Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation

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Summary

1. Community composition of epiphytic bryophyte communities, sampled systematically in nine localities across 2800 km from east to west of the Amazon forest, was mostly explained by their height zone along the vertical microenvironmental gradient from the base to the top of the host tree.

2. Despite the lack of correlation between geographical distance and dissimilarity in species composition, communities within the same locality were significantly more similar than communities from different localities in all height zones, with the highest values of similarity found between outer canopy communities.

3. While height zone on the host tree explained most of the variation in species composition at local scale, elevation and temperature were the variables most strongly related to species composition at a geographical scale.

4. Using the concepts of meta/local community of the Neutral Theory of Biodiversity and Biogeography, we showed that establishment limitation was strongest at the extremes of the vertical gradient. We estimated that communities of the tree base and the outer canopy drew individuals from outside the habitat species pool at a rate of 0.28 and 0.22, respectively, in contrast with values between 0.55 and 0.76 of other height zones.

5. Our results offered contrasting evidence for the hypothesis that species inhabiting the canopy have higher chances of engaging in long-distance dispersal events. If the stronger establishment limitation at the extremes of the gradient is not compensated by facilitated dispersal compared to other zones, as our results suggest, communities on the base and on the outer canopy might be, through time, subjected to stronger selection.

6. Synthesis. This study indicated that the community composition of epiphytic bryophytes in the Amazon is mainly regulated by environmental conditions, both at local and at geographical scales. Dispersal, although predominantly local, did not show geographical structure across the area.

Key-words: altitudinal gradient, Amazon, canopy, determinants of plant community diversity and structure, liverworts, metacommunity, mosses, neotropics, neutral theory, vertical gradient

Introduction

The species composition of plant communities is shaped by the interplay of environmental filters, dispersal limitation and stochastic events. In bryophytes, environment acts from large scales, such as along altitudinal gradients (Wolf 1993; 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; Sporn et al. 2010) or through phorophyte preference (Szóvényi, Hock & Tóth 2004; Gabriel & Bates 2005). Dispersal limitation affects the abundance of species in local communities depending on their level of connectivity with the metacommunity (Löbel, Snäll & Rydin 2006; Zartman & Nascimento 2006), and dispersal strategy may influence species composition of communities, according to time since the substrate has become available for colonization (Hetsemekers, Dopagne & Vanderpoorten 2008). Because multiple processes are involved in the assemblage of communities, most of the studies in community ecology explain only a small part of the variation found in nature.

In the Guianas, we have shown that height zone on the host tree was the main driver of species composition of epiphytic bryophyte communities at both local and regional scales, explaining variation better than geographical distance, across 640 km of forest (Mota de Oliveira et al. 2009). Although the relationship between species composition and
the height zones of the host tree – the so-called vertical gradient – was shown to be very strong in the Guianas, the predictability of species occurrence remains limited, due to a considerable amount of unexplained variation. Specialists – species that can be predicted to occur in a given height zone and more strongly contribute to the relationship – corresponded to less than half of the pool of species and are not evenly distributed along the height zones. The assembly of different communities along the vertical gradient on the host tree might be not only related to the microenvironmental features of the height zones, but also to their role in facilitating the dispersal of propagula (spores or vegetative parts). It has been suggested that dispersal should be higher among individuals inhabiting the canopy, due to higher wind velocity (Gradstein 2006). Any attempt to explain more of the variation in community composition and therefore predictability of species occurrence in the Amazon should investigate the effect of higher geographical-scale gradients, including climatic variables, as well as the role of dispersal along the height zones.

It is a challenge to tackle bryophyte diversity in such a multiscale context. We believe that using the concept of a metacommunity, in a hierarchical approach, is appropriate to investigate the relative roles of environment and dispersal in local community composition (Ricklefs 1987; Whittaker, Willis & Field 2001). It treats the local community under study not only confined to its own individuals and habitat, but also as influenced by a higher level, that is the sum of other surrounding comparable communities. Yet, there are many ways to approach the 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. At first sight, the establishment of something like a ‘habitat species pool’ 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, since the species selected are then known to be able to occur in that given habitat, and their absence has a greater chance of being the effect of unsuccessful dispersal. 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 (SAD). In the framework of the Neutral Theory of Biodiversity and Biogeography (Hubbell 2001), the species abundance distribution of any given community can be described by two parameters, $\theta$ and $m$. The parameter $\theta$ is a measure of the diversity of the metacommunity, while $m$ stands for the recruitment rate at which individuals in the local community were recruited from the metacommunity. Within the same metacommunity (same $\theta$), $m$ gives an indication of how ‘isolated’ is the local community in relation to the complete species pool, based on its SAD. Calculating $m$ for multiple local communities originating from the same metacommunity, as proposed in Chave & Jabot (2006), allows their comparison. In the original theoretical concept, this ‘isolation’ was related to dispersal limitation alone, due to the assumption of ecological equivalence of all individuals, regardless of their species identity. In a further interpretation of the parameter, Jabot, Etienne & Chave (2008) suggested that $m$ could represent the sum of processes shaping species abundances in the local community under study, that is dispersal limitation and establishment limitation.

