Tropical bryophyte floras: a homogeneous assemblage of highly mobile species? Insights from their spatial patterns of beta diversity

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The impact of Pleistocene climate changes substantially varied between tropical regions, resulting in striking differences in angiosperm species richness caused by post-glacial recolonization delays. Tropical bryophytes, which have been perceived as extremely good dispersers due to biased rates of monoecy and hence spore production, differ strikingly from angiosperms in their similar patterns of species richness among tropical regions. Here, we analyse the patterns of beta diversity of tropical bryophytes to determine whether their high dispersal capacities have balanced patterns of species richness and erased any difference of post-glacial recolonization patterns between tropical regions. The partitioning of beta diversity for 7485 tropical moss species among 164 operational geographical units (OGUs) and 3276 liverwort and hornwort species in 154 OGUs revealed a slight, but significantly higher beta diversity among than within tropical regions. The nestedness component of beta diversity did not significantly differ between tropical regions. This indicates that, although regional migration rates were sufficient to erase differences of the impact of Pleistocene climate changes between tropical regions, the similar bryophyte species richness of tropical regions cannot be interpreted in terms of unrestricted migrations and that oceans act as a barrier to routine dispersal, which is sufficient to shape large-scale floristic patterns. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016

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INTRODUCTION

The uneven distribution of species richness across the globe has long been recognized a time ago, and the latitudinal gradient of biodiversity that

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culminates in the profusion of the variety of life in the equatorial tropics appears as one of the few truly universal ecological rules (Mittelbach *et al.*, 2007; but see Mateo *et al.*, 2016; and references therein). Although tropical rain forests are renowned for high species richness, this is neither uniformly distributed nor is it always the case (Corlett & Primack, 2010). For example, tropical Africa includes 32 400 angiosperm species across around 22 million km^2 (Klopper *et al.*, 2007) compared to 90 000 in 17.84 million km^2 in the Neotropics (Raedig *et al.*, 2010) and 42 000 species in 3 million km^2 in Malesia (Linder, 2014).

The comparative biotic poverty in tropical Africa has been interpreted as a result of extinctions caused by historical climate shifts towards increasing drought (Maley, 1996; Morley, 2000). All the tropical regions of the world experienced severe vegetation shifts during the glacial cycles of the Pleistocene, with forest contractions during cold periods. The recolonization of grasslands and savannas that prevailed during the driest and coolest periods of the Pleistocene has been challenged by the low dispersal capacities of many rainforest species. While, in the Neotropics, a few common tree species dominate immense areas of forest (ter Steege *et al.*, 2013) and may even display transoceanic distributions following long-distance dispersal (Dick *et al.*, 2007), the spatial aggregation of many woody tropical species, characterized by low levels of anemochory, high levels of zoochory and the production of large diaspores (Butler *et al.*, 2007; Muscarella & Fleming, 2007; Beaune *et al.*, 2013), reflects dispersal limitations (Myers *et al.*, 2013). Delays in the recolonization of forest areas led to nested patterns (Midgley *et al.*, 2004) due to the fact that species assemblages of the poorest sites are subsets of those of the richest sites. African rainforests were, however, substantially more impacted than Neotropical ones (Parmentier *et al.*, 2007; Kissling *et al.*, 2012). In particular, pollen and geochemical evidence suggests that, during the last glacial maximum, the African rainforest area was reduced by *c*. 84%, whereas the Amazon humid forest area probably shrank to 54% of its present-day extent (Anhuf *et al.*, 2006). Extinction processes are, furthermore, expected to be stronger in Africa than in Amazonia because of the smaller African rain forest area (*c*. 24 million ha in Africa vs. 668 million ha in Amazonia), resulting in smaller population sizes, which in turn enhances extinction risk (Parmentier *et al.*, 2007).

