted by the model (+); actual field data abundances (log-transformed, o) for all sites minus Ecuador and Saul.

Bazzania hookeri in São Gabriel da Cachoeira, and *Syrrhopodon cryptocarpus* in Urucu.

In the simulation procedure, random draws from the metacommunity resulted in a species richness far higher than most of the richness values observed, a much higher Fishers' alpha and number of singletons, and much lower abundance of the most common species (Figure S1, Table 1). We therefore rejected the null hypothesis that the composition of each locality is a random draw from the metacommunity. The values of m obtained with Tetame ranged from 0.16 to 0.26, with an average of 0.2, which is also inconsistent with the dispersal-unlimited null model.

Simulating hypothetical local communities through a neutral model with 250 individuals and m of 0.2 (see Supplementary material), gave results that were compatible with the field data. Almost all species abundances in the field data were consistent with the range of possibilities produced by the model (Figure 2). The percentage of hypothetical local communities in which a given species was present showed a strong correlation with the percentage of local communities where that species was actually present in the real data (Figure 3). Therefore, a neutral model alone could account for most of the abundance values found in the local communities. Species richness was consistent with the neutral model in eight out of the nine localities. Only Ecuador yielded more species than their community structure would predict based on neutral theory (Figure 4).

Local species richness did not correlate with any of the tested climatic parameters. The variation of total annual precipitation, dry season length and minimum precipitation of the driest quarter recorded for the Amazon forest did not cause the variation of species richness. Species recorded as singletons in our dataset were not endemics, according to our bibliographic search. The ten most abundant species in the metacommunity were widespread, collected in at least six out of the nine localities. The highest percentage of restricted species (sampled exclusively at one given locality) was 37.8% in Ecuador, while this value

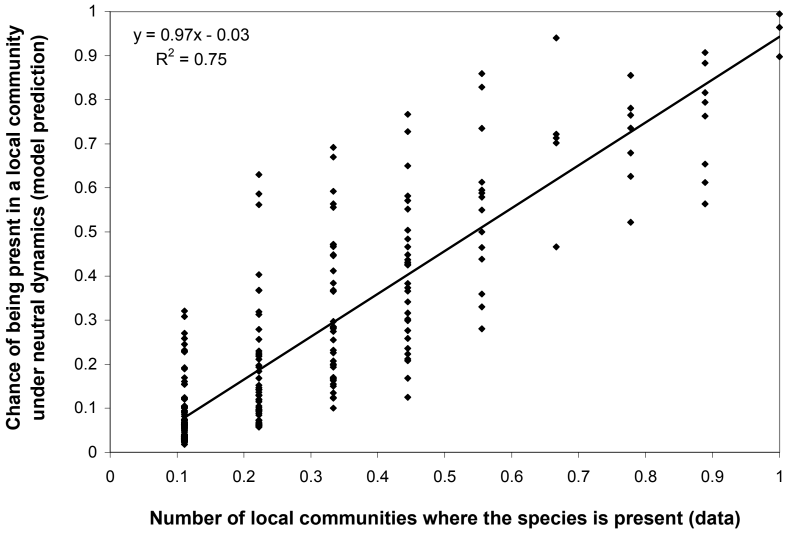


Figure 3. Correlation between the number of local communities where a given species is present in our dataset and its chance of being present in a local community, as predicted by the neutral model.

was around 14% for the other localities. Tested in the 1000 random communities, restricted species composed on average 9.6% of a standard local community, with a 95% confidence interval from 2.66 to 16.56%. Finally, Ecuador also yielded the highest percentage of facultative epiphylls, 16.5%, while in general the percentage ranged from 5.7% to 10.8% (Table 1).

The average Sørensen similarity between localities was 0.31 for the field data and 0.33 for 1000 values of the hypothetical local communities. Although showing almost the same average (Figure 5), the similarity values calculated from field data were slightly lower (MCAnova, $p<0.05$) and showed a wider range of values, but the two datasets did not appear to originate from different distributions (Kolmogorov-Smirnov test, D = 0.5556, $p > 0.05$).

We found no significant relationship between the matrix of similarity of community composition and the matrix of geographical distance (Mantel r = 0.25, p = 0.13). Thus, localities close by were not significantly more similar than localities further away, although distances ranged from 15 to 2835 km. At the level of the trees, however, floristic similarity showed a significant distance decay (Mantel r = 0.37, p < 0.0001). While similarities ranged from 0 to 0.45 at any distance tested, values above 0.55, reaching a maximum of 0.7, were found only between communities on trees from the same locality (Figure 6).

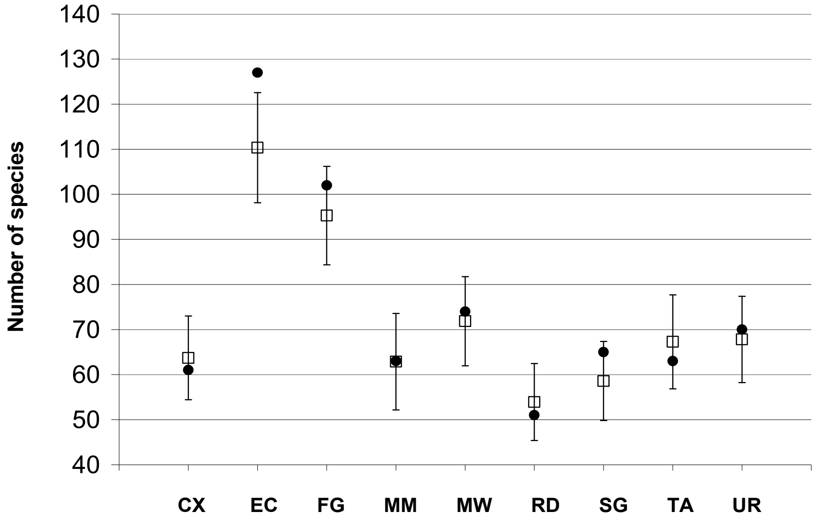


Figure 4. Average and 95% confidence interval of the number of species predicted by the model (open squares) and number of species recorded in each locality (black dots). Modeled data was produced for each locality separately, and consisted of 250 hypothetical local communities built based on their real number of individuals (J) and *m* as estimated by maximum likelihood.

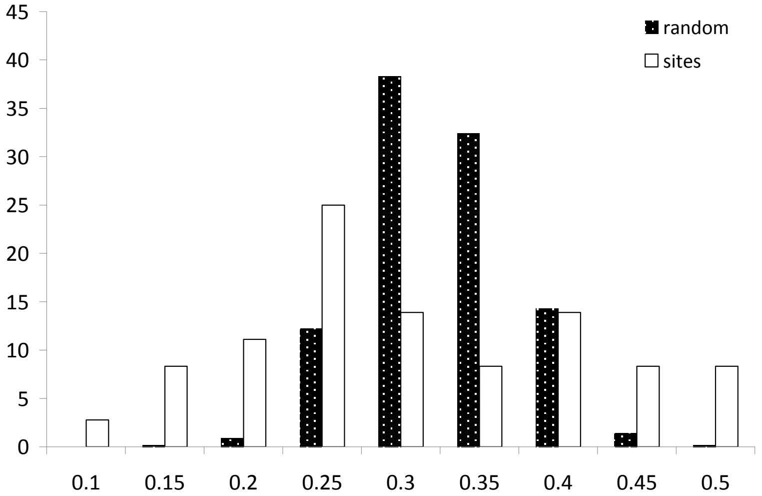


Figure 5. Frequency distribution (%) of Sørensen similarity between pairs of 1000 randomly built communities (grey bars) and between pairs of communities sampled in the field (dashed bars).

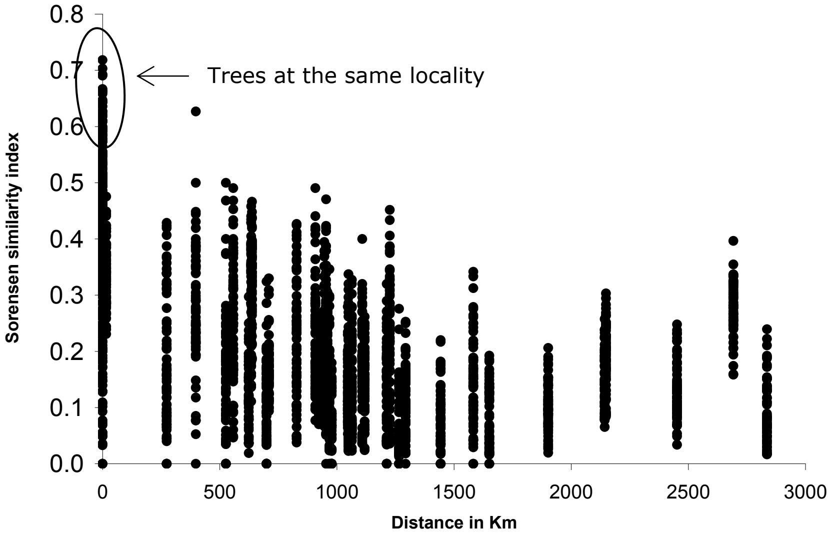


Figure 6. Correlation between geographical distance among the host trees and similarity measured by Sørensen similarity index among the bryophyte community composition.

Discussion

The entire Amazon comprises a single metacommunity for epiphytic bryophytes, with species able to disperse across the region. This diversity pattern is unique, since species richness does not follow the predominant climatic gradients. Furthermore, the structure of a majority of local communities can be explained by the neutral theory.

In our step-wise analysis of the data, we initially tested the community structure of our local communities against a null model of no dispersal limitation. Theoretically, very high immigration rates (of 0.95 to 1) would produce local communities built as random draws of the metacommunity. As bryophytes show long distance dispersal and fast colonization rates, one could indeed expect very high immigration rates. Examples of these features in the literature are abundant, such as the colonization of a lava substrate by 60 species in La Reunion in just 19 years (Ah-Peng *et al.* 2007); or the formation of a completely different bryoflora, within 65 years, with an average of one immigrant species per year coming at least from 5 km away from the place of establishment (Miller & McDaniel 2004). This great dispersal potential of bryophytes in space, however, did not lead to communities built of propagules arriving indistinctly from the metacommunity. Recruitment of new individuals is mainly a result of dispersal from within 15 km distance, which is in agreement with the recruitment of 44% of bryophytes on slag heaps from within 6 km distance estimated by Hutsemekers et al. (2008). Therefore, we rejected the null hypothesis of random draws from the metacommunity and found low immigration rates instead (average m of 0.2).

Testing the predictions of the neutral theory on the basis of a metacommunity with dispersal limitation, i.e. immigration rate (m) of 0.2, gave more consistent results. Support for the estimation was given by the strong correlation between the number of local communities where a given species is present in our dataset and its chance of being present in a hypothetical local community, as predicted by the neutral model. The observed abundances of all species for the majority of the sites, as well as the number of species, were in agreement with the predictions. Those species with low abundance in the metacommunity and high local abundance also fell within the predictions of neutral dynamics. Once a species establishes locally, its chance of becoming locally abundant suddenly increases, since it can be recruited both from the meta- and from its own local community (Hubbell 2001).

Neutral dynamics could not account for the richness in Ecuador. It is well known that also for trees Ecuadorian Amazon yields higher diversity than other regions (Gentry 1988; ter Steege *et al.* 2003), in this case possibly due to paleo-climatic stability and speciation/extinction balance (Stropp *et al.* 2009). Such historical processes can definitely not be claimed for differences on bryophyte alpha diversity in the Amazon, since the species treated here are all part of a single metacommunity. Here we believe there is a strong role for the microenvironment in the high species richness found in Ecuador. Among bryophytes, the epiphyllous habit – inhabiting the surface of living leaves – is strongly associated with moist environments (Coley *et al.* 1993). In our data, the percentage of typically epiphyllous species growing on bark was the highest in Ecuador (Table 1). For instance, *Odontolejeunea rhomalea* and *O. lunulata*, *Colura greig-smithii*, *Radula mammosa*, found on the bark of the host trees only in Ecuador, are typical epiphylls. Published records of these same species indicate their presence in Central and Eastern Amazonia (so there is no dispersal barrier), but growing on leaves (Zartman & Ilkiu-Borges 2007). This result suggests that the high moisture of Ecuador increases the occurrence of species from another substrate, possibility that is obviously not accounted by the neutral model, but the most likely explanation.

We found distance playing some role at a local scale, but not across the basin (Figure 6). In another article we also show that the similarity between plots on trees of the same locality is significantly higher than between plots of different localities, even when environment is kept constant (Mota de Oliveira & ter Steege, submitted, chapter 4 this thesis). This pattern is probably tightly related to the dispersal curves of bryophytes. Most of the propagules fall very close to their origin, while the rest can travel very far by chance in an air turbulence or attached to insects (Miles & Longton 1992; Sundberg 2005). Over medium to large distances, propagules show the same chance of arrival. This is consistent with the fact that, in our data, no distance decay in similarity could be observed at distances from 15 to 2835 km. Therefore, the lack of spatial explicitly of the neutral theory, as pointed out by Chave & Leigh (2002), does not have further consequences on our predictions. The scale at which distance may play a role, influencing species richness (local), is already addressed by the immigration rate (*m*) in the spatially implicit version.

We posit that richness and relative species abundances in most of the localities are so well explained by the neutral model because of the lack of strong environmental gradient pertinent to bryophytes at this scale. The most important gradient for these plants in an Amazonian forest is given by microenvironmental changes within a locality, along the height zones of a tree (Mota de Oliveira et al. 2009). When an entire locality is treated as one local community, it spans the full range of the environmental gradient. Consequently, community dynamics at this scale is mainly regulated by stochastic recruitment of individuals influenced by the abundances of the species they belong to, in the metacommunity.

The predictions of a neutral model for epiphytic bryophytes in the Amazon

The fact that the local communities are so well predicted by the neutral theory leads to a number of implications/predictions. The average bryophyte community of 250 occurrences found in a sample of 8 trees in the Amazon is expected to have around 65 species and 21 singletons and with the most common species having between 10-30 occurrences (Table

S1). Roughly 80% of the established individuals are recruited from within an area of 15 km. Only 20% of the established individuals originate from further, having no definite distance decay.

Cheilolejeunea rigidula will be found in practically any set (99.5%) of eight trees inhabitable by bryophytes in a terra firme Amazonian landscape. An estimate for the number of trees > 10 cm DBH is 4.3 10^{11} trees (Hubbell *et al.* 2008). Assuming that *Cheilolejeunea rigidula* occurs in just 1 out of the 8 trees (a very careful underestimate), an estimate for its total occurrence would be 5 10^{10}. That is 2 orders of magnitude more than the estimated abundance of the most common tree species (Hubbell *et al.* 2008). *Cheilolejeunea rigidula* is thus arguably the most common land plant of the Amazon. To the other extreme, rare species such as *Pycnolejeunea papillosa*, will be present in very few places which can be anywhere across the basin, due to their erratic dispersal. For these rare species, where one cannot predict the occurrence of populations through environmental variables, the risk of extinction is exceedingly difficult to assess and runs along with the loss of forest habitat.

Acknowledgments

The authors are grateful to CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior / Brasil - for funding the first author; Marinus Werger and Jerome Chave for discussions and comments on an earlier draft of the manuscript.

Supplementary material – Neutral model of bryophyte communities in the Amazon

The model

We built a neutral model in Matlab (The MathWorks, Inc., Natick, USA) based on Hubbell's (2001) 'Neutral Theory of Biodiversity and Biogeography'. The model consists of a computer routine that simulates the mechanisms underlying neutral theory in order to build local communities from a given metacommunity, and of a metacommunity, the abundances of which are the sum of the occurrences of all individuals of all species in the local communities.

The local communities were simulated based on two parameters, J and *m*. J is the number of individuals to be present in the local community and *m* is the probability that an individual is recruited from the metacommunity. Initially, the local community is empty and the first individual is recruited at random from the metacommunity. After that, recruitments can come from the local or the metacommunity, with probability *m* from the metacommunity and 1-m from the local community. When J individuals are reached, the local communities go through neutral dynamics with 10^8 time steps, each time with a random death of one individual and a random recruitment from the local or metacommunity, again with probability *m* from the metacommunity and 1-m from the local community.

We ran our Matlab model to generate hypothetical local communities with J=250 and *m* varying from 0.1 to 1. In local communities under neutral dynamics, species richness, Fisher's alpha (Fα) and number of singletons are positively correlated with *m* (Figure S1). The abundance of the most common species decreases with *m*, since a higher rate of recruitment from the metacommunity (higher *m*) decreases the chance of recruitment of the most abundant species in the local community.

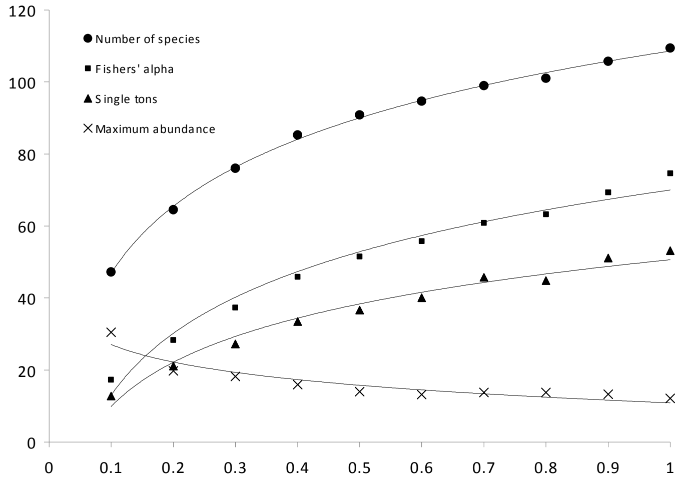


Figure S1. Community ecology properties vary predictably with *m*. The number of species, Fishers' alpha, and number of singletons increase with increasing *m*. Maximum abundance (the abundance of the most common species decreases with increasing *m*). Values are the average of 25 simulations each.

Tetame vs. Matlab

We used the program Tetame (Chave & Jabot 2006) to calculate *m* for our local communities. To verify the working of our Matlab model with Tetame, we compared the values of *m* calculated by Tetame for those communities with known *m* created by our Matlab model. We found a very good accordance between the values of m used in the simulations and the ones estimated with Tetame (Figure S2). The variation in *m* as calculated by Tetame is due to the fact that the program uses a maximum likelihood function for calculating *m*, which gives the most likely solution. In practical sense, when an individual is added to the local community in our model, the source is known (recruitment from meta- or local community). In the mathematical solution the source is inferred because it is based only in the relative abundance distributions (RAD) of the meta- and local community. In the latter case, there is more than one possible *m* that can generate a given local RAD from the RAD of the metacommunity.

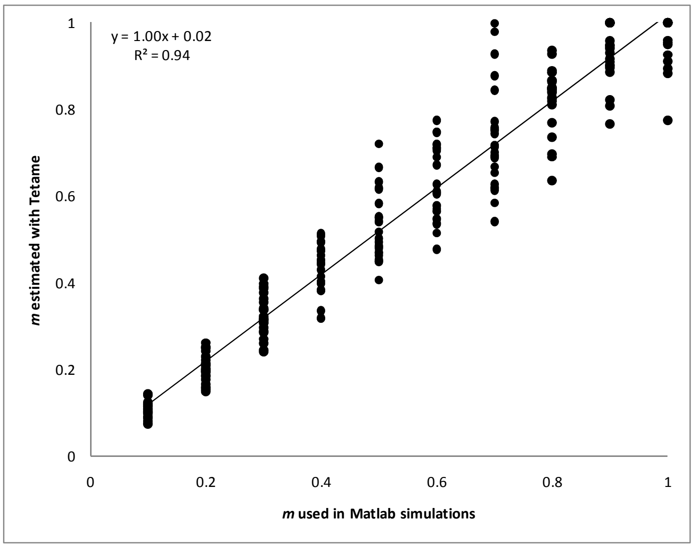


Figure S2. Relationship between values of *m* used in the Matlab neutral model with 10^8 runs and values of *m* as estimated by Tetame for these local communities. Note that the slope of this line is 1!

One thousand bryophyte communities

We used the average value of *m* (0.2) and the average number of individuals of the local communities (250) in our data to simulate 1000 local communities. We calculated the proportion of communities in which each species occurs under neutral dynamics and compared this with the proportion in which they occurred in our field data. These results are part of the manuscript. Using this procedure, we can assess the chance of a species being present in a local community depending on its abundance in the metacommunity (Figures S3). As expected, the most abundant species is present in practically all communities generated (*Cheilolejeunea rigidula*, N=148, simulated presence 99.5%, Figure S3A). Uncommon species can become locally abundant, as it is shown both in the modeled communities (Figure S3B) and in our field data (manuscript). Once an uncommon species establishes, it has a higher chance of increasing abundance, since most of the recruitments are from the local community.

The chance of a species being recorded as a singleton is highest when a species is medium abundant. With low abundance in the metacommunity, the species occur in very few local communities, thus its chance of being recorded even as a singleton is small. On the other hand, with high abundance in the metacommunity, very common species can hardly be recorded as singletons, due to higher chances of repeated immigration (Figure S3C). Finally, the simulated metacommunity (corrected for size by multiplying the sum of abundances with 3064/1000*250) is a near exact copy of the actual metacommunity (N=3064) (Figure S3D).

Based on a neutral dynamics, the average bryophyte community of 250 occurrences is expected to have 65 species with 21 singletons and with the most common species having some 20 occurrences (Table S1).

Table S1. Average diversity characteristics of 1000 modeled bryophyte communities (J =250, m=0.2).

	average	**SD**	**low conf**	**high conf**
S	65.315	4.737	56.031	74.599
# singletons	21.605	4.360	13.060	30.150
Fishers' alpha	28.869	3.470	22.068	35.671
Abundance sp1	20.251	5.486	9.499	31.003

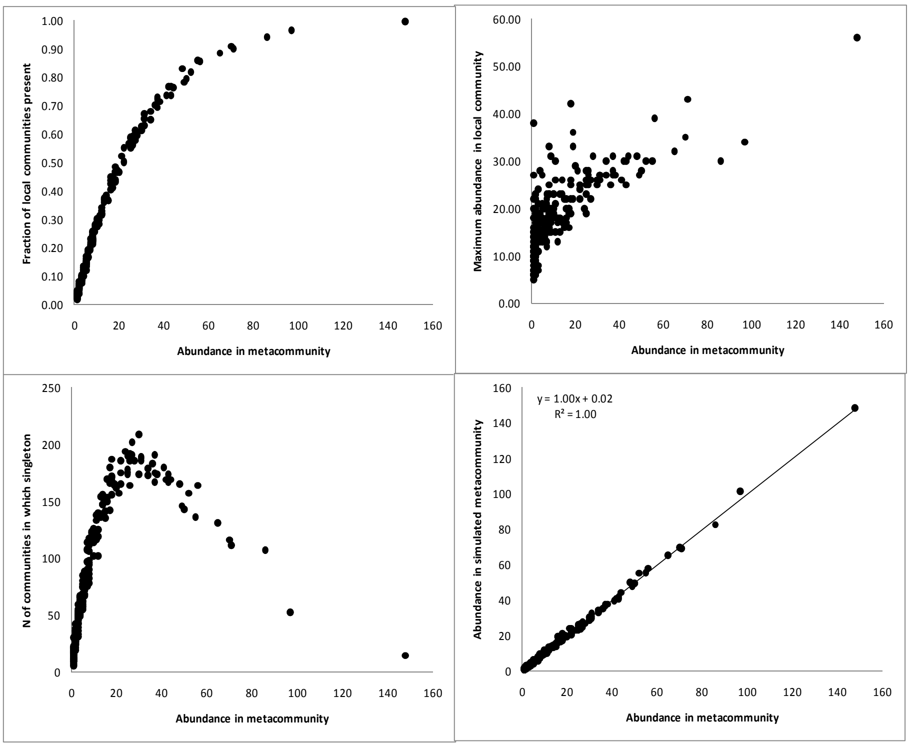


Figure S3. Results of simulating 1000 neutral bryophyte communities with *m* = 0.2 and J =250. **A.** Number of times that a species is present in a local community as a function of its abundance in the metacommunity. **B.** Abundance of a species in the metacommunity (x axis) and the maximum abundance achieved in the modeled local communities (y axis). **C.** Abundance of a species in the metacommunity (x axis) and its chance of being recorded as a singleton (y axis). **D.** The simulated metacommunity (corrected for size by multiplying the sum of abundances with 3064/1000*250) is a near exact copy of the actual metacommunity (N=3064).