In the Amazon, we assume that epiphytic bryophytes behave as one single metacommunity in the sense of Wilson (1992) and Leibold et al. (2004), which means that species can disperse over the full area into local communities. This assumption is supported by the lack of endemics and the relative homogeneity in composition reported in a floristic study (Oliveira & ter Steege 2013). In this study, we use the approach of Jabot, Etienne & Chave (2008) for the parameter $m$, to attempt to estimate how dispersal and establishment limitation shape composition of communities along the gradient and across localities.

Here, we aim at increasing the predictability of epiphytic bryophyte species occurrence in terra firme forests of the Amazon. To achieve that, we investigated (i) whether the vertical gradient explains most of the variation in species composition of epiphytic bryophytes both at local and at geographical scales; (ii) whether climatic variables and elevation are related to species assemblages at geographical scale; (iii) whether dispersal limitation can be detected as distance decay in similarity at the geographical scale; and (iv) how dispersal limitation as well as establishment limitation rates vary according to height zone, based on the estimated recruitment rates from the metacommunity into local communities.

Materials and methods

STUDY AREA

The Amazon is a tropical rain forest covering an area of approximately 6 million km$^2$ in northern South America. It shows a mosaic of landscapes, in which the non-flooded forest on plateaus, known as ‘terra firme forest’, predominates. The sampling for this study was carried out in nine *terra firme* forest localities, spread across the Amazon from the mouth of the Amazon River to Ecuador, as follows: three localities in the Guianas, three localities in an east–west transect along the Amazon River, two localities to the west of the transect, at two main tributaries, in Brazil, and finally one locality in Ecuador, as the most western point of the transect. Coordinates and abbreviations of the localities, as well as values of selected climatic variables and elevation, are given in Table 1.

SAMPLING

We sampled epiphytic bryophytes in five height zones, from the bottom to the canopy of eight canopy trees in each of the nine localities (1 sample $\times$ 5 height zones $\times$ 8 trees $\times$ 9 localities). Each sample was obtained by collecting four patches of approximately
Table 1. Site characteristics for the nine sites studied

| Site | LON   | LAT   | Elev | APt | M1M | M3M | AT  | Tmin | Tmax |
|------|-------|-------|------|-----|-----|-----|-----|------|------|
| CX   | -51.46204 | -1.71986 | 33   | 2993 | 26.9 | 149.9 | 26.8 | 21.7 | 33.0 |
| FG   | -53.19099 | 3.63333  | 276  | 2822 | 8.1  | 137.7  | 24.3 | 18.9 | 30.9 |
| MM   | -58.70394 | 5.17887  | 136  | 2745 | 11.4 | 70.1   | 26.2 | 21.1 | 31.8 |
| MW   | -58.70394 | 5.17887  | 136  | 2745 | 11.4 | 70.1   | 26.2 | 21.1 | 31.8 |
| TA   | -54.96278 | -2.50917 | 12   | 2097 | 7.6  | 38.6   | 26.3 | 20.9 | 32.6 |
| RD   | -59.96920 | -2.92761 | 67   | 2542 | 15.6 | 98.8   | 27.3 | 22.6 | 32.8 |
| UR   | -62.35000 | -3.57000 | 32   | 2754 | 33.9 | 172.6  | 26.6 | 21.9 | 32.2 |
| SG   | -65.63000 | -0.14000 | 73   | 2758 | 43.4 | 297.1  | 26.7 | 21.5 | 32.0 |
| EC   | -75.95000 | -0.72000 | 344  | 2410 | 27.0 | 160.2  | 24.4 | 18.9 | 30.2 |

Elev, elevation from digital elevation model; APt, annual precipitation; M1M, rain (mm of rain for the driest month from 1999–2009); M3M, mm of rain for the driest three-month period from 1999–2009; AT, annual average temperature; Tmin, lowest temperature in the coldest quarter; Tmax, highest temperature in the warmest quarter. Elev, AT, Tmax and DEM from Bioclim (Hijmans et al. 2005), APt, M1M, M3M from TRMM data (http://trmm.gsfc.nasa.gov/).