Bryophytes offer an original model to address questions concerning patterns of floristic diversity in the tropics. In mosses, of which the 2109, 2583 and 2676 tropical African, Neotropical and tropical Asian species contribute 32%, 39% and 41% of the global tropical moss species pool, respectively (Geffert *et al.*,

2013), species richness patterns are much more balanced among tropical regions than in angiosperms, pointing to differences in the assembly mechanism of tropical biota between the two groups. In fact, bryophytes in general (Medina, Draper & Lara, 2011) and tropical bryophytes in particular (Schuster, 1983) seem, in contrast to rainforest tree species, especially well equipped for dispersal, so that niche preference rather than dispersal limitation shapes species distribution patterns (Mota de Oliveira *et al.*, 2009). Using null model analyses based on metacommunity concepts for Amazonian epiphytic bryophyte communities, Mota de Oliveira & ter Steege (2015) concluded that 'long-distance dispersal of bryophytes in the Amazon does not lead to geographical structure in species composition'. Lowland tropical bryophytes have indeed been considered as 'highly specialized elements with higher than normal levels of monoecism' (Schuster, 1983). Such a departure of the sexual systems of tropical mosses and liverworts from the general patterns in these groups is expected to have a substantial impact on their reproductive success. Indeed, mosses and liverworts disperse by specialized asexual diaspores and spores, which are assumed to be involved in short- and long-distance dispersal, respectively (Schuster, 1983). Spore production is tightly linked to sexual systems because sexual reproduction depends on sperm being able to reach the ova by swimming through a continuous film of water. In monoecious species, which represent about one-third of all moss and liverwort species, this functional constraint is weak, as the distance between male and female sexual organs on the same plant is minimal. Although it should not be assumed that monoecious species are selfing simply because the male and female gametangia are simultaneously mature and although one case of self-incompatibility was recently reported (Stark & Brinda, 2013), monoecious bryophyte species are assumed to be capable of self-fertilization, as evidenced by the high Fis values observed in the sporophytic phase of all monoecious species investigated so far (Hutsemékers, Hardy & Vanderpoorten, 2013; Johnson & Shaw, 2015; Klips, 2015). In dioecious species, conversely, the likelihood of fertilization is inversely proportional to the distance between male and female plants. As a result, sporophyte production is significantly lower in dioecious than in monoecious species (Longton, 1997; Laaka-Lindberg, Hedderson & Longton, 2000). Monoecious bryophyte species have therefore been perceived as better dispersers than dioecious ones (Schuster, 1983). However recent evidence suggests that, in line with the high proportion of pantropical species in the mostly dioecious family Calymperaceae, production of specialized asexual diaspores contributes to long-distance dispersal (Laenen *et al.*,

2016). This situation would explain why dioecious species are filtered out along a gradient of geographical isolation, as shown by the balanced proportion of monoecious and dioecious bryophyte species on oceanic islands (Patiño *et al.*, 2013). Increased rates of monoecy, combined with other traits such as precocious germination of spores, while still in the capsule, have led to the hypothesis that tropical bryophytes are particularly well equipped for long-distance dispersal and rapid and efficient establishment (Schuster, 1983). A mechanism potentially triggering high dispersal capacities in tropical bryophytes is that, due to the accumulation of large amounts of debris and low light intensities on the forest floor, tropical bryophytes tend towards epiphytism, which would have been selective for short-term life cycles and high dispersal capacities.

Here, we address the question of how the high long-distance capacities of tropical bryophytes impact on their global patterns of species diversity. More specifically, we test the following hypotheses.

1. If the similar patterns of bryophyte species richness result from dynamic floristic interchanges among tropical regions, we expect that the strong environmental gradients that characterize tropical regions rather than geographical isolation between regions shape their patterns of species richness and, hence, that total beta diversity between regions is not significantly higher than within regions (Hypothesis 1).

2. If tropical bryophytes, unlike angiosperms, did not experience delays in the recolonization of areas that underwent severe vegetation shifts during the last glacial cycles, we expect that, despite the fact that sub-Saharan Africa was substantially more impacted than the Neotropics and tropical Asia by historical climate change, sub-Saharan African floristic assemblages are not significantly more nested than those of the two other tropical regions (Hypothesis 2).

MATERIAL AND METHODS

FLORISTIC DATA

Tropical areas were defined according to the traditional latitudinal limits of 23.5 degrees, but followed some modifications by Condamine *et al.* (2012) so that tropical areas included sub-Saharan Africa, Madagascar, the Neotropics, southern India (including Sri Lanka), the Malayan region (i.e. southern China, Malaysian Peninsula and Indochina) and Australasia (including northern Australia, Melanesian Islands, Papua New Guinea and Wallacea). Focusing on the tropical areas, we partitioned the

data into the Neotropics, sub-Saharan tropical Africa and tropical Asia.