Sampling Bryophytes in Urucu, Brazil

4

4. Effects of environment and dispersal on the community composition of epiphytic bryophytes across the Amazon

with Hans ter Steege

Abstract

In order to understand the roles of dispersal limitation and environmental filtering upon epiphytic bryophyte communities along the different height zones of the host trees, as well as across the Amazon basin, we sampled communities from the base to the top of canopy trees in nine localities, varying in distance from 15 to approximately 2800 Km. Differences between local communities that belong to the same metacommunity can be captured by their species abundance distribution. We approached dispersal limitation and establishment limitation in local communities by analysing the relationship between the metacommunity and selected groups of local communities. These groups of local communities encapsulate, respectively, the effect of microenvironment (to estimate dispersal limitation) and the effect of distance (to estimate establishment limitation). At local scale, the results showed a consistent gradient in species composition from the base to the top of the trees, in all localities studied. The gradient is set mostly by a strong establishment limitation at the extremities, zones 1 and 6, combined with lower establishment limitation in the middle trunk and high dispersal of species between adjacent zones. At large scale – species composition of geographical localities – dispersal limitation is the main process at play. Approximately 80% of the recruitment occurring in a local community correspond to species already locally established. The probability of long distance dispersal events increases with increasing height zone, which makes canopy communities the most similar in terms of species composition across the basin.

Introduction

The composition of bryophyte communities is influenced by environment as well as dispersal. Environment acts from large scales, such as along altitudinal gradients (Kessler 2000; Bruun *et al.* 2006; Ah-Peng *et al.* 2007), to small scales such as along relative humidity gradients (Sonnleitner *et al.* 2009), height zones in a host tree (Cornelissen & ter Steege 1989; Mota de Oliveira *et al.* 2009) or through phorophyte preference (Szövényi *et al.* 2004; Gabriel & Bates 2005). Dispersal limitation affects the abundance of species in local communities depending on their level of connectivity with the metacommunity (Löbel *et al.* 2006; Zartman & Nascimento 2006). Dispersal strategy may also determine species composition of communities according to the time that the substrate has been available for colonization (Hutsemekers *et al.* 2008). The relative roles of these two factors in structuring bryophyte communities, however, are seldom investigated together.

The concept of a metacommunity, in a top-down approach, is very appropriate to test the relative roles of environment and dispersal in local community composition (Ricklefs 1987; Whittaker *et al.* 2001). It treats the local community under study not confined to its own individuals and habitat, but also influenced by higher scale level, i.e. the sum of all other surrounding comparable communities. Yet, there are many ways to approach the advocated hierarchical link between metacommunity and local community. One source of difference is in the definition of the metacommunity itself. While some authors list all species occurring in a given region (Wilson 1992; Hubbell 2001), others conceive a habitat species pool (Zobel 1997), which comprises the species able to occur in the habitat of the local community under discussion, as determined by their ecological requirements. The establishment of something like a "habitat species pool" at first sight may restrict the possibility of investigating environmental filtering from the metacommunity to the local community. It may become useful, however, as a further tool to estimate pure dispersal limitation. We will approach both concepts to answer our research questions, according to the process addressed.

Differences between communities that belong to the same metacommunity can be captured by the comparison of their species abundance distribution. Under the framework of the Neutral Theory of Biodiversity and Biogeography (Hubbell 2001), species abundance distribution of any given community can be described by two parameters, θ and *m*. In a local community with constant number of individuals, a random death of one individual is replaced by a random recruitment of one new individual. The new individual can pertain either to a species already present in the local community or to a species present in any other local community, i.e. in the metacommunity. The probability with which these new individuals in the local community are recruited from the metacommunity is represented by the parameter *m*. Therefore, *m* gives an indication of how much "isolated" a local community is in relation to the metacommunity. In the original neutral theory, this "isolation" was accounted for by dispersal limitation alone. Recently, Jabot et al. (2008) presented a method to calculate *m* for multiple local communities originating from the same metacommunity. The authors showed that, through this approach, the parameter can also be used to account for establishment limitation, related to environmental filtering.

The epiphytic bryophytes in the Amazon behave as one single metacommunity (Mota de Oliveira & ter Steege, this thesis, Chapter 3) in the sense of Wilson (1992) and Leibold et al. (2004), that species can disperse over the full area into local communities, despite the fragmented nature of the habitat (in this case substrate – separate trees). Dispersal spreads individuals of the different species across the basin regardless of the main climatic gradients. In a recent study, most of the richness and community composition recorded in a locality could be predicted by the species abundance distribution in the metacommunity (Mota de Oliveira & ter Steege, this thesis, Chapter 3). We have also shown the importance of niche assembly driving community composition when we look into smaller plot units. The strong influence of microhabitat on the occurrence of species leads to much higher turnover of bryophyte species along the 30 m of vertical gradient on the host trees than across a 640 km distance (Mota de Oliveira *et al.* 2009). The position in the vertical gradient (height zone) may also have an influence on dispersal and Gradstein (2006) suggested that dispersal should be higher in the canopy, due to higher wind velocity.

In this paper we will use the framework of the Neutral Theory (Hubbell 2001) to investigate the different roles of dispersal and establishment limitation in structuring bryophyte communities in the height zones of trees and in entire geographical localities. Based on the fact that Amazonian terra firme forests have similar canopy structure, with a predictable microenvironmental gradient from the base to the top of trees, we expect a gradient in community composition of epiphytic bryophytes according to height zones in all localities studied. Furthermore, we expect that species inhabit, on average, the same height zone at different localities across the basin. If the gradient is indeed supported in all localities, we ask whether the environmental filtering is different for the different height zones and whether height zones in the tree differ in the input from long distance dispersal. Finally, we summarize at which scales and along which gradients environment and dispersal most influence community similarity.

Methods

Study area

The fieldwork was conducted across the Amazon Basin, in three localities in the Guianas and six localities along an East-West transect, from the mouth of the Amazonas River to Ecuador (see figure 1 in chapter 2). The sampling procedure took place in forests growing on non-flooded plateaus (terra firme forest).

Sampling

We sampled epiphytic bryophytes from the base to the top of eight canopy trees in each of the nine localities. Trees were divided into height zones, used as a surrogate for the microclimatic gradient found from the base to the canopy of the forest. The height zones were established as follows: from the base up to 1.5 metre (zone 1), via the lower and upper trunk (zones 2 and 3) to the base of the crown (zone 4) and finally the outer sun-lit twigs (zone 6) (for details see Mota de Oliveira *et al.* 2009). The material from the sites Saul (FG), Mabura Mora (MM) and Mabura Wallaba (MW) had been collected earlier, during three MSc projects at Utrecht University (Cornelissen & ter Steege 1989; Montfoort & Ek 1989; Bleij 1991), in a higher number of trees and also including the middle crown as a height zone (zone 5). In order to have a balanced experimental setup, we used a sub-set of the data of these three sites, which consisted of eight randomly chosen trees per locality and five height zones (zones 1 to 4 and zone 6). The bryophyte communities were sampled in 4 patches of approximately 10 cm^2 per height zone. These 4 patches within a height zone formed a bulk sample, which we treated as one plot.

The specimens present in the plots were identified using identification keys, monographs (Reese 1993a; Gradstein 1994; Dauphin 2003) and floras (Allen *et al.* 1994; Gradstein *et al.* 2001a; Buck 2003; Gradstein & Costa 2003). The specimens from the Guianas, which were already identified in the Nationaal Herbarium Nederland, were re-checked and compared to the new material. The composition of a plot consisted of a list of the species recorded. We used presence/absence for the plot data. We considered the use of an abundance measure inappropriate, due to the impossibility of separating individuals for most of the species and due to the variation in plant size. In order to have quantitative information on community structure, i.e. species abundance distribution, per locality or per zone, we used frequency as a surrogate of abundance, summing the number of plots in which each species was recorded. Thus, abundance value of a species in the species abundance distribution of a given locality can range from 1 to 40 (40 is present in all 5 plots of all 8 trees of that locality). Accordingly, abundance value of a species in the species abundance distribution of a given zone can range from 1 to 72 (72 is present in all 9 localities and all 8 plots per locality of that height zone).

Data analysis

In order to test if the vertical gradient in species composition holds in every locality studied, we carried out detrended correspondence analysis (DCA), an indirect ordination method (McCune & Grace 2002). We used DCA, as this method models species occurrence as a unimodal, Gaussian, response curve over gradients, just as we expect species to behave. The distribution of the plots in the ordination space is calculated only according to the species composition of each plot, without a priori assumption of an external gradient. The main gradient will be shown along the first ordination axis. Our expectation was that this first axis would be related to height zone. Since the environmental gradient to be tested - height zones - was expressed by classes, we tested the correlation between the scores of the first axis and the height zones using Monte Carlo regression analysis, available in the freeware EcoSim (Gotelli & Entsminger 2006). The method randomizes the data matrix 1000 times and it calculates R^2 and slope for each randomization. Observed and simulated values are compared for the level of significance.

Indicator species analysis (ISA, McCune & Grace 2002) was used to classify species into generalists and specialists. This analysis also provides an indicator value (IV) for the species with a significant preference for a height zone. The indicator value ranges from 0 to 100, according to the strength of the preference. Using a direct gradient analysis with zonation as single gradient, we calculated the weighted average height zone for species recorded in at least three localities. In order to test if species maintain their preferred height zone across the basin we calculated and correlated, for each species: the average height zone of the species in a given locality and the average height zone of that species in all other localities omitting the first locality, to avoid dependence. Monte Carlo regression test was again used to test for significance.

Sørensen distance measure was used to calculate similarity between plots based on presence / absence data. The similarity between communities was calculated for the following distance categories: adjacent plots in the same tree; non-adjacent plots in the same tree; plots in the same height zone in different trees at the same locality; plots in different height zones in different trees at the same locality; plots in the same height zone at different localities; plots in different height zones and different localities. Because measurements were not independent, a standard ANOVA was not valid. We used the freeware EcoSim (Gotelli & Entsminger 2006) to perform Monte Carlo ANOVAs and tested the significance of the differences in similarity between plots in the different distance categories.

We approached dispersal limitation through an analysis of the species abundance distribution of the localities, since there is no environmental gradient influencing species composition at this scale (chapter 3). Accordingly, we approached establishment limitation through an analysis of the species abundance distributions of the height zones, where dispersal is eliminated by pooling plots from the different localities. The use of the parameter *m*, derived from the Neutral Theory, to compare species abundance distributions, allowed differentiation between dispersal and environmental filters, as proposed by Jabot et al. (2008). Knowing in advance that the closer *m* gets to 1, the more similar local community and metacommunity are is an intuitive way of interpreting the parameter. We calculated the parameter *m* for the given local communities with the freeware Tetame (Chave & Jabot 2006).

In order to calculate *m* for the localities, each local community was composed by all individuals of all plots in a site (Fig. 1a). Here, the summing up of all plots along the microenvironmental gradient of each locality allowed us to estimate dispersal limitation from metacommunity to local community, without influence of establishment limitation. In order to calculate *m* for the height zones, each "local" (theoretical) community was composed by plots of all sites per height zone (Fig. 1b). Here, the summing up of all plots per height zone across the basin allowed us to estimate establishment limitation from metacommunity to a given height zone, without influence of dispersal limitation.

We also used *m* to compare the immigration rates of the different habitats for each locality. We compared understory - zones 1, 2 and 3 - with canopy - zones 4 and 6 (Fig. 1c); and lower canopy - zone 4 - with upper canopy - zone 6 (Fig. 1d). In this calculation the metacommunity was composed of all plots of all localities occurring in the zones pertaining to the habitat to be analysed (habitat species pool concept, again to avoid the effects of establishment limitation). Local communities were composed of all plots in the zones of the habitat to be analysed in a given locality.

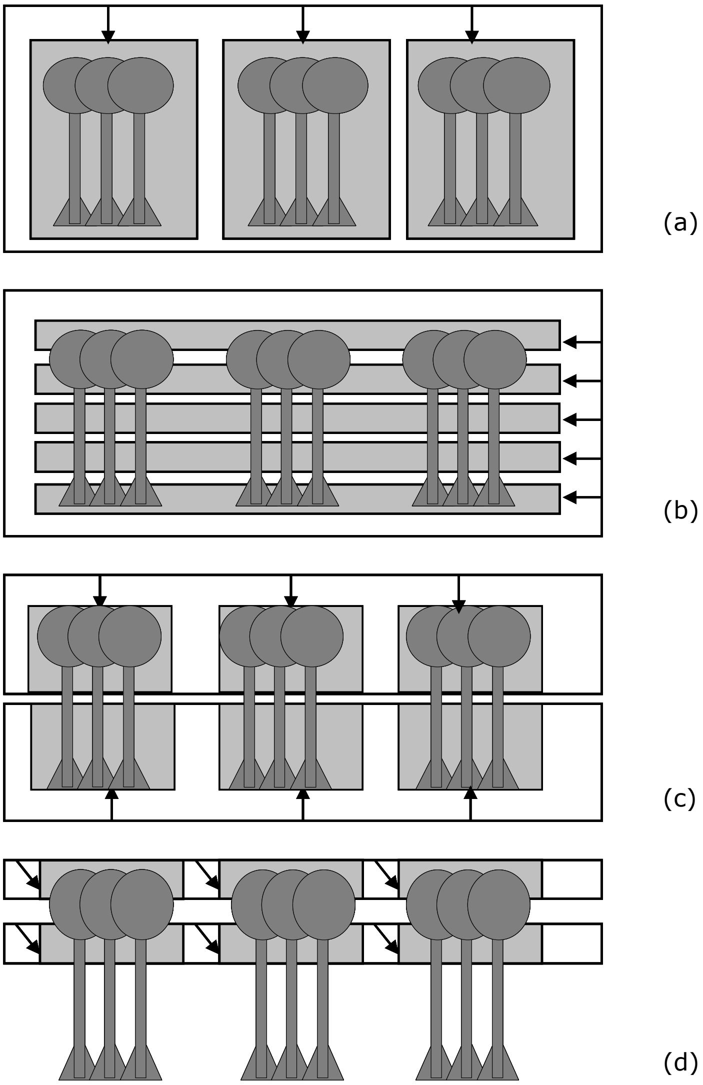


Figure 1. Schematic view of the calculations of the likelihood of the species abundance distributions. In (a) and (b), the metacommunity concept is the full species pool; in (c) and (d) the metacommunity concept is the habitat species pool. Larger white rectangles represent metacommunities, grey rectangles represent local communities. Arrows show the link metacommunity – local community involved in the calculation. For further explanation see text.

Results

In all localities studied the strongest intrinsic gradient in species composition was indeed found along the vertical zonation of trees (Fig. 2) with some variability in the strength of the relationship. The explained variation of the first axis of the DCAs ranged from 25% to 58% and the correlation coefficient between the ordination scores of the first axis and the height zones varied from 0.30 to 0.85 (Table 1). All correlations were tested with Monte Carlo regression and all slopes and R-squares were significant at $p<0.001$. Height zone does not explain the plot ordination when data from all localities is analysed together. A DCA analysis applied to the full dataset did not show any clear biological or distance gradient along the first axis (data not shown).

Species inhabited preferably the same average height zone across the localities. We found a correlation coefficient of $R^2=0.51$ for the 103 species analyzed (Fig. 3). The relationship had R^2 and slope significant at $p<0.001$ as tested with Monte Carlo regression. Among the 155 species recorded for more than one site, 57 were considered specialists (37%) and 98 (63%) generalists. Specialists were mainly found at the extremes of the gradient, zones 1 and 6. Only 14% of the specialists had preference for another zone, 7 species in zone 4 and 1 species in zone 2. Specialist species made up to 22% of the species found in zone 6 and 13% of the species found in zone 1. Specialists occurring at the base showed a much higher taxonomical diversity; they belong to seven different bryophyte families, while among the canopy specialists only three families – Lejeuneaceae, Jubulaceae and Pterobryaceae – were represented (Appendix 1 for detailed information). Typical widespread and abundant species of the base of the trees are *Octoblepharum pulvinatum*, *Pictolejeunea picta*, *Sematophyllum subsimplex*, *Taxithelium planum*, *Fissidens guianensis*, *Haplolejeunea cucullata*, *Pilosium chlorophyllum* and *Cheilolejeunea neblinensis*. In the canopy, the most typical species are *Lopholejeunea subfusca, Caudalejeunea lehmaniana*, *Frullania caulisequa,*

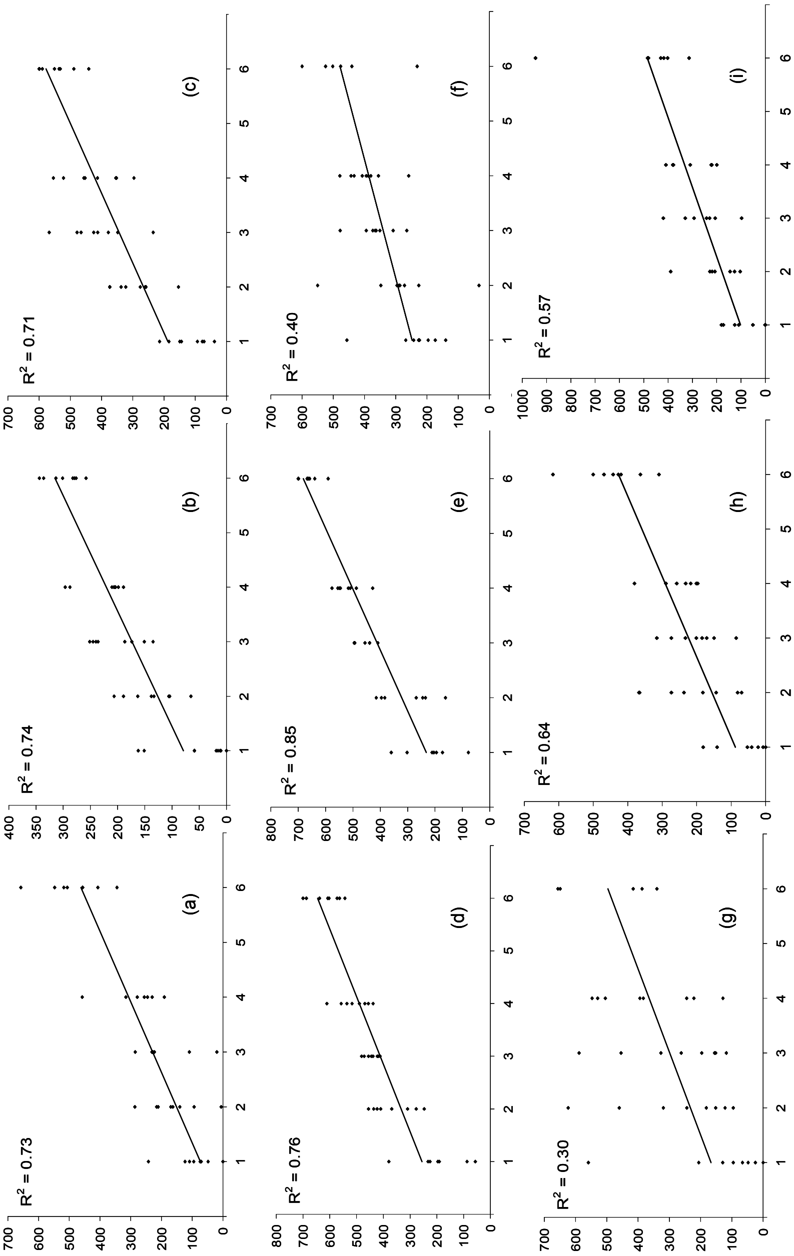


Figure 2. Correlation between height zone and DCA score (1st axis) for the nine localities (a) Caxiuanã; (b) Ecuador; (c) French Guiana; (d) Mabura Mora; (e) Mabura Wallaba; (f) Reserva Ducke; (g) São Gabriel da Cachoeira; (h) Tapajós; (i) Urucu.

Pycnolejeunea contigua, *Diplasiolejeunea rudolphiana*, *Leptolejeunea elliptica*, *Microlejeunea bullata* and *Drepanolejeunea fragilis.*

Table 1. Values of λ and the explained variation of the first axis of the DCA; correlation coeficient between scores of the first axis of DCA and height zone for each locality.

Locality	**Λ**	**axis 1**	**r_s**
CX	0.796	0.36	0.73
EC	0.478	0.33	0.74
FG	0.722	0.51	0.71
MM	0.659	0.52	0.76
MW	0.736	0.58	0.85
RD	0.593	0.25	0.40
SG	0.828	0.28	0.30
TA	0.690	0.34	0.64
UR	0.817	0.25	0.57

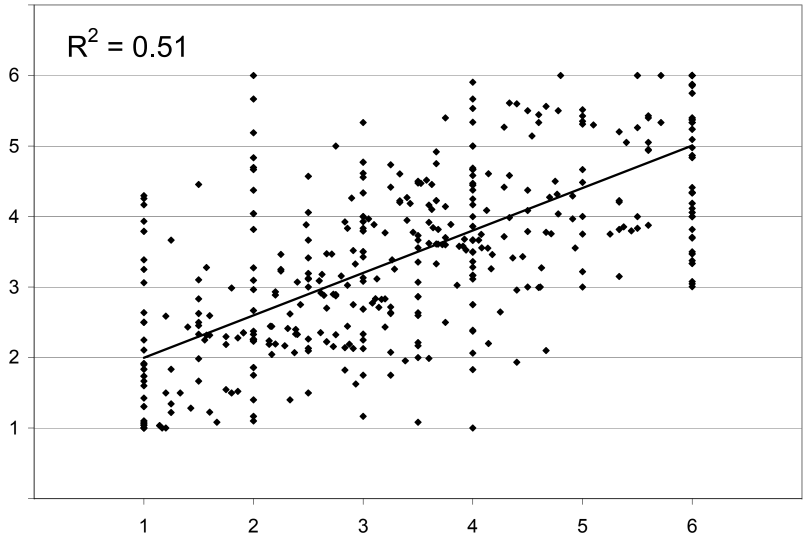


Figure 3. Correlation of pairs of weighted average height zone values for each species occurring in three or more sites. Weighted average height zone of a species in a given locality in axis x and weighted average height zone of the same species in all other localities in axis y. Dots represent species.