10 × 10 cm² in each height zone. Five height zones were established in each tree: from the base up to 1.5 m (zone 1), via the lower and upper trunk (zones 2 and 3) to the base of the crown (zone 4) and finally the outer sunlit twigs (zone 6) (Mota de Oliveira et al. 2009).

Identification of specimens present in the samples and standardization of data from the Guianas followed the procedure already described in (Oliveira & ter Steege 2013). The composition of a sample consisted of a list of the species recorded. We did not record abundance here, due to the impossibility of separating individuals for most of the species and due to the variation in plant size. Thus, we assumed that each occurrence of a species in one sample is the result of a single colonization event. Because bryophytes grow vegetatively, the size of one colony does not relate directly to the number of colonization events, and colonization events, or recruitment, are exactly what matters for the calculation of the parameter m. In order to have quantitative information on community structure, that is species abundance distribution, per locality or per height zone, depending on the analysis, we used frequency as a measure of abundance, summing the number of samples in which each species was recorded. Thus, we calculated abundance by pooling sampling units and counting the number of individual records of a species in a given site (all site samples) or in a given height zone (all height zone samples). As a consequence, the abundance value of a species in the species abundance distribution of a given locality can range from 1 to 40 (40 indicates occurrence in all five plots of all eight trees of that locality). Similarly, an abundance value of a species in the species abundance distribution of a given height zone can range from 1 to 72 (72 indicates occurrence in all nine localities and all eight plots per locality of that height zone).

DATA ANALYSIS

In order to test whether the vertical gradient in species composition holds at local scale, we carried out the indirect ordination method detrended correspondence analysis (McCune & Grace 2002) with data from every locality studied, separately. We used DCA because this method makes no a priori assumption of an external gradient, and the distribution of the communities in the ordination space is calculated solely according to species composition, assuming unimodal response curves, as we expected to be the case along the height zones. 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. Further, we selected climatic variables to perform the analysis at a geographical scale. We performed principal component analysis with 10 environmental variables and selected the five variables that correlated most strongly with the first four axes: ‘elevation’ and ‘annual average temperature’ (Tavg) with axis 1 (we dropped other temperature variables that were strongly colinear with Tavg); ‘precipitation in the driest three-month period’ (Min3Mon) with axis 2 (and dropped all other strongly collinear rainfall variables); ‘mean diurnal temperature range’ (Trange) with axis 3; and ‘annual precipitation’ with axis 4. All precipitation data corresponded to 10 year of TRMM data and all temperature data from Bioclim (Hijmans et al. 2005). After selecting the environmental variables, we performed another DCA ordination with the complete Amazonian data set, pooling plots by height zone by locality. We then performed the ‘envfit’ function of the R library vegan (Oksanen et al. 2013), to search for a relationship between the environmental variables, including height zone, and species composition of the localities. Sorensen dissimilarity in species assemblage was calculated for plots in the same locality and for plots in different localities, by height zone. Furthermore, the correlation between Sorensen dissimilarity values calculated for localities – pooled samples – and geographical distance between localities (distance decay) was tested with Mantel test (Legendre 1998).

Finally, we calculated the parameter m derived from the neutral theory for different subsets of metacommunity/local communities (Fig. 1), allowing differentiation between dispersal and environmental filters acting upon the recruitment rate of a local community Jabot, Etienne & Chave (2008), using the freeware TeTame (Chave & Jabot 2006). An intuitive way of interpreting the parameter is by knowing in advance that, on a scale from 0 to 1, the closer m gets to 0, the more isolated is the local community in relation to the metacommunity. A random draw of the metacommunity would return a value of m very close or equal to 1. First, we addressed recruitment rate by calculating the parameter m for complete assemblages, in which the metacommunity was formed by the complete data set and each local community was built by all individuals of all plots in one locality (Fig. 1a). Further, in order to investigate the role of environmental filtering in the recruitment rate from the metacommunity to local communities along the height zones, we built (theoretical) local communities by pooling data from all localities per height zone – in this way, we avoided the effect of dispersal limitation in the calculation by eliminating distance (Fig. 1b). Finally, in order to investigate the role of dispersal limitation in the recruitment rate from the metacommunity to local communities along the height zones, we built the metacommunity according to the concept of habitat species pool: data from all localities per height zone – in this way, we avoided the effect of dispersal limitation in the calculation by eliminating distance (Fig. 1b).
of establishment limitation, while local communities were composed of all plots in the zones of the habitat to be analysed in a given locality (Fig. 1c).