For mosses, information on the distribution of 7485 tropical species among 164 operational geographical units (hereafter, OGUs) was retrieved from Geffert *et al.* (2013). For liverworts, the most comprehensive database of species distributions available to date, which has been built in the context of the Early Land Plants Today project (von Konrat, Söderström & Hagborg, 2010), was employed to document the distribution of 3276 liverwort species, keeping only verified species names (Söderström *et al.*, 2016), at the level of 154 tropical OGUs worldwide. Hornworts should, for consistency, have been analysed separately. They are, however, a small group of *c*. 150 species the diversity of which pales in comparison with liverworts (6000 species) and mosses (10 000 species). The number of hornwort species in our data set did not warrant separate analyses (1–3% of the total liverwort number depending on the tropical region), and since hornworts exhibit a suite of functional vegetative traits and ecological features that are similar to those of liverworts, the data from the two groups were merged (hereafter, liverworts).

The liverwort data set, provided in Supporting Information (Appendix S1), is derived from a pool of resources and cross-referencing, involving a combination of species checklists, annotated checklists with synonyms, monographs, revisions, specialist and broad taxonomic papers. The present working data sets includes: a bibliography of 13 500 publications; *c*. 35 000 published liverwort names (including 'accepted' taxa, infraspecific ranks, synonyms, invalid and illegitimate names); > 400 000 geographical observations (a single observation is a record of one taxon from one OGU); and almost 500 geo-political units (e.g. state, province, country). As a more specific example, > 3500 journal articles and monographs have been used so far as input for this data.

DATA ANALYSIS

To test Hypothesis 1, we computed total beta diversity (Jaccard dissimilarity, β_{jac}) within and among tropical regions (Neotropics, tropical Africa and tropical Asia). Multiple-site dissimilarities were computed 100 times for randomly sampled subsets of 20 OGUs from the original pool of each region to evaluate how β_{jac} varies within each tropical region. Second, we calculated multiple-site dissimilarities computed 100 times for randomly sampled subsets of 20 OGUs, ten of which were sampled from each of two continents, to determine how dissimilarities in β_{jac} vary between pairs of regions. The significance of the within-continent and between-continent differences in β_{jac} was estimated as the degree of overlap

between the parameter distributions estimated through the bootstrapping with replacement procedure mentioned above. The rationale of these analyses is that if beta diversity were driven by within-continent environmental variation, then the inclusion of OGUs from different continents (among-continents analyses) would not increase beta diversity compared to the within-continent analyses.

To test Hypothesis 2, we partitioned total beta diversity (β_{jac}) into contributions by turnover (β_{jtu}) and nestedness-driven dissimilarity (β_{jne}) following Baselga (2010, 2012) and Baselga & Leprieur (2015). Nestedness occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites. Spatial turnover is the replacement of some species by others as a consequence of environmental sorting or spatial and historical constraints (Baselga, 2010). In the first case (nestedness), total diversity would just be equal to that of the richest local assemblage, whereas in the second case (spatial turnover), total diversity would be the result of pooling the different local assemblages and thus be higher than that of any local assemblage. Due to the coarse grain size of our OGUs, we expect to observe high and similar levels of species turnover across tropical regions. However, if, as palaeontological evidence suggests, vegetation shifts were substantially more severe in tropical Africa than in the two other tropical regions, we expect that the nestedness component of beta diversity is significantly higher in tropical Africa than in tropical Asia and in the Neotropics. All computations were performed in R (R Core Team, 2013) using the package 'betapart' 1.3 (Baselga & Orme, 2012).