The Sørensen similarity between communities is highest among adjacent plots, with an average value of 0.41 (Fig. 4). Communities from plots on different trees in one locality and in the same height zone were more similar, with values of 0.29 on average, than communities established on the same tree but on non-adjacent plots, which had an average similarity of 0.18. When only communities from different trees at the same site were compared, similarity was on average of 0.29 for communities established at the same height zone and only 0.16 for communities established at different height zones. The difference of 0.13 in Sørensen similarity value is strictly influenced by the differences in height zone. Communities on different trees at the same locality, no matter the height zone, were more similar than communities in different localities, even when these were compared within the same height zone. The lowest similarity values were found between plots from different localities.

The calculation of the parameter *m* for the different localities showed that recruitment of individuals showed a similar rate in all localities, with an average of 20% recruited from the metacommunity (Fig. 1a, Table 2). Height zones 1 and 6 had a much higher rate of recruitment (*m*) from their own habitat pool than from the metacommunity compared to the other zones. While the other zones drew on average 65% of the recruitments from the metacommunity, zones 1 and 6 drew on average only 25% from the metacommunity (Fig. 1b, Table 2).

When different habitats were analysed within their own metacommunities, i.e. within the definition of habitat species pool, the values of *m* vary according to habitat. We found in all localities that *m* is lower in the understorey zones – 1,2,3 – than in the canopy. Also, in all localities, *m* is lower in the lower canopy – zone 4 – than in the outer canopy – zone 6 (Table 3). The values of *m* calculated in these different sets were always higher in the habitat most exposed to wind. The chance of having all comparisons of values according to expectation is significantly lower than by chance (Exact binomial $p = 0.59 = 0.004$ for each comparison).

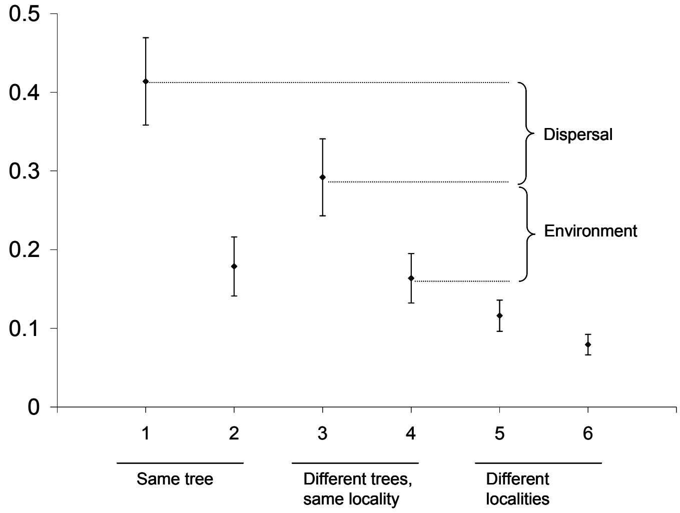


Figure 4. Similarity between communities (y axis) calculated from all pairs of plots on six distance categories (x axis). Bars represent standard deviation. 1) adjacent plots on the same tree; 2) non-adjacent plots on the same tree; 3) plots on different trees of the same locality, same height zone; 4) plots on different trees of the same locality, different height zone; 5) plots from different localities, same height zone; 6) plots from different localities, different height zones.

Table 2. Number of species (S), number of individuals (J), and *m* value per height zone.

Zones	S	J	*m*	Std_m
1	144	598	0.28	0.02
2	135	569	0.76	0.02
3	122	533	0.63	0.03
4	138	679	0.55	0.02
6	136	685	0.22	0.02

Table 3. Values of *m* for the different localities, its respective habitats, and comparison of *m* values. Understory: zones 1, 2, 3; canopy: zones 4, 6; outer canopy: zone 6.

Locality	***m* local**	$m_{1,2,3}$	$m_{4,6}$	m_6	$m_{1,2,3} < m_{4,6}$	$m_4 < m_6$
CX	0.21	0.17	0.48	0.59	yes	Yes
EC	0.16	0.22	0.37	0.57	yes	Yes
FG	0.22	0.32	0.36	0.54	yes	Yes
MM	0.11	0.12	0.25	0.26	yes	Yes
MW	0.19	0.24	0.32	0.37	yes	Yes
RD	0.19	0.25	0.38	0.46	yes	Yes
SG	0.26	0.32	0.47	0.77	yes	Yes
TA	0.26	0.36	0.44	0.54	yes	Yes
UR	0.27	0.33	0.54	0.59	yes	Yes

Discussion

The species composition of epiphytic bryophyte communities is mainly driven by the vertical microenvironmental gradient along the trees in each of the localities investigated across the Amazon (Fig. 2). In such a large area, however, the composition of plots becomes also heavily subjected to the species composition of the locality, i.e. the local species pool. The latter explains why microenvironment is not the main variable driving plot species composition when basin-wide data is analysed together in an ordination procedure. We estimated that approximately 80% of the recruitment occurring in a plot corresponds to species already locally established, i.e. in a surrounding of circa 10 Km radius (Mota de Oliveira & ter Steege, this thesis, chapter 3). The exception on this pattern was shown by the three localities in the Guianas (Mota de Oliveira *et al.* 2009). Even 640 Km apart, microenvironment (the vertical gradient) was still the first explanatory variable for community composition. The explanation for this particular case is that the two forests in Guyana are compositionally sub-sets of French Guianas' forest. Therefore, local recruitment, though being high, did not cause compositional differences that could override the differences in height zone composition.

The highest values of similarity shown by communities from adjacent plots probably result from the lack of sudden changes in the microenvironmental gradient and the facilitated dispersal due to the very short distance involved. Short distances are easily covered not only by spores, but also by asexual propagules such as gemmae or caducous leaves. Basically, species can easily migrate from one zone to the next. The mechanism seems to work mainly at these very small distances, since non-adjacent plots in the same tree have stronger environmental differences. These differences are already enough to cause non-adjacent plots in the same tree to be less similar than plots in different trees but from the same height zone. The lowest values of similarity, being found between communities from different localities, confirmed the results suggesting a predominant recruitment from the local community into the species composition of the plots.

The establishment limitation is set by the extremes and may be related to particular processes such as desiccation pressures in the outer canopy and space and light limitation in zone 1, at the base of the tree. In a recent paper (Mota de Oliveira *et al.* 2009), we briefly discussed that the main environmental filter in the outer canopy seems to be light intensity, based on the disappearance of some understory elements in gaps or tree-fall areas and the recorded shift of canopy species downwards, when light penetrates deeper (Acebey *et al.* 2003). Additionally, we speculate here that time for colonization also plays a role, the outer canopy being the most recent substrate available. Several species restricted to the canopy in our dataset, such as *Vitalianthus urubuensis* and *Leptolejeunea elliptica*, were recorded in the literature as epiphylls growing in the understory. Apparently this observation poses a paradox, since epiphylls are associated with moist habitats. Epiphylls are also associated with high population dynamics, and dispersal processes may affect their abundance more than habitat quality (Zartman & Nascimento 2006). Therefore we suggest that the relationship "epiphyll – moisture" is not always applicable. For instance, Sonnleitner et al. (2009), studying epiphylls from three distinct forest habitats, found *Leptolejeunea elliptica* more frequently in the habitat with highest variation of relative humidity and not associated with the most humid habitat. The author pointed out that the occurrence of this same species being positively associated with humidity in Barro Colorado Island (Marino & Allen 1992) poses a discrepancy that should be solved with the comparison of precise microclimatic records. Our data suggest that *Leptolejeunea elliptica* can tolerate wide relative humidity fluctuations, corresponding to its identification as an indicator species for the outer canopy. Based on that, we suggest that there was no discrepancy in the cited studies, but just that relative humidity is not the main driver of the occurrence of the species. Furthermore, we propose that the community of the outer canopy yields specialist species with different strategic advantages, from physiological features such as desiccation tolerance to population dynamical features such as high turn over and fast colonization of recent available substrates.

At the other extreme, the process behind establishment limitation on the base of the trees is an open research field. Competition is not commonly considered to be important for bryophyte communities (Slack 1990). During and Lloret (2001) review evidence that competitive exclusion hardly takes place in many types of bryophyte vegetation and state that probably density-dependent facilitation effects may counteract interspecific competition. The evidence that the aggregate growth of bryophytes favours water and nutrient capture comes from temperate forest, however. These studies focus mainly on species growing on forest soils with a higher light availability and lower water availability than tropical forests. Thus, the evidence may not hold for a moist and dark understory of a bark surface in the Amazon. Here, contrary to temperate forests, water is not limiting, but light is. Therefore, enhanced water capture through the aggregate growth is less of an issue, while the decreased light levels, caused by the same aggregate growth, in an already light limited surface such as a bark, may impose constraints to establishment of new individuals.

Epiphytic bryophyte species differ in many features such as spore size, frequency of sexual and asexual reproduction, protonema growth rate, etc. These differences influence dispersal and establishment on an available spot (Snall *et al.* 2004; Löbel *et al.* 2009), but the influence will depend on characteristics of the habitat to be occupied and at the scale where community will be investigated. Within localities we showed that, along the height zones, microenvironment plays the major role in the general structuring of community composition. In a more detailed analysis of this main gradient we found evidence that establishment limitation drives the species abundance distribution of zones 1 and 6, while dispersal overrides establishment limitation in the middle trunk zones 2, 3 and 4. Across localities, we showed that there is no identifiable gradient on species composition that can be related to establishment limitation. At this scale, dispersal has a constant and major role and the species abundance distribution of the localities resemble the metacommunity almost equally. Despite this constant role of dispersal across localities, there is a clear differentiation regarding the origin of most of the long distance dispersal events. We supported that long distance dispersal increases with increasing height along the vertical gradient of a tree, through the comparison of *m* as a measure of dispersal within habitat pool (Table 2). This is in accordance with the well known pattern of increased wind speed along the canopy profile (Cionco 1972; Kruijt *et al.* 2000 for the Amazon). The importance of wind for the dispersal of bryophytes is so remarkable that a study in the Southern hemisphere showed that floristic similarities had a stronger association with maximum wind connectivity between areas than with their geographical proximity (Munoz *et al.* 2004). Canopy and outer canopy communities are more similar across the basin due to a better connectivity and facilitated dispersal through wind.

Acknowledgments

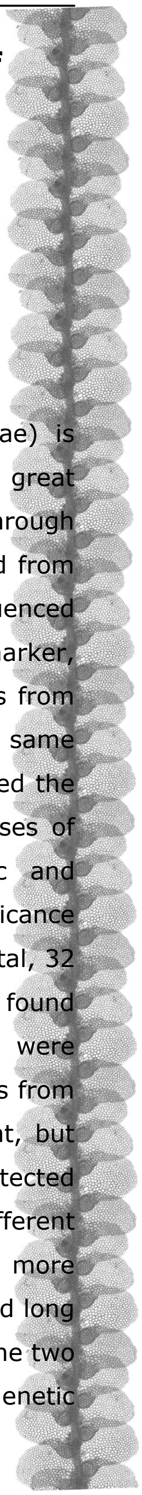
The authors are grateful to CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior / Brasil - for funding the first author; Marinus Werger and Heinjo During for discussions and comments on an earlier draft of the manuscript; Elena Drehwald and Anna Luiza Ilkiu-Borges for suggestions on the identification of some Lejeuneaceae species.

Sampling Bryophytes in São Gabriel da Cachoeira, Brazil

5

5. Dispersal and connectivity of populations of *Cheilolejeunea rigidula* (Lejeuneaceae) in Amazonian forests: a pilot study

with Andries Temme, Roy Erkens and Hans ter Steege



Abstract

Cheilolejeunea rigidula (Nees et Mont.) R.M.Schust. (Lejeuneaceae) is very abundant and widespread in the Amazon, providing a great opportunity to investigate how populations are connected through dispersal. Individual shoots of *Cheilolejeunea rigidula* were obtained from herbarium collections of five localities in the Amazon basin. We sequenced two chloroplast markers, *atpB-rbcL* and *psbA* and one nuclear marker, ITS, in order to compare differences in genetic distance of samples from the same locality and from different localities, as well as from the same habitat and different habitats - understory and canopy. We evaluated the amount of population genetic structure through hierarchical Analyses of Molecular Variance (AMOVA). The correlation between genetic and geographical distance from 400 to 1500 km was tested for significance with a Mantel test carried out through permutation regression. In total, 32 samples of *Cheilolejeunea rigidula* were successfully sequenced. We found that genetic distances between shoots from the same locality were significantly lower than the average genetic distance between shoots from different localities, indicating the predominance of local recruitment, but no geographical pattern such as isolation by distance was detected between 400 and 1500 km. When only pairs of shoots from different localities were compared, pairs of canopy shoots were significantly more similar than pairs of understory shoots, as predicted by the facilitated long distance dispersal in the canopy. Surprisingly, pairs of shoots from the two different habitats, canopy and understory, show the highest genetic distance, a pattern to be further investigated.

Introduction

Cheilolejeunea rigidula (Nees et Mont.) R.M.Schust. (Lejeuneaceae) is the most abundant bryophyte species on the bark of canopy trees in the unflooded forests of the Amazon (Mota de Oliveira & ter Steege, chapter 3, this thesis). The species is predicted to occur in any sample of 8 trees in the Amazon and, indeed, has been found in every inventory that included epiphytic liverworts in the Amazon (Santiago 1997, Yano & Camara 2004, Ilkiu-Borges 2000, Zartman 2008) and Atlantic forest of Brazil so far (Porto & Oliveira 1998, Costa 1999, Visnadi 2005, Porto et al. 2006, Yano & Porto 2006). Such an abundant and widespread species provides a great opportunity to investigate how populations are connected through dispersal.

Experimental studies on bryophyte dispersal show that the majority of the spores and asexual propagula fall very close to the mother plant, within a radius of a few metres (McQueen 1985, Kimmerer 1991, Stoneburner et al. 1992). A variable percentage of the diaspores will be spread over large distances (Miles & Longton 1992). How high this percentage is and how far these diaspores travel is relevant for an understanding of long distance dispersal, across a given region, from hundreds to thousands of metres. Since trapping experiments, able to measure diaspore deposition, are severely space limited, information within these distances is usually inferred from species distribution maps. The emerging distribution patterns can be then correlated to differences among species, such as diaspore type (spores or several other asexual propagules), diaspore size or frequency of diaspore production (Snall 2004, Lobel 2009). Distribution maps, although pattern-wise informative, are limited in investigating dispersal processes of a single species because they lack information on the historical connectivity among the populations under study. They are insufficient, for instance, to determine whether intercontinental distribution is due to separation of populations during drift of land masses or to long distance dispersal, a very common question in bryophyte biogeography. Whether several populations occurring on an island are the result of one colonization event followed by local dispersal or of multiple colonization events is also impossible to answer only based on presence/ absence data. Here, molecular studies may provide data on similarity / connectivity between populations and, therefore, help to explain the dispersal process that generated the observed pattern (McDaniel & Shaw 2005, Grundmann et al. 2008).

Amazonian epiphytic bryophytes show wide distribution ranges, being mostly neotropical or pantropical (Gradstein 2002). We have shown that communities of epiphytic bryophytes across the Amazon behave as one metacommunity, where 80% of the recruitment is originating from individuals of species already established in the local community (Mota de Oliveira & ter Steege, chapter 3, this thesis) and the rest may come from anywhere in the basin, without a clear geographic structure. When immigration was estimated for these epiphytic communities on different strata of the forest, i.e. different height zones in the host tree, we found evidence that long distance dispersal events are more frequently originating from individuals in the canopy than from individuals in the understory. From these results, it can be predicted that for a single species, such as *Cheilolejeunea rigidula*, individuals from the same locality will be genetically more similar to each other than individuals from different localities, because new recruitments are mainly originating from parent plants established in the surroundings. Furthermore, we expect no correlation between genetic similarity and geographical distance of individuals from different localities. Finally we predict that, when only populations of different localities are compared, plants of *Cheilolejeunea rigidula* in the canopy will be genetically more similar than plants in the understory, due to the higher chance of long distance dispersal to the canopy.

Methods

Sampling strategy

Individual shoots of *Cheilolejeunea rigidula* were obtained from herbarium collections of five localities in the Amazon basin (Figure 1). The collections consisted of a 40 cm^2 sample patch of epiphytic bryophyte communities taken from the understory or canopy of a host tree, in which the presence of *Cheilolejeunea rigidula* had been previously recorded. For this work, each herbarium collection provided us with one sample (= one shoot) of *Cheilolejeunea rigidula*. We planned to extract DNA from ten samples in each of the five localities, in order to analyse a total of 50 samples. Several samples failed to have DNA extracted, probably due to the small size of the shoot. This fact led us to develop a new protocol for this species, but we were still left with an unbalanced design of 32 successfully sequenced samples (Appendix 1). Only one sample from São Gabriel da Cachoeira was successfully sequenced, and the locality was excluded from some analyses. Collections at the same locality were known to be separated by 5 km at most, while shoots from different localities were separated by variable distances ranging from 400 to 1500 km.

Figure 1. Map of the study area, showing the sampling localities from East to West in the Amazon and Guiana Shield (Chapter 1, this thesis). Locations from which samples were not successfully sequenced are shown in light gray. Location 3 and 4 are treated as 1 locality here (Mabura).

DNA extraction, amplification and sequencing

It was necessary to design a modified extraction protocol for this species. DNA extraction was difficult, probably due to the small size and extremely low weight of individual shoots (generally 0.1-<0.01µg). Air-dried individual shoots were placed in a 0.5 ml Eppendorf tube and disrupted by vigorous up and down motion with a sterile blunt ended rod. Further extraction of total genomic DNA was carried out using the GenElute® Plant Genomic DNA Miniprep Kit (Sigma-aldrich Co., St Louis, MO, USA) with the standard protocol downscaled to one tenth of the volume to prevent dilution of DNA. Final elution was carried out in 30 µl. Two chloroplast markers, *atpB-rbcL* (primers 672F and 910R, Wolf *in* http://bioweb.usu.edu/wolf.htm) and *psbA* (primers 501F and trnHR, C.Cox *in* http://bryophytes.plant.siu.edu/methods.html), and one nuclear marker, ITS (divided into two sequential fragments, ITS1 primers Bryo-18SF, Bryo-5.8SR; ITS2 primers Bryo-5.8SF, Bryo-26SR) (Hartman et al. 2006), were employed in this study.

PCR of the chloroplast markers *atpB-rbcL* and *psbA* was performed in 25 µl solution containing 2.5 µM Reaction Buffer, 3.5 µM $MgCl_2$, 0.2 µM dNTP's each, 0.1 µM primer, 1.0 µl 0.4% bovine serum albumin and 5 µl template solution using a ½ unit Taq polymerase. PCR mixes for the nuclear marker ITS were also 25 µl, with 2.0 µM $MgCl_2$, 0.2 µM primer, 3 µl template solution and 1.0 µl added DMSO to prevent the formation of secondary structures. PCR was performed by 1 minute initial denaturation at 94 °C followed by 35 cycles of 1 minute denaturation at 93 °C, 1 minute annealing at 50 °C and 3 minutes extension at 72 °C. Final extension was done during 7 minutes at 72 °C. PCR of ITS was performed by 3 minutes initial denaturation at 96 °C followed by 30 cycles of 1 minute denaturation at 95 °C, 2 min annealing at 60 °C and 5 min extension at 72 °C. Final extension was done in a single step of 5 minutes at 72 °C. Due to low yields, the obtained PCR product was re-amplified using the same mixes and programs. PCR products were purified using either an Ilustra™ GFX™ PCR DNA and Gel Band Purification Kit (GE

Healthcare LTD, UK) or an E-Gel® CloneWell 0.8 % SYBR Safe™ (Invitrogen, USA). Sequencing was carried on an ABI 3730XL automated DNA sequencer using BIGDYE terminators (ABI, USA) using the same primers as mentioned above.

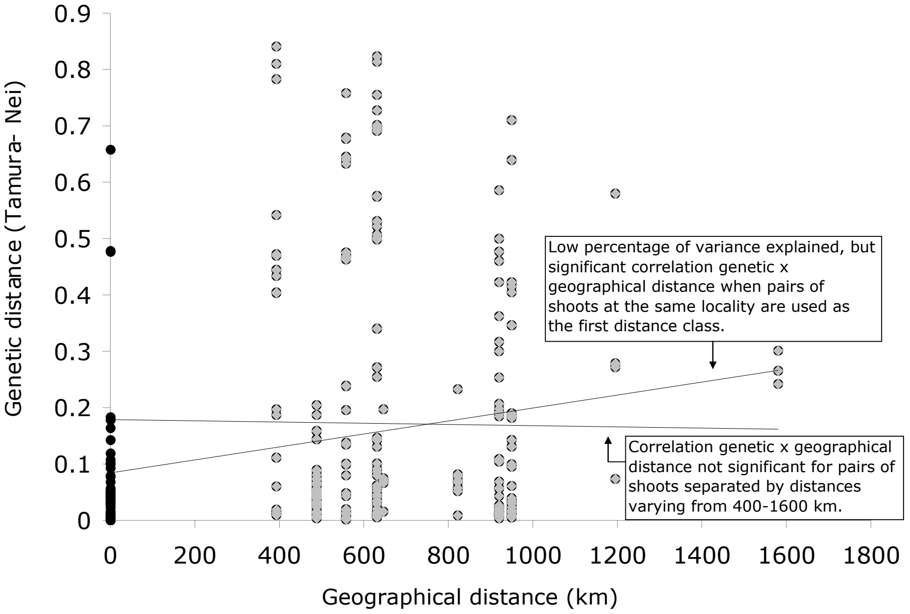
Data analysis

Tracer files were edited manually using SeqMan version 2.0 (DNASTAR inc., USA). Individual sequences were aligned manually using Maclade version 4.0 (Maddison & Maddison 2002), following an initial alignment using the Clustal W algorithm (Larkin et al. 2007). In order to evaluate the amount of population genetic structure, different hierarchical Analyses of Molecular Variance (AMOVA) were calculated with the software Arlequin version 3.11 (Excoffier et al. 2005). Fst was calculated as a weighted average over all loci as described in Weir & Cockerham (1984). Genetic distance between pre-defined groups of samples was calculated using the Tamura-Nei parameter over all combined loci for pairwise genetic differentiation in PAUP* version 4.0b10 (Swofford 2003). The significance of the differences in genetic distance values of samples from the same locality and samples from different localities, as well as the differences in genetic distance values of samples from the understory and canopy were analysed with permutation Anova using EcoSim version 7.72 (Goteli & Entsminger 2009). The correlation between genetic and geographical distance from 400 to 1500 km was tested for significance with a Mantel test carried out through permutation regression also with EcoSim 7.72 (Goteli & Entsminger 2009).