**Results**

In every locality studied, the strongest intrinsic gradient in species composition of epiphytic bryophytes was the vertical zonation on the host trees (Fig. 2), with some variability in the strength of the relationship. The correlations between the scores of the first axis of the DCAs and the height zone of the samples were tested with Monte Carlo regression, and all slopes as well as all R squares were significant at $P < 0.001$. The explained variation given by the first axis 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). The lowest values of explained variation and correlation coefficients were found in central Amazon localities, especially in Uruçu, São Gabriel da Cachoeira and Reserva Ducke (Fig. 2).

When the same analysis was performed for the complete data set — scaling up by using all data by zone for each complete locality, instead of plots — the height zones were not correlated with the first axis of the DCA and therefore not the main explanatory variable for species composition. Yet, they showed a significant correlation with the scores of the second axis of the DCA ($P < 0.001$, Fig. 3). The variables that best correlated with axis 1 were elevation, mean yearly temperature and minimum temperature (Table 2).

The similarity between communities of the same locality was significantly higher than that between communities of different localities in samples of all height zones. The highest similarity values corresponded to comparison between communities of height zone 6 from the same locality (Fig. 4). The positive correlation between floristic and geographical distances found had values close to 0, which we do not consider biologically relevant (data not shown).

The calculation of the parameter $m$ for the species abundance distribution of each locality in relation to the complete metacommunity, eliminating the vertical gradient, showed that recruitment of individuals from the metacommunity attained similar rates across the localities, 0.2 on average (data not shown). Pooling localities together, to eliminate the effect of long-distance dispersal limitation, and thus estimate establishment limitation per height zone, showed that zones 1 and 6 drew individuals from outside their own habitat species pool at a rate of 0.28 and 0.22, respectively, whereas the other height zones showed rates between 0.55 and 0.76 (Figs 1b and 5). Using the habitat species pool approach to eliminate the effect of establishment limitation, and thus estimate recruitment of individuals from long-distance dispersal per height zone, resulted in rates of long-distance dispersal between 0.44 and 0.59 without a clear pattern along the gradient (Figs 1c and 5).

**Discussion**

**LOCAL AND REGIONAL VIEWS OF THE VERTICAL GRADIENT**

In all localities studied across the Amazon, the vertical micro-environmental gradient was the main driver of the local variation in species composition of epiphytic bryophyte communities. Yet, we found that the strength of the relationship varied across localities, being weakest in central Amazon. The influence of the vertical microenvironmental gradient on the species composition of epiphytic bryophytes

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Fig. 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), the metacommunity concept is the habitat species pool. Larger white rectangles represent metacommunities, and grey rectangles represent local communities. Arrows show the link metacommunity–local community involved in the calculation. For further explanation, see text.

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has been documented in a few tropical forests in South and Central America and Indonesia (Cornelissen & ter Steege 1989; Costa 1999; Acebey, Gradstein & Krömer 2003; Holz & Gradstein 2005; Sporn et al. 2010), as well as in temperate forests (McCune et al. 2000). Although frequently reported, the amount of variation in communities explained by the relationship between height zone and species composition is not always quantified, which makes it difficult to compare the intensity of the relationship across areas. The pattern might be absent or very weak, such as shown by studies in the Atlantic forest of north-eastern Brazil (Alvarenga, P orto & de Oliveira 2009; Silva & P orto 2013). The authors suggest that human impact and fragmentation of the forest can lead to higher canopy openness rates and consequently to loss of diversity, mainly of species with narrow niche. In the present study, because all localities sampled were actually part of a continuous primary forest, we believe that the variation we found in the strength of the relationship were not due to human impact, but to features of the forest structure and dynamics that can vary across the Amazon (Anderson 2012). Canopy height, for instance, shows the highest values in the Guianas (38–41 m), followed by eastern Amazon (31–35 m) around Tiputini (EC). The lowest canopy (26–31 m) occurs around our localities in central Amazon – São Gabriel da Cachoeira and Manaus (SG and RD) – where the strength of the vertical gradient was also the lowest. Comparing this pattern to our results, it is possible that higher canopies produce a stronger microenvironmental gradient in the forest and therefore a clearer turnover on species composition.