RESULTS

Total beta diversity (β_{jac}) among OGUs was higher between than within continents (Fig. 1; Table 1). In both moss and liverwort floras, β_{jac} in the Neotropics was from marginally to significantly lower than in Neotropical-tropical Asia and Neotropical-sub-Saharan Africa comparisons. β_{jac} in mosses was significantly lower in tropical Asia than in tropical Asia-Neotropical and tropical Asia-sub-Saharan Africa comparisons. For liverworts, these differences were only marginally significant (Table 1). In both
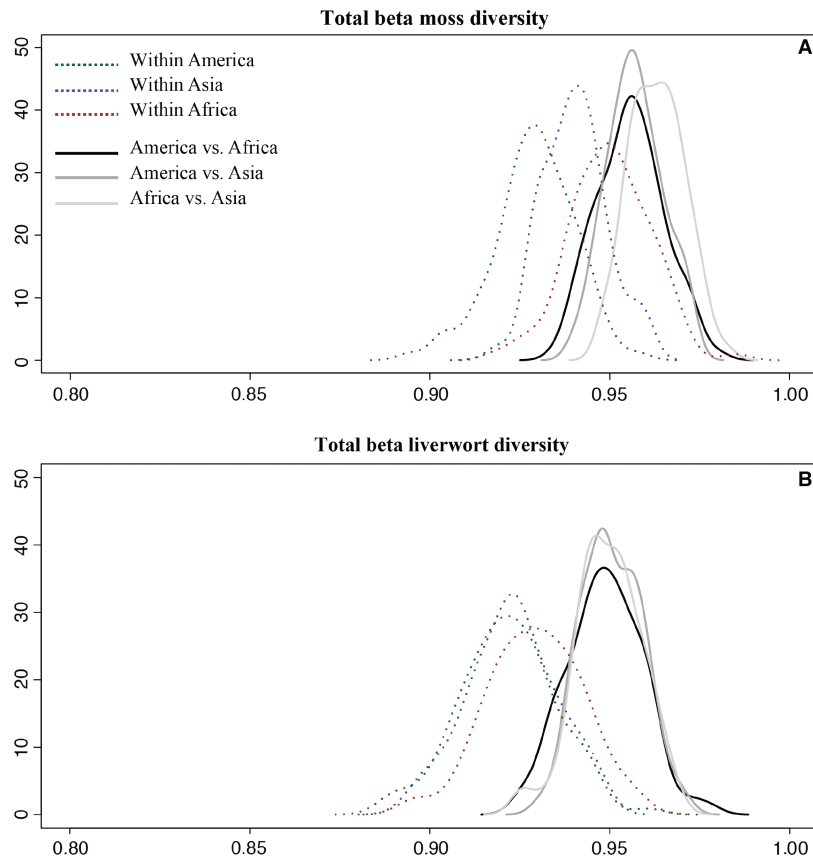

Figure 1. Comparison of total beta diversity (β_{jac}) in mosses (A) and liverworts (B) among OGUs within and among tropical regions, respectively.

Table 1. Significance tests (*P*-value) for the difference in total moss and liverwort beta diversity (β$_{jac}$) within vs. between tropical sub-Saharan Africa (Africa), the Neotropics and tropical Asia (Asia; see Fig. 1)

	Moss β$_{jac}$	Liverwort β$_{jac}$
Within Africa vs. between Africa–Asia	0.15	0.13
Within Africa vs. between Africa–Neotropics	0.38	0.15
Within Asia vs. among Asia–Africa	0.03	0.05
Within Asia vs. among Asia–Neotropics	0.05	0.06
Within Neotropics vs. among Neotropics–Africa	0.05	0.03
Within Neotropics vs. among Neotropics–Asia	0.04	0.01

moss and liverwort floras, there were no significant differences in β$_{jac}$ in sub-Saharan Africa in comparison with tropical Africa-Asia and tropical Africa-Neotropics.

Within tropical regions, the species turnover component of beta diversity (β$_{jtu}$) was systematically higher than nestedness-driven dissimilarity (β$_{jne}$; Fig. 2). β$_{jac}$ (Fig. 1), β$_{jtu}$ and β$_{jne}$ (Fig. 2) among OGUs within tropical regions were similar in sub-Saharan Africa, the Neotropics and Asia. However, β$_{jac}$ in mosses among OGUs in sub-Saharan Africa

was marginally higher than β$_{jac}$ among OGUs in the Neotropics (*P* = 0.05) and in tropical Asia (*P* = 0.07) (Table 2).