Results

In total, 32 samples of *Cheilolejeunea rigidula* were successfully sequenced. Genetic distances between plants from different localities, separated by 400 to 1500 km, were not correlated to geographical distance (Mantell test, $p=0.55$). The influence of geographical distance on genetic distance is only detected if shoots of the same locality, corresponding to the smallest distance class, are taken into account in the analysis (Mantell test, $p<0.001$) (Figure 2). Therefore, the relationship genetic distance x geographical distance is only due to the differences between shoots from the same locality (within) and shoots from different localities (among). Based on this result, all the "among differences" were pooled in subsequent analyses.

We found that genetic distances between shoots from the same locality were on average 0.05, significantly lower than the average genetic distance between shoots from the different localities, which was 0.17 ($p<0.001$) (Table 1). Pairs of shoots of different sites sampled from the canopy were significantly more similar than those sampled in the understory. Surprisingly, pairs of shoots from the two different habitats, canopy and understory, both when compared from different and the same locality show the highest genetic distance calculated ($p<0.001$) (Table 1). Furthermore, the 'within locality' genetic distances between both pairs of shoots from the canopy and pairs of shoots from the understory were very similar. Hence, the significant overall difference in genetic distance is given by pairs of shoots from different localities. These more detailed results, however, could not yet be statistically tested due to our unbalanced dataset.



Low percentage of variance explained, but significant correlation genetic x geographical distance when pairs of shoots at the same locality are used as the first distance class.

Correlation genetic x geographical distance not significant for pairs of shoots separated by distances varying from 400-1600 km.

Figure 2. Relationship between genetic distance and geographical distance of pairs of shoots from different localities (grey dots) and the same relationship including pairs of shoots of the same locality – distance zero (black dots).

Table 1. Average genetic distance of pairs of shoots calculated for the different geographical distance classes – comparisons within and among localities (columns) and for the different habitats – comparisons of pairs of canopy shoots (CC), understory shoots (UU) and pairs formed by one shoot from the understory and one from the canopy (UC) (rows). Values highlighted in grey were tested statistically; values in bold italic format were interesting non-testable differences, referred to in the results.

	CC	**UU**	**UC**	**distance**
Within	0.036	0.028	***0.112***	0.053
Among	***0.105***	0.201	0.228	0.172
Habitat	0.084	0.143	0.215	←p<<0.001 ↑

Discussion

The genetic structure of *Cheilolejeunea rigidula* populations seems to be in agreement with our predictions, which were: predominantly local recruitment, lack of geographical structure at large scales (isolation-by-distance pattern not detected) and higher chance of long distance dispersal in canopy populations than in trunk populations.

The predominant local recruitment fits with long standing and general knowledge of plant dispersal, as well as with direct experiments on dispersal distance of bryophyte spores. Despite the fact that (wind-) dispersal distances reported vary mainly in a range of a few meters (McQueen 1985, Kimmerer 1991, Stoneburner et al. 1992), the transport of spores or even plant fragments by animals can lead to greater distances, of hundreds of metres (van Tooren & During 1988, Heinken et al. 2001) or even beyond, as in the case of dispersal of viable fragments through ingestion and defecation by flying-foxes (Parsons et al. 2007) or the case of ant-mediated dispersal (Rudolphi 2009). Based on that, the range of distances between our shoots from the same locality can very well represent this area where most of the propagula are distributed.

The fact that dispersal is mainly occurring within the surroundings of the mother plant, however, does not immediately convey that increased distance will be followed by a proportional decrease in dispersal probability. Several models that describe the relationship dispersal x geographical distance have been put forward, including differences of characteristics of species and functional groups (Bossenbroek et al. 2001, Nathan et al. 2002, Tackenberg 2003). As reviewed by Nathan & Muller-Landau (2000), propagule density very frequently declines leptokurtically with distance, showing an extended tail of long distance dispersal. This pattern was already suggested by Miles & Longton (1992) for bryophyte diaspores. But how far this extended tail goes and how fat the tail is, remain questions. Answering these questions is one of the main challenges in dispersal ecology, often neglected in bryological literature, due to either experimental constraints or an acclaimed rarity of long distance dispersal events. Molecular studies have demonstrated long distance dispersal to be more frequent than previously supposed in bryophytes (Skotnicki et al. 2000, McDaniel & Shaw 2005, Sabovljevi & Frahm 2008), despite the experimental work of van Zanten (1976), showing that liverworts are usually vulnerable to the stresses experienced during long distance dispersal, such as low tolerance of spores to UV and desiccation. The lack of geographical structure in the genetic distances of *Cheilolejeunea rigidula* reported in our results may indicate that when recruitments are the consequence of long distance dispersal, diaspores have the same probability of migrating in a range of hundreds of kilometres. Apparently, when diaspores become airborne, trajectory is less influenced by deterministic features such as weight, shape or angle of release and more influenced by the wind currents and stochastic break-downs and spores are capable of surviving this.

In *Cheilolejeunea rigidula*, as in most of the bryophytes, dispersal is predominantly carried out by wind. In agreement with the fact that wind speed is higher in the canopy than in the understory (Cionco 1972; Kruijt et al. 2000 for the Amazon), long distance dispersal events seem to occur more frequently with diaspores from plants of *Cheilolejeunea rigidula* established in the canopy, which causes the lower genetic distance among these shoots than among shoots from the understory (table 1). If we propose that genetic distance among canopy populations is lower than among understory populations because of facilitation of long distance dispersal events, we cannot expect differences between these genetic distances within locality. That is exactly what we found when separating the components within and among localities lumped in both habitat classes (Table 1). On the other hand, diaspores from plants occurring in the canopy did not necessarily “arrive” at canopy spots after long distance dispersal. The genetic distances between pairs of shoots from the different habitats, understory and canopy, even within localities were the highest in our study, even within localities. The limitation given by our number of samples prevents testing, but it is important to be aware of possible differentiation in genotypes depending on microenvironmental conditions, as reported by Sastad et al. (1999) for *Sphagnum* populations.

The Fst values reported here indicate a higher level of population structure than commonly found for liverworts (see review in Bischler & Boisselier-Dubayle 1997). However, comparison of Fst values of different species is limited by the use of different molecular markers. The only study to date of an Amazonian bryophyte, *Radula flaccida*, reports much lower population structure (Zartman 2006). If methodological differences could be ruled out, the high population dynamics typical of this epiphyllous species, explains its lower population structure when compared to *Cheilolejeunea rigidula*, due to a more efficient and frequent dispersal.

This is the first population genetic study of bryophytes in the Amazon at this spatial scale. Although the results are interesting and promising, the low success in sequencing, resulting in a relatively low number of sequences does not allow us to test all questions at a depth we had hoped for. Further research then should add a greater number of sampled localities, in order to confirm the lack of geographical structure in long distance dispersal events of the species, and a finer scale of distance classes within localities, in order to have detailed measurement of distance decay at the spatial range where it occurs.

Acknowledgments

The authors are grateful to CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior / Brasil - for funding the first author; Jan Maas for all support during the laboratory work and Marinus Werger for discussions and comments on an earlier draft of the manuscript.

Appendix 1. Origin of *Cheillejeuenea rigidula* shoots, successfully sequenced. Z: zone, T or C indicates whether a shoot was found on the trunk or in the canopy.

site	**collection nr**	**collector**	**Z**	**Markers**		
				atpB	**pbsA**	**ITS**
Mabura Hill (-58.694, 5.294)						
	c687	Cornelissen & ter Steege 1985	C	+	-	+
	C686	Cornelissen & ter Steege 1985	C	+	+	+
	C769	Cornelissen & ter Steege 1985	C	+	-	+
	C685	Cornelissen & ter Steege 1985	C	+	+	+
	C768	Cornelissen & ter Steege 1985	C	+	-	-
	C768	Cornelissen & ter Steege 1985	C	+	+	+
	C789	Cornelissen & ter Steege 1985	T	+	+	+
	C789	Cornelissen & ter Steege 1985	T	+	+	-
	C833	Cornelissen & ter Steege 1985	T	+	+	+
	C642	Cornelissen & ter Steege 1985	C	+	+	-
	C641	Cornelissen & ter Steege 1985	C	+	-	+
	C684	Cornelissen & ter Steege 1985	C	+	+	+
Reserva Ducke (-59.969, -2.928)						
	217516	Mota de Oliveira 2005	C	-	+	+
	217529	Mota de Oliveira 2005	C	+	-	+
	217533	Mota de Oliveira 2005	T	+	-	+
	217534	Mota de Oliveira 2005	C	+	+	+
	217509	Mota de Oliveira 2005	T	+	+	+
	217505	Mota de Oliveira 2005	T	+	+	+
	217506	Mota de Oliveira 2005	C	+	-	+
Caxiuana (-51.462, -1.720)						
	186230	Mota de Oliveira 2006	C	+	-	+
	186239	Mota de Oliveira 2006	C	-	+	+
	186254	Mota de Oliveira 2006	T	+	-	-
	186258	Mota de Oliveira 2006	C	-	-	+
	186263	Mota de Oliveira 2006	C	+	-	-
Tapajos (-54.963, -2.509)						
	217804	Mota de Oliveira 2005	C	+	+	+

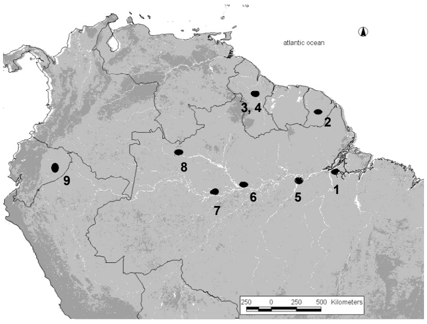
217804	Mota de Oliveira 2005	T	-	+	+
217806	Mota de Oliveira 2005	T	-	-	+
Tree 1	Mota de Oliveira 2005	T	-	-	+
Tree 8	Mota de Oliveira 2005	T	-	-	+
217779	Mota de Oliveira 2005	C	+	+	-
217789	Mota de Oliveira 2005	C	+	+	+
217789	Mota de Oliveira 2005	C	+	-	-
Soa Gabriel (-65.630, -0.140)					
tree 6	Mota de Oliveira 2006	T	-	-	+

View from the LBA tower at São Gabriel da Cachoeira, Brazil

6

6. General discussion

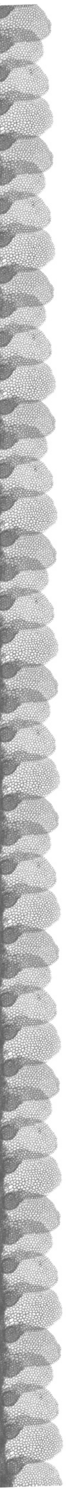
This thesis reports on the first systematic sampling, species identification and analysis of community composition of epiphytic bryophytes from East to West across the Amazon basin. Eight trees in each of nine localities (Figure 1) were sampled in five height zones from the base of the tree to the outer canopy.



1. Caxiuana, Brazil
2. Saul, French Guyana (FG)
3. Mabura Mora, Guiana (MM)
4. Mabura Wallaba, Guiana (MW)
5. Floresta Nacional do Tapajos (TA)
6. Reserva Ducke, Brazil (RD)
7. Província petrolífera de Urucu, Brazil (UR)
8. Parque Nacional do Pico da Neblina, Brazil (SG)
9. Tiputini Biodiversity Station, Ecuador (EC)

Figure 1. Map of the study area, showing the sampling localities from East to West in the Amazon and Guiana Shield.

The sampling resulted in 3104 records, 3066 of which resulted in the identification of 225 species and 38 morpho-species and 40 records remained unidentified. The species belonged to 29 families. The most common families in number of records were Lejeuneaceae (55%), Calymperaceae (8%), Leucobryaceae (4%) and Sematophyllaceae (4%), and these were the only families recorded in all localities. The most common species was *Cheilolejeunea rigidula*, followed by *Ceratolejeunea cornuta*, *Octoblepharum pulvinatum*, *Octoblepharum albidum*, *Archilejeunea fuscescens, Sematophyllum subsimplex, Lopholejeunea subfusca* and *Symbiezidium barbiflorum*. These eight species together accounted for 21% of the records.



The vertical gradient along the host tree – bryophytes are strongly niche-assembled.

Over the entire Amazon basin bryophytes show a clear compositional gradient along the host trees (Chapter 2, 4). While the gradient in itself is gradual, many species show one significantly preferred height zone on the host tree, across the basin (Chapter 4, Appendix 1). Most of these specialists are found in zone 1, the base of the stem, and in zone 6, the outer twigs, the extremes of the gradient, in terms of microclimate.

The vertical gradient in bryophytes is long known, both in terms of species composition and life forms (Barkman 1958, Richards 1984, Gradstein 2001, Sporn et al. 2009). The restriction of some bryophyte species to the canopy has also been observed before in the Amazon forest (Cornelissen & ter Steege 1989). This and the shift of bryophyte occurrences to lower height zones in a tree, as a result of opening of the canopy (Acebey et al. 2003), supports the long standing idea of a niche-based relationship between occurrence and microenvironmental conditions. Based on this view, epiphytic species were traditionally classified as "shade epiphytes" when restricted to the bottom part of the host tree, "generalists" when occurring in many height zones, and "sun epiphytes" when restricted to the canopy (Richards 1984). The mechanisms leading to the restriction of a given species to one of the habitats, however, are not necessarily related to light intensity as suggested by the denomination. Canopy specialists may be directly related to the requirement of high light levels for development, such as reported for *Frullania* species (Romero et al. 2006), but can be also related to the availability of empty substrata, such as in *Leptolejeunea elliptica* and other species with high population dynamics. The possible physiological causes for the preferences are discussed in chapters 2 and 4.

Although the physiological basis for the strong preference of many species for a given height zone is as yet unknown, the preference was clearly constant across the Amazon Basin (Chapter 4), supporting strong niche assembly of bryophyte communities on host trees in the Amazon.

Epiphytic bryophyte communities in a *terra firme* Amazonian forest – neutral dynamics of species abundances

While the occurrence of bryophytes on host trees is strongly niche based, interestingly, richness and relative species abundances of epiphytic bryophytes in most of the nine Amazonian localities studied were very well explained by the Neutral Model of Biodiversity and Biogeography (Hubbell 2001), as shown in chapter 3. Plant diversity across the Amazon basin was never tested for neutral dynamics, probably due to the clear gradients in diversity from East to West (Phillips et al. 2002, ter Steege et al. 2003) and in composition from the Northeastern to the Southwestern borders of the basin (ter Steege et al. 2006). Because of the strong niche-assembly of bryophytes, similar patterns to those of trees may be expected. The species composition and structure of bryophyte communities at this scale, however, were shown mainly to be regulated by stochastic recruitment of individuals from the same locality or from immigration, influenced by the abundances of the species they belong to in the metacommunity. The lack of a strong compositional gradient pertinent to epiphytic bryophyte vegetation when all records per locality are treated as one local community leads to the conclusion that community compositions are fully consistent with neutral theory. The absence of a geographical pattern does not rule out the importance of dispersal, however. Most of the individuals recruited in a locality come from within the same locality, which confirms the general pattern of predominance of short distance dispersal in bryophytes (McQueen 1985, Kimmerer 1991, Sundberg 2005, Hutsemekers 2008, among others) but nearly panmictic dispersal at medium and large distances, since at those scales probabilities of successful immigration are equally low.

The Neutral Theory must not be seen as an alternative to niche theory. More, it should be used as a first approach to explain species richness and relative abundances of a given local community, influenced by species richness and relative abundances of a larger (meta) community, as a source of new individuals. There has been criticism on the Neutral Theory's simplistic assumptions, such as ecological equivalence and environmental saturation. Epiphytic bryophytes hardly attend to the assumption of spatial saturation. Also ecological equivalence of individuals finds little support in the literature and in this thesis (Chapter 2, 4), due to the well known differences in species performance, such as spore establishment or photosynthetic responses (Wiklund & Rydin 2004, Gabriel & Bates 2003, Thomas et al. 1994). Apparently, that would hamper the use of the theory as a first approximation to explain the influence of the metacommunity on local communities. Nevertheless, among recent theoretical developments, it was shown that breaking assumptions, such as the zero-sum game (spatial saturation) and the ecological equivalence, may not affect predictions, unless immigration from the meta to the local community is absent or extremely low (Gravel et al. 2006, Zillio & Condit 2007). This is caused by the importance of immigration (or a "species input" parameter) in regulating community composition and abundance distribution in a local community. This "top-down" approach is very useful in macroecological studies (Ricklefs 1987, Whittaker et al. 2001, Blackburn 2005) and also employed by the Neutral Theory. Furthermore, expanding on the possibilities of the theory, it was recently shown (Jabot et al. 2008) that the parameter corresponding to "species input" or immigration (*m*), can be interpreted beyond the strict concept of dispersal limitation, as proposed initially. The parameter can also account for establishment limitation (environmental filtering), acting upon the diaspore or its further development (Ettiene 2007, Jabot et al. 2008), as used in chapter four.

The reason why environmental differences across the Amazon are not strong enough to cause a diversity gradient in epiphytic bryophyte communities across geographical space is not very clear. The strong role for neutral dynamics was also puzzling, especially when compared to other surveys in bryophytes. Species richness in the temperate region of England, for instance, was shown to be correlated to the annual number of rainy days (> 1 mm) (Callaghan & Ashton 2008) in a much more restricted area. Biomes next to the Amazon such as the Andes and the Atlantic forest of Brazil, also show strong diversity gradients across much shorter distances than the ones investigated across the Amazon (Wolf 1993, Kessler 2000, Costa & Lima 2005). Those diversity gradients are clearly set by the altitudinal gradient, and usually attributed to the correlated gradient in relative humidity and temperature, which can vary in different mountains and may result in a shift of species richness along the altitudinal zones (Andrew et al. 2003).

The exception to the neutrality across the Amazon is given by the locality in Ecuador. Strictly, the higher species richness is associated with a higher number of individuals in plots of the same size as the ones in the rest of the Amazon. This could be favoured by successful establishment of species from another substrate, such as epiphylls, due to local high and constant relative humidity conditions. Therefore, the extra source of species was not in agreement to the model. The same can be suggested for French Guiana which, although within the prediction of the neutral theory in our simulations, is significantly richer than an average Amazonian locality.

Epiphytic bryophyte communities in a *terra firme* Amazonian forest - predictions

Using neutral theory as a deterministic model is not useful, because two local communities from the same metacommunity can present totally different species composition. Quantitative predictions can be carried out, however, and tested. In chapter 3 it was shown that the average epiphytic bryophyte community of 250 occurrences found in a sample of 8 trees in the Amazon is expected to have around 65 species including 21 singletons, with the most common species having between 10-30 occurrences. We could not compare this prediction to other studies in the Amazon (because of the lack thereof), but a study carried out in the Atlantic rain forest of Brazil, surprisingly, showed results very compatible with ours: Alvarenga & Porto (2009) sampled epiphytic bryophyte communities from different forest fragments from the bottom to the top of trees. They found, in the most preserved forest (that was comparable to our ecosystem), exactly 63 species, of which 18 were singletons, *Cheilolejeunea rigidula* being the most abundant species with 15 records.

Furthermore, two predictions raised by the results of chapter 3 were tested in the most abundant species of the dataset, *Cheilolejeunea rigidula,* using molecular data as a measurement of distance among individuals. The results were in agreement with the predictions of predominance of local recruitment and lack of geographical structure in the immigration across the basin. It means that, when analyzed within hundreds of metres, genetic distances between individuals of the same species may have a relationship with spatial distances, as shown by Snall et al. (2005), but across larger geographical distances the relationship is lost, due to the general low chance of long-distance dispersal.

The vertical gradient along the host tree and neutral dynamics across the basin – relative roles of environment and dispersal

The general picture given by the results is the combination of strong niche assembly in different height zones on a host tree to communities of an entire locality driven by neutral dynamics. Ultimately, the composition of a community of epiphytic bryophytes in a given height zone of a host tree in a given locality is driven by the following pattern: The environment has a stronger role at the extremes of the gradient, so that communities of zones 1 and 6 – bottom and canopy – have the strongest influence of establishment limitation. The influence of dispersal overrides establishment limitation in the middle trunk zones 2, 3 and 4. In all zones, the possibility of a species to occur is significantly higher for species already established in the surroundings of the same locality (within circa 15 km radius) than for species arriving through long distance dispersal. Finally, the chance of a species not yet present at the locality of the community to occur, i.e. through long distance dispersal, significantly increases with increasing height zone of the community.

Future research

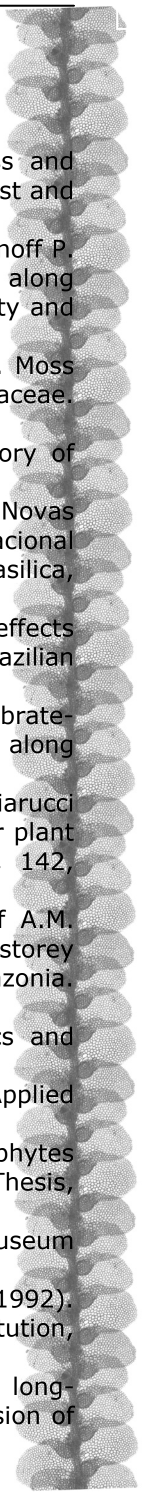
This thesis provides a background for future long-term and large scale research of bryophytes in the Amazon. Based on the fact that the occurrence of epiphytic bryophytes is more influenced by micro-environmental differences at the local scale, an interesting step further is the investigation of other forest types in the surroundings of the "terra firme" forests sampled here. This could answer whether the vertical gradient along the height zones is the main ecological gradient at the local scale or whether environmental differences, such as a lower canopy or higher relative humidity given by topography, would also play an important role as environmental filters acting upon the neutral dynamics across the basin.

Another issue to tackle is the spatial structure at the local scale. Since the results showed a lack of geographical structure in community composition as well as in genetic distance for the most common species, it is interesting to ask at which scale distance would show influence on recruitment. That would be possible through a systematic sampling scheme with distance classes between 1 and 15 km, which is the estimated "local scale" and the comparison of communities of the same height zone – given the fact that dispersal curves may vary from habitat to habitat.

Future research at large scale, across the basin, should add localities in the southeast and northeast of the basin to reassess the predictability of the neutral theory.

Forest interior in Urucu

7. References



Acebey A., Gradstein S.R. & Krömer T. (2003). Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of Tropical Ecology, 19, 9-18.

Ah-Peng C., Chuah-Petiot M., Descamps-Julien B., Bardat J., Stamenoff P. & Strasberg D. (2007). Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Reunion. Diversity and Distributions, 13, 654-662.

Allen B.H., Allen N.S., Crum H., Pursell R.A. & Reese W.D. (1994). Moss Flora of Central America. Part 1. Sphagnaceae-Calymperaceae. Missouri Botanical Garden, Missouri, USA.

Alonso D. & McKane A.J. (2004). Sampling Hubbell's neutral theory of biodiversity. Ecology Letters, 7, 901-910.

Alvarenga L.D.P., Lisboa R.C.L. & Tavares A.C.C. (2007). Novas referências de hepáticas (Marchantiophyta) da Floresta Nacional de Caxiuanã para o Estado do Pará, Brasil. Acta Botanica Brasilica, 21, 649-656.