While the vertical zonation remained the most important explanatory gradient at regional scale in the Guianas (Mota de Oliveira et al. 2009), this was not the case across the Amazon. The explanation for the pattern found in the Guianas is that the two forests in Guyana are compositionally subsets of French Guianas’ forest. Therefore, local recruitment, though being high, did not cause compositional differences that could override the differences in height zone composition, because of the ‘homogeneity’ of the species pool in the three localities. In this study, across a much wider geographical area, subjected to a larger species pool, the effect of local recruitment becomes clearer. As shown in our results, samples from the same
locality, in all height zones, are significantly more similar than samples from different localities. The predominant local recruitment explains why microenvironment is not the main variable driving community composition when data from all localities were analysed together. The fact that vertical zonation correlated with the second axis of the ordination indicates that height zone remains, also at regional scale, among the most important drivers of species composition.

GEOGRAPHICAL PATTERNS: LOWLAND FORESTS WITH AN ELEVATION TOUCH?

The lack of geographical structure found in our data, given by the low correlation coefficient of the distance decay in similarity at distances from 15 to 2835 km, is probably tightly related to the dispersal curves of bryophytes. 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 also suggested for bryophyte diasporas by Miles & Longton (1992). Most of the propagules fall very close to their origin, while the rest can travel very far, by chance, in air turbulence or attached to insects (Miles & Longton 1992; Sundberg 2005). Over medium to large distances, propagules show the same chance of arrival because they become airborne, and therefore, trajectory is less influenced by deterministic features such as weight, shape or angle of release and more influenced by the wind currents and stochastic breakdowns. Based on these speculations and on our results, we believe that long-distance dispersal of bryophytes in the Amazon does not lead to geographical structure in species composition.

Surprisingly for a lowland forest, elevation and temperature had the strongest correlation with species composition, among all environmental/climatic variables tested. Although the importance of elevation on bryophyte diversity and composition has been frequently pointed out in the literature, the localities in this study belong all to the lowland forest. The establishment of the first altitudinal belt varies among studies according to region or taxa sampled, and the limit of the lowland forest belt in bryophyte studies was already established at 300–500 m, based on data from NE Peru and Borneo (Frahm & Gradstein 1991); at 300 m in Papua New Guinea (Enroth 1990); and at 50 m in the Atlantic forest of southeastern Brazil (Costa & Lima 2005). It is not desirable to reach a consensus about the limit of the first belt, due to intrinsic regional differences in biogeography, local topography and climate (Kessler 2000). In our case, does the small range in elevation (around 300 m) cause a significant turnover on species composition? Probably not. There is evidence

Table 2. Values of $\lambda$ and the explained variation of the first axis of the DCA per locality

| Locality | $\lambda$ | Axis 1 |
|----------|----------|-------|
| CX       | 0.796    | 0.36  |
| EC       | 0.478    | 0.33  |
| FG       | 0.722    | 0.51  |
| MM       | 0.659    | 0.52  |
| MW       | 0.736    | 0.58  |
| RD       | 0.593    | 0.25  |
| SG       | 0.328    | 0.28  |
| TA       | 0.690    | 0.34  |
| UR       | 0.817    | 0.25  |
enough to believe that the highest localities, Tiputini, in Ecuador, and Saül, in French Guiana, still harbour most of the lowland bryoflora. In addition to that, however, they may have a local microclimate that favours the establishment of some sub-montane and/or Andean elements, such as the genera *Porotrichum* and *Neckeropsis* and an increased occurrence of *Plagiochila* (Oliveira & ter Steege 2013). Slight changes in temperature might prevent some of these species to be abundant or even to occur in other lowland forests (Wagner, Zotz & Bader 2013). Some areas of Saül, for instance, were recognized as ‘tropical lowland cloud forest’ due to the significantly higher frequency of fog, which increases water availability and consequently epiphytic biomass and diversity (Ah-Peng *et al.* 2007; Medina *et al.* 2013). The locality in Ecuador, Tiputini, might also show these conditions, but robust physical measurements are still lacking.