DISCUSSION

The analyses presented here are among the first to describe the spatial structuring of bryophyte communities at a large scale (see Aranda *et al.*, 2013; Mateo *et al.*, 2016), but intimately depend on the limitations in our knowledge of species identities (the Linnean shortfall) and distributions (the Wallacean shortfall) (Diniz-Filho *et al.*, 2013). This issue, which is already present for well known taxa like angiosperms in well known areas like Europe (Petřík, Pergl & Wild, 2010), is particularly pronounced in tropical areas (Küper *et al.*, 2006) and culminates in organisms with reduced morphologies and, hence, uncertain taxonomy like bryophytes (Vanderpoorten & Shaw, 2010). During the period of active bryological exploration of extra-European regions during the 19th century indeed, hundreds of new 'geographical species' were described based in large part on the assumption that populations from distant regions must represent species distinct from familiar European taxa (Shaw, 2001) and also because many species were described by taxonomists who could not have at that time a worldwide vision of their group of interest, resulting in an overestimation of local endemics. In this context, O'Shea (1997a, b)
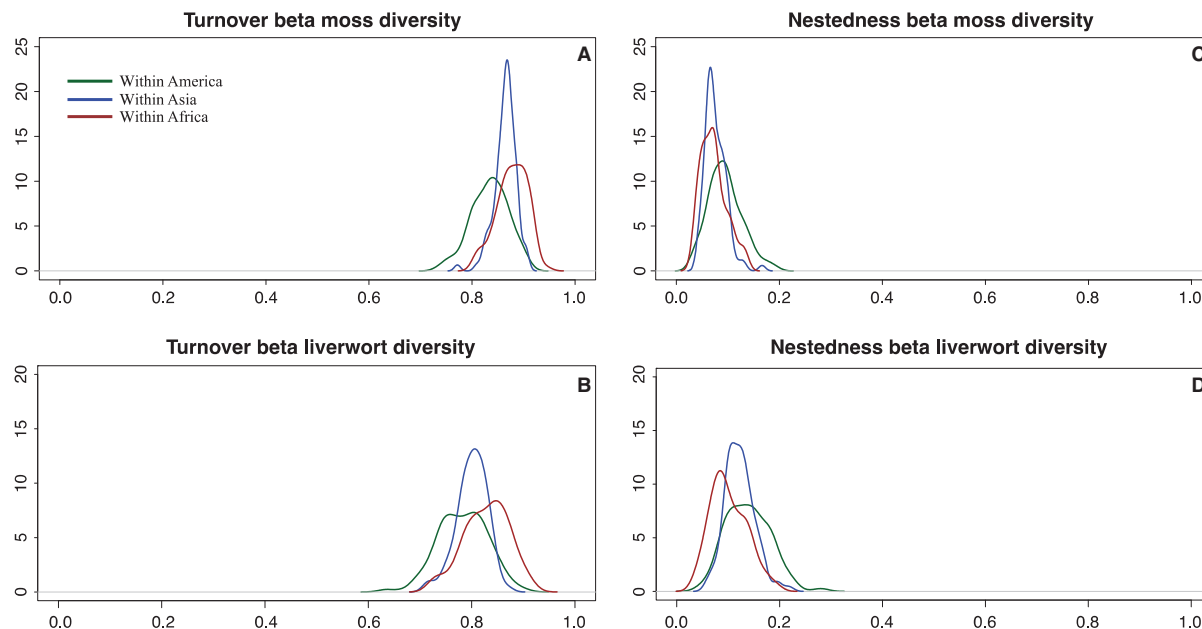

Figure 2. Partitioning of total beta diversity in tropical mosses (A, C) and liverworts (B, D) into its species turnover (β$_{jtu}$) and nestedness (β$_{jne}$) components within each of the three continental regions considered (America, Asia and Africa).

Table 2. Significance tests (*P*-value) for the pairwise comparisons of total beta diversity (β_{jac}; Fig. 1), species beta turnover (β_{jtu}; Fig. 2) and species beta nestedness (β_{jne}; Fig. 2) among OGUs in mosses and liverworts within the Neotropics, tropical sub-Saharan Africa and tropical Asia.

	Africa–Neotropics	Asia–9Neotropics	Africa–Asia
Total beta diversity (β_{jac})			
Mosses	0.05	0.36	0.07
Liverworts	0.40	0.16	0.74
Turnover beta diversity (β_{jtu})			
Mosses	0.71	0.74	0.84
Liverworts	0.46	0.32	0.63
Nestedness beta diversity (β_{jne})			
Mosses	0.39	0.31	0.28
Liverworts	0.56	0.54	0.56

predicted an overall reduction of 77% of endemism to *c.* 43% of the existing list of mosses for Africa. Such an overestimation of local endemism is likely to lead to an overestimation of beta diversity. There are also substantial floristic gaps in the Neotropics, e.g. the Pacific coastal region of north-western South America, Peru, the tepuis of the Guayana Highland (Gradstein, Churchill & Salazar, 2001) and large tracts of the driest areas (Germano, Silva & Peralta, 2016). Nevertheless, the global similarity of the patterns independently observed in mosses and liverworts suggest that, despite the limitations of the data, the patterns observed are robust.