Alvarenga L.D.P., Pôrto K.C. & de Oliveira J. (2010). Habitat loss effects on spatial distribution of non-vascular epiphytes in a Brazilian Atlantic forest. Biodiversity and Conservation, 19, 619-635.

Andrew N.R., Rodgerson L. & Dunlop M. (2003). Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. Journal of Biogeography, 30, 731-746.

Bacaro G., Rocchini D., Bonini I., Marignani M., Maccherini S. & Chiarucci A. (2008). The role of regional and local scale predictors for plant species richness in Mediterranean forests. Plant Biosyst., 142, 630-642.

Benavides J.C., Duque M., Alvaro J., Duivenvoorden J.F. & Cleef A.M. (2006). Species richness and distribution of understorey bryophytes in different forest types in Colombian Amazonia. Journal of Bryology, 28, 182-189.

Bischler H. & Boisselier-Dubayle M.C. (1997). Population genetics and variation in liverworts. Advances in Bryology, 6.

Blackburn T.M. & Gaston K.J. (2004). Macroecology. Basic and Applied Ecology, 5, 385-387.

Bleij B. (1991). Vertical distribution and ecology of epiphytic bryophytes and lichens in a Mora forest near Mabura Hill, Guyana. MSc Thesis, Universiteit Utrecht Utrecht.

Boggan J. (1996). Checklist of the plants of the Guianas. National Museum of Natural History, Smithsonian Institution.

Boggan J., Funk V., Kelloff C., Hoff M., Cremers G. & Feuillet C. (1992). Checklist of the Plants of the Guianas. Smithsonian Institution, Washington, DC.

Bossenbroek J.M., Kraft C.E. & Nekola J.C. (2001). Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. Ecological Applications, 11, 1778-1788.

Bruun H.H., Moen J., Virtanen R., Grytnes J.A., Oksanen L. & Angerbjörn A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. Journal of Vegetation Science, 17, 37-46.

Buck W.R. (2003). Guide to the plants of Central French Guiana. The New York Botanical Garden Press, New York.

Callaghan D.A. & Ashton P.A. (2008). Knowledge gaps in bryophyte distribution and prediction of species-richness. Journal of Bryology, 30, 147-158.

Chave J. & Jabot F. (2006). Tetame: estimation of Θ and m by maximum likelihood in the neutral model with dispersal limitation. In. Toulouse, France: Université Paul Sabatier,(http://www. edb. ups-tlse. fr/equipe1/chave/tetame. htm).

Chave J. & Leigh E.G. (2002). A spatially explicit neutral model of ß-diversity in tropical forests. Theoretical Population Biology, 62, 153-168.

Churchill S.P. (1994). The mosses of Amazonian Ecuador. In: AAU Reports. University of Aarhus Aarhus.

Churchill S.P. (1998). Catalog of Amazonian Mosses. Journal of the Hattori Botanical Laboratory, 85, 191-238.

Cionco R.M. (1972). A wind-profile index for canopy flow. Boundary-Layer Meteorology, 3, 255-263.

Coley P.D., Kursar T.A. & Machado J.L. (1993). Colonization of tropical rain forest leaves by epiphylls: effects of site and host plant leaf lifetime. Ecology, 619-623.

Condit R., Pitman N., Leigh E.G., Chave J., Terborgh J., Foster R.B., Nuñez P., Aguilar S., Valencia R. & Villa G. (2002). Beta-diversity in tropical forest trees. Science, 295, 666-669.

Cornelissen J.H.C. & Gradstein S.R. (1990). On the occurrence of bryophytes and macrolichens in different lowland rain forest types at Mabura Hill, Guyana. Tropical Bryology, 3, 29-35.

Cornelissen J.H.C. & ter Steege H. (1989). Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. Journal of Tropical Ecology, 5, 131-150.

Costa D.P. (1999). Epiphytic bryophyte diversity in primary and secondary lowland rainforests in southeastern Brazil. The Bryologist, 102, 320-326.

Costa D.P. (2003). Floristic composition and diversity of Amazonian Rainforest bryophytes in the state of Acre, Brazil. Acta Amazonica, 33, 399-414.

Costa D.P. & Lima F.M. (2005). Moss diversity in the tropical rainforests of Rio de Janeiro, southeastern Brazil. Revista Brasileira de Botânica, 28, 671-685.

Costa F.R.C., Magnusson W.E. & Luizao R.C. (2005). Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology, 93, 863-878.

Dauphin G. (2003). Ceratolejeunea. Flora Neotropica Monograph 90, 1-86.

Drucker D.P., Costa F.R.C. & Magnusson W.E. (2008). How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. Journal of Tropical Ecology, 24, 65-74.

During H.J. & Lloret F. (2001). The species-pool hypothesis from a bryological perspective. Folia Geobotanica, 36, 63-70.

Etienne R.S. (2005). A new sampling formula for neutral biodiversity. Ecology Letters, 8, 253-260.

Etienne R.S. & Alonso D. (2005). A dispersal-limited sampling theory for species and alleles. Ecology Letters, 8, 1147-1156.

Etienne R.S., Apol M.E.F., Olff H. & Weissing F.J. (2007). Modes of speciation and the neutral theory of biodiversity. Oikos, 116, 241.

Excoffier L., Laval G. & Schneider S. (2005). Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evolutionary bioinformatics online, 1, 47.

Fanshawe D.B. (1952). The vegetation of British Guiana: a preliminary review. Imperial Forestry Institute, University of Oxford.

Florschütz-de Waard J. & Bekker J.M. (1987). A comparative study of the bryophyte flora of different forest types in west Suriname. Cryptogamie, Bryologie, Lichénologie, 8, 31-45.

Florschütz-de Waard J. (1990). A catalogue of the bryophytes of the Guianas II. Musci. Tropical Bryology, 3, 89-104.

Frahm J. (2008). Bryophyte phytomass in tropical ecosystems. Biological Journal of the Linnean Society, 104, 23-33.

Fuentes A. & Muñoz J. (2002). Contribution to the bryoflora of Bolivia. I. Lowland mosses from two protected areas in the Department of Santa Cruz. Journal of Bryology, 24, 165-167.

Gabriel R. & Bates J.W. (2003). Responses of photosynthesis to irradiance in bryophytes of the Azores laurel forest. Journal of Bryology, 25, 101-105.

Gabriel R. & Bates J.W. (2005). Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. Plant Ecology, 177, 125-144.

Gentry A.H. (1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75, 1-34.

Glime J.M. (2007). Bryophyte ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists.

Goffinet B. (2000). Origin and phylogenetic relationships of bryophytes. In: Bryophyte biology (eds. Shaw AJ & Goffinet B). Cambridge Univ Press Cambridge, UK, pp. 124-149.

Gotelli N.J. (2001). Research frontiers in null model analysis. Global Ecology and Biogeography, 337-343.

Gotelli N.J. & Entsminger G.L. (2000). EcoSim: Null models software for ecology. Acquired Intelligence Inc. & Kesey-Bear.

Gotelli N.J. & Entsminger G.L. (2006). EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT, 5465.

Gradstein S.R. (1994). Lejeuneaceae: Ptychantheae, Brachiolejeuneae. Flora Neotropica Monograph 62, 1-216.

Gradstein S.R. (2006). The lowland cloud forest of French Guiana: a liverwort hotspot. Cryptogamie, Bryologie, Lichénologie 27, 141-152.

Gradstein S.R., Churchill S.P. & Salazar-Allen N. (2001a). Guide to the bryophytes of tropical America. NYGB Press, New York.

Gradstein S.R., Churchill S.P. & Salazar Allen N. (2001b). Guide to the bryophytes of tropical America. New York Botanical Graden Press, New York.

Gradstein S.R. & Costa D.P. (2003). Hepaticae and Anthocerotae of Brazil. The New York Botanical Garden Press, New York.

Gradstein S.R., Griffin D., Morales M.I. & Nadkarni N.M. (2001c). Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. Caldasia, 23, 203-212.

Gradstein S.R., Meneses R.I., Arbe Q. & Arbe B.A. (2003). Catalogue of the Hepaticae and Anthocerotae of Bolivia. Journal of the Hattori Botanical Laboratory, 93, 1-68.

Gradstein S.R., Montfoort D. & Cornelissen J.H.C. (1990). Species richness and phytogeography of the bryophyte flora of the Guianas, with special reference to the lowland forest. Tropical Bryology, 2, 117-126.

Gravel D., Canham C.D., Beaudet M. & Messier C. (2006). Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters, 9, 399-409.

Griffin III D. (1979). Guia preliminar para as briófitas freqüentes em Manaus e adjacências. Acta Amazonica, 9, 1-67.

Grundmann M., Ansell S.W., Russell S.J., Koch M.A. & Vogel J.C. (2007). Genetic structure of the widespread and common Mediterranean bryophyte *Pleurochaete squarrosa* (Brid.) Lindb. (Pottiaceae)- evidence from nuclear and plastidic DNA sequence variation and allozymes. Molecular ecology, 16, 709-722.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25.

Holz I. & Gradstein S.R. (2005). Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. Plant Ecology, 178, 89-109.

Holz I., Gradstein S.R., Heinrichs J. & Kappelle M. (2002). Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. The Bryologist, 105, 334-348.

Hubbell S.P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton University Press.

Hubbell S.P., He F.L., Condit R., Borda-de-Agua L., Kellner J. & ter Steege H. (2008). How many tree species and how many of them are there in the Amazon will go extinct? Proc. Natl. Acad. Sci. U. S. A., 105, 11498-11504.

Hutsemekers V., Dopagne C. & Vanderpoorten A. (2008). How far and how fast do bryophytes travel at the landscape scale? Diversity and Distributions, 14, 483-492.

Ilkiu-Borges A.L. & Lisboa R.C.L. (2004a). *Cololejeuneae* (Lejeuneaceae, Hepaticae) na Estação Científica Ferreira Penna, Melgaço, PA, Brasil. Acta Botânica Brasilica, 18, 887-902.

Ilkiu-Borges A.L. & Lisboa R.C.L. (2004b). Os gêneros *Cyclolejeunea, Haplolejeunea, Harpalejeunea, Lepidolejeunea* e *Rectolejeunea* (Lejeuneaceae, Hepaticae) na Estação Científica Ferreira Penna, Pará, Brasil. Acta Botânica Brasilica, 18.

Ilkiu-Borges A.L., Tavares A.C.C. & Lisboa R.C.L. (2004). Briófitas da Ilha de Germoplasma, reservatório de Tucuruí, Pará, Brasil. Acta Botânica Brasilica, 18, 689-692.

Jabot F., Etienne R.S. & Chave J. (2008). Reconciling neutral community models and environmental filtering: theory and an empirical test. Oikos, 117, 1308.

Jetten V.G. (1994). Modelling the effects of logging on the water balance of a tropical rain forest: a study in Guyana. Tropenbos Foundation.

Johansson D.R. (1974). Ecology of vascular epiphytes in West African rain forest. Acta Phytogeographica Suecica, 59, 1-136.

Jongman R.H.G., ter Braak C.J.F. & van Tongeren O.F.R. (1987). Data analysis in community and landscape ecology. Pudoc Wageningen, Netherlands.

Kessler M. (2000). Altitudinal zonation of Andean cryptogam communities. Journal of Biogeography, 27, 275-282.

Kimmerer R. (1994). Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pellucida*. Bryologist, 97, 20-25.

Kimmerer R.W. (1991). Reproductive ecology of *Tetraphis pellucida*. II. Differential success of sexual and asexual propagules. The Bryologist, 94, 284-288.

Kimmerer R.W. (2005). Patterns of dispersal and establishment of bryophytes colonizing natural and experimental treefall mounds in northern hardwood forests. Bryologist, 108, 391-401.

Kruijt B., Malhi Y., Lloyd J., Norbre A.D., Miranda A.C., Pereira M.G.P., Culf A. & Grace J. (2000). Turbulence statistics above and within two Amazon rain forest canopies. Boundary-Layer Meteorology, 94, 297-331.

Larkin M.A., Blackshields G., Brown N.P., Chenna R., McGettigan P.A., McWilliam H., Valentin F., Wallace I.M., Wilm A. & Lopez R. (2007). Clustal W and Clustal X version 2.0. Bioinformatics, 23, 2947.

Legendre P. (1998). Numerical ecology. 2nd edn. Elsevier Science, Amsterdam.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.E., Holt R.D., Shurin J.B., Law R. & Tilman D. (2004). The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters, 7, 601-613.

Leon-Vargas Y., Engwald S. & Proctor M.C.F. (2006). Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. Journal of Biogeography, 33, 901-913.

León-Yánez S., Gradstein S.R. & Wegner C. (2006). Hepáticas (Marchantiophyta) y Antoceros (Anthocerotophyta) del Ecuador. Publicaciones del Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Lisboa R.C.L. (1976). Estudos sobre vegetacão das campinas amazônicas. V. Brioecologia de uma campina amazônica. Acta Amazonica, 6, 171-191.

Lisboa R.C.L. (1984). Avaliação da brioflora de uma área de floresta de terra firme. I. Musci. Boletim do Museu Paraense Emílio Goeldi, serie Botânica, 1, 23-35.

Lisboa R.C.L. (1985). Avaliação da brioflora de uma área de floresta de terra firme. II-Hepaticae. Boletim do Museu Paraense Emílio Goeldi, Série Botânica2, 1, 99-114.

Lisboa R.C.L. (1991). Histórico da briologia na Amazônia brasileira. Boletim do Museu Paraense Emílio Goeldi, Série Botânica, 7, 69-77.

Lisboa R.C.L. (1993). Musgos acrocárpicos do Estado de Rondônia. Ministério da Ciência e Tecnologia, Conselho Nacional de Desenvolvimento Científico e Tecnológico, Museu Paraense Emílio Goeldi, Belem, Brasil.

Lisboa R.C.L. (1994). Boletim do Museu Paraense Emilio Goeldi, série Botânica 10, 15 - 42.

Lisboa R.C.L. & Ilkiu-Borges A.L. (1997). Novas ocorrências de Bryophyta (musgos) para o Estado do Pará, Brasil. Acta Amazonica, 27, 81-102.

Lisboa R.C.L., Lima M.J.L. & Maciel U. (1999). Musgos da Ilha de Marajó-II, Município de Anajás, Pará, Brasil. Acta Amazonica, 29, 201-206.

Lisboa R.C.L. & Maciel U.N. (1994). Musgos da Ilha de Marajó-I, Afuá. Boletim do Museu Paraense Emílio Goeldi, série Botânica, 10, 43-55.

Lisboa R.C.L. & Yano O. (1987). Novas ocorrências de briófitas na Amazônia brasileira. Boletim do Museu Paraense Emílio Goeldi, série Botânica, 3, 141-156.

Löbel S., Snäll T. & Rydin H. (2006). Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. Ecology, 94, 856-868.

Löbel S., Snäll T. & Rydin H. (2009). Mating system, reproduction mode and diaspore size affect metacommunity diversity. Journal of Ecology, 97, 176-185.

Longton R.E. (1992). Reproduction and rarity in British mosses. Biological Conservation, 59, 89-98.

Lowman M.D. & Rinker H.B. (2004). Forest canopies. Elsevier Academic Press, Oxford.

Maddison W.P. & Maddison D.R. (1992). MacClade: analysis of phylogeny and character evolution. Evolution (PMBD, 185908476).

Marino P.C. & Allen N.S. (1992). Tropical Epiphyllous Hepatic Communities Growing on Two Species of Shrub in Barro Colorado Island, Panama: The Influence of Light and Microsite. Lindbergia, 17, 91-95.

McCune B. & Grace J.B. (2002). Analysis of ecological communities. MjM Software Design.

McCune B., Rosentreter R., Ponzetti J.M. & Shaw D.C. (2000). Epiphyte habitats in an old conifer forest in western Washington, USA. The Bryologist, 103, 417-427.

McDaniel S.F. & Shaw A.J. (2005). Selective sweeps and intercontinental migration in the cosmopolitan moss *Ceratodon purpureus* (Hedw.) Brid. Molecular Ecology, 14, 1121-1132.

McGill B.J., Maurer B.A. & Weiser M.D. (2006). Empirical evaluation of neutral theory. Ecology, 87, 1411-1423.

McKane A.J., Alonso D. & Solé R.V. (2004). Analytic solution of Hubbell's model of local community dynamics. Theoretical Population Biology, 65, 67-73.

McQueen C.B. (1985). Spatial pattern and gene flow distances in *Sphagnum subtile*. The Bryologist, 88, 333-336.

Menzel M. (1984). Katalog der Lebermoose von Peru. Willdenowia, 1, 473-523.

Menzel M. & Schultze-Motel W. (1992). Preliminary checklist of the mosses of Peru. Journal of The Hattori Botanical Laboratory, 71, 175-254.

Miles C.J. & Longton R.E. (1992). Deposition of moss spores in relation to distance from parent gametophytes. Journal of Bryology, 17, 355-368.

Miller N.G. & McDaniel S.F. (2004). Bryophyte dispersal inferred from colonization of an introduced substratum on Whiteface Mountain, New York. American Journal of Botany, 91, 1173-1182.

Montfoort D. & Ek R.C. (1989). Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest, French Guiana. MSc Thesis, Universiteit Utrecht, Utrecht.

Moraes E.N.R. & Lisboa R.C.L. (2005). Musgos (Bryophyta) da Serra dos Carajás, estado do Pará, Brasil. Boletim do Museu Paraense Emílio Goeldi.

Mori S.A. & Boom B.M. (1987). The forest. Memoirs of the New York Botanical Garden, 44, 9-29.

Mota de Oliveira S., ter Steege H., Cornelissen J.H.C. & Robbert Gradstein S. (2009). Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. Journal of Biogeography, 36, 2076-2084.

Munoz J., Felicisimo A.M., Cabezas F., Burgaz A.R. & Martinez I. (2004). Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science, 304, 1144.

Nathan R. & Muller-Landau H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution, 15, 278-285.

Nathan R., Perry G., Cronin J.T., Strand A.E. & Cain M.L. (2003). Methods for estimating long-distance dispersal. Oikos, 103, 261-273.

Oliveira S.M. & Porto K.C. (2001). Reproductive phenology of the moss *Sematophyllum subpinnatum* in a tropical lowland forest of north-eastern Brazil. Journal of Bryology, 23, 17-22.

Parsons J.G., Cairns A., Johnson C.N., Robson S.K.A., Shilton L.A. & Westcott D.A. (2007). Bryophyte dispersal by flying foxes: a novel discovery. Oecologia, 152, 112-114.

Pereira Alvarenga L.D. & Pôrto K.C. (2007). Patch size and isolation effects on epiphytic and epiphyllous bryophytes in the fragmented Brazilian Atlantic forest. Biological Conservation, 134, 415-427.

Phillips O.L., Hall P., Gentry A.H., Sawyer S.A. & Vasquez R. (1994). Dynamics and species richness of tropical rain forests. Proceedings of the National Academy of Sciences, 91, 2805-2809.

Pinzón M., Linares E.L. & Uribe J. (2003). Hepáticas del Medio Caquetá (Amazonía colombiana). Caldasia, 25, 297-311.

Pitman N.C.A., Terborgh J., Silman M.R. & Nuñez V.P. (1999). Tree species distributions in an upper Amazonian forest. Ecology, 80, 2651-2661.

Pitman N.C.A., Terborgh J.W., Silman M.R., Núñez V P., Neill D.A., Cerón C.E., Palacios W.A. & Aulestia M. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology, 82, 2101-2117.

Pohjamo M., Laaka-Lindberg S., Ovaskainen O. & Korpelainen H. (2006). Dispersal potential of spores and asexual propagules in the epixylic hepatic *Anastrophyllum hellerianum*. Evolutionary Ecology, 20, 415-430.

Pôrto K.C. & Oliveira S.M. (1998). Biodiversidade e biologia reprodutiva de briófitas da reserva ecológica de Dois Irmaos. Reserva ecológica de Dois Irmaos: estudos em um remanescente de mata atlântica em área urbana. Recife: SETMA, Editora Universitária/UFPE, 115–135.

Proctor M.C.F. (2000). The bryophyte paradox: tolerance of desiccation, evasion of drought. Plant Ecology, 151, 41-49.

Rahbek C. & Graves G.R. (2001). Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Sciences, 98, 4534.

Reese W.D. (1993). Calymperaceae. Flora Neotropica Monograph 58, 1-101.

Richards P.W. (1984). The ecology of tropical forest bryophytes. New Manual of Bryology, 2, 1233–1270.

Ricklefs R.E. (1987). Community diversity: relative roles of local and regional processes. Science, 235, 167.

Romero C., Putz F.E. & Kitajima K. (2006). Ecophysiology in relation to exposure of pendant epiphytic bryophytes in the canopy of a tropical montane oak forest. Biotropica, 38, 35-41.

Rosenzweig M.L. (1995). Species diversity in space and time. Cambridge University Press, Cambridge.

Rudolphi J. (2009). Ant-mediated dispersal of asexual moss propagules. The Bryologist, 112, 73-79.

Ruokolainen K., Tuomisto H., Macía M.J., Higgins M.A. & Yli-Halla M. (2007). Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? Journal of Tropical Ecology, 23, 13-25.

Santiago R.L. (1997). Estudo ecológico de briófitas do estado de Roraima, MSc Thesis. In. Universidade Federal de Pernambuco, Recife.

Santos J.C., Coloma L.A., Summers K., Caldwell J.P., Ree R. & Cannatella D.C. (2009). Amazonian amphibian diversity is primarily derived from Late Miocene Andean lineages. PLoS Biology, 7.

Santos R.C.P. & Lisboa R.C.L. (2003). Musgos (Bryophyta) do Nordeste Paraense, Brasil: I-Zona Bragantina, Microrregião do Salgado e Município de Viseu. Acta Amazonica, 33, 415-422.

Sastad S.M., Pedersen B. & Digre K. (1999). Habitat-specific genetic effects on growth rate and morphology across pH and water-level gradients within a population of the moss *Sphagnum angustifolium* (Sphagnaceae). American Journal of Botany, 86, 1687.

Skotnicki M.L., Selkirk P.M. & Ninham J.A. (1999). RAPD analysis of genetic variation and dispersal of the moss *Bryum argenteum* in Ross Island and Victoria Land, Antarctica. Polar Biology, 21, 417-422.

Slack N.G. (1990). Bryophytes and ecological niche theory. Botanical Journal of the Linnean Society, 104, 187-213.

Snall T., Fogelqvist J., Ribeiro P.J. & Lascoux M. (2004). Spatial genetic structure in two congeneric epiphytes with different dispersal strategies analysed by three different methods. Molecular Ecology, 13, 2109-2119.

Söderström L. (1989). Regional distribution patterns of bryophyte species on spruce logs in northern Sweden. The Bryologist, 92, 349-355.

Sonnleitner M., Dullinger S., Wanek W. & Zechmeister H. (2009). Microclimatic patterns correlate with the distribution of epiphyllous bryophytes in a tropical lowland rain forest in Costa Rica. Journal of Tropical Ecology, 25, 321-330.

Sporn, G.S., Bos, M.M. & Gradsrein, S.R. (2010). Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. Biodiversity and Conservation 19, 745-760.

Spruce R. (1885). Hepaticae amazonicae et andinae. Trans. Proc. Bot. Soc. Edinburgh, 15, 589.

Stoneburner A., Lane D.M. & Anderson L.E. (1992). Spore dispersal distances in *Atrichum angustatum* (Polytrichaceae). The Bryologist, 95, 324-328.

Stropp J., Ter Steege H. & Malhi Y. (2009). Disentangling regional and local tree diversity in the Amazon. Ecography, 32, 46.

Sundberg S. (2005). Larger capsules enhance short-range spore dispersal in Sphagnum, but what happens further away? Oikos, 108, 115.

Sundberg S., Hansson J. & Rydin H. (2006). Colonization of *Sphagnum* on land uplift islands in the Baltic Sea: time, area, distance and life history. Journal of Biogeography, 33, 1479-1491.

Swofford D.L. (2003). PAUP* 4.0 b10. In: Phylogenetic analysis using parsimony (* and other methods). Sinauer Associates Sunderland, Massachusetts.

Szövényi P., Hock Z.S. & Tóth Z. (2004). Phorophyte preferences of epiphytic bryophytes in a stream valley in the Carpathian Basin. Journal of Bryology, 26, 137-146.

Tackenberg O., Poschlod P. & Bonn S. (2003). Assessment of wind dispersal potential in plant species. Ecological Monographs, 73, 191-205.

ter Steege H. (2000). Plant diversity in Guyana, with recommendations for a national protected area strategy. Tropenbos Foundation, Wageningen.

ter Steege H. & Cornelissen J.H.C. (1989). Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica, 21, 331-339.

ter Steege H., Pitman N., Sabatier D., Castellanos H., van der Hout P., Daly D.C., Silveira M., Phillips O., Vasquez R. & van Andel T. (2003). A spatial model of tree a-diversity and tree density for the Amazon. Biodiversity and Conservation, 12, 2255-2277.

ter Steege H., Pitman N.C.A., Phillips O.L., Chave J., Sabatier D., Duque A., Molino J.F., Prévost M.F., Spichiger R. & Castellanos H. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. Nature, 443, 444-447.

Terborgh J. & Andresen E. (1998). The composition of Amazonian forests: patterns at local and regional scales. Journal of Tropical Ecology, 14, 645-664.

Tuomisto H., Ruokolainen K. & Yli-Halla M. (2003a). Dispersal, environment, and floristic variation of western Amazonian forests. Science, 299, 241-244.

Uribe M.J. & Gradstein S.R. (1998). Catalogue of the Hepaticae and Anthocerotae of Colombia. Bryophytorum Bibliotheca, 53, 1-99.

Van Zanten B.O. (1978). Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. Journal of the Hattori Botanical Laboratory, 44, 455-482.

van Zanten B.O. & Pócs T. (1981). Distribution and dispersal of bryophytes. In: Advances in bryology (ed. Schultze-Motel W) Cramer, Vaduz, pp. 479-562.

Visnadi S.R. (2005). Brioflora da Mata Atlântica do estado de São Paulo: região norte. Hoehnea, 32, 215-231.

Weir B.S. & Cockerham C.C. (1984). Estimating F-statistics for the analysis of population structure. Evolution, 38, 1358-1370.

Whitmore T.C. (1998). An introduction to tropical rain forests. Oxford University Press, Oxford. 2nd edn.

Whittaker R.J., Willis K.J. & Field R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28, 453-470.

Wiklund K. & Rydin H. (2004). Ecophysiological constraints on spore establishment in bryophytes. Functional Ecology, 18, 907-913.

Wilson D.S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology, 73, 1984-2000.

Wolf J.H.D. (1993). Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. Annals of the Missouri Botanical Garden, 80, 928-960.

Yano O. (1985). *Octoblepharum* (Leucobryaceae) do alto rio Negro, Amazonas (Brasil). Acta Amazonica, 15, 1-21.

Yano O. (1992). Briófitas da Ilha de Maracá, Roraima, Brasil. Acta Amazonica, 22, 535-539.

Yano O. & Camara P. (2004). Briófitas de Manaus, Amazonas, Brasil. Acta Amazonica, 34, 445-457.

Yano O. & Lisboa R.C.L. (1988). Briófitas do território Federal do Amapá, Brasil. Boletim do Museu Paraense Emílio Goeldi, série Botânica, 4, 243-270.

Yano O. & Pôrto K.C. (2006). Diversidade das briófitas das matas serranas do Ceará, Brasil. Hoehnea, 33, 7-39.

Young S.B. & Klay J.R. (1971). Bryophytes in the 1969 crater of Deception Island, Antarctica: an apparent case of rapid long-distance dispersal. Ohio Journal of Science (Ohio Academy of Science), 71.

Zartman C. & Ilkiu-Borges A.L. (2007). Guia para as Briófitas Epífilas da Amazônia Central. Editora INPA, Manaus Brasil.

Zartman C.E. (2003). Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. Ecology, 84, 948-954.

Zartman C.E. & Ackerman I.L. (2002). A New Species of *Vitalianthus* (Lejeuneaceae, Hepaticae) from the Brazilian Amazon. The Bryologist, 105, 267-269.

Zartman C.E. & Nascimento H.E.M. (2006). Are habitat-tracking metacommunities dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian forest fragments. Biological Conservation, 127, 46-54.

Zillio T. & Condit R. (2007). The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. Oikos, 116, 931-940.

Zobel M. (1997). The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? Trends in Ecology and Evolution, 12, 266-269.

Zotz G. & Vollrath B. (2003). The epiphyte vegetation of the palm Socratea exorrhiza - correlations with tree size, tree age and bryophyte cover. Journal of Tropical Ecology, 19, 81-90.

Zuquim G., Costa F.R.C., Prado J. & Braga-Neto R. (2009). Distribution of pteridophyte communities along environmental gradients in Central Amazonia, Brazil. Biodiversity and Conservation, 18, 151-166.

Tapajos River

Appendix 1 – Floristics and microhabitat specialization of Amazonian epiphytic bryophytes

An estimated 800 bryophyte species occur in the Amazon region (Gradstein et al. 2001). The last published count of species for the Brazilian Amazon recorded 514 species among mosses, liverworts and hornworts (Costa 2003). Lately, this number has increased, since species have been cited as new records for the region and new species have been described and recorded (Zartman 2002, Ilkiu-Borges 2008, Ilkiu-Borges pers. commun.). Yet, there had been no attempt up to now for a general and quantitative description of the Amazonian bryoflora.

Based on our sampling of epiphytic bryophytes along the vertical gradient of eight trees in localities across the Amazon, we tested ecological hypothesis concerning species occurrence in the localities inventoried and, at a finer scale, species occurrence along the microenvironmental gradient found in the host trees. Here we use this extensive data set to describe the Amazonian epiphytic bryoflora. We address general features such as total relative abundances of species and families, and the relative abundances of species and families in the different height zones of the host trees. Moreover, we identify specialist and generalist species and families and provide their abundance and occurrence in the different height zones.

Data presented here originates from the same dataset used for chapters 3 and 4 of this thesis, where descriptions of the study area and sampling procedure can be found. Classification of species and families in microhabitat specialists was based on weighted averaging techniques and indicator species analysis (chapter 4).

A total of 351 plots on 72 trees yielded 3104 occurrences of bryophytes. These belonged to 29 families, 97 genera and 263 (morpho-) species.

The most common families in number of records were Lejeuneaceae (1700 records, 55% of the total), Calymperaceae (265, 9%), Leucobryaceae (197, 6%), Plachiogilaceae (149, 5%) and Sematophyllaceae (147, 5%). The same ranking was found when the floristic composition was analysed separately for the height zones 1, 2, 3 and 4. In height zone 6, however, Jubulaceae was the second most common family, with 8% of the records, while Pterobryaceae and Macromitriaceae were as common as Calymperaceae, with 3% of the records.

In the full dataset, Lejeuneaceae and Calymperaceae were not only the most common families, but also the richest, with respectively 133 and 27 species, followed by Plagiochilaceae, Lepidoziaceae and Macromitriaceae with 17, 11 and 10 species respectively.

Eleven families were indicators for zone 1 and several families, despite not being indicators, had a weighted average of occurrence between height zones 2 and 3 (Table 1). The understory (zones 1, 2, 3) was richer than the canopy in number of families. Three families - Lejeuneaceae, Pterobryaceae and Jubulaceae - were indicators for the outer canopy, although Lejeuneaceae will not be treated at family level in this analysis. Despite the statistically significant preference for zone 6, the family included many indicator species for zone 1. One family - Macromitriaceae - was indicator for height zone 4.

The most common species were *Cheilolejeunea rigidula*, *Ceratolejeunea cornuta*, *Octoblepharum pulvinatum*, *Octoblepharum albidum*, *Archilejeunea fuscecens, Sematophyllum subsimplex, Lopholejeunea subfusca* and *Symbiezidium barbiflorum*. These eight species together accounted for 21% of the records.
Out of the 263 species, 78 were significant indicator species for a particular zone. Zone 6 had most of the indicator species (37) followed by zone 1 (26), zone 4 (11), zone 2 (3), and finally zone 3 (1). The majority

of indicator species in zone 6 belonged to Lejeuneaceae - 25 out of the 37.

Some species were restricted to zone 6 and widespread across the basin, which was the case in *Vitalianthus urubuensis*, *Caudalejeunea lehmanniana* and all five species recorded of the genus *Diplasiolejeunea* (with the exception of 1 record out of 46, of *Diplasiolejeunea cavifolia* in zone 4). Many of these species are very frequently found as epiphylls in the understory. The most abundant indicator species of zone 6 in number of records, however (*Lopholejeunea subfusca*, *Frullania caulisequa, Pycnolejeunea contigua, Microlejeunea bullata*), were all found in at least three height zones. Among the indicator species of zone 1, there was no predominant family and only 7 out of 26 species belonged to Lejeuneaceae. The most abundant indicator species of zone 1 (*Sematophyllum subsimplex*, *Pictolejeunea picta*, *Taxithelium planum*, *Plagiochila laetevirens*) were also found in other height zones.

Table 1. Zonation of bryophyte families in the Amazon. **N**: total number of records for the family. **WA**: Mid-point of zonation for the family as calculated by weighted average for the family. **1-6**: number of records per height zone. Bold values indicate significant Indicator Analysis value.

Family	N	WA	1	2	3	4	6
Calypogeiaceae	5	1.0	**5**				
Leucophanaceae	5	1.0	**5**				
Racopilaceae	1	1.0	1				
Stereophyllaceae	13	1.1	**12**	1			
Hookeriaceae	7	1.3	**5**	2			
Leucomiaceae	12	1.4	**8**	3	1		
Thuidiaceae	14	1.5	**10**	2	1	1	
Fissidentaceae	34	1.6	**25**	5		2	2
Thamnobryaceae	3	1.7	1	2			
Metzgeriaceae	16	1.9	7	6	2		1
Lepidoziaceae	36	2.1	**18**	6	5	7	1
Sematophyllaceae	147	2.5	**51**	34	28	21	13
Leucobryaceae	197	2.5	**58**	47	42	44	6
Hypnaceae	43	2.5	15	8	8	10	2
Neckeraceae	59	2.5	17	16	12	11	3
Geocalycaceae	35	2.5	13	8	3	8	3
Plagiochilaceae	149	2.6	**49**	32	27	27	14
Radulaceae	59	2.6	14	18	11	12	4
Calymperaceae	265	2.8	58	64	**63**	60	20
Daltoniaceae	27	2.9	7	8	4	3	5
Dicranaceae	9	3.2	1	2	2	3	1
Phyllodrepaniaceae	8	3.3		1	4	3	
Meteoriaceae	37	3.5	1	9	9	13	5
Cephaloziaceae	6	3.5		2	1	2	1
Lejeuneaceae	1700	3.7	212	288	295	398	**507**
Pterobryaceae	49	4.3	3	4	7	15	**20**
Macromitriaceae	40	4.9			1	**21**	18
Jubulaceae	84	5.3		1	6	19	**58**
Cephaloziellaceae	1	6.0					1

Table 2. Zonation of bryophyte species in the Amazon. **N**: total number of records for the species. **WA**: Mid-point of zonation for the species as calculated by weighted average for the species. **1-6**: number of records per height zone. Bold values indicate significant Indicator Analysis value. IS indicates the zone for which the species is indicative ($P < 0.05$).

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Phyllodon truncatulus	2	1	2				
Hypnaceae species 01	1	1	1				
Octoblepharum cilyndricum	1	1	1				
Plagiochila species 00	1	1	1				
Plagiochila species 02	1	1	1				
Prionolejeunea microdonta	4	1	**4**				
Racopilum tomentosum	1	1	1				
Calymperes rubiginosum	1	1	1				
Cyrtohypnum scabrosulum	3	1	**3**				
Cyrtohypnum schistocalyx	2	1	2				
Taxithelium pluripunctatum	1	1	1				
Vesicularia vesicularis	4	1	**4**				
Cyclolejeunea luteola	5	1	**5**				
Mnioloma parallelogramma	4	1	**4**				
Echinocolea asperrima	2	1	2				
Xylolejeunea crenata	5	1	**5**				
Zoopsidella macella	2	1	2				
Plagiochila simplex	2	1	2				
Prionolejeunea denticulata	2	1	2				
Calypogeia laxa	1	1	1				
Arachniopsis species 01	1	1	1				
Bazzania species 01	1	1	1				
Aphanolejeunea species 01	2	1	2				
Fissidens weirii	3	1	**3**				
Fissidens diplodus	2	1	2				
Fissidens zollingeri	3	1	**3**				
Fissidens prionodes	1	1	1				
Syrrhopodon elatus	2	1	2				
Leucophanes molleri	5	1	**5**				
Lepidopilum radicale	2	1	2				

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Micropterygium trachyphyllum	1	1	1				
Micropterygium parvistipulum	2	1	2				
Radula mammosa	1	1	1				
Pilosium chlorophyllum	13	1.08	**12**	1			
Pictolejeunea picta	22	1.09	**20**	2			
Prionolejeunea muricatoserrulata	7	1.14	**6**	1			
Plagiochila species 06	4	1.25	3	1			
Radula husnotii	4	1.25	3	1			
Syrrhopodon leprieuri	4	1.25	3	1			
Ochrobryum gardneri	7	1.29	**5**	2			
Callicostella pallida	7	1.29	**5**	2			
Plagiochila species 09	3	1.33	2	1			
Calymperes species 01	3	1.33	2	1			
Taxithelium planum	26	1.35	**19**	6		1	
Chryso-hypnum diminutivum	5	1.4	3	2			
Leucobryum martianum	17	1.41	**11**	5	1		
Leucomium strumosum	12	1.42	**8**	3	1		
Plagiochila laetevirens	26	1.42	**16**	9	1		
Haplolejeunea cucullata	14	1.43	**12**	1			1
Fissidens guianensis	19	1.47	**14**	4			1
Ceratolejeunea cerathanta	2	1.5	1	1			
Microlejeunea aphanella	2	1.5	1	1			
Bazzania aurescens	2	1.5	1	1			
Octoblepharum cocuiense	11	1.55	**6**	4	1		
Plagiochila species 06	8	1.63	**5**	2		1	
Thallose liverwortsp01	3	1.67	2		1		
Homaliodendron piniforme	3	1.67	1	2			
Calymperes palisotii	3	1.67	2		1		
Lophocolea liebmanniana	7	1.71	4	2		1	
Aphanolejeunea contractiloba	9	1.78	5	2	1	1	
Cyrtohypnum involvens	9	1.78	5	2	1	1	
Metzgeria species non identified	9	1.78	3	5	1		
Prionolejeunea aemula	5	1.8	2	2	1		
Lejeunea controversa	11	1.82	**6**	4			1
Micropterygium leiophyllum	6	1.83	**5**				1
Syrrhopodon incompletus	20	1.85	**9**	7	2	2	

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Plagiochila species 05	7	1.86	3	2	2		
Oryzolejeunea species 01	1	2		1			
Bazzania cuneistipula	2	2	1		1		
Leucoloma cruegerianum	4	2	1	2	1		
Pireella cymbifolia	2	2	1		1		
Calymperes smithii	1	2		1			
holostipous species 01	4	2	2	1		1	
Symbiezidium species 01	1	2		1			
unidentified species 02	4	2	1	2	1		
Trachylejeunea species 02	1	2		1			
Syrrhopodon species 01	3	2	1	1	1		
Lepidopilum surinamense	1	2		1			
Calymperes lonchophyllum	30	2	11	**12**	5	1	1
Taxilejeunea asthenica	1	2		1			
Aphanolejeunea kunertiana	1	2		1			
Trachylejeunea aneogyna	25	2.04	9	8	6	2	
Neckeropsis disticha	12	2.08	5	4	2		1
Syrrhopodon simmondsii	10	2.1	4	2	3	1	
Aphanolejeunea camillii	9	2.11	4	3	1		1
Radula flaccida	9	2.11	1	**6**	2		
Metzgeria decipiens	7	2.14	4	1	1		1
Lepidopilum scabrisetum	5	2.2	1	2	2		
unidentified species 05	5	2.2	1	2	2		
Lepidopilum affine	8	2.25	3	3	1		1
Ceratolejeunea minuta	26	2.27	9	7	6	3	1
Sematophyllum subsimplex	65	2.28	**22**	15	16	12	
Lepidolejeunea involuta	10	2.3	3	5		1	1
Calymperes platyloma	14	2.36	3	5	4	2	
Octoblepharum pulvinatum	86	2.37	24	24	20	18	
Cyclolejeunea convexistipa	8	2.38	3	2		3	
Cheilolejeunea neblinensis	37	2.43	7	**14**	9	7	
Trichosteleum papillosum	37	2.49	9	13	7	6	2
Lopholejeunea nigricans	2	2.5	1			1	
Ceratolejeunea desciscens	2	2.5	1			1	
Fissidens steerei	4	2.5	2	1			1
Syrrhopodon species 02	2	2.5		1	1		

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
unidentified species 01	22	2.55	5	9	3	3	2
Calymperes afzelli	11	2.55	4	1	2	4	
Neckeropsis undulata	31	2.55	9	7	8	5	2
Bazzania hookeri	18	2.56	4	5	4	5	
Lophocolea bidentata	25	2.56	9	6	3	4	3
Pireella pohlii	10	2.6	2	3	2	3	
Macrocolura sagittispula	5	2.6	1	2		2	
Plagiochila species 01	15	2.67	4	2	4	5	
Porotrichum substriatum	16	2.69	3	5	2	6	
Lejeunea cerina	7	2.71	2	2	1	1	1
Stictolejeunea squamata	25	2.72	8	5	4	5	3
Archilejeunea parviflora	34	2.74	8	10	5	8	3
Isopterygium tenerum	18	2.78	4	3	6	4	1
Microlejeunea globosa	5	2.8	2	1		1	1
Calymperes othmeri	5	2.8	1	1	1	2	
Radula javanica	43	2.84	9	10	9	12	3
Syrrhopodon cryptocarpus	27	2.85	3	6	10	8	
Ceratolejeunea laetefusca	48	2.85	11	11	10	11	5
Archilejeunea crispistipula	14	2.86	2	4	4	3	1
Syrrhopodon ligulatus	49	2.9	6	13	14	14	2
Lejeunea maxonii	1	3			1		
Harpalejeunea tridens	3	3	1			2	
Syrrhopodon africanus	1	3			1		
Ceratolejeunea species 01	1	3			1		
Cheilolejeunea discoidea	1	3			1		
Taxilejeunea obtusangula	1	3			1		
Oryzolejeunea saccatiloba	3	3	1	1			1
Aphanolejeunea microscopia var *africanus*	1	3			1		
Calymperes mitrafugax	6	3		2	2	2	
Calymperes guildingii	2	3		1		1	
Calymperes species 02	1	3			1		
Lejeunea longifissa	2	3		1		1	
Plagiochila subplana	22	3.05	1	5	8	8	
Plagiochila disticha	43	3.05	9	9	10	8	7
Octoblepharum albidum	71	3.06	11	12	20	**23**	5
Calymperes erosum	38	3.13	4	7	11	**14**	2

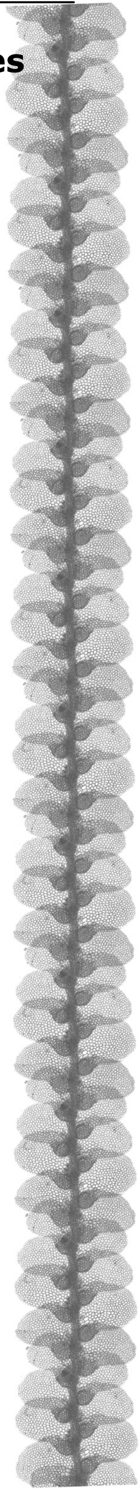
Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Archilejeunea fuscescens	70	3.23	6	18	18	19	9
Mniomalia viridis	8	3.25		1	4	3	
Lejeunea phyllobola	18	3.28		4	7	6	1
Rhacopilopsis trinitensis	13	3.31	1	3	2	6	1
Harpalejeunea oxyphylla	19	3.32	1	6	4	5	3
Lejeunea reflexistipula	14	3.36	1	1	6	5	1
Symbiezidium barbiflorum	55	3.42	10	11	10	9	15
unidentified species 03	7	3.43	1	1	1	3	1
Zelometeorium patulum	37	3.46	1	9	9	13	5
Cheilolejeunea oncophylla	2	3.5			1	1	
Cheilolejeunea clausa	16	3.5		5	4	4	3
Syrrhopodon cymbifolius	2	3.5			1	1	
Lejeunea boryana	2	3.5	1				1
Odontoschisma falcifolium	6	3.5		2	1	2	1
Pycnolejeunea macroloba	52	3.63	2	7	15	**20**	8
Ceratolejeunea cubensis	31	3.65	5	5	4	8	9
Acroporium pungens	6	3.67			**4**	1	1
Frullania patens	3	3.67			1	2	
Ceratolejeunea guianensis	31	3.68		5	10	11	5
Archilejeunea species 01	7	3.71		1	2	3	1
Ceratolejeunea cornuta	97	3.74	4	17	21	**34**	21
Lejeunea flava	16	3.75	2	3	4	1	6
Pycnolejeunea papillosa	4	3.75		1	1	1	1
Lejeunea laetevirens	44	3.8	5	8	8	8	**15**
Cheilolejeunea adnata	28	3.82	3	5	4	7	9
Cheilolejeunea rigidula	148	3.82	5	25	35	**46**	37
Crossomitrium patrisiae	8	3.88	1	2		2	3
Neurolejeunea breutelii	8	3.88			3	4	1
Microlejeunea acutifolia	17	3.88		4	4	4	5
Cheilolejeunea holostipa	50	3.9	3	4	10	**22**	11
Mastigolejeunea auriculata	42	3.93	1	6	12	11	12
Cheilolejeunea trifaria	41	3.98		4	11	**17**	9
Leptoscyphus species 01	1	4				1	
Lepidolejeunea ornata	1	4				1	
Schlotheimia torquata	1	4				1	
Schlotheimia rugifolia	1	4				1	