**ESTABLISHMENT LIMITATION AND DISPERSAL LIMITATION ALONG THE GRADIENT**

The results obtained from the calculation of the parameter $m$, based on the species abundance distributions of the metacommunity and sets of local communities, suggested that the establishment limitation is higher at the extremes of the gradient. The hypothesis was earlier proposed based on the fact...
that species with a significant preference for a given height zone inhabit either the base or the canopy (Mota de Oliveira & ter Steege 2013). In this study, we found support for this hypothesis and estimated further that only circa of 22% and 28% of the individuals were drawn from outside of the habitat species pool.

It has been advocated that the main environmental filters in the outer canopy are light intensity and drought, based on the disappearance of some understory elements in gaps or tree-fall areas and the recorded shift of canopy species downwards, when light and drought penetrate deeper (Acebey, Gradstein & Krömer 2003). Recently, it was shown that species inhabiting the canopy of the forest, in French Guiana, withstand desiccation events better than understory species (Pardow & Lakatos 2013). At the other extreme, what are the processes that limit establishment of certain species on the base of the trees? Competition is not commonly considered to be important for bryophyte communities (Slack 1990). During & Lloret (2001) review evidence that competitive exclusion hardly takes place in bryophyte vegetation and state that 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. Consequently, the evidence may not hold for the opposite condition – a moist and dark understory of a bark surface in the Amazon. Here, contrary to temperate forests, water is not limiting, but light is. We propose that 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 in the understory, may impose constraints to establishment of new individuals.

Dispersal limitation estimated using the parameter m concerned only long-distance dispersal, due to the approach metacommunity–local community (see methods). We expected to find a clear differentiation regarding the origin of most of the long-distance dispersal events due to the well-known pattern of increased wind speed along the canopy profile (Cionco 1972; Krujt 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 (Muñoz et al. 2004). The values of m obtained in this study suggested, contrary to our expectations, that the rate of recruitment from long-distance dispersal events is not increased in the canopy. In an earlier analysis, we had proposed that long-distance dispersal increases with increasing height along the vertical gradient of a tree, based on a comparison between understory and canopy communities (Mota de Oliveira 2010). A reconsideration of the procedure, however, showed that we used metacommunities of different sizes in the analysis, which may have caused a bias due to the tendency of higher values of m with the decreasing size of the metacommunity.

In this study, by analysing the recruitment rate from the metacommunity into local communities of different zones, we did not find support for the hypothesis of facilitated (long-distance) dispersal in the canopy. However, at local scale, canopy communities showed the highest similarity values, which lends support to the hypothesis that canopy bryophyte communities are more connected due to facilitated dispersal through wind. The contrasting results seem to indicate that the dispersal of canopy-inhabiting species is facilitated only at local scale, 10–15 km in our study. Despite the fact that (wind) dispersal distances reported are within a few metres (McQueen 1985; Kimmerer 1991; Stoneburner, Lane & Anderson 1992), the transport of spores or even plant fragments by animals can lead to greater distances, of hundreds of metres (van Tooren & During 1988; Heikken 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). These measurements could very well represent the area to which we refer as local scale. Future population studies on dispersal abilities of canopy and understory species can help understand why apparently height zone has a stronger effect on dispersal at local scale.

Finally, one can still argue that the higher values of similarity among canopy communities are again caused by microenvironment, rather than increased dispersal. If the canopy was shown to be more homogeneous in terms of environment (understorey environment is more subjected to differences as the presence/absence of creeks, distance of a gap, more variability in bark surface in comparison with the thin branches of the outer canopy, etc.), the higher heterogeneity in the understory could decrease similarity among communities. In this case, establishment limitation and not dispersal limitation would be the process behind the pattern found. Therefore, it is desirable to treat both explanations as working hypotheses.

CONSEQUENCES AND CAVEATS OF THE METACOMMUNITY – LOCAL COMMUNITY APPROACH

Although the manipulation of subsets of the data helps disentangling the effects of establishment and dispersal limitation, the recruitment rates calculated with the parameter m cannot be used to calculate the relative contribution of each process in the assemblage of the communities. Note that m is used here as an abstract value to measure the isolation of a local community in relation to the metacommunity that was assigned to it; thus, comparison of m values is restricted to each analysis. The approach revealed, however, that the stronger establishment limitation at the extremes of the gradient is not compensated by facilitated dispersal.

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