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ABSTRACT

Bryophytes include about 20,000 species characterized by their poikilohydric condition, high long-distance dispersal capacities, and cold tolerance. Despite these specific life-history traits, large-scale biogeographic patterns in bryophytes are consistent with those observed in other groups, wherein they have been interpreted in terms of historical factors. Comparative phylogeographic analyses in bryophytes and angiosperms suggest, however, that spatially congruent patterns may not necessarily arise from common processes. This is best illustrated by the strikingly lower rates of endemism at all taxonomic and spatial scales in bryophytes due to their failure to diversify *in-situ* and the rapidity at which they enlarge their distribution range. In particular, the striking transoceanic disjunctions that are typical for many bryophyte species and their low community turnover at broad geographic scales both point to the higher capacities of bryophytes for long-distance dispersal than angiosperms. Such high long-distance dispersal capacities are reflected in the lower spatial genetic structure of bryophytes as compared to angiosperms at large geographic scales. This explains why, as opposed to the expectations of MacArthur & Wilson's model, bryophyte species richness is not necessarily lower on islands than on continents, suggesting that community assembly is more constrained by ecological filtering than dispersal limitations in bryophytes. The low relevance of historical factors for global patterns of bryophyte species richness has contributed to the idea that, as opposed to the predictions of one of the most general rules in ecology, bryophyte species richness does not decrease with latitude due to a strong tropical niche conservatism. Recent evidence for the existence of a latitudinal species richness gradient in bryophytes raises, however, the question of why bryophytes diversified faster in the tropics. This and other avenues of research in bryophyte biogeography are discussed.

I. Introduction

Biogeography is the science that aims at describing the spatial distributions of biota (a pattern) and understanding the means by which these distributions were achieved (a process) (Humphries and Parenti, 1999). The first discoveries that contributed to the development of biogeography as a science began in the mid-18th century, as Europeans explored the world and discovered the diversity of life. In particular, Alexander von Humboldt (1769-1859) and Augustin P. De Candolle (1778-1841) established the foundations of biogeography through their holistic approaches of the geography of biotas at different spatial scales. Their work had a major impact on the development of Darwin's (1809-1882) and Wallace's (1823-1913) theories that have remained fundamental to the developments of modern ecology and evolution (Cox *et al.*, 2016). In the ongoing context of global change, biogeography emerges as a key discipline, as understanding how species disperse, diversify, and adapt in a changing environment appear as increasingly pressing issues (Lexer *et al.*, 2013; Jablonski *et al.*, 2017).

Here, we focus on the ecological and evolutionary biogeography of bryophytes. We aim at establishing the link with previous reviews on bryophyte distribution patterns (Tan and Pócs, 2000; Medina *et al.*, 2011), speciation (Shaw, 2001), phylogeography (Medina *et al.*, 2011), and global change (He *et al.*, 2016), to produce a comprehensive review embedded in the context of the most recent conceptual (Whittaker *et al.*, 2017) and methodological developments, including ecological

modeling (Guisan *et al.*, 2017), and molecular biology (Edwards *et al.*, 2016), applied to the field of biogeography.

II. Relevance of bryophyte life-history traits and ecophysiology to biogeography

A. What is a bryophyte?

Bryophytes are the generic name for non-vascular land plants with a haplo-diplophasic life cycle with a dominant gametophytic phase. These key features are shared by mosses, liverworts, and hornworts, but whether these three lineages are monophyletic remains an area of controversy (Cox *et al.*, 2014; Liu *et al.*, 2014; Wickett *et al.*, 2014; Morris *et al.*, 2018).

Bryophytes are considered the closest modern relatives of the ancestors to the earliest terrestrial plants. Linking the vascular plants to their algal ancestors, they mark the transition to land (Kenrick and Crane, 1997). The oldest unambiguous bryophyte fossil is a simple thalloid liverwort of 420 Ma (million years ago), but molecular dating analyses push the origin of land plants into the Cambrian, 470.0–515.1 Ma (Morris *et al.*, 2018). Mosses and liverworts underwent bursts of diversification since the mid-Mesozoic (Feldberg *et al.*, 2014; Laenen *et al.*, 2014; Silva *et al.*, 2017). The diversification rates further increased in specific lineages toward the Cenozoic to reach, in the most recently derived lineages, values that are comparable to those reported in angiosperms. This suggests that low-diversification rates do not fully account for the comparatively low species richness of bryophytes (about 20,000 species) as compared to angiosperms (about 350,000 species), leading Laenen *et al.* (2014) to hypothesize that as in gymnosperms, the low extant bryophyte species richness might have resulted from massive extinctions.

B. Reproduction and dispersal

Bryophytes primarily disperse by means of spores whose expulsion out of the capsule is actively enhanced by the hygroscopic movements of elaters and pseudo-elaters in liverworts and hornworts, respectively (Vanderpoorten and Goffinet, 2009), and the peristome in mosses (Johansson *et al.*, 2016). Different animal-mediated dispersal mechanisms, including epizoochory (Heinken *et al.*, 2001; Rudolphi, 2009; Pauliuk *et al.*, 2011) and endozoochory (Parsons *et al.*, 2007; Boch *et al.*, 2015; Wilkinson *et al.*, 2017), were reported and may play an important role at short distances in ecosystems with low wind connectivity, such as dense forests. At larger spatial scales, evidence of bryophyte diaspores embedded in the plumage of long distance transequatorial migrant shorebirds (Lewis *et al.*, 2014) points to the key role of zoochory in explaining bipolar bryophyte distributions (Heinken *et al.*, 2001). Spores are, however, primarily dispersed by wind, as evidenced by the striking parallelism between species composition patterns with wind connectivity rather than with geographic proximity (Muñoz *et al.*, 2004). The long-distance dispersal (hereafter LDD) capacities of wind-dispersed spores vary as a function of their diameter (Sundberg, 2010; Zanatta *et al.*, 2016) and possibly also their ornamentation (Zanatta *et al.*, 2016).

Spore densities sharply decrease with increasing distance from the mother sporophyte (Figure 1). The majority of the spores, however, disperses beyond the nearest vicinity of the mother sporophyte (Sundberg, 2005; Lönnell *et al.*, 2012). In *Sphagnum*, for example, only 6.8–22.4% of the spores are deposited within a 3.2 m range (Sundberg, 2005). Bryophyte spore deposition curves thus typically exhibit long and fat tails, resulting in high, distance-dependent colonization probabilities near the source, and much lower, but still substantial, distance-independent colonization probabilities once spore is airborne away from the source. This was best illustrated by trapping spore experiments in *Discelium nudum* (Lönnell *et al.*, 2012, 2014), wherein the mean colonization rates at a distance up to 10 m from the source exceeded 50%. Colonization rates exhibited a significant distance-dependent relationship up to 50 m from the source, whereas the tail of the probability density function showed no relation to distance (Figure 1).

The shape of the dispersal kernel, in particular its tail, is a primary determinant of expansion dynamics and the spatial genetic structure of spreading populations (for review see Szövényi *et al.*, 2012). In thin-tailed kernels, rare establishment by a few founders ahead of the expanding front dominates the dispersal process and is expected to lead to a dramatic reduction in genetic diversity. By contrast, when LDD events are more frequent, establishment of individuals ahead of the colonization front and from a wider array of sources is expected. Frequent LDD events can preserve genetic diversity at the regional scale because of the mixing of genetically diverse propagules ('reshuffling effect', see Bialozyt *et al.*, 2006). If, moreover, efficient LDD is coupled with random colonization, an inverse isolation effect is predicted to develop (Sundberg, 2005), wherein increasing genetic diversity per colonizer is expected with increasing distance from a genetically variable source. The inverse isolation effect could partly explain the wide distribution of many bryophyte species, the lack of an obvious distance effect on species richness on islands, the relatively low level of
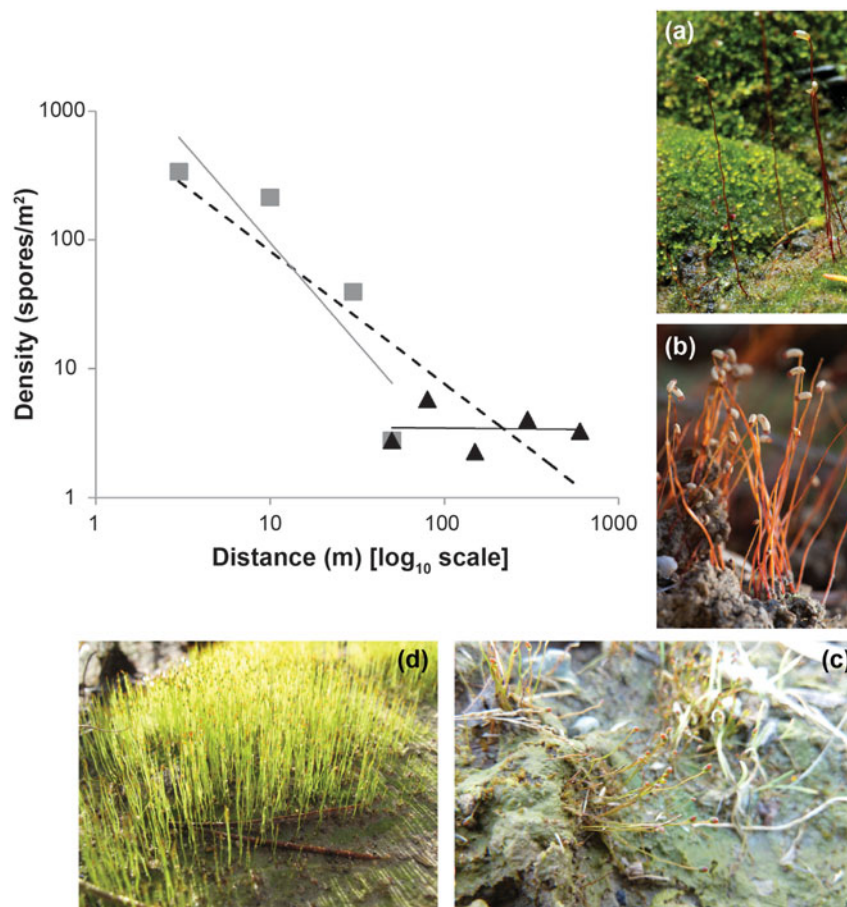
Figure 1. Estimated spore densities (spores/m^2) as a function of the distance from the source in a trapping spore experiment in the moss *Discelium nudum* (reproduced with permission from Lönnel *et al.* (2012)). Images of fructified specimens (a,b) and habitat (c,d) of *D. nudum* are provided. Photo credits: Martin Hutten (a,b), Steve Joya (c), and Doroshina Ya (d).

(allopatric) speciation in bryophytes as compared to seed plants, and the weak relationship between latitude and diversity (Sundberg, 2005).

Dispersal by spores is, nevertheless, not an option for a range of species that fail to produce sporophytes. For instance, 14% of the moss species of the British flora never undergo sexual reproduction (Longton and Schuster, 1983). Dioicous species, in particular, often fail to reproduce sexually. In a study on the reproductive biology of British mosses, Longton (1997) found that 87% of the British species, wherein sporophytes are unknown, are dioicous, whereas sporophytes are regarded as occasional to common in 83% of the monoicous species. Fertilization indeed involves that the sperm swims to the archegonia. In monoicous species, such a functional constraint is virtually lacking, as the distance between female and male gametangia is minimal. For dioicous species, which represent about 70% of liverworts and 60% of mosses, the likelihood of fertilization is, by contrast, inversely proportional to the distance between male and female shoots. Fertilization is, in many instances, complicated by the spatial segregation of the sexes, which may

result from a sex-specific physiology (Stark and McLetchie, 2006; but see Bisang *et al.*, 2015). Asexual methods of gametophyte reproduction are thus of utmost importance in bryophytes. Some species, in particular, are only known to reproduce vegetatively.

Vegetative propagules and spores are assumed to play complementary roles. Spores contribute to LDD but are produced during a limited period, especially in liverworts, which have a short-lived sporophyte. In contrast, specialized vegetative propagules are produced continuously, exhibit a larger size than spores (Longton and Schuster, 1983; but see Pohjamo *et al.*, 2006), and do not have mechanisms that promote their release. They are, therefore, thought to contribute mainly to short-distance dispersal and population persistence (Longton and Schuster, 1983; Kimmerer, 1991; Kimmerer, 1994; Longton, 1997; Löbel and Rydin, 2009). Since, according to Baker's law, 'occurrence in localities most likely to have been reached by more or less long-distance dispersal is correlated with the development of self-compatibility' (Baker, 1955; Baker, 1967), geographical range should correlate with sexual condition and, given that LDD mostly depends on

spores, monoicous bryophyte species should have larger ranges than dioecious species (for review see Longton and Schuster, 1983). Laenen *et al.* (2016b) failed, however, to demonstrate a significant relationship between range size and sexual condition. In fact, recent evidence suggests that vegetative propagules might also contribute to wind LDD. For instance, the moss *Sphagnum subnitens* rapidly dispersed across Northwest America over more than 4000 km *via* the clonal spread of a single genotype (Karlin *et al.*, 2011). Stieha *et al.* (2014) further presented evidence for potential LDD by vegetative propagules through the mathematical analysis of dioicous metapopulations.

C. Ecophysiology

1. Water uptake and drought tolerance

Upon the conquest of land, bryophytes faced the challenge of water availability, which is one of the most important evolutionary pressures on terrestrial life (Alpert, 2005). While angiosperms primarily adapted to drought by resisting to desiccation, bryophytes developed desiccation tolerance, which refers to the ability to dry to equilibrium with air that is moderately to extremely dry and then resume normal metabolic activity after rehydration. Desiccation tolerance has important ecological and evolutionary consequences (Oliver *et al.*, 2005; Proctor *et al.*, 2007).

Bryophytes are poikilohydric, which means that their water content is directly regulated by ambient humidity. Although species with specialized conducting cells may pump-up water from their substrate (Sokołowska *et al.*, 2017), the vast majority of species rely on atmospheric precipitations for water uptake, which takes place through the entire gametophyte. Therefore, the cuticle that seals the vascular plant body is most often reduced or even lacking on the gametophyte of bryophytes. This alternative ecophysiological strategy enables them to grow on rocks and tree trunks that are inhospitable for most vascular plants.

Bryophytes thus desiccate at the same time as or shortly after their substratum. Physiological activity, and hence growth, is restricted to periods of hydration, with the plant entering dormancy upon desiccation. Many, and perhaps most bryophytes can recover a normal metabolism upon rehydration after losing a substantial part of their cell water content (Proctor, 2000). Species, however, vary greatly in the degree of desiccation they can endeavour. *Sphagnum* and tropical cloud forest *Leucobryum*, which occur in habitats that are unlikely to experience long-term water deficit, form compact tufts and exhibit anatomical adaptations for water storage, seem better adapted for short-term drought-resistance

rather than desiccation tolerance. In fact, they can survive desiccation for only a few hours or a few days. By contrast, *Syntrichia caninervis*, a desert species, can remain at around −540 Mpa (equilibrated to the atmosphere above silica gel at 2–4% relative humidity) for up to six years and still recover normal activity and growth upon rehydratation (Oliver *et al.*, 2005). As a most extreme example, 23 year-old herbarium collections of the liverwort genus *Riccia* were found to be still viable (Alpert, 2005).

2. Temperature

A common feature among most bryophytes is their ability to grow at low temperature. More than half of the 40 temperate species investigated by Furness and Grime (1982) showed a growth reduction of less than 50% at 5 °C compared to growth at their optimal temperature. La Farge *et al.* (2013), Roads *et al.* (2014), and Cannone *et al.* (2017) further evidenced a unique successful regeneration of subglacial bryophytes following up to six centuries of ice entombment, expanding our understanding of their role in recolonization of glaciated landscapes. Regeneration of subglacial bryophytes indeed broadens the concept of Ice Age refugia (Tzedakis *et al.*, 2013), traditionally confined to survival of land plants in sites above and beyond glacier margins. Altogether, the high LDD capacities of bryophytes, their poikilohydric condition, and their higher cold tolerance than angiosperms, suggest at first sight that bryophytes should exhibit different biogeographical patterns than other taxonomic groups, and in particular, angiosperms.

III. Species distributions and biogeographic patterns

A. Biogeographic regionalizations and centers of endemism

1. Patterns

The definition of biogeographic regions at different spatial scales based upon their biotic composition has most recently gained increasing attention to provide, through the statistical analysis of distribution data, a spatially explicit framework for a range of basic and applied questions in historical and ecological biogeography, evolutionary biology, systematics, and conservation (e.g. Kreft and Jetz, 2010; Holt *et al.*, 2012; Linder *et al.*, 2012). Given that species evolve within areas from which they subsequently disperse, the taxonomic composition of an area's flora and fauna reflects the degree to which it (i) acts as a centre of origin; (ii) has been colonized by dispersing organisms; or (iii) has been subject to large-scale environmental forces

(Mackey *et al.*, 2008). This raises the question whether, as opposed to the early view of common plant kingdoms and animal regions, biogeographic patterns are taxon-specific. In particular, Cox (2001, 2010) emphasized the relevance of dispersal ability to delineate biogeographical patterns. In spore-dispersed organisms like bryophytes and pteridophytes, van Zanten and Pócs (1981) and Wolf *et al.* (2001) proposed that dispersal homogenizes floristic composition, erasing any signature of historical signal in distribution data, and in particular, of vicariance.

Biogeographical regionalizations in bryophytes at the world (Vanderpoorten et al., 2010) and continental (Mateo *et al.*, 2013) scales unexpectedly revealed, however, biogeographic patterns that are consistent with those already observed in other groups of organisms, where they have been interpreted in terms of historical factors. Thus, an analysis of the distribution of 360 liverwort genera in 21 major biogeographic units worldwide revealed a major split between Laurasian and Gondwanan areas (Vanderpoorten *et al.*, 2010). At first sight, this finding points to the substantial role for the Tethys seaway as a biogeographic barrier that was reinforced during the Cretaceous by the emergence and radiation of a dense angiosperm belt in the tropics (Proches, 2006). Another apparent signature of ancient vicariance is the sister relationship of bryophyte floristic assemblages between sub-Saharan Africa and South America. This pattern (for a detailed floristic account see Gradstein, 2017) has traditionally been interpreted in terms of the break-up sequence of northwest Gondwana and the opening of the South Atlantic ocean, 110 Ma (for a review see Sanmartín and Ronquist, 2004).

At the continental scale, biogeographic regionalization analyses for the European bryophyte flora resolved Mediterranean, alpine, boreal, and continental regions, which largely overlap with those defined for vascular plants. At the regional scale, Van Rooy and Van Wyk (2010) similarly found a high degree of correspondence between the regions resolved by biogeographic regionalization analyses based on bryophyte and angiosperm distribution patterns in southern Africa. However, the Cape phytochorion, which has long been identified as the smallest of the six plant floristic kingdoms based on its unique density of endemic species (Takhtajan, 1986; but see Cox, 2001 and Linder *et al.*, 2012), is less distinctive in analyses of bryophyte species distributions and only separated at the level of a domain within the Afromontane Region (Van Rooy and Van Wyk, 2010). Macaronesia, another floristic region also defined by its high levels of endemism in its angiosperm flora (Takhtajan, 1986), was not resolved as a

homogeneous entity in moss distribution analyses, wherein the Azores and Madeira clustered in a group with Europe, whereas the Canary Islands clustered with northern Africa and western Asia (Vanderpoorten *et al.*, 2007).

Overall, it thus appears that biogeographic regionalizations referred from the analysis of bryophyte species distributions are largely congruent with those reported in other taxonomic groups, in sharp contrast with the hypothesis that substantial differences in ecophysiology, dispersal ability, and distributions between vascular plants and bryophytes would result in different biogeographic patterns.

2. Processes

A review of the literature reporting instances of transoceanic disjunctions among species including ancestral area reconstructions and molecular dating analyses is provided in Table 1. It reveals that, although floristic patterns at the world scale are largely congruent with the expectations of a continental drift scenario, the timing of the disjunctions is largely more recent than continental split events, and hence, that repeated events of LDD account for the observed disjunct patterns. The strong signal of transoceanic dispersal events in biogeographic patterns is, at first glance, surprising because LDD has long been assumed to generate chaotic, wide-ranging and pattern-limited relationships in area cladograms. For instance, Tangney (2007) suggested that 'giving priority to dispersal as the means by which distributions are formed has several undesirable effects' because it devalues distribution data since the possibility of the reliability of patterns in distributions is lessened if dispersal is assumed to be a major determining driver. Two main factors may explain the strong geographic structuring of the area cladogram resulting from the analysis of liverwort genus distributions worldwide (Vanderpoorten *et al.*, 2010), despite the role of LDD in shaping the observed disjunct patterns.

First, the number of speciation events largely exceeds that of transcontinental dispersal events to explain current patterns of disjunct species distributions (Table 1), suggesting that the speciation rate is higher than the transoceanic dispersal rate, readily creating a geographic structure (Norhazrina *et al.*, 2016). Second, and as best illustrated by the Neotropical/sub-Saharan disjunction, migrations tend to be asymmetric, from the same source to the same sink area (Table 1). In a meta-analysis of the Neotropical-sub-Saharan African disjunction in angiosperms, Renner (2004) similarly concluded that wind dispersal occurred in the direction from South America to Africa, but rarely in the opposite direction. Constrained by prevailing wind, asymmetrical dispersal

Table 1. A brief summary of important episodes of continental landmass breakups against speciation and biogeographic disjunction events in bryophytes.

N° speciation events	Dispersal events	Disjunction timing (95% HPD)	Genus (Reference)
Neotropics –sub-Saharan Africa breakup: 110 Ma Sanmartín and Ronquist (2004)			
Neotropics: 2			
Africa: 0	1 (Neotropics to Africa)	15	*Bryopteris* (Hartmann et al., 2006)
Neotropics: 9			
Africa: 3	4 (Neotropics to Africa)	8.4–24.8; 2.6–17.2; 5.4–15.2; 2.3–6.6	*Ceratolejeunea* (Scheben et al., 2016)
Neotropics: 12	1 (Neotropics to Africa)	0.5–20.3	*Leptoscyphus* (Devos and Vanderpoorten, 2009)
Africa: 0			
Neotropics: 3	2 (Neotropics to Africa)	18.7; 35.3*	*Leptolejeunea* (Bechteler et al., 2017)
Africa: 0			
Neotropics: 4			
Africa: 0	1 (Neotropics to Africa)	16–26	*Marchesinia* (Heinrichs et al., 2009)
South America – New Zealand breakup: 80 Ma Sanmartín and Ronquist (2004)			
Chile: 2			
New Zealand: 0	1 (Chile to New Zealand)	1.2–39.9	*Nothoceros* (Villarreal and Renner, 2014)
New Zealand: 0	0–2 (?)	32.4–70.8; 21.1–47.3	*Frullania* (Carter et al., 2017)
North America – Europe: 40–15 Ma Milne (2006)			
Europe: 3			
North America: 7	2 (North America to Europe and vice versa)	3.5–8.2	*Homalothecium* (Huttunen et al., 2008)

The number and regions of cladogenetic speciation events (i.e. indicating number of taxonomically recognized species within clades that diversified within the same biogeographical region), number and direction of dispersal events (i.e. indicating a non-counting dispersal event among conspecific accessions) and timing of those dispersal events are provided.
*indicates that 95% HPD is not provided in the original reference.

may in fact produce predictable, repeated distribution patterns that are likely to account for many of the range disjunctions and patterns of endemism currently observed (Cook and Crisp, 2005; McGlone, 2005; Sanmartín et al., 2007). For example event-based tree-fitting methods applied across a sample of 23 southern hemisphere plant groups suggested that easterly moving weather systems, probably often associated with forest fires in eastern Australia causing massive updraft and carrying plants and animals with it (McGlone, 2005), constrained the dispersal of plants from Australia to New Zealand, favouring the evolution of endemism in the latter area (Sanmartín et al., 2007; McDowall, 2008). Accordingly, New Zealand, despite its comparatively much smaller size than Australia, contains four times more endemic bryophyte genera (Figure 2).

At the continental scale, the scarcity of phylogeographic analyses in bryophytes as compared to angiosperms makes it difficult to identify the historical and evolutionary mechanisms underlying the observed distribution patterns. Europe, including the oceanic Macaronesian region, is arguably the continent with the highest level of knowledge on species distributions and the highest number of available phylogeographies and has long served as a model for articulating concerns about the genetic implications of current climatic changes. Recent evidence in angiosperms suggests, however, that European postglacial

recolonization patterns may not apply in other regions of the northern hemisphere (Lumibao et al., 2017), calling for an urgent effort to improve the phylogeographic knowledge of European bryophytes and document bryophyte phylogeographies in North America and Asia.

In European bryophytes, four postglacial recolonization patterns have been identified (for a review see Kyrkjeeide et al., 2014). The two first patterns, which involve a postglacial recolonization of northern areas from either southern refugia (Cronberg, 2000; Grundmann et al., 2007) or scattered northern micro-refugia (Désamoré et al., 2012), correspond to the two patterns typically reported for angiosperms (Hewitt, 2000; Bhagwat and Willis, 2008). In the third pattern, which has to date been reported in the genus *Polytrichum* only, no significant correlation between genetic diversity at the population level and latitude was found, leading van der Velde and Bijlsma (2003) to conclude that postglacial dispersal has been sufficient to prevent substantial genetic differentiation among populations by genetic drift and to wipe out an initially present genetic structure that may have resulted from the latest glacial period. Changes in communities depending on major climatic shifts during the Quaternary era are, in fact, evident from the succession of (macro-)remains preserved in peat. Each climatic phase had its characteristic range of habitats,
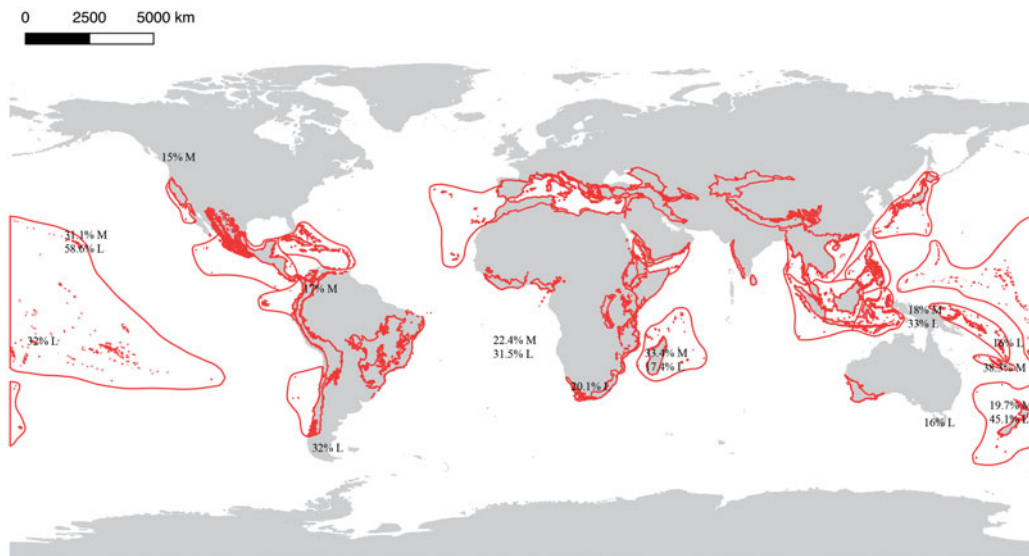
Figure 2. Worldwide patterns of bryophyte hot spots of endemism compared to Myers's *et al.* (2000) angiosperm hot spots. Only areas with levels of bryophyte species endemism higher than 15% in mosses (M) and liverworts (L) are represented (redrawn and updated from Vanderpoorten and Hallingbäck (2009).

and these appear to have been colonized by bryophytes at a remarkable speed as soon as they developed and became available (Jonsgard and Birks, 1996; Ellis and Tallis, 2000). Such a high ability to track areas of suitable climates might have important consequences on the ability of bryophytes to face climate change (Patiño *et al.*, 2016).

The fourth postglacial recolonization pattern in bryophytes is an extension of Hulten's model (see Abbott and Brochmann, 2003, for review) involving a high dispersal capacity of the circum-arctic angiosperm flora from the Beringian refugium, a region encompassing Northeast Russia and Northwest America, to the entire amphi-Atlantic element. In this pattern, North America (Stenøien *et al.*, 2011) and the northeastern Atlantic islands (Hutsemékers *et al.*, 2011; Laenen *et al.*, 2011), which experienced buffered climate conditions at the Last Glacial Maximum (Fernández-Palacios *et al.*, 2011), contributed to the postglacial recolonization of Europe. As an extreme case, phylogeographical evidence further suggests that the Atlantic fringe bryophyte flora largely assembled from Macaronesian ancestors during glacial–interglacial cycles from the mid to the Late Pleistocene (Patiño *et al.*, 2015b), resulting in an Atlantic element that is geographically similar in extent to the one defined based upon analyses of angiosperm distributions, but has a completely different geographical origin.

A complex mixture of origins thus characterizes the postglacial history of European bryophytes, reflecting their high LDD capacities. The differences in the postglacial recolonization mechanisms in bryophytes and

angiosperms suggest that their spatially congruent distribution patterns may not necessarily reveal common processes. It, therefore, appears that although bryophytes responded quicker to climate change than angiosperms and may have had a completely different biogeographic history than the latter, the similarities of their present distribution patterns confirms a central thesis in ecology that climate exerts the dominant control on distributions at the continental scale (Woodward, 1987). Based on the high similarities of the biogeographic regionalizations obtained for angiosperms and mammals in Europe, Heikinheimo *et al.* (2012) similarly concluded that, at such scales, environmental forcing results in coherent animal and plant distributions patterns. A signature of the high dispersal capacities of bryophytes in their extant distribution patterns can, however, be found in phytochoria defined in angiosperms based upon their high levels of endemism, as best illustrated by the Cape Floristic Kingdom and the Macaronesian region. In fact, one of the most striking biogeographic features of bryophytes is their patterns of endemism.

B. Endemism

1. Patterns of endemism in the bryophyte floras across spatial and taxonomic scales

Bryophyte and angiosperm endemism patterns differ in two main features. First, worldwide patterns of endemism at the genus level reveal an imperfect match with Myers *et al.* (2000)'s world biodiversity hotspots that are defined based upon endemism and threat levels (Figure 2). For example the

Mediterranean and Central America are listed among the most important hotspots for angiosperms, but do not exhibit spectacular levels of endemism in bryophytes. By contrast, several temperate areas, including Patagonia, the Pacific Northwest American region, and Tasmania (Figure 2), exhibit high levels of bryophyte endemism, but are not listed as priority areas for conservation with respect to angiosperm floras. Within Australia similarly, only three of the eight grid cells with the highest scores for bryophyte endemism occurred in an endemism centre identified for angiosperms, whereas southwestern Western Australia, which is recognized as a global diversity hotspot, is not a region of high endemism for bryophytes (Stevenson et al., 2012).

Second, levels of endemism shown by all three bryophyte lineages are consistently and largely below those reported for angiosperms across all taxonomic and spatial scales (Table 2). In Australia for example, the 1% of generic endemism in liverworts pales in comparison with the 22.6% in angiosperms. Even in the Neotropics, which display the highest number of endemic genera amongst the world's liverwort floras (24.6%), levels of generic endemism in the angiosperm flora are more than twice higher. The same tendency is observed on oceanic and continental islands that are typically characterized by their extremely high levels of endemism in angiosperms. For example the Mediterranean islands (e.g. Cyprus, Crete, Corsica, and Sardinia) each exhibit 7–12% of endemism at the species level in angiosperms, but to date, only a single endemic moss species of debatable taxonomic status has been described from Corsica (Sotiaux et al., 2009). In the Canary Islands, the 1.5% of bryophyte species endemism pales in comparison with the 40% endemism rates observed in angiosperms (Patiño et al., 2014a). Even in Hawaii, one of the world's richest hotspots of island endemic taxa, the percentages of endemic moss (31.1%), and liverwort species (58.6%) are substantially lower than the 90 and 77% levels reported for angiosperms (Wagner et al., 2005) and ferns (Geiger et al., 2007), respectively, and likely still overestimated due to the urgent need for taxonomic revisions in the archipelago (S.R. Gradstein, pers. comm.).

2. Why are there so few bryophyte endemics?
2.1. Taxonomic shortcomings.
Since taxonomic issues in describing and understanding biodiversity patterns are expected to culminate as organisms decrease in size and morphological complexity (Whittaker et al., 2005), taxonomic shortcomings provide a simple explanation for the low levels of endemism reported in bryophytes. Even in arguably well-worked floras, such as that of North America (Carter et al., 2016), the description of new species is not close to being completed.

An increasing number of studies reported that apparently widely distributed bryophyte species correspond to complexes of multiple species with much narrower distribution ranges (Carter, 2012; Medina et al., 2012; Hedenäs et al., 2014; Lang et al., 2015; Caparrós et al., 2016; Patiño et al., 2017). In the liverwort genus Plagiochila, Renner et al. (2017) estimated that real diversity in Australasian species is 29% higher than currently recognized. In the Cape area in particular, the numerous descriptions of new species (Hedderson and Zander, 2007b; Hedderson and Zander, 2008a; Zander and Hedderson, 2011a; Hedderson, 2012) and genera (Hedderson and Zander, 2007a, 2008b, c; Zander and Hedderson, 2009, 2011b) during the last decade suggest that rates of both native and endemic diversity are likely to increase with further taxonomic work.

The global trend is, however, mostly toward a reduction in endemic species numbers. During the period of active bryological exploration of extra-European regions during the 19th century, hundreds of new 'geographical species' were described based in large part on the assumption that populations from distant regions must represent species distinct from European taxa (Shaw, 2001). In this context, O'Shea (1997a, b) predicted an overall reduction of 77% to around 43% of endemism in sub-Saharan African mosses. Thus, inaccurate taxonomy alone cannot explain the strikingly low rates of bryophyte endemism.

2.2. Speciation rates.
The low rates of endemism in bryophytes, along with the geographic distribution of hot-spots of endemism, are at first sight consistent with the traditional interpretation that bryophytes exhibit low evolutionary rates (for review see Shaw, 2001). In particular, Schuster (1983b) interpreted the higher levels of endemism in the southern than in the northern hemisphere (Figure 2) in terms of ancient divergence following the long isolation of former Gondwana fragments, whose separation was completed 90 Ma. In the northern hemisphere in contrast, North America and Eurasia were still connected about 5 Ma ago, and Schuster (1983b) proposed that northern hemisphere endemism results from extensive Pleistocene extinctions caused by recurrent glaciations (paleoendemism).

The limited fossil record that is available for bryophytes tends to support the relictual nature of the Laurasian disjunctions. For example the presence of fossil material of the Japanese endemic liverwort Nipponolejeunea subalpina in Baltic amber from the

Table 2. Levels or range estimates (in percentage) of endemism at different taxonomic and spatial scales in liverworts, mosses, hornworts, and angiosperms.

Region	Liverworts		Mosses		Hornworts		Angiosperms	
	Genus	Species	Genus	Species	Genus	Species	Genus	Species
Oceanic islands								
Galapagos	0 (6)	8.0 (6)	0 (7)	3.0 (7)	0 (6)	28.5 (6)	–	51 (46)
Hawaii	0 (40)	58.6[c] (40)	1.5 (9)	31.1 (9)	0 (40)	0[b] (40)	–	90 (10)
La Réunion	0 (14)	5.5 (14)	0 (14)	12.5 (14)	0 (14)	0 (14)	2.2 (48)	26.8 (48)
Tristan da Cunha	0 (16)	10.1 (16)	–	–	0 (16)	2 (16)	0 (53)	34.7 (53)
Falkland Isl.	0 (55)	3.1 (55)	–	–	0 (55)	0 (55)	0 (52)	8 (52)
Canary Islands	0 (17)	0.7 (17)	0 (17)	1.7 (17)	0 (17)	0 (17)	5.4 (17)	45.5 (17)
Azores	0 (43)	1.8 (17)	0 (43)	1.7 (17)	0 (17)	0 (17)	0 (17)	35.5 (17)
Madeira	0 (42)	1.6 (17)	1.5 (42)	1.7 (17)	0 (17)	0 (17)	1.5 (17)	22.5 (17)
Ascension island	0 (20)	8.7 (20)	0 (20)	26 (20)	0 (20)	25 (21)	0 (37)	25.0 (37)
St. Helena	0 (22)	32.5 (22)	0 (22)	22.4 (22)	0 (22)	33 (22)	0 (36)	52–59 (36)
São Tomé	0 (26)	2.1 (26)	0 (26)	14.1 (26)	0 (26)	0 (26)	0.2 (34)	13.3 (34)
Príncipe	0 (26)	2.1 (26)	0 (26)	0 (26)	0 (26)	0 (26)	0 (34)	13.3 (34)
Continental islands								
Japan	1.5 (38)	10.1 (38)	0.6 (38)	7.7 (38)	0 (38)	0 (38)	–	32 (50)
Sulawesi	0 (15)	0.5 (15)	0 (15)	1 (15)	0 (15)	0 (15)	0.4[g] (47)	12.6 (47)
Madagascar	0 (24)	17.4 (24)	0 (24)	33.4 (24)	0 (24)	0 (24)	15 (25)	84 (25)
New Zealand	6.8 (18)	45.1 (18)	5.7 (18)	19.7 (18)	0 (18)	50[a] (18)	10 (5)	83 (51)
Sicily	0 (33)	0 (33)	0 (32)	0 (32)	0 (33)	0 (33)	0.3 (58, 60)	7.6 (31)
New Caledonia	1 (11)	13–39 (11)	0.7 (64)	38.3 (12)	0 (11)	21.4 (11)	14.3 (13)	62.8 (13)
Corsica	0 (8)	0 (8)	0 (8)	0.2 (8)	0 (8)	0 (8)	0 (58, 59)	12.5 (31)
Sardinia	0 (33)	0 (33)	0 (32)	0 (32)	0 (33)	0 (33)	0 (58)	11.5 (31)
Balearic Islands	0 (33)	0 (33)	0 (32)	0 (32)	0 (33)	0 (33)	0.20 (62)	7.1 (62)
Cyprus	0 (33)	0 (33)	0 (32)	0 (32)	0 (33)	0 (33)	0[f] (56)	7.1 (56)
Crete	0 (33)	0 (33)	0 (32)	0 (32)	0 (33)	0 (33)	0.3 (58, 61)	10.5 (31)
Continental areas								
Cape Kingdom	0 (1)	20.1[d] (49)	2.3 (35)	7.0 (27)	0 (1)	0 (1)	16.2 (2)	70 (27)
Australia	1 (1)	23–28 (28)	2.5 (29)	22.7 (28)	0 (19)	61.9 (19)	22.6 (3)	93.2 (27)
Neotropics	24.6 (1)	80–85 (44)	25.0 (30)	–	0 (41)	54.3 (41)	52.8 (65)	90 (45)
North America	1.5 (54)	5.8 (54)	8.1 (23)	21.4 (23)	0 (41)	40 (41)	13e (57)	50 (57)

Reference numbers corresponding to the citation list are provided in brackets. Dashes indicate that there is no available information for that species group and archipelago.
[a]Including *Phaeomegaceros hirticalyx*, but excluding *Dendroceros granulatus* and *D. validus* (J.C. Villarreal, pers. comm.).
[b]Excluding *Anthoceros spongiosus* (J.C. Villarreal, pers. comm.).
[c]In the absence of any recent taxonomic revision of the Hawaiian liverwort flora, the endemism rates are likely over-estimated. S.R. Gradstein (pers. comm.) estimates that the actual rate of Hawaiian endemic liverwort is around 15–20%.
[d]Rate calculated across the entire South African region, thus largely overestimating the endemism rate in the Cape region.
[e]Estimates derived from the currently published volumes of Flora of North America.
[f]Considering that the only endemic genus, *Lindbergella*, should be merged with *Poa* (Soreng et al., 2015).
[g]Calculated from data from M. Roos and P. van Welzen (pers. comm.).

(1) Vanderpoorten et al. (2010); (2) Born et al. (2006); (3) Orchard (1999); (4) Takhtajan (1986); (5) Moreira-Muñoz (2007); (6) Gradstein and Ziemmeck (2016), updated by S.R. Gradstein (pers. comm.); (7) Ziemmeck and Harpel (2014); (8) Sotiaux et al. (2009); (9) Staples et al. (2004); (10) Sakai et al. (2002); (11) Thouvenot et al. (2011); (12) Thouvenot and Bardat (2010); (13) Jaffré et al. (2001); (14) Ah-Peng and Bardat (2005) updated by C. Ah-Peng (pers. comm.); (15) Gradstein et al. (2005), Ariyanti et al. (2009); (16) Váňa and Engel (2013); (17) Vanderpoorten et al. (2011); (18) Gibbs et al. (2017); (19) J.C. Villarreal (pers. comm.); (20) Pressel et al. (2016); (21) Villarreal et al. (2017); (22) Wigginton (2013); (23) Carter et al. (2016); (24) Marline et al. (2012), with updates by L. Marline (pers. comm.); (25) Callmander et al. (2011); (26) Sérgio and Garcia (2011); (27) Van Rooy and Van Wyk (2012); (28) https://www.environment.gov.au/system/files/pages/2ee3f4a1-f130-465b-9c7a-79373680a067/files/06-nlsaw-plants.pdf; (29) http://www.anbg.gov.au/abrs/Mosses_online/00_AMO_all%20GENERA.html; (30) Schofield (2004); (31) Jeanmonod et al. (2015); (32) Ros et al. (2013); (33) Ros et al. (2007); (34) Figueiredo et al. (2011); (35) J. Van Rooy, pers. Comm.; (36) Lambdon (2012); (37) J. Sim, pers. comm.; (38) Higuchi (2011); (39) Stotler and Crandall-Stotler (2005); (40) Staples and Imada (2006); (41) J.C. Villarreal, pers. comm. (42) Sérgio et al. (2008); (43) Gabriel et al. (2005); (44) estimates from Gradstein (2013, 2016); Gradstein et al. (2001, 2007); (45) Ulloa et al. (2018); (46) http://darwinfoundation.org/datazone/checklists/Magnoliophyta/; (47) Roos et al. (2004); (48) Boullet (2016); (49) Wigginton, pers. comm.; (50) Kato and Ebihara (2011); (51) Wilton and Breitwieser (2000); (52) http://www.falklandsconservation.com/wildlife/plants/native-vascular-plant-checklist; (53) McIntosh and Malan (2012); (54) Stotler and Crandall-Stotler (2017); (55) Engel (1990); (56) Hand et al. (2011); (57) Morin et al. (2015); (58) Médail (2017); (59) Jeanmonod and Gamisans (2007); (60) Conti et al. (2005); (61) Turland et al. (1993); (62) calculated from unpublished data of J.A. Rossello (pers. comm.); (63) Bell and Hyvönen (2010); (64) Bell et al. (2012); (65) C. Ulloa and P. Jörgensen, pers. comm.

European Eocene unambiguously attests that the distribution of the genus, currently restricted to eastern Asia, was much broader in the Tertiary (Grolle and Meister, 2004). Additional Baltic amber fossils, although sometimes incomplete and difficult to assign taxonomically, also attest to the paleoendemic nature of an array of taxa currently restricted to eastern Asia (Frahm, 2000; Frahm, 2004). Mounting evidence that geographically disjunct species diverged long after continental split events (Table 1), resulting from isolation following LDD events, however, suggests that paleoendemism and extremely low speciation rates associated with continental drift cannot be invoked to explain the low levels of bryophyte endemism.

While the perception of bryophytes as 'sphinxes of the past' with no evolutionary capacity can today be abandoned, diversification rate analyses indicated that,

with the exception of a few lineages (Wall, 2005; Laenen *et al.*, 2014), overall estimates of net species diversification are approximately half those reported in ferns and about 30% those described for angiosperms (Laenen *et al.*, 2014). This finding suggests that bryophytes underwent massive extinctions and/or exhibit slower speciation rates. Assessing the impact of extinctions is challenging in the absence of a suitable fossil record, and we, therefore, focus below on two potential mechanisms that could account for slow speciation rates.

2.2.1. Speciation mode.

The theory of 'punctuated equilibrium' (Gould and Eldredge, 1993) proposes that species change suddenly during short bursts associated with speciation ('cladogenetic change'; for a review see Bokma, 2008). In plants, it is best exemplified in angiosperms, where adaptive radiations have led to spectacular cases of sympatric endemic speciation (Losos and Ricklefs, 2009; Givnish, 2010; Stroud and Losos, 2016). By contrast, speciation may also arise through the spatial isolation and progressive divergence of populations along the periphery of a species range. The gradual evolution of a new species from a founder event has been called 'phyletic' or 'anagenetic speciation' (Stuessy *et al.*, 2006; Gehrke and Linder, 2011; but see Emerson and Patiño, 2018). Although several processes beyond adaptive radiation can produce highly diverse clades, and although fast diversification may also take place following extensive opportunities for geographic isolation and allopatric speciation (Simões *et al.*, 2016), adaptive radiations are typically characterized by rapid and extensive speciation within lineages.

Following Stuessy *et al.* (2006), Patiño *et al.* (2014a) used island endemism as a proxy for speciation and inferred cladogenesis (sympatric speciation) and anagenesis (allopatric speciation) when there were at least two congeneric endemic species or a single endemic species within a genus, respectively. In bryophytes, the predominance of allopatric speciation was evidenced by the much higher proportion of genera with single archipelago species endemics (73%) than in angiosperms (55%). Archipelagic allopatric speciation contributed 49% of bryophyte and 40% of endemic pteridophyte species, but only 17% of angiosperms species. Overall, therefore, allopatric speciation has played a much more substantial role in the evolution of endemic bryophyte diversity on oceanic islands than in angiosperms, contributing to the lower speciation rates than in angiosperms.

Cladogenesis is promoted by two mains factors. First, the relative contribution of anagenesis and cladogenesis to endemic speciation depends on geographic isolation (Heaney, 2000). Cladogenesis increases with spatial isolation, as a few colonists may radiate in the absence of competition in isolated islands. Anagenesis, in turn, occurs at an intermediate distance from source areas, as a result of the trade-off between the number of events potentially fostering anagenetic change and the intensity of migration preventing speciation through undisrupted gene flow (Rosindell and Phillimore, 2011). Given the dispersal capacities of bryophytes, it is likely that even the most geographically isolated islands are not sufficiently isolated genetically to promote cladogenesis.

Second, cladogenesis increases with high levels of environmental heterogeneity and topographical complexity, ultimately fostering adaptive radiations (Stuessy *et al.*, 2006; Rosindell and Phillimore, 2011). Previous experimental work suggested that, in contrast with the vast majority of seed plants, bryophytes do not tend to develop ecotypes, but rather display an inherent broad ability to cope with environmental variation. In the moss *Bryum argenteum*, plants from clean and heavily polluted environments exhibit indistinguishable growth responses to media supplemented with heavy metals (Shaw and Albright, 1990). In the desert moss *Syntrichia caninervis*, morphological variation of populations from extreme microhabitats results from plasticity (Reynolds and Mcletchie, 2011). In a transplant experiment of 10 species along an elevation gradient in Panama, mortality was higher and growth lower in the transplanted samples, but a few transplanted samples of most species survived the whole experiment and finished with growth rates similar to controls, pointing to rapid temperature acclimation (Wagner *et al.*, 2014). This suggests that 'general purpose' genotypes confer on bryophytes an inherent high level of tolerance, making the evolution of specialized races unnecessary. Physiological and morphological plasticity, therefore, appears to be much more important than genetic specialization for bryophytes (Shaw, 1992; Reynolds and McLetchie, 2011), potentially hampering the chances of adaptive radiation. Recent evidence for increased genetic divergence (Szövényi *et al.*, 2009; Hutsemékers *et al.*, 2010; Pisa *et al.*, 2013; Mikulášková *et al.*, 2015; Magdy *et al.*, 2016) and speciation (Johnson *et al.*, 2015) along environmental gradients in bryophytes suggests, however, that adaptation could play a more important role in shaping genetic patterns in bryophytes than previously thought.

2.2.2. Limited opportunities for speciation associated with high levels of gene flow.

Kisel and Barraclough (2010) proposed that speciation has a spatial scale that depends on levels of gene flow, so that organisms with

Table 3. Comparison of the fine-scale genetic structure in bryophytes and angiosperms, as measured by Vekemans and Hardy's (2004) *Sp* statistics. NS denotes a non-significant slope.

Taxon	Species/life history traits	*Sp* statistics	Range (m)	Reference
Bryophytes	*Rhynchostegium riparioides*	0.029	0.01–12,000	Hutsemékers *et al.* (2013)
	Barbilophozia attenuata	0.009–0.030	0.01–60	Korpelainen *et al.* (2011)
	Calliergon megalophyllum	0.051	10–2900	Korpelainen *et al.* (2013)
	Fontinalis antipyretica	0.077	10–3850	Korpelainen et al. (2013)
	Fontinalis hypnoides	0.020	10–2850	Korpelainen *et al.* (2013)
	Orthotrichum handiense	0.144	0.01–1200	Patiño *et al.* (2013c)
	Crossocalyx hellerianus	0.012–0.968	0.01–500	Holá *et al.* (2015)
	Orthotrichum speciosum	NS	0.01–1500	Snäll *et al.* (2004)
	Orthotrichum obtusifolium	0.013	0.01–1500	Snäll *et al.* (2004)
Angiosperms	Wind-dispersed seeds	0.012 ± 0.012		Vekemans and Hardy (2004)
	Wind-dispersed pollen	0.006 ± 0.004		Vekemans and Hardy (2004)
	Self-fertilized angiosperms	0.143 ± 0.080		Vekemans and Hardy (2004)
	Outcrossing angiosperms	0.013 ± 0.010		Vekemans and Hardy (2004)

high dispersal capacities require strong geographic isolation and/or very large areas to speciate. Another factor potentially contributing to the low levels of endemism in bryophytes is, therefore, that chances of genetic divergence, and hence, speciation, are hampered by high migration rates. Sundberg (2005) in fact proposed that the 'inverse isolation hypothesis' could explain the relatively low level of (allopatric) speciation in bryophytes as compared to angiosperms. Later, Vanderpoorten *et al.* (2011) similarly hypothesized that dispersal between the Macaronesian archipelagos and between the archipelagos and the Atlantic and Mediterranean seaboards of Europe and North Africa promotes gene flow and hampers genetic isolation, resulting in the low levels of endemism observed.

As mentioned in Section II.B, the shape of the dispersal kernel, and in particular its tail, is a primary determinant of expansion dynamics and spatial genetic structure of colonizing populations. In extremely LDD efficient organisms characterized by a fat-tailed dispersal kernel, random dispersal of spores is expected, owing to the well-mixed and diverse propagule pool, to erase any signal of isolation by distance (Sundberg, 2005). To address this question and test the hypothesis that intense gene flow could hamper chances of allopatric speciation, we performed a review of the literature on spatial genetic structure in bryophytes. We built on Korpelainen *et al.* (2005) to review available data on spatial genetic structure in bryophytes, from regional to entire species distribution ranges. We generated a dataset of similar size by sampling about 100 studies in angiosperms by using the keywords 'angiosperm' and 'AMOVA' in Scopus.

Spatial genetic structuring at the local scale can usefully be characterized by the *Sp* statistics, a measure of the dispersal capacity derived from the slope of the regression between pairwise kinship coefficients and geographic distance standardized by the mean kinship coefficient observed at the first distance class (Vekemans and Hardy, 2004). The *Sp* statistics measured in bryophytes are compared to those reported for angiosperms depending on their dispersal syndromes and sexual systems in Table 3.

Although bryophyte spores are more comparable in size to pollen grains (*ca*. 10-100 μm) than to seeds, the smallest of which measure 100 μm, the *Sp* statistics reported to date in bryophytes lie in the range of those reported for wind-dispersed seeds, well-above those reported for wind-dispersed pollen. While the significant spatial genetic structuring reported in all of the species but one listed in Table 3 is expected given the high spore deposition near the vicinity of the mother sporophyte (see Section II.B), their apparent low dispersal capacities with regard to their size are more intriguing. It must be noted, however, that other factors than dispersal syndromes affect patterns of spatial genetic structure. In particular, Vekemans and Hardy (2004) showed that the *Sp* statistics is significantly higher in selfing than in outcrossing species. Since clonality is of utmost importance in bryophytes, as suggested by their life-history traits (see Section II.B) and further evidenced by the significance of the linkage disequilibrium among loci within populations in all of the studies available to date (Snäll *et al.*, 2004; Hutsemékers *et al.*, 2010; Hutsemékers *et al.*, 2011; Johnson *et al.*, 2012; Terracciano *et al.*, 2012, but see Gunnarsson *et al.*, 2005), clonality undoubtedly leads to an underestimation of actual dispersal capacities based on fine-scale spatial genetic analyses.

At larger (regional) scales, Szövényi *et al.* (2012) failed to find evidence for isolation-by-distance in two
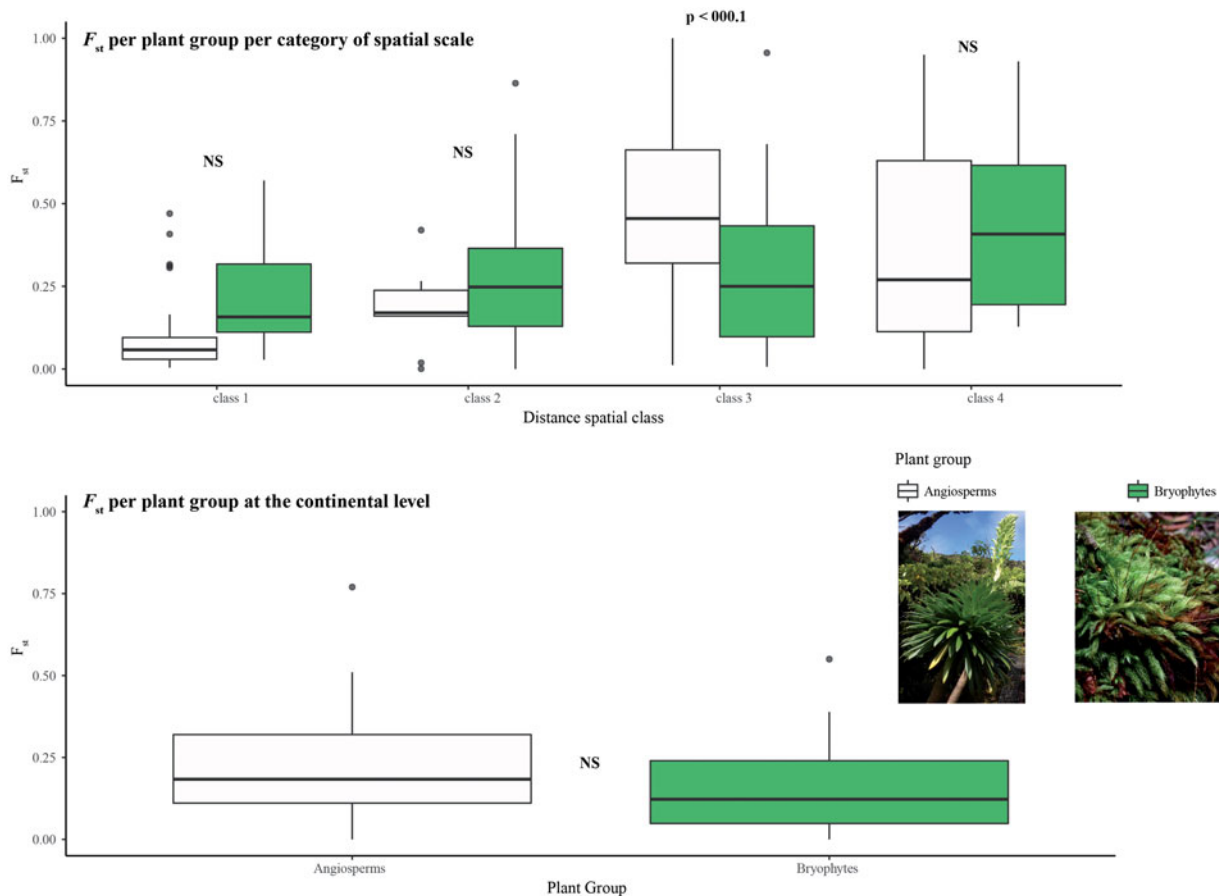
Figure 3. (a) Comparison of the spatial genetic structure (F_{st} among populations) in bryophytes and angiosperms at different spatial scales (see Table 4 for raw data and source information): (1) Local scale (<10 km); (2) regional scale (10–200 km); (3) country to continental scale (200–5000 km); (4) intercontinental scale. (b) Comparison of the spatial genetic structure (F_{st} among groups of populations) of bryophytes and angiosperms between continents (see Table 5 for raw data and source information). Photo credit: Jairo Patiño.

out of the three species investigated, but significant isolation-by-distance patterns were reported elsewhere at the regional (Pisa et al., 2013; Pisa et al., 2015) and intercontinental (Kyrkjeeide et al., 2016) scales, even when controlling for clonality by working at the level of genets instead of ramets (Hutsemékers et al., 2010). The significance of the relationship between distance and genetic similarity from the local to the regional, and sometimes even intercontinental scales, is consistent with distance-dependent experimental kernels based on spore trapping experiments (Sundberg, 2005, 2013), but is at odds with experimental studies suggesting that the tail of the probability density function is independent from the distance to the source, as shown in Figure 1 (Lönnell et al., 2012). Barbé et al. (2016) similarly concluded that the degree of similarity between extant and propagule rain communities was not explained by geographic distance. The main difference between spore trapping experiments and indirect measurements of dispersal from genetic estimators is the time scale, as the former generates an instantaneous picture of 'spore rain', whereas the latter returns

a historical reconstruction of the colonization process. It, therefore, appears that on the long term, and although other factors, such as wind connectivity may also play a major role (see Section II.B), spore dispersal is determined by the distance from the source.

Nevertheless, comparisons of F_{st} values among populations of bryophytes and angiosperms (Figure 3(a)) revealed that spatial genetic structuring in bryophytes tends to become lower than that reported in angiosperms at increasing large spatial scales. Although this tendency was also observed at the largest scale, F_{st} among populations at the largest distance class (Figure 3(a)) and among intercontinental groups (Figure 3(b)) did not reveal significantly lower genetic structures in bryophytes than in angiosperms. We suggest that the test lacks statistical power at such scales precisely because comparatively few angiosperm species exhibit transoceanic distribution ranges. This is best illustrated by the North Atlantic disjunction, wherein 43% of the species of mosses that are found in North America are also found in Europe, while 70% of the moss species found in Europe also occur in North

Table 4. Comparison of the spatial genetic structure of bryophyte and angiosperm populations (F_{st}) at different spatial scales, as shown in Figure 2a: (1) local scale (<10 km); (2) regional scale (10–200 km); (3) country to continental scale (200–5000 km); and (4) intercontinental scale.

Species	F_{st}	Type of marker	Geographic scale (1–4)	Reference
Bryophytes				
Pleurochaete squarrosa	0.44	Allozymes	3	Grundmann et al. (2007)
Pleurochaete squarrosa	0.50	ITS	3	Grundmann et al. (2007)
Pleurochaete squarrosa	0.25	cpDNA sequences	3	Grundmann et al. (2007)
Pleurochaete squarrosa	0.34	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.36	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.33	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.41	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.26	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.18	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.40	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.38	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.13	Allozymes	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.22	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.36	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.36	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.54	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.18	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.12	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.71	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.54	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.17	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.50	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.36	ITS	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.03	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.41	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.21	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.30	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.30	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.12	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.25	cpDNA sequences	2	Grundmann et al. (2007)
Pleurochaete squarrosa	0.20	cpDNA sequences	2	Grundmann et al. (2007)
Crossocalyx hellerianus	0.18	SSRs	2	Holá et al. (2015)
Crossocalyx hellerianus	0.06	SSRs	2	Holá et al. (2015)
Crossocalyx hellerianus	0.25	SSRs	3	Holá et al. (2015)
Sphagnum wulfianum	0.72	SSRs	4	Kyrkjeeide et al. (2012)
Sphagnum angermanicum	0.15	SSRs	4	Stenøien et al. (2011)
Polytrichum uliginosum	0.09	Allozymes	3	van der Velde and Bijlsma (2003)
Polytrichum commune	0.07	Allozymes	3	van der Velde and Bijlsma (2003)
Polytrichum formosum	0.39	Allozymes	3	van der Velde and Bijlsma (2003)
Polytrichum juniperinum	0.34	Allozymes	3	van der Velde and Bijlsma (2003)
Polytrichum piliferum	0.09	Allozymes	3	van der Velde and Bijlsma (2003)
Polytrichum commune	0.05	SSRs	3	van der Velde and Bijlsma (2003)
Polytrichum formosum	0.05	SSRs	3	van der Velde and Bijlsma (2003)
Polytrichum juniperinum	0.17	SSRs	3	van der Velde and Bijlsma (2003)
Rhynchostegium riparioides	0.57	SSRs	2	Hutsemékers et al. (2010)
Rhynchostegium riparioides	0.43	SSRs	1	Hutsemékers et al. (2013)
Orthotrichum handiense	0.57	SSRs	1	Patiño et al. (2013c)
Barbilophozia attenuata	0.13	SSRs	1	Korpelainen et al. (2011)
Calliergon megalophyllum	0.17	SSRs	1	Korpelainen et al. (2013)
Fontinalis antipyretica	0.28	SSRs	1	Korpelainen et al. (2013)
Fontinalis hypnoides	0.14	SSRs	1	Korpelainen et al. (2013)
Asterella liukiuensis	0.68	Allozymes	3	Itouga et al. (2002)
Conocephalum japonicum	0.06	Allozymes	3	Itouga et al. (2002)
Lunularia cruciata	0.96	Allozymes	3	Itouga et al. (2002)
Porella canariensis	0.60	Allozymes	3	Freitas and Brehm (2001)
Preissia quadrata	0.93	Allozymes	4	Boisselier-Dubayle and Bischler (1997)
Reboulia hemisphaerica	0.45	Allozymes	3	Itouga et al. (2002)
Bryum argenteum	0.13	RAPD	3	Skotnicki et al. (1999a)
Fontinalis antipyretica	0.22	ISSRs	2	Korpelainen et al. (2005)
Hennediella heimii	0.15	RAPD	3	Dale et al. (1999)
Hylocomium splendens	0.07	Allozymes	3	Cronberg et al. (1997)
Hylocomium splendens	0.04	Allozymes	2	Cronberg (2002)
Leucodon atrovirens	0.11	Allozymes	3	Akiyama (1994)
Leucodon luteus	0.04	Allozymes	3	Akiyama (1994)
Leucodon nipponicus	0.21	Allozymes	3	Akiyama (1994)
Leucodon temperatus	0.04	Allozymes	2	Akiyama (1994)
Leucodon sapporensis	0.10	Allozymes	3	Akiyama (1994)
Leucodon sciuroides	0.44	Allozymes	3	Cronberg (2000)

Table 4. Continued.

Species	F_{st}	Type of marker	Geographic scale (1–4)	Reference
Meesia triquetra	0.45	Allozymes	3	Montagnes *et al.* (1993)
Mielichhoferia elongata	0.93	Allozymes	4	Shaw and Schneider (1995)
Octoblepharum albidum	0.06	RAPD	2	Korpelainen and Salazar Allen (1999)
Plagiomnium ciliare	0.25	Allozymes	3	Wyatt *et al.* (1989)
Pohlia drummondii	0.11	ISSRs	3	Korpelainen *et al.* (2005)
Plagiomnium ellipticum	0.17	Allozymes	4	Wyatt *et al.* (1992)
Plagiomnium insigne	0.33	Allozymes	3	Wyatt *et al.* (1992)
Plagiomnium medium	0.13	Allozymes	4	Wyatt *et al.* (1992)
Plagiomnium tezukae	0.09	Allozymes	2	Odrzykoski et a. (1993)
Polytrichum juniperinum	0.41	Allozymes	4	Derda and Wyatt (2003)
Polytrichum juniperinum	0.43	Allozymes	3	Derda and Wyatt (2003)
Polytrichum juniperinum	0.41	Allozymes	3	Derda and Wyatt (2003)
Polytrichum juniperinum	0.30	Allozymes	3	Derda and Wyatt (2003)
Polytrichum juniperinum	0.44	Allozymes	3	Derda and Wyatt (2003)
Polytrichum piliferum	0.28	Allozymes	4	Derda and Wyatt (1999)
Polytrichum strictum	0.49	Allozymes	4	Derda and Wyatt (2003)
Polytrichum strictum	0.01	Allozymes	3	Derda and Wyatt (2003)
Polytrichum strictum	0.13	Allozymes	3	Derda and Wyatt (2003)
Polytrichum strictum	0.28	Allozymes	3	Derda and Wyatt (2003)
Sarconeuron glaciale	0.41	RAPD	3	Skotnicki *et al.* (1999b)
Sarconeuron glaciale	0.15	RAPD	2	Skotnicki *et al.* (1999b)
Sphagnum affine	0.51	Allozymes	4	Thingsgaard (2001)
Sphagnum affine	0.55	Allozymes	3	Thingsgaard (2001)
Sphagnum affine	0.10	Allozymes	2	Thingsgaard (2001)
Sphagnum affine	0.25	Allozymes	2	Thingsgaard (2001)
Sphagnum affine	0.66	Allozymes	2	Thingsgaard (2001)
Sphagnum affine	0.86	Allozymes	2	Thingsgaard (2001)
Sphagnum angustifolium	0.13	RAPD	2	Stenoien and Sastad (1999)
Sphagnum angustifolium	0.22	Allozymes	4	Stenoien and Sastad (1999)
Sphagnum angustifolium	0.27	Allozymes	2	Stenoien and Sastad (1999)
Sphagnum angustifolium	0.14	Allozymes	2	Stenoien and Sastad (1999)
Sphagnum fallax	0.54	RAPD	2	Stenoien and Sastad (1999)
Sphagnum lindbergii	0.00	RAPD	2	Stenoien and Sastad (1999)
Sphagnum angermanicum	0.06	ISSRs	3	Gunnarsson *et al.* (2005)
Sphagnum angermanicum	0.03	ISSRs	1	Gunnarsson *et al.* (2005)
Acanthorrhynchium papillatum 0.06		SSRs	2	Leonardía *et al.* (2013)
Pleurozium schreberi	0.07	SSRs	1	Kotelko *et al.* (2008)
Leptodon smithii	0.31	ISSRs	2	Spagnuolo *et al.* (2007b)
Pleurochaete squarrosa	0.00	ISSRs	2	Spagnuolo *et al.* (2007a)
Angiosperms				
Minuartia biflora	0.45	AFLP	3	Schönswetter *et al.* (2006a)
Minuartia biflora	0.81	AFLP	3	Schönswetter *et al.* (2006a)
Minuartia biflora	0.45	AFLP	3	Schönswetter *et al.* (2006a)
Minuartia biflora	0.81	AFLP	3	Schönswetter *et al.* (2006a)
Ranunculus glacialis	0.51	AFLP	3	Schönswetter *et al.* (2004)
Carex atrofusca	0.97	AFLP	3	Schönswetter *et al.* (2006b)
Carex atrofusca	0.63	AFLP	4	Schönswetter *et al.* (2006b)
Campanula alpina f	0.45	AFLP	3	Ronikier *et al.* (2008)
Dryas octopetala	0.47	AFLP	1	Skrede *et al.* (2006a)
Chamaedaphne calyculata	0.31	AFLP	1	Wróblewska (2014)
Sorbus aucuparia	0.02	Allozymes	1	Raspé and Jacquemart (1998)
Sorbus aucuparia	0.00	Allozymes	2	Raspé and Jacquemart (1998)
Sorbus aucuparia	0.04	Allozymes	3	Raspé and Jacquemart (1998)
Sorbus aucuparia	0.01	Allozymes	3	Raspé and Jacquemart (1998)
Sorbus aucuparia	0.06	Allozymes	3	Raspé and Jacquemart (1998)
Leavenworthia alabamica	0.45	Allozymes	3	Koelling *et al.* (2011)
Leavenworthia crassa	0.36	Allozymes	3	Koelling *et al.* (2011)
Acer campestre	0.71	cpDNA	3	Petit *et al.* (2003)
Acer pseudoplatanus	0.67	cpDNA	3	Petit *et al.* (2003)
Alnus glutinosa	0.81	cpDNA	3	Petit *et al.* (2003)
Betula pendula	0.42	cpDNA	3	Petit *et al.* (2003)
Calluna vulgaris	0.59	cpDNA	3	Petit *et al.* (2003)
Carpinus betulus	1.00	cpDNA	3	Petit *et al.* (2003)
Corylus avellana	0.89	cpDNA	3	Petit *et al.* (2003)
Crataegus monogyna	0.24	cpDNA	3	Petit *et al.* (2003)
Cytisus scoparius	0.57	cpDNA	3	Petit *et al.* (2003)
Fagus sylvatica	0.74	cpDNA	3	Petit *et al.* (2003)
Fraxinus sp.	0.86	cpDNA	3	Petit *et al.* (2003)
Hedera sp.	0.57	cpDNA	3	Petit *et al.* (2003)
Ilex aquifolium	0.60	cpDNA	3	Petit *et al.* (2003)

(continued)

Table 4. Continued.

Species	F_{st}	Type of marker	Geographic scale (1–4)	Reference
Populus tremula	0.11	cpDNA	3	Petit et al. (2003)
Prunus avium	0.29	cpDNA	3	Petit et al. (2003)
Prunus spinosa	0.32	cpDNA	3	Petit et al. (2003)
Quercus sp.	0.84	cpDNA	3	Petit et al. (2003)
Rubus sp.	0.31	cpDNA	3	Petit et al. (2003)
Salix caprea	0.09	cpDNA	3	Petit et al. (2003)
Sorbus torminalis	0.33	cpDNA	3	Petit et al. (2003)
Tilia cordata	0.57	cpDNA	3	Petit et al. (2003)
Ulmus sp.	0.47	cpDNA	3	Petit et al. (2003)
Eryngium alpinum	0.42	AFLP	2	Gaudeul et al. (2000)
Campanula pollinensis	0.16	ISSRs	2	Bellusci et al. (2007)
Hippophae rhamnoides	0.15	RAPD	3	Bartish et al. (1999)
Tetraena mongolica	0.17	ISSRs	2	Ge et al. (2003)
Linanthus parryae	0.16	Allozymes	1	Heywood (1991)
Liatris cylindracea	0.07	Allozymes	1	Heywood (1991)
Desmodium nudiflorum	0.01	Allozymes	1	Heywood (1991)
Cynosurus cristatus	0.01	Allozymes	1	Heywood (1991)
Plantago lanceolata	0.06	Allozymes	1	Heywood (1991)
Fagus sylvatica	0.00	Allozymes	1	Heywood (1991)
Impatiens capensis	0.03	Allozymes	1	Heywood (1991)
Delphinium nelsoni	0.07	Allozymes	1	Heywood (1991)
Triticum dicoccoides	0.41	Allozymes	1	Heywood (1991)
Psychotria nervosa	0.01	Allozymes	1	Heywood (1991)
Alseis blackiana	0.03	Allozymes	1	Heywood (1991)
Brosimum alicastrum	0.05	Allozymes	1	Heywood (1991)
Erythrina costaricensis	063	Allozymes	1	Heywood (1991)
Hybanthus prunifolius	0.06	Allozymes	1	Heywood (1991)
Platypodium elegans	0.05	Allozymes	1	Heywood (1991)
Psychotria horizontalis	0.03	Allozymes	1	Heywood (1991)
Rinorea sylvatica	0.08	Allozymes	1	Heywood (1991)
Swartzia simplex	0.04	Allozymes	1	Heywood (1991)
Tachigalia versicolor	0.06	Allozymes	1	Heywood (1991)
Ipomopsis aggregata	0.03	Allozymes	1	Heywood (1991)
Sanicula gregaria	0.11	Allozymes	1	Heywood (1991)
Osmorhiza claytonii	0.06	Allozymes	1	Heywood (1991)
Cryptotaenia	0.31	Allozymes	1	Heywood (1991)
Thymus vulgaris	0.24	cpDNA	2	Tarayre et al. (1997)
Thymus vulgaris	0.02	Allozymes	2	Tarayre et al. (1997)
Lepanthes rubripetala	0.27	Allozymes	2	Tremblay and Ackermann (2001)
L. rupestris	0.17	Allozymes	2	Tremblay and Ackermann (2001)
L. eltomensis	0.22	Allozymes	2	Tremblay and Ackermann (2001)
Ilex leucoclada	0.32	RAPD	1	Turimaru et al. (2003)
Liquidambar formosana	0.06	SSRs	3	Sun et al. (2016)
Lespedeza buergeri	0.52	cpDNA	3	Jin et al. (2016)
Lespedeza buergeri	0.46	ITS	3	Jin et al. (2016)
Capparis spinosa	0.67	cpDNA	3	Wang et al. (2016)
Tapiscia sinensis	0.32	cp SSRs	3	Zhang et al. (2015)
Betula pubescens	0.40	cpDNA	3	Maliouchenko et al. (2007)
Betula pendula	0.43	cpDNA	3	Maliouchenko et al. (2007)
Betula nana	0.42	cpDNA	3	Maliouchenko et al. (2007)
Rubus arcticus	0.48	AFLP	3	Lindqvist-Kreuze et al. (2003)
Draba flava	0.61	AFLP	4	Skrede et al. (2006b)
Draba flava	0.58	SSRs	4	Skrede et al. (2006b)
Draba flava	0.21	SSRs	4	Skrede et al. (2006b)
Draba nivalis	0.63	AFLP	4	Skrede et al. (2006b)
Draba nivalis	0.71	SSRs	4	Skrede et al. (2006b)
Draba nivalis	0.27	SSRs	4	Skrede et al. (2006b)
Draba subcapitata	0.55	AFLP	4	Skrede et al. (2006b)
Draba subcapitata	0.63	SSRs	4	Skrede et al. (2006b)
Draba subcapitata	0.32	SSRs	4	Skrede et al. (2006b)
Empetrum nigrum	0.15	AFLP	4	Alsos et al. (2007)
Vaccinium uliginosum	0.05	AFLP	4	Alsos et al. (2007)
Rubus chamaemorus	0.11	AFLP	4	Alsos et al. (2007)
Betula nana	0.11	AFLP	4	Alsos et al. (2007)
Dryas octopetala	0.16	AFLP	4	Alsos et al. (2007)
Salix herbacea	0.11	AFLP	4	Alsos et al. (2007)
Cassiope tetragona	0.01	AFLP	4	Alsos et al. (2007)
Arabis alpina	0.00	AFLP	4	Alsos et al. (2007)
Saxifraga rivularis	0.21	AFLP	4	Alsos et al. (2007)
Eutrema salsugineum	0.95	nDNA	4	Wang et al. (2015)
Eutrema salsugineum	0.93	cpDNA	4	Wang et al. (2015)

America (Frahm and Vitt, 1993). By contrast, only 6.5% of the species of vascular plants, are shared between the North American and European floras (Qian, 1999). Therefore, there are few phylogeographic studies on transoceanic disjunct angiosperm species (e.g. Wang *et al.*, 2015), and most of them concern circum-Arctic species, which appear to be, in line with Hulten's Arctic refugium model (see Section III.A.2), among the best angiosperm dispersers (Alsos *et al.*, 2007). Although our F_{st} comparisons are further limited by the fact that the different studies reviewed employed different markers, it is, therefore, tempting to see, in the lower population genetic structuring of bryophytes as compared to angiosperms at large spatial scales, a signature of the higher LDD capacities of the former.

Based on these comparisons, we conclude with Shaw *et al.* (2015) that, although bryophytes 'in no way conform to an everything is everywhere pattern', analyses of their patterns of spatial genetic structure suggest that their higher LDD capacities than angiosperms are reflected in lower genetic structuring at large geographic scale. The idea that these high LDD capabilities of bryophytes lead to intense gene flow at large geographic scales, hampering chances of speciation, is, however, at odds with analyses of sexual systems. In fact, monoicous liverworts exhibit higher diversification rates than dioicous ones (Laenen *et al.*, 2016a), suggesting that the higher sporophyte production of the former as compared to the latter, which enhances their dispersal capacities, so that monoicous species are proportionally more common on oceanic islands than on continents (Patiño *et al.*, 2013a), is more likely to trigger allopatric speciation than hampering it due to intense gene flow. If the low levels of endemism in bryophytes do not seem to be explained by decreased chances of speciation associated with intense gene flow, their high LDD capacities lead, however, to an increase of their distribution ranges, thereby affecting their endemic status.

2.3. Post-speciation dispersal. Several lines of evidence suggest that many once endemic bryophyte species enlarge their range and hence, lose their endemic status. In particular, the low levels of endemism observed in island bryophyte floras is paralleled by strikingly lower levels of single-island endemics than in angiosperms. Such a pattern can be visualized by endemic species 'presence in k-island' graphs, which are typically right-skewed in the oceanic island endemic angiosperm flora because most endemics are restricted to a single island (Figure 4(a), Carine and Schaefer (2010)). In contrast, 'presence in k-island' curves for endemic bryophytes are left-skewed (Figure 4(b,c)), indicating that most endemic

species tend to be widespread, and illustrating their capacities to disperse toward other islands and archipelagos soon after the colonization event or speciation process.

Genetic evidence further suggests that the rich European Atlantic fringe bryophyte flora mostly assembled from Macaronesian ancestors during glacial–interglacial cycles from the mid to the Late Pleistocene, resulting in a large suite of species that are shared today between the mid-Atlantic archipelagos and western Europe (Patiño *et al.*, 2015b). Altogether, the spatial distribution of endemic species across archipelagos, along with phylogeographic evidence for a relatively recent migration of once endemic Macaronesian species toward Europe, indicate that island endemic bryophyte species remain restricted to their island of origin during a short period of time. This hypothesis is in line with the notion that bryophyte species exhibit larger ranges and recolonized glaciated areas from much more geographically distant source populations than their angiosperm counterparts (Section III.B.2.2.2). It thus appears that the strikingly low level of endemism in bryophytes is a consequence of both (i) lower diversification rates than angiosperms largely associated to their failure to radiate, and (ii) high LDD capacities, which enable them to disperse quickly after speciation and reach large distribution ranges. Such a major evolutionary pathway would not only result in the loss of their endemic status, but also has important consequences on their patterns of species richness and turnover.

IV. Species richness patterns

A. Species–area relationships

The increase in species richness with increasing area, known as the species–area relationship, is regarded as one of the few laws in ecology (Storch *et al.*, 2012; Triantis *et al.*, 2012; Whittaker and Triantis, 2012), with fundamental implications for our understanding of global biodiversity patterns (Rosenzweig, 1995). In bryophytes, significant species–area relationships were consistently reported from large (Aranda *et al.*, 2013; Patiño *et al.*, 2014b) to small (Virtanen and Oksanen, 2007) spatial scales, although the importance of area may decrease or even disappear on very small scales (trees and boulders) in dynamic habitats where assemblages are not at equilibrium (Kimmerer and Driscoll, 2000; Löbel *et al.*, 2006b). In line with their higher LDD capacities and associated larger range sizes, the slope of the species–area relationship

(Figure 5) in bryophytes is flatter than in angiosperms (Patiño et al., 2014b).

MacArthur and Wilson's (1967) equilibrium theory of island biogeography further predicts that due to the low colonization rates on isolated islands, the slope of the species–area relationship increases with geographical isolation. In a meta-analysis of the species–area relationship among land plants, Patiño et al. (2014b) observed that geographical isolation significantly impacted the intercept of angiosperms, but not that one of bryophytes. Since the intercept of the species–area relationship in the logarithmic space can be interpreted as the carrying capacity, this suggests that, in bryophytes, the realized island carrying capacity does not decrease with geographical isolation because of declining colonization rates. This is consistent with previous studies (Patiño et al., 2013b), in which the contribution of geographical remoteness to explaining spatial patterns of species richness was substantially lower than that of factors accounting for environmental heterogeneity. In arid scrubland fragments, geographic distance significantly explained 10.4% of the floristic dissimilarities for angiosperms, but only 2.1% in bryophytes, again demonstrating that angiosperms, even at the community level, are more sensitive to geographic isolation than bryophytes (Granzow-de la Cerda et al., 2016). Sundberg et al. (2006) similarly concluded that area and habitat type drive diversity patterns of peat moss species on Baltic Sea islands rather than geographical isolation.

One major consequence of the low contribution of geographic isolation to observed species richness patterns in bryophytes is that, as opposed to the expectations of MacArthur and Wilson's (1967) model and patterns observed in angiosperms, bryophyte species richness is not necessarily lower on islands than on continents (Patiño et al., 2015a). The lack of a decrease of species richness with geographic isolation has important evolutionary consequences, because island organisms are expected to respond to empty niche space through a series of major transformations in their life-history traits, such as the loss of dispersal power, changes in body size, and shifts in sexual systems, which are collectively referred to as island syndromes (Whittaker and Fernandez-Palacios, 2007, but see García-Verdugo et al., 2017 and Burns, 2018). Despite the non-significance of geographic isolation in explaining species richness patterns, key differences in life-history traits were observed between endemic island species and their closest continental relatives and between continental and island populations of the same species (Patiño et al., 2013a). Since shifts in the expression of reproductive traits observed in island bryophytes (e.g. higher investment in asexual reproduction, higher frequency of fertile shoots) cannot be interpreted as a response to empty niche space, such changes may reflect a response to the specific climate conditions that prevail on islands. A global comparison of island and mainland environments indeed revealed that wet climates typical of tropical and, especially, temperate rainforest biomes are overrepresented on islands, whereas hot and dry desert climates are underrepresented (Weigelt et al., 2013), which could have catalyzed the emergence of a bias in bryophyte traits associated to such environmental conditions.

Species–area relationships were also observed at smaller spatial scales in fragmented landscapes, wherein species richness across plots of standardized size increases as a function of the area of the fragment (Tangney et al., 1990; Berglund and Jonsson, 2001; Moen and Jonsson, 2003; Zartman and Nascimento, 2006). For example area explained up to 83% of the variation in bryophyte species richness in lake islands in New Zealand at a scale of a few kilometers (Tangney et al., 1990), and 70% in old-growth boreal forest islands surrounded by Sphagnum wetland in Sweden (Berglund and Jonsson, 2001). In line with the idea that geographic isolation does not account for the observed patterns of species richness at large scales, isolation estimates did not correlate with species richness at the landscape scale. This suggests that the degree of isolation in the studied landscape is below the level where it influences species community composition.

The importance of area, but not spatial isolation, raises the question of the impact of fragmentation on species richness. Fragmentation may impact species richness through increased stochastic extinctions and decreased recolonization (rescue effect) due to the break-up and isolation of formerly continuous populations, or altered physical conditions associated with an increase in 'edge environments'. Given the low contribution of geographic isolation to the variation of species richness, ecological factors associated with edge effects would intuitively play a much more important role than demographic factors associated with the rescue effect. Zartman and Nascimento (2006) attempted at disentangling these two factors by investigating variation in Amazonian rainforest epiphyllous abundance, which was strongly correlated with species richness ($R^2 = 0.73$). In sharp contrast to this prediction, they showed that, in line with other tropical epiphyllous studies (Malombe et al., 2016), the lower abundance in epiphylls in small fragments is not well explained by distance to the nearest edge. Zartman and Shaw (2006) further showed that, while extinction

Table 5. Comparison of the spatial genetic structure (F_{st} among groups of populations) of bryophytes and angiosperms between continents.

Species	Spatial scale	F_{st}	Type of marker	Reference
Bryophytes				
Amphidium lapponicum	N America/Europe	0.25	n+cpDNA sequences	Desamore et al. (2016)
Amphidium mougeotii	N America/Europe	0.11	n+cpDNA sequences	Desamore et al. (2016)
Calypogeia fissa	N America/Europe	0.12	cpDNA sequences	Desamore et al. (2016)
Orthotrichum lyellii	N America/Europe	0.29	n+cpDNA sequences	Desamore et al. (2016)
Plagiothecium denticulatum	N America/Europe	0.11	n+cpDNA sequences	Desamore et al. (2016)
Plagiothecium undulatum	N America/Europe	0.09	n+cpDNA sequences	Desamore et al. (2016)
Timmia austriaca	N America/Europe	0.25	n+cpDNA sequences	Desamore et al. (2016)
Timmia bavarica	N America/Europe	0.19	n+cpDNA sequences	Desamore et al. (2016)
Bryum argenteum	All continents	0.15	ITS	Pisa et al. (2014)
Radula lindenbergiana	Macaronesia/Europe/South Africa	0.20	cpDNA sequences	Laenen et al. (2011)
Rhynchostegium riparioides	Iberian peninsula/Morocco/Canary Islands/Madeira/Azores	0.18	SSRs	Hutsemékers et al. (2011)
Grimmia montana	N America/Europe/South Africa/Asia	0.32	cpDNA sequences	Vanderpoorten et al. (2008)
Sphagnum miyabeanum	N America/Asia	0.25	SSRs	Shaw et al. (2014)
Sphagnum contortum	N America/Europe	0.16	SSRs	Szövényi et al. (2008)
Sphagnum cuspidatum	N America/Europe	0.04	SSRs	Szövényi et al. (2008)
Sphagnum magellanicum	N America/Europe	0.03	SSRs	Szövényi et al. (2008)
Sphagnum platyphyllum	N America/Europe	0.24	SSRs	Szövényi et al. (2008)
Sphagnum subsecundum	N America/Europe	0.11	SSRs	Szövényi et al. (2008)
Sphagnum fimbriatum	N America/Europe	0.04	SSRs	Szövényi et al. (2008)
Sphagnum wulfianum	N America/Europe/Asia	0.05	SSRs	Kyrkjeeide et al. (2016)
S. quinquefarium	N America/Europe/Asia	0.55	SSRs	Kyrkjeeide et al. (2016)
S. fuscum	N America/Europe/Asia	0.16	SSRs	Kyrkjeeide et al. (2016)
S. rubiginosum	N America/Europe/Asia	0.21	SSRs	Kyrkjeeide et al. (2016)
S. angustifolium	N America/Europe/Asia	0.08	SSRs	Kyrkjeeide et al. (2016)
Dicranum scottianum	Macaronesia/Europe	0.36	nDNA	Patiño et al. (2015b)
Dicranum scottianum	Macaronesia/Europe	0.03	cpDNA	Patiño et al. (2015b)
Fissidens serrulatus	Macaronesia/Europe	0.14	cpDNA	Patiño et al. (2015b)
Homalia lusitanica	Macaronesia/Europe	0.26	cpDNA	Patiño et al. (2015b)
Myurium hochstetteri	Macaronesia/Europe	0.06	nDNA	Patiño et al. (2015b)
Ptychomitrium polyphyllum	Macaronesia/Europe	0.04	nDNA	Patiño et al. (2015b)
Ptychomitrium polyphyllum	Macaronesia/Europe	0.00	cpDNA	Patiño et al. (2015b)
Saccogyna viticulosa	Macaronesia/Europe	0.04	cpDNA	Patiño et al. (2015b)
Sematophyllum substrumulosum	Macaronesia/Europe	0.39	nDNA	Patiño et al. (2015b)
Sematophyllum substrumulosum	Macaronesia/Europe	0.12	nDNA	Patiño et al. (2015b)
Sematophyllum substrumulosum	Macaronesia/Europe	0.07	cpDNA	Patiño et al. (2015b)
Tetrastichium fontanum	Macaronesia/Europe	0.29	nDNA	Patiño et al. (2015b)
Tetrastichium fontanum	Macaronesia/Europe	0.09	cpDNA	Patiño et al. (2015b)
Tetrastichium virens	Macaronesia/Europe	0.00	nDNA	Patiño et al. (2015b)
Tetrastichium virens	Macaronesia/Europe	0.00	cpDNA	Patiño et al. (2015b)
Ulota calvescens	Macaronesia/Europe	0.01	cpDNA	Patiño et al. (2015b)
Angiosperms				
Silene acaulis	N America/Europe	0.51	cpDNA	Gussarova et al. (2015)
Rubus chamaemorus	N America/Europe/Asia	0.15	AFLP	Ehrich et al. (2008)
Dryas octopetala	N America/Europe/Asia	0.32	AFLP	Skrede et al. (2006a)
Draba flava	N America/Europe/Asia	0.21	SSRs	Skrede et al. (2006b)
Draba nivalis	N America/Europe/Asia	0.27	SSRs	Skrede et al. (2006b)
Draba subcapitata	N America/Europe/Asia	0.32	SSRs	Skrede et al. (2006b)
Empetrum nigrum	N America/Europe/Asia	0.15	AFLP	Alsos et al. (2007)
Vaccinium uliginosum	N America/Europe/Asia	0.05	AFLP	Alsos et al. (2007)
Rubus chamaemorus	N America/Europe/Asia	0.11	AFLP	Alsos et al. (2007)
Betula nana	N America/Europe/Asia	0.11	AFLP	Alsos et al. (2007)
Dryas octopetala	N America/Europe/Asia	0.16	AFLP	Alsos et al. (2007)
Salix herbacea	N America/Europe/Asia	0.11	AFLP	Alsos et al. (2007)
Cassiope tetragona	N America/Europe/Asia	0.01	AFLP	Alsos et al. (2007)
Arabis alpina	N America/Europe/Asia	0.00	AFLP	Alsos et al. (2007)
Saxifraga rivularis	N America/Europe/Asia	0.21	AFLP	Alsos et al. (2007)
Eutrema salsugineum	N America/Asia	0.77	nDNA	Wang et al. (2015)
Eutrema salsugineum	N America/Asia	0.37	cpDNA	Wang et al. (2015)

probabilities were independent from fragment size, experimental leaf patches in fragments of ≥100 ha experienced nearly double (48%) the colonization probability observed in small fragments (27%). These findings suggest that the cause of epiphyll species loss in small fragments (≤10 ha) is reduced colonization due to inter-fragment dispersal limitations, and hence, that the immigration potential of epiphyll species is impacted by increased habitat insularity.

Although epiphyte communities need to track patches of suitable trees in a dynamic landscape for metapopulation persistence (Snäll et al., 2005), the idea
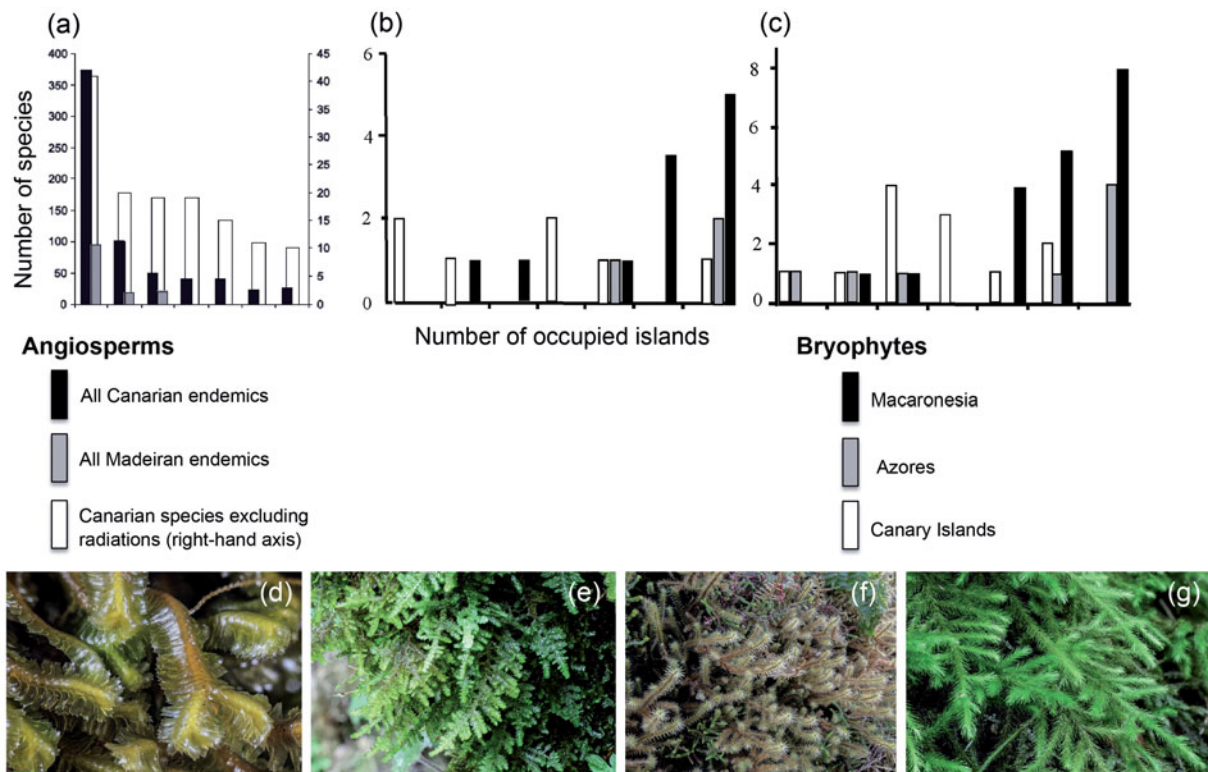
Figure 4. Endemic species 'presence in k-island' distributions for oceanic island archipelagos illustrating, in each case, the number of endemic species having a distribution spanning 1, 2, 3, or more islands. (a) All Canarian endemics (black bars), Madeiran (grey), and Canarian species excluding radiations endemic angiosperm (white). (b) Macaronesian endemic liverworts and (c) Macaronesian endemic mosses. Images show examples of liverwort (d) *Bazzania azorica*) and moss (e) *Neckera intermedia*; (f) *Breutelia azorica*; and (g) *Echinodium spinosum*) species endemic to the Macaronesian region (reproduced and adapted with permission from Cambridge University Press from Vanderpoorten *et al.* (2011)). Photo credit: Dick Haaksma.

that epiphyte communities are strongly constrained by dispersal capacities is supported by several lines of evidence. In fact, epiphytic communities are significantly spatially structured (Heegaard and Hangelbroek, 1999; Snäll *et al.*, 2003, 2004; Löbel *et al.*, 2006a, b; Patiño *et al.*, 2018; but see Kiebacher *et al.*, 2017). Löbel *et al.* (2006a) pointed out that the scale of the observed structured pattern corresponds to the distance of a few meters, at which the density of diaspores from parental sporophytes is the highest (see Section II.B). Although its effect may vary among species and be lower than the sum of the effects of all local environmental variables, connectivity was the most important factor explaining epiphyte distribution patterns in boreal systems (Snäll *et al.*, 2003; Snäll *et al.*, 2004; but see Mota de Oliveira *et al.*, 2009, in tropical epiphytes). This pattern is further confirmed by strong spatial structure patterns of genetic variation at local scales consistently reported in bryophytes in general, and epiphytic bryophytes in particular (Table 3). Functionally, epiphytic mosses typically exhibit peristomial reduction, one of the morphological modifications related to hygrochasy in mosses (Hedenäs, 2012). The release of spores under wet conditions might be seen as a safe-site strategy,

forcing spores to land in appropriate patches in the near vicinity where their survival is favored (Medina and Estébanez, 2014), so that establishment, which occurs at high humidity, is a stronger evolutionary bottleneck than dispersal distance (Johansson *et al.*, 2016).

The different contribution of geographic isolation at different spatial scales shows a striking parallelism with the spore dispersal kernel (see Section II.B), supporting Sundberg's (2005) prediction of the lack of an obvious distance effect on species richness on islands, but suggesting that the higher spore densities observed in the nearest vicinity of the mother sporophyte also shapes local species diversity and composition patterns.

The fact that increased insularity disrupts the dispersal patterns of epiphytes at small spatial scales is a stark reminder of the impacts of fragmentation on connectivity. Even though epiphytes and epiphylls occupy microhabitats, such as tree trunks and leaves, preserving large areas of at least several hectares of boreal forests (Baldwin and Bradfield, 2007) and at least 100 hectares in Amazonian rainforests (Zartman and Nascimento, 2006) is necessary for maintaining connectivity, and hence, promoting the long-term persistence of epiphyte