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Frullanoides liebmanniana	1	4				1	
Colura tortifolia	1	4				1	
Cheilolejeunea acutangula	2	4				2	
Leptoscyphus porphyrius	2	4				2	
Drepanolejeunea lichenicola	2	4				2	
Bazzania species 02	1	4				1	
unidentified species 01	1	4				1	
Syrrhopodon flexifolius	3	4				**3**	
Fissidens radicans	2	4				2	
Radula species 01	2	4		1			1
Lejeunea caespitosa	12	4.17	1	3	1	1	**6**
Lopholejeunea subfusca	56	4.2	4	8	7	14	**23**
Harpalejeunea stricta	10	4.2		2	2	2	4
Holomitrium arboreum	5	4.2			1	3	1
Plagiochila montagnei	17	4.24	2	1	2	5	7
Jaegerina scariosa	3	4.33			1	1	1
Pilotrichum evanescens	3	4.33			1	1	1
Drepanolejeunea orthophylla	3	4.33			1	1	1
Macromitrium cirrosum	5	4.4				**4**	1
Microlejeunea epiphylla	24	4.46		3	7	2	**12**
Drepanolejeunea fragilis	30	4.47	1	5	5	3	**16**
Orthostichopsis tetragona	19	4.47		1	3	8	7
Neurolejeunea seminervis	8	4.5				**6**	2
Microlejeunea bullata	36	4.5	1	4	5	9	**17**
Octoblepharum stramineum	4	4.5				3	1
Ceratolejeunea confusa	8	4.5			2	3	3
Macromitrium pellucidum	7	4.57				**5**	2
Syrrhopodon parasiticus	25	4.6	2	2	3	4	**14**
Groutiella obtusa	8	4.63			1	4	3
Ceratolejeunea coarina	3	4.67		1			2
Groutiella apiculata	3	4.67				2	1
Lopholejeunea eulopha	3	4.67				2	1
Pycnolejeunea species 01	12	4.75		2	1	2	**7**
Rectolejeunea flagelliformis	26	4.81		3	3	5	**15**
Acrolejeunea torulosa	8	4.88			1	3	4
Frullania apiculata	18	4.94		1	3	3	**11**

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Rectolejeunea berteroana	11	5		1	1	2	**7**
Acrolejeunea emergens	2	5				1	1
Ceratolejeunea malleigera	2	5				1	1
Drepanolejeunea crucianella	2	5				1	1
unidentified species 04	2	5				1	1
Syrrhopodon graminicola	2	5				1	1
Symbiezidium transversale var. hookerianum	25	5.08		2	1	6	**16**
Frullania caulisequa	34	5.18			2	11	**21**
Thysananthus amazonicus	17	5.24			1	5	**11**
Leptolejeunea elliptica	21	5.24		2		4	**15**
Macromitrium punctatum	8	5.25				3	**5**
Sematophyllum subpinnatum	7	5.29			1	1	**5**
Pycnolejeunea contigua	27	5.3		1	1	6	**19**
Leucolejeunea unciloba	3	5.33				1	2
schizostipous species 01	3	5.33				1	2
Rectolejeunea emarginuliflora	14	5.36		1	1	1	**11**
Colura greig-smithii	6	5.5			1		**5**
Henicodium geniculatum	15	5.6				3	**12**
Groutiella tomentosa	6	5.67				1	**5**
Frullania kunzei	12	5.67				2	**10**
Diplasiolejeunea cavifolia	6	5.67				1	**5**
Frullania nodulosa	10	5.8				1	**9**
Verdoornianthus griffinii	10	5.8				1	**9**
Diplasiolejeunea pellucida	8	6					**8**
Caudalejeunea lehmanniana	16	6					**16**
Cyclolejeunea peruviana	1	6					1
Cololejeunea cardiocarpa	1	6					1
Archilejeunea auberiana	1	6					1
Meiothecium boryanum	1	6					1
Frullania riojaneirensis	5	6					**5**
Metalejeunea cucullata	1	6					1
Meiothecium urceolatum	4	6					**4**
Odontolejeunea rhomalea	2	6					**2**
Leptolejeunea obfuscata	2	6					**2**
Brachiolejeunea conduplicata	1	6					1
Cylindrocolea planifolia	1	6					1

Full name	**N**	**WA**	**1**	**2**	**3**	**4**	**6**
Lejeunea monimiae	1	6					1
Odontolejeunea lunulata	1	6					1
Diplasiolejeunea cobrensis	5	6					**5**
Colura cylindrica	1	6					1
Cololejeunea species 01	1	6					1
unidentified species 08	1	6					1
Frullania subg. *Chonanthelia*	1	6					1
Lejeunea magnoliae	1	6					1
unidentified species B	2	6					**2**
Drepanolejeunea species 01	1	6					1
unidentified species 07	1	6					1
Macromitrium podocarpi	1	6					1
Frullania gibbosa	1	6					1
Diplasiolejeunea brunnea	10	6					**10**
Diplasiolejeunea rudolphiana	18	6					**18**
Vitalianthus urubuensis	6	6					**6**

Appendix 2 – Full names and authors of species found in this study



Calymperaceae

Calymperes afzelli Sw.
Calymperes erosum Müll. Hal.
Calymperes guildingii Hooker & Greville
Calymperes lonchophyllum Schwaegr.
Calymperes mitrafugax Florschutz
Calymperes othmeri Herzog
Calymperes palisotii Schwaegr.
Calymperes platyloma Mitt.
Calymperes rubiginosum (Mitten) Reese
Calymperes smithii Bartram
Calymperes species 01 INPA 217763
Calymperes species 02 INPA 217755
Syrrhopodon africanus (Mitt.) Paris
Syrrhopodon cymbifolius C. Muller
Syrrhopodon elatus Montagne
Syrrhopodon flexifolius Mitten
Syrrhopodon graminicola Williams
Syrrhopodon leprieuri Mont.
Syrrhopodon species 01 MPEG 186275
Syrrhopodon species 02 INPA 217501
Syrrhopodon cryptocarpus Dozy & Molk.
Syrrhopodon incompletus Schwaegr. var. *incompletus*
Syrrhopodon ligulatus Mont.
Syrrhopodon parasiticus Brid.
Syrrhopodon simmondsii Steere

Calypogeiaceae

Calypogeia laxa Gottsche & Lindenb.
Mnioloma parallelogrammum (Spruce) R. M Schust

Cephaloziaceae

Odontoschisma falcifolium Steph.

Cephaloziellaceae

Cylindrocolea planifolia (Steph.) R.M. Schust.

Daltoniaceae

Crossomitrium patrisiae (Brid.) Müll. Hal.
Lepidopilum affine Müll. Hal.
Lepidopilum radicale Müll. Hal.
Lepidopilum scabrisetum (Schwaegr.) Steere
Lepidopilum surinamense Müll. Hal.
Pilotrichum evanescens (Müll. Hal.) Crosby

Dicranaceae

Holomitrium arboreum Mitt.
Leucoloma cruegerianum (Müll. Hal.) A. Jaeger

Fissidentaceae

Fissidens diplodus Mitt.
Fissidens guianensis Mont.
Fissidens prionodes Mont.
Fissidens radicans Mont.
Fissidens steerei Grout
Fissidens weirii Mitt.
Fissidens zollingeri Mont.

Geocalycaceae

Leptoscyphus porphyrius (Nees) Grolle
Leptoscyphus species 01
Lophocolea bidentata (L.) Dumort.
Lophocolea liebmanniana Gottsche

Hookeriaceae

Callicostella pallida (Hornsch.) Angström

Hypnaceae

Chryso-hypnum diminutivum (Hampe) W.R. Buck
Hypnaceae species 01
Isopterygium tenerum (Sw.) Mitt.

Phyllodon truncatulus (Müll. Hal.) W.R. Buck
Rhacopilopsis trinitensis (Müll. Hal.) E. Britton & Dixon
Vesicularia vesicularis (Schwägr.) Broth.

Jubulaceae
Frullania apiculata (Reinw., Blume & Nees) Nees
Frullania caulisequa (Nees) Nees
Frullania gibbosa Nees
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.
Frullania nodulosa (Reinw., Nees & Blume) Gottsche et al.
Frullania patens Lindenb.
Frullania riojaneirensis (Raddi) Spruce
Frullania subg. *Chonanthelia*

Lejeuneaceae
Acrolejeunea emergens (Mitt.) Steph.
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiff.
Aphanolejeunea camillii (Lehman) R.M.Schuster
Aphanolejeunea contractiloba (A.Evans) R.M.Schuster
Aphanolejeunea kunertiana Steph.
Aphanolejeunea microscopia var. *africanus* (Taylor) A.Evans
Aphanolejeunea species 01 INPA 217693
Archilejeunea auberiana (Mont.) A. Evans
Archilejeunea crispistipula (Spruce) Steph.
Archilejeunea fuscescens (Hampe & Lehm.) Fulford
Archilejeunea parviflora (Nees.) Schiffn.
Archilejeunea species 01 INPA 217802
Brachiolejeunea conduplicata (Steph.) Gradstein
Caudalejeunea lehmanniana (Gottsche) A.Evans
Ceratolejeunea cerathanta (Nees & Mont.) Schiffn.
Ceratolejeunea coarina (Gottsche) Schiff.
Ceratolejeunea confusa R.M.Schust.
Ceratolejeunea cornuta (Spruce) Steph.
Ceratolejeunea cubensis (Mont.) Schiff.
Ceratolejeunea desciscens (Sande-Lac) Schiff.
Ceratolejeunea guianensis (Nees & Mont.) Steph.
Ceratolejeunea laetefusca (Aust) Schust.

Ceratolejeunea malleigera (Spruce) Steph.
Ceratolejeunea minuta G. Dauphin
Ceratolejeunea species 01
Cheilolejeunea acutangula (Nees) Grolle
Cheilolejeunea adnata (Kunze ex Lehm.) Grolle
Cheilolejeunea clausa (Nees & Mont.) R.M.Schust.
Cheilolejeunea discoidea (Lehm &. Lindenb) Kachroo &. R M. Schust
Cheilolejeunea holostipa (Spruce) Grolle & R.L. Zhu
Cheilolejeunea neblinensis Ilkiu-Borges & Gradstein
Cheilolejeunea oncophylla (Angstr.) Grolle & E. Reiner
Cheilolejeunea rigidula (Mont.) R.M.Schust.
Cheilolejeunea trifaria (Reinw., Blume & Nees) Mizut.
Cololejeunea cardiocarpa (Mont.) Steph.
Cololejeunea species 01 http://hanstersteege.jalbum.net
Colura cylindrica Herz.
Colura greig-smithii Jovet-Ast
Colura tortifolia (Nees & Mont.) Steph.
Cyclolejeunea convexistipa (Lehm. & Lindenb.) Evans
Cyclolejeunea luteola (Spruce) Grolle
Cyclolejeunea peruviana (Lehm. & Lindenb.) A. Evans
Diplasiolejeunea brunnea Steph.
Diplasiolejeunea cavifolia Steph.
Diplasiolejeunea cobrensis Gottsche ex Steph.
Diplasiolejeunea pellucida (C.F.W. Meissn. ex Spreng.) Schiffn.
Diplasiolejeunea rudolphiana Steph.
Drepanolejeunea crucianella (Taylor) A. Evans
Drepanolejeunea fragilis Bischl.
Drepanolejeunea lichenicola (Spruce) Steph.
Drepanolejeunea orthophylla Bischl.
Drepanolejeunea species 01 MPEG 186262
Echinocolea asperrima (Spruce) R.M. Schust.
Frullanoides liebmanniana (Lindenb. & Gottsche) Slageren
Haplolejeunea cucullata (Steph.) Grolle
Harpalejeunea oxyphylla (Nees & Mont.) Steph.
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.
Harpalejeunea tridens (Besch. & Spruce) Steph.
Lejeunea boryana Mont.

Lejeunea caespitosa Steph.
Lejeunea cerina (Lehm. & Lindenb.) Gottsche et al.
Lejeunea controversa Gottsche
Lejeunea flava (Sw.) Nees
Lejeunea laetevirens Nees & Mont.
Lejeunea longifissa Steph.
Lejeunea magnoliae Lindenb. & Gott.
Lejeunea maxonii (A. Evans) X.-L. He
Lejeunea monimiae (Steph.) Steph.
Lejeunea phyllobola Nees & Mont.
Lejeunea reflexistipula (Lehm. & Lindenb.) Gottsche et al.
Lepidolejeunea involuta (Gottsche) Grolle
Lepidolejeunea ornata (H.Rob) R.M.Schust
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.
Leptolejeunea obfuscata (Spruce) Steph.
Leucolejeunea unciloba (Lindenb.) A. Evans
Lopholejeunea nigricans (Lindenb.) Schiffn.
Lopholejeunea quelchii Steph.
Lopholejeunea subfusca (Nees) Schiffn.
Macrocolura sagittispula (Spruce) R.M.Schust.
Mastigolejeunea auriculata (Wils.) Schiffn.
Metalejeunea cucullata (Reinw et. al) Grolle
Microlejeunea acutifolia Steph.
Microlejeunea aphanella (Spruce) Steph.
Microlejeunea bullata (Taylor) Steph.
Microlejeunea epiphylla Bischl.
Microlejeunea globosa (Spruce) Steph.
Neurolejeunea breutelii (Gott.) Evans
Neurolejeunea seminervis (Spruce) Schiffn.
Odontolejeunea lunulata (Weber) Schiffn.
Odontolejeunea rhomalea (Spruce) Steph.
Oryzolejeunea saccatiloba (Steph.) Gradstein
Oryzolejeunea species 01
Pictolejeunea picta (Gottsche ex Steph.) Grolle
Prionolejeunea aemula (Gottsche) A. Evans
Prionolejeunea denticulata (Web.) Schiff.
Prionolejeunea microdonta (Gottsche) Steph.

Prionolejeunea muricatoserrulata (Spruce) Steph.
Pycnolejeunea contigua (Nees) Grolle
Pycnolejeunea macroloba (Mont.) Schiffn.
Pycnolejeunea papillosa X.-L. He
Pycnolejeunea species 01 INPA 186240
Rectolejeunea berteroana (Gottsche ex Steph.) A. Evans
Rectolejeunea emarginuliflora (Gottsche ex Schiffn) Evans
Rectolejeunea flagelliformis A. Evans
Stictolejeunea squamata (Willd.) Schiffner
Symbiezidium barbiflorum (Lindenb. & Gott.) Evans
Symbiezidium species 01 INPA 217504
Symbiezidium transversale var. *hookerianum* (Gottsche) Gradst. & van Beek
Taxilejeunea asthenica Spruce (Steph.)
Taxilejeunea obtusangula (Spruce) A. Evans
Thysananthus amazonicus (Spruce) Schiffn.
Trachylejeunea aneogyna (Spruce) Grolle
Trachylejeunea species 02 MPEG 186234
Verdoornianthus griffinii Gradst.
Vitalianthus urubuensis Zartman & I. L. Ackerman
Xylolejeunea crenata (Spruce) Steph.

Lejeuneaceae species 01 INPA 217817, http://hanstersteege.jalbum.net/
Lejeuneaceae species 02 INPA 217594
Lejeuneaceae species 03 Mota de Oliveira pers. coll. ECT02Z4
Lejeuneaceae species 04 INPA 217625
Lejeuneaceae species 05 Mota de Oliveira pers. coll. ECT02Z1
Lejeuneaceae species 07 MPEG 186263
Lejeuneaceae species 08 INPA 217800
Lejeuneaceae species B MPEG 186234
Lejeuneaceae holostipous species 01 http://hanstersteege.jalbum.net/
Lejeuneaceae schizostipous species 01 INPA 217501

Lepidoziaceae
Arachniopsis species 01 INPA 217507
Bazzania aurescens Spruce
Bazzania cuneistipula (Gottsche, Lindenb. & Nees) Trevis.
Bazzania hookeri (Lindenb.) Trevis.

Bazzania species 01 INPA 217566
Bazzania species 02 INPA 217501
Micropterygium leiophyllum Spruce
Micropterygium parvistipulum Spruce
Micropterygium trachyphyllum Reimers
Zoopsidella macella (Steph.) R.M. Schuster

Lepidoziaceae species 01 INPA 217624

Leucobryaceae
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.
Ochrobryum gardneri (C. Müll.) Mitt
Octoblepharum albidum Hedw.
Octoblepharum cocuiense Mitt.
Octoblepharum cylindricum Schimp. ex Mont.
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.
Octoblepharum stramineum Mitt.

Leucomiaceae
Leucomium strumosum (Hornsch.) Mitt.

Leucophanaceae
Leucophanes molleri Müll. Hal.

Macromitriaceae
Groutiella apiculata (Hook.) Crum & Steere
Groutiella obtusa (Mitt.) Florsch.
Groutiella tomentosa (Hornsch.) Wijk.& Marg.
Macromitrium cirrosum (Hedw.) Brid.
Macromitrium pellucidum Mitt.
Macromitrium podocarpi Müll. Hal.
Macromitrium punctatum (Hook & Grev.) Brid.
Schlotheimia rugifolia (Hook.) Schwaegr.
Schlotheimia torquata (Hedw.) Brid.

Meteoriaceae
Zelometeorium patulum (Hedw.) Manuel

Metzgeriaceae

Metzgeria decipiens Schiff.

Metzgeriaceae species 01 INPA 217647

Neckeraceae

Neckeropsis disticha (Hedw.) Kindb.

Neckeropsis undulata (Hedw.) Reichdt.

Porotrichum substriatum (Hampe) Mitt.

Phyllodrepaniaceae

Mniomalia viridis (Mitt.) Müll. Hal.

Plagiochilaceae

Plagiochila disticha (Lehm. & Lindenb.) Lindenb.

Plagiochila laetevirens Lindenb.

Plagiochila montagnei Nees

Plagiochila simplex (Sw.) Lindenb.

Plagiochila subplana Lindenb.

Plagiochila species 00

Plagiochila species 01 http://hanstersteege.jalbum.net

Plagiochila species 02 http://hanstersteege.jalbum.net

Plagiochila species 05 http://hanstersteege.jalbum.net

Plagiochila species 06 http://hanstersteege.jalbum.net

Plagiochila species 06 http://hanstersteege.jalbum.net

Plagiochila species 09 http://hanstersteege.jalbum.net

Pterobryaceae

Henicodium geniculatum (Mitt.) W.R. Buck

Jaegerina scariosa (Lorentz) Arzeni

Orthostichopsis tetragona (Sw. ex Hedw.) Broth.

Pireella cymbifolia (Sull.) Cardot

Pireella pohlii (Schwaegr.) Card.

Racopilaceae

Racopilum tomentosum (Hedw.) Brid.

Radulaceae

Radula flaccida Lindenb. & Gott.
Radula husnotii Castle
Radula javanica Steph.
Radula mammosa Spruce
Radula species 01 Mota de Oliveira personal collection ECT03Z2

Sematophyllaceae

Acroporium pungens (Hedw.) Broth.
Meiothecium boryanum (Müll. Hal.) Mitt.
Meiothecium urceolatum (Schawaegr.) Mitt.
Sematophyllum subpinnatum (Brid.) Britt.
Sematophyllum subsimplex (Hedw.) Mitt.
Taxithelium planum (Brid.) Mitt.
Taxithelium pluripunctatum (Renauld & Cardot) W.R.Buck
Trichosteleum papillosum (Hornsch.) A. Jaeger

Stereophyllaceae

Pilosium chlorophyllum (Hornsch.) C. Mull.

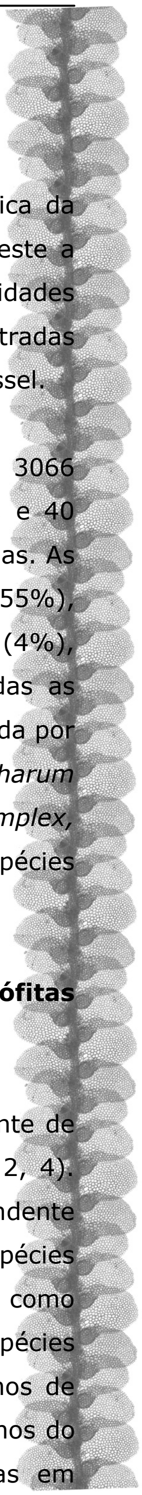
Thamnobryaceae

Homaliodendron piniforme (Brid.) Enroth

Thuidiaceae

Cyrtohypnum involvens (Hedw.) W.R.Buck & H.A. Crum
Cyrtohypnum scabrosulum (Mitten) W.R. Buck et Crum
Cyrtohypnum schistocalyx (Müller Hal.) W.R. Buck & Crum

Octoblepharum albidum on lower stem in Guyana



Resumo em Português

A tese aqui apresentada contém a primeira amostragem sistemática da estrutura de comunidades de briófitas epífitas num transecto de leste a oeste da Bacia Amazônica. Em cada uma das nove localidades selecionadas na Amazônia, comunidades de briófitas foram amostradas em oito árvores, em cinco diferentes zonas de altura, da base ao dossel.

O processamento da amostragem gerou 3104 registros, dos quais 3066 resultaram na identificação de 225 espécies e 38 morfo-espécies, e 40 permaneceram não identificados. As espécies pertenciam a 29 famílias. As famílias mais comuns em número de registros foram Lejeuneaceae (55%), Calymperaceae (8%), Leucobryaceae (4%) e Sematophyllaceae (4%), sendo estas as únicas famílias com ocorrência registrada em todas as localidades. A espécie mais comum foi *Cheilolejeunea rigidula*, seguida por *Ceratolejeunea cornuta*, *Octoblepharum pulvinatum*, *Octoblepharum albidum*, *Archilejeunea fuscescens, Sematophyllum subsimplex, Lopholejeunea subfusca* e *Symbiezidium barbiflorum*. Estas oito espécies corresponderam a 21% do total de registros.

Gradiente vertical ao longo do forófito – comunidades de briófitas são determinadas pelo microambiente

As comunidades de briófitas epífitas apresentaram um claro gradiente de composição ao longo dos forófitos na Bacia Amazônica (Capítulos 2, 4). Muitas espécies habitavam uma zona de altura específica, independente da localidade investigada (Capítulo 4, Anexo 1). Dentre as 155 espécies registradas para mais de uma localidade, 57 foram identificadas como especialistas (37%) e 98 (63%) como generalistas. A maioria das espécies especialistas são encontradas nos extremos do gradiente em termos de microclima, ou seja, na zona 1, base do tronco, e zona 6, galhos finos do dossel. Apenas 8 espécies foram identificadas como especialistas em outras zonas de altura. Portanto, o gradiente vertical é estabelecido através de uma interação entre filtro ambiental e dispersão em todas as zonas de altura, com a importância relativa de cada um desses processos dependendo da zona de altura em questão. Enquanto o filtro ambiental é o principal fator determinante da composição de espécies na base do tronco e no dossel, a possibilidade de dispersão dada pela abundância da espécie nos arredores – inclusive no mesmo forófito – é o principal fator determinante da composição de espécies ao longo do tronco nas zonas 2, 3 e 4.

Comunidades de briófitas epífitas em floresta de terra firme na Amazônia – dinâmica neutra de abundância de espécies

Enquanto a ocorrência de briófitas nos forófitos apresenta uma estrutura fortemente influenciada pelo microambiente e portanto um gradiente de composição, a riqueza e abundância de espécies da maioria das nove localidades investigadas não apresentaram padrão espacial definido ao longo de gradiente climáticos da Bacia Amazônica. Nesta escala, a riqueza de espécies e a estrutura das comunidades corresponderam ao que seria previsto pelo Modelo Neutro de Biodiversidade e Biogeografia proposto por Hubbell (capítulo 3). Este resultado significa que a comunidade de briófitas epífitas de uma localidade (soma de todas as comunidades amostradas nos forófitos de uma mesma localidade) pode ser formada pelo recrutamento ao acaso de indivíduos originados localmente ou por imigração, sob a única influência da abundância total da espécie na localidade e na metacomunidade (soma de todas as comunidades amostradas nas localidades), respectivamente.

A ausência de um padrão geográfico, no entanto, não exclui a importância do fenômeno da dispersão no processo de formação da comunidade. De acordo com os resultados, a maioria dos novos indivíduos numa localidade são originados localmente, confirmando o predomínio de curtas distâncias (cerca de 15 Km) de dispersão em briófitas e chances igualmente baixas em média a longas distâncias (> 15 a 1.000 Km).

A localidade inventoriada no Ecuador forneceu o contraponto à dinâmica neutra. Aparentemente, a maior riqueza de espécies foi associada ao fato de ter sido registrado um maior número de indivíduos nos plots. Provavelmente, devido a uma alta e constante umidade relativa do ar, o estabelecimento de espécies típicas de outro substrato, como epífilas, é facilitado, o que não poderia ser previsto pelo modelo.

A tendência dada pelos resultados nesta tese é a de coexistência de dois processos: em escala local, a formação de comunidades de briófitas epífitas nos forófitos foi fortemente determinada pela interação entre filtro ambiental e abundância local (dispersão), enquanto que na escala da bacia a formação das comunidades foi influenciada principalmente pela abundância das espécies na metacomunidade. Em todas as zonas de altura, a probabilidade de uma espécie já estabelecida nos arredores (cerca de um raio de 15 Km) ocorrer é maior do que a de uma espécies que depende de um fenômeno de dispersão de longa distância. Finalmente, a freqüência de ocorrência de um fenômeno de dispersão de longa distância aumenta de acordo com a zona de altura no forófito.

O uso da teoria neutra como um modelo determinístico é inútil, uma vez que duas comunidades locais originadas da mesma metacomunidade podem apresentar composição de espécies completamente diferentes. No entanto, predições quantitativas de número de espécies e estrutura podem ser geradas e testadas com dados de campo. No capítulo 3 foi proposto que uma comunidade padrão de briófitas epífitas proveniente da amostragem de oito forófitos, numa localidade de floresta de terra firme na Amazônia, é composta em média por 65 espécies, 21 espécies com apenas uma ocorrência, e com a espécies mais comum apresentando entre 10 e 30 registros.

Utilizando a espécie mais abundante da base de dados, *Cheilolejeunea rigidula,* duas das predições propostas no capítulo 3 foram testadas através de dados moleculares de distância genética entre indivíduos. Os resultados estiveram de acordo com as predições: recrutamento de novos indivíduos majoritariamente local e ausência de uma estrutura geográfica de imigração através da bacia. Finalmente, os maiores valores de distância genética foram obtidos entre indivíduos do dossel e do sub-bosque, um interessante resultado a ser melhor investigado.

Esta tese fornece base para pesquisa de longo termo e de larga escala em ecologia de briófitas na Amazônia devido à padronização da amostragem. Baseado no fato de que a ocorrência de briófitas epífitas sofre uma maior influência em escala local, de acordo com diferenças microambientais, um complemento futuro interessante para esta pesquisa seria a investigação de outros tipos de vegetação na Amazônia, adjacentes a floresta de terra firme, mas com microclima diferenciado, como os igapós. Outro ponto a ser abordado é a estrutura espacial em escala local. Para tanto, seria necessário um esquema de amostragem sistemática em classes de distância entre 1 e 15 Km e a comparação de comunidades pertencentes à mesma zona de altura, já que probabilidades de dispersão podem variar de acordo com o habitat.

Nederlandse samenvatting

Dit proefschrift beschrijft het resultaat van de eerste systematische verzameling van epifytische bryofyten in de Amazone. Acht bomen in negen locaties werden van boomvoet tot boomkroon bemonsterd.

Van de in totaal 3104 waarnemingen werden er 3066 geïdentificeerd als behorend tot 225 soorten en 38 morfo-soorten. Veertig waarnemingen bleven ongeïdentificeerd. De soorten behoorden tot 29 families. De meest algemene familie (in termen van individuen) was de Lejeuneaceae (55%), gevolgd door Calymperaceae (8%), Leucobryaceae (4%) en Sematophyllaceae (4%). Dit waren ook de enige families die op alle locaties werden aangetroffen. De meest algemene soort was *Cheilolejeunea rigidula*, gevolgd door *Ceratolejeunea cornuta*, *Octoblepharum pulvinatum*, *Octoblepharum albidum*, *Archilejeunea fuscescens, Sematophyllum subsimplex, Lopholejeunea subfusca* en *Symbiezidium barbiflorum*. Deze acht soorten waren goed voor 21% van alle waarnemingen.

De verticale gradiënt in de gastheerboom – bryofyten zijn sterk standplaats bepaald

Over de gehele Amazone vertonen bryofyten een duidelijke verticale zonering over de gastheerbomen (Hoofdstuk 2, 4). Veel soorten hebben een duidelijke, significante voorkeur voor één bepaalde hoogte in de boom (Hoofdstuk 4, Appendix 1). De meeste van deze specialisten worden op de stamvoet of in de uiterste twijgen van de boomkroon aangetroffen, dus op de uitersten van de microklimatologische gradiënt.

De verticale gradiënt over gastheerbomen en het exclusieve voorkomen van sommige soorten in de ondergroei (schaduw-epifyten) en op de uiterste twijgen (zonne-epifyten) is al eerder gevonden. Het mechanisme dat tot deze scheiding leidt is echter niet noodzakelijkerwijs het licht zoals de aanduidingen schaduw- en zonne-epifyt doen vermoeden.

Hoewel de fysiologische basis voor de sterke preferentie van veel soorten vooralsnog onbekend is (Hoofdstuk 2) is de preferentie van veel soorten constant over de Amazone. Dit suggereert een sterke rol voor de faktor standplaats in de samenstelling van epifytische gemeenschappen op gastheerbomen in de Amazone.

Epifytische gemeenschappen in Amazone droogland bos – neutrale dynamiek van abundanties van soorten

Terwijl het voorkomen van bryofyten op gastheerbomen sterk standplaats gerelateerd is, werden de soortenrijkdom en relatieve soort-abundanties van negen Amazonische locaties prima voorspeld door het 'Neutrale model van Biodiversiteit en Biogeografie' van Hubbell (Hoofdstuk 3). Neutrale dynamiek was bij planten nog niet eerder op deze schaal getest, waarschijnlijk vanwege de sterke, en bekende, geografische gradiënt in soortensamenstelling. De samenstelling van bryofytische gemeenschappen op deze schaal bleek het best verklaard te worden door een stochastisch vestigingsmodel, dat sterk bepaald wordt door de abundanties van de soorten in een meta-community. Dit betekent echter niet dat verspreiding van sporen geheel zonder ruimtelijke component is. De meeste dispersie van sporen vindt binnen een locatie plaats, en dat is consistent met wat bekend is van bryofyten – een dominantie van verspreiding over korte afstand maar vrijwel ongelimiteerde verspreiding voor de overige sporen.

De redenen waarom verschillen in omgevingsfactoren over de Amazone zo weinig invloed op de samenstelling van de bryofyten gemeenschappen hebben is niet geheel duidelijk. In gematigde en Andiene systemen is deze invloed namelijk erg prominent. Ecuador was de uitzondering op de neutrale regel. Hier werden veel meer individuen gevonden en daarmee samenhangend een grotere soortenrijkdom. Mogelijk is een hoge relatieve vochtigheid hieraan debet. Dit kan ook het geval zijn in de locatie in Frans Guiana, die hoewel binnen de voorspelling van de neutrale theorie, significant soortenrijker was dan de gemiddelde Amazonische locatie.

Epifytische bryofyten gemeenschappen in droogland Amazone bos - voorspellingen

Het gebruik van de neutrale theorie als deterministisch model is niet nuttig, omdat locale gemeenschappen vanuit de metapopulatie een totaal andere soortensamenstelling kunnen krijgen. Het is echter wel mogelijk kwantitatieve voorspellingen te doen en deze te testen. In Hoofdstuk 3 werd berekend dat de gemiddelde epifytische gemeenschap van 250 waarnemingen op acht bomen zo’n 65 soorten zal hebben, waarvan 21 soorten met slechts één individu. De meest algemene soort zal zo’n 20-30 keer voorkomen. Hoewel we deze voorspellingen niet uitgebreid konden toetsen bleken de resultaten van een studie in het Atlantische bos in Brazilië extreem goed met onze verwachtingen overeen te komen: 63 soorten, waarvan 18 met één individu. *Cheilolejeunea rigidula* was de meest algemene soort met 15 waarnemingen.

Twee voorspellingen van het neutrale model uit Hoofdstuk 3 werden getoetst met de meest algemene soort uit de dataset, *Cheilolejeunea rigidula,* gebruik makend van moleculaire technieken. De resultaten van deze test lijken een bevestiging van een voornamelijk lokale verjonging en een gebrek aan verband tussen de genetische verwantschap en afstand tussen locaties in de Amazone. Dit betekent dat er tussen individuen die binnen enkele honderden meters van elkaar voorkomen een relatie is tussen afstand en genetische verwantschap, maar dat dit over grotere afstanden niet meer merkbaar is door de, over het algemeen, kleine kans op lange afstand migratie.

De verticale gradiënt in de gastheerboom en neutrale dynamiek over het Amazone bekken – de relatieve bijdrage van omgevingsfactoren en migratie

Uit de resultaten van dit onderzoek blijkt een combinatie van sterke standplaatsvoorkeur van soorten in de gastheerboom, terwijl de gehele gemeenschap door een neutraal proces lijkt te worden gevormd. Uiteindelijk wordt de samenstelling van een epifytengemeenschap in een bepaalde hoogtezone van de gastheerboom door het volgende patroon bepaald: de omgeving heeft een sterke invloed in de extremen van de hoogtegradiënt over de boom met als gevolg dat de gemeenschappen van de boomvoet en de twijgen de sterkste 'vestigingslimitatie' vertonen; verspreiding is belangrijker in de middelste zones langs de boom; in alle zones geldt dat als een soort al binnen een straal van 15 km voorkomt, de kans hoger is dat deze zich kan vestigen dan dit het geval is door lange-afstand-migratie; de kans dat een soort zich op een locatie door lange-afstand-migratie vestigt neemt toe met de hoogte in de gastheerboom.

Toekomstig onderzoek

Dit proefschrift legt een basis voor lange-termijn en grootschalig toekomstig onderzoek aan bryofyten in de Amazone. Omdat het voorkomen van bryofyten sterk door het microklimaat op de lokale schaal wordt bepaald, is het interessant om andere bostypen te vergelijken met het drooglandbos dat hier onderzocht is. Dit kan de vraag beantwoorden of de verticale hoogtegradiënt de voornaamste lokale gradiënt is, of dat geringere kroonhoogte of hogere luchtvochtigheid door topografie ook een belangrijke rol spelen in de vestiging.

Een andere punt van onderzoek is de ruimtelijke populatiestructuur op kleine schaal. Omdat dit onderzoek aantoont dat er weinig ruimtelijke structuur zit in de samenstelling van gemeenschappen en de genetische afstand tussen individuen, is het interessant om te onderzoeken op welke schaal dit wel een rol speelt. Dit zou mogelijk zijn door het systematisch verzamelen van gemeenschappen of populaties van één soort op vaste afstanden tussen 1 en 15 kilometer en in dezelfde hoogte zone.

Onderzoek op grotere schaal zou zich op het systematisch verzamelen van meer locaties in het zuidoosten en noordoosten van het Amazone bekken moeten richten om de voorspelbaarheid van de neutrale theorie verder te toetsen.

Collecting bryophytes in Tiputini, Ecuador

Acknowledgements

I finish this thesis with a grateful feeling for the way life went on. The story of this doctorate began somewhere when I moved to Manaus. I was working with hydrochemistry at INPA – National Institute for Research in Amazonia - but my botanical "upbringing" started pushing my interests back to the bryophytes. Of course the decision of trying a doctorate was not so easy and at that time many people helped me to take it. I thank firstly and profoundly my parents Maria Celia Mota and Sven Wolff for the full and always confident support. Since the beginning they told me that I could and should take this challenge if this would make me happy. Simple as it sounds; this view gave me a lot of strength. I knew they would stand by me whenever it was needed. Muito obrigada, meus queridos, por todo o amor e confiança. My brother Julio and my sister Clara had, besides emotional, very practical participation in the beginning and at the end of this thesis. In the beginning, Julio helped me typing some bryophyte occurrence records from old papers, since I wanted to have some information on species distribution before starting the real work in the Netherlands. I would also like to thank my parents in Aracaju. From there I counted on the support of my father José Olyntho de Oliveira Neto, Ana Lucia Oliveira, my sisters Rachel and Narjara and my brother Olyntho, given by the really cosy and relaxing time we spent together. Along all these years without seeing each other, Ana made me feel a little closer to them sending lovely mails with news, strength and the best wishes. Obrigada meus queridos, com carinho e saudades, pelos dias que passamos juntos. Many thanks also to my dearest friend Débora Drucker, for so many great discussions, scientific or not, and support on my decision for the doctorate. Very important and special was the motivation given by two of my former teachers: Kátia Cavalcanti Pôrto (with whom I started studying bryophytes), knowing about personal difficulties I was going through, called me from Recife a couple of times talking about publications, doctorate... trying to put me "on track" again. José Maria Cardoso da Silva helped me by discussing the outline of the project and by making me believe that it would become true. Thank you both. In 2004 I wrote the proposal for my doctorate to Capes – the Brazilian agency funding this type of research – and in 2005 it was approved. Here I thank Capes and the Brazilian government for the secure and fundamental funding during these four years.

Starting the PhD in the Netherlands was an exciting challenge. The cold weather was fortunately compensated by the warm welcome at the Herbarium. Thanks Marion Jansen-Jacobs, Paul and Hiltje Maas, Paddy Haripersaud, Roy Erkens, Tinde van Andel, Erik Simonis, Rob van Aubel and all other staff for the cosy and stimulating work environment during my first three months. I had a lovely time among you all.

After this period of first snow I went back to Manaus to do fieldwork. There I counted first of all on my family, and here I thank them again for gladly opening space at home for a daughter, a son-in-law, and two grandchildren!!! We lived there during the first months of 2006, while I was up and down, from Manaus to the field stations and back. My mother always very happy to take care of the children – for all that love I thank her so much. The fieldwork itself would not be possible without the cooperation of many institutions and people. During the first fieldwork period I went to Reserva Ducke, Urucu and Tapajos. In Manaus I thank the institution INPA, for the permit to work at Reserva Ducke; and the researchers Carlos Franciscon, for the process regarding the bryophyte collections and Rogério Gribel, for an interesting discussion of my work. In Urucu I thank Petrobras, the Brazilian state oil company, for the permit to collect in their exploitation unit and for providing aerial transportation, lodging and field assistance. Flying almost two hours over closed canopy to finally reach the "gap" formed by the exploitation unit is unique. The forest is tremendously vast and beautiful. In order to work in Floresta Nacional do Tapajós, I stayed at the field base of LBA project and I would like to thank Paulo Coutinho for all arrangements, tips concerning the area, help with renting a car and a very nice chat in the meantime.

Somehow everything went smoothly in Tapajós, despite an enormous amount of rain! The area where Tapajós river meets Amazonas river is fantastic! In the second fieldwork period, at the end of 2006, I collected in São Gabriel da Cachoeira and Caxiuanã. In São Gabriel da Cachoeira, Sr. Luiz, Juliana Stropp and Hans ter Steege participated and helped. Thank you all for those days! Days later, in Caxiuanã, I had my hardest fieldwork, emotionally speaking. I was for the first time more than 20 days far from my children and that was painful and a bit demotivating. On top of that, part of the planning did not work and here I am very grateful for the help of people at MPGE - Museu Paraense Emilio Goeldi - such as Cida Lopes, Nilson Gabas Jr. and Regina Lobato. Finally I had my last fieldwork in July 2007, in Ecuador. I never came across so many mammals in such a short time! I thank David Romo for all arrangements concerning my stay at Tiputini Biodiversity Station. I also thank Gijs Meijer and Chequita Bhikhi for joining this fieldwork and my research through their MSc projects. The care of Chequita for slide preparation was very nice to witness. And I cannot forget the enchantment of Gijs for the rainforest. That was motivating! I would also like to thank all field assistance, especially the one given by Everaldo Santos. Well, after having all material sampled, the identification was a difficult, yet beautiful task. Concerning the difficult bit, I thank Elena Drehwald and Anna Luiza Ilkiu-Borges for giving their precious opinion about the identity of some Lejeuneaceae, based on some photographs I sent them. Along the way, I would like to thank very much Hans Cornelissen, Dimitri Montfoort and Bert Bleij for all effort in finding back old notebooks and for making the data from the Guianas available.

At University of Utrecht, I thank Marinus J. A. Werger for accepting to be my promoter. His careful reading, very interesting remarks and objectivity were important for the improvement of the chapters. I would also like to thank Heinjo During for comments on some chapters and insightful discussions about the bryophytes. Concerning the hard DNA extraction, I owe many thanks to Andries Temme, Jan Maas and Roy Erkens, and also

for giving valuable assistance and discussions. In short, I had very good times with all people from the Ecology and Biodiversity department. Thank you all for the discussions during the meetings and the friendly routine. Claudia Soliz-Gamboa and Juliana Stropp, queridas, thanks a lot for your lovely friendship. Thanks for being by my side for great and funny times and for the times when I had wet eyes!!! A bit of South American winning (jogo de cintura) was essential to survive impossible data analysis, winter, and deadlines. Out of work I also met people who made my days lighter, specially the mothers of Maria and Daniel's school friends. I thank Miriam Cornelis, Mireille and Tatiana, for all effort to follow my rudimentary Dutch, giving me the feeling that I can be at home in this country too! And I would like to thank very much Nicole Kelling for her great friendship. My sister Clara, very much at the end, helped me "motion wise", when I was already nine months pregnant and still finishing the general discussion. Thanks, Clara, for picking up the children from school, from sport, from friends' houses... and all the help. Probably, with all rush to write, some people who I wanted to include here were left out. Sorry my friends, and thanks anyway.

Enfim, ofereço esta tese a Maria Vitória, Daniel e Isabel, sendo infinitamente grata pelo amor que nos une. Meus filhos, encontro em vocês o maior incentivo que posso imaginar para esta vida, obrigada.

Lately, there is one person who was along all lines and dreams of this work. Hans ter Steege, I thank you first as supervisor, for accepting me as AIO; for all concern and practical help on my staying in the Netherlands; for an enthusiastic and always helpful coaching; for extremely interesting discussions and important additions to my original project. Hans, I thank you now as my beloved partner, for making daily life so light and beautiful, for the sweetest words I could ever hear and lots of incentive at difficult moments. Thank you for using your admirable combination of working very hard yet joyfully in the layout of this thesis! Thanks for being there, in such a special way, always by my side.

Curriculum Vitae

Sylvia Mota de Oliveira was born on September 7, 1975 in Aracaju, State of Sergipe, in the Northeast of Brazil. She got her bachelor degree in Biological Sciences in 1999 at Universidade Federal Rural de Pernambuco, in Recife. During the bachelor course she got research scholarships for projects on bryophyte phenology and population ecology(1). She also participated in other projects at the Biology of Bryophytes Laboratory(2). The next step was a master degree, at the Universidade Federal de Pernambuco, obtained in 2001 with a dissertation on the population structure of two Pottiaceae species(3). Thereafter she moved from Recife to Manaus, State of Amazonas, and in 2002 she started working at INPA – Instituto Nacional de Pesquisas da Amazônia. There she had a fellowship under the project LBA, which encompassed research on the hydrochemistry of black waters as well as scientific and technical coordination of the field activities of two instrumented experimental catchments in a forest reserve(4). In 2005 she received funding from the Brazilian Government to work on the present doctoral thesis(5).

In the canopy, Tiputini, Ecuador

Publications

(1) Oliveira SM, Pôrto KC. 1998. Reprodução Sexuada em Musgos Acrocárpicos do Estado de Pernambuco, Brasil. Acta Botanica Brasilica 12: 385-392.

(1) Oliveira SM, Pôrto KC. 2001. Reproductive phenology of *Sematophyllum subpinnatum* (Brid.) Britt. in the Atlantic Rain Forest, Recife, Pernambuco State, Brasil. Journal of Bryology 23: 17-22.

(1) Oliveira SM, Pôrto KC. 2002. Population profile of *Bryum apiculatum* Schwaegr. in an Atlantic Forest Remnant, Pernambuco, Brazil. Journal of Bryology 24: 251.

(1) Pôrto KC, Oliveira SM. 2002. Reproductive phenology of *Octoblepharum albidum* (Bryopsida, Leucobryaceae) in a tropical lowland forest of north-eastern Brazil. Journal of Bryology 24: 291-294.

(2) Pôrto KC, Oliveira SM. 1998. Biodiversidade e biologia reprodutiva de briófitas da reserva ecológica de Dois Irmãos. In: Machado, I. C.; Lopes, A. V.; Pôrto, K. C.. (Ed.). Reserva ecológica de Dois Irmãos: Estudos em um remanescente de Mata Atlântica em área urbana. Recife: Universitária - UFPE, 1998, v. 1, p. 115-135.

(2) Pôrto KC, Germano SR, Oliveira SM. 2000. New records of Bryophytes for Pernambuco State, Brazil. Tropical Bryology 18: 107-114.

(3) Oliveira SM, Pôrto KC. 2005. Sporophyte production and population structure of two species of Pottiaceae in an Atlantic Forest remnant in Pernambuco, Brazil. Cryptogamie 26: 239-247.

(4) Waterloo MJ, Oliveira SM, Drucker DP, Nobre AD, Cuartas LA, Hodnett MG, Langedijk I, Jans WP, Tomasella J, Araújo AC, Pimentel TP, Múnera JC. 2006. Export of carbon in runoff from an Amazonian rainforest catchment. Hydrological Processes 20: 2581–2597.

(4) Tomasella J, Hodnett MG, Cuartas LA, Nobre AD, Waterloo M, Oliveira SM 2008. The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour. Hydrological Processes 22: 2133-2147.

(4) Oliveira SM, Waterloo MJ, Monteiro MTF, Drucker DP, Nobre AD, Cuartas LA, Tomasella J, Hodnett MG, Nascimento AHM, Munera JC. Hydrochemical aspects of runoff generation in an Amazonian blackwater catchment. *Submitted to Biogeochemistry*

(5) Oliveira SM, ter Steege H, Cornelissen, JHC, Gradstein SR. 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. Journal of Biogeography 36: 2076-2084.

CAPES

Universiteit Utrecht