Thus, and as opposed to our primary hypothesis, total beta diversity of mosses and liverworts was slightly, but in the Neotropics and Asia significantly, higher between than within tropical regions. This situation suggests that the similar moss and liverwort species richness between tropical areas as compared with angiosperms cannot be interpreted in terms of unrestricted migrations among tropical regions and indicates that, although instances of transoceanic dispersal among tropical regions have been recurrently inferred from species-level phylogenetic analyses (Heinrichs *et al.*, 2005, 2009; Hentschel *et al.*, 2007), oceans act as a barrier to routine dispersal. This barrier, which is further reflected by the strong geographical structure among tropical regions found in phylogenetic analyses of tropical bryophyte genera (Dong *et al.*, 2012; Câmara & Shaw, 2013; Aranda *et al.*, 2014; Scheben *et al.*, 2016), is sufficient to shape substantial large-scale floristic differences. This result, combined with the higher levels of species turnover reported among tropical pleurocarpous moss assemblages as compared to extra-tropical ones (Hedenäs, 2007), is at

odds with the hypothesis that tropical bryophytes are better dispersers than extra-tropical ones based on their syndromes for high long-distance dispersal capacities (Schuster, 1983). Two reasons might explain why Schuster's hypothesis is not supported here. First, Schuster (1983) assumed that monoecious species, which prevail in the lowland tropical bryophyte flora, are better dispersers than dioecious ones. Such an assumption was, however, challenged by correlation analyses between sexual systems and distribution ranges (Laenen *et al.*, 2016). Second, Schuster's assumption was largely based on the observation that a large proportion of tropical species are shared among tropical areas. Bryophyte species indeed globally tend to exhibit larger distribution ranges than angiosperms (Shaw, 2001). For instance, 144 liverwort species, representing about 10% of the Neotropical flora and 16% of the flora of tropical Africa, are shared between South America and sub-Saharan Africa (Gradstein, 2013). Although molecular data in some instances confirmed the conspecificity of highly disjunct bryophyte populations (e.g. Lewis, Rozzi & Goffinet, 2014; Patiño *et al.*, 2016; Vigalondo *et al.*, 2016), mounting evidence suggests, however, that many of those widespread bryophyte species in fact correspond to complexes of species that are not necessarily monophyletic and exhibit much narrower distributions (Hutsemékers *et al.*, 2012; Medina *et al.*, 2012, 2013; Hedenäs *et al.*, 2014; Heinrichs *et al.*, 2015; Patiño & Vanderpoorten, 2015; Scheben *et al.*, 2016).

Despite evidence for long-distance dispersal limitations among tropical regions in the world moss and liverwort floras, but in line with our second hypothesis, Neotropical, tropical African and tropical Asia moss and liverwort assemblages exhibited similar patterns of nestedness. This finding suggests that, although vegetation shifts were much more dramatic in tropical Africa than in tropical Asia and in the Neotropics during the glacial cycles of the Pleistocene, the high dispersal capacities of tropical bryophytes at the regional scale (Mota de Oliveira & ter Steege, 2015) have been sufficient to erase any difference that would have resulted from recolonization delays.

CONCLUSIONS

Although tropical bryophytes displayed a high capacity to recolonize efficiently areas exposed to substantial vegetation shifts during the Pleistocene, our results are not consistent with the hypothesis that the similar patterns of species richness observed among tropical bryophyte floras are due to the sharing of a common pool of species with high dispersal capacities. Instead, this study suggests that tropical

bryophyte floras evolved independently, but at a similar rate across tropical areas, and opens the door to further research to determine whether, like angiosperms (Kissling *et al.*, 2012), regional bryophyte assemblages exhibit a significant phylogenetic clustering in the different tropical regions of the world.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Distribution of the 3276 liverwort and hornwort species in the 154 tropical OGUs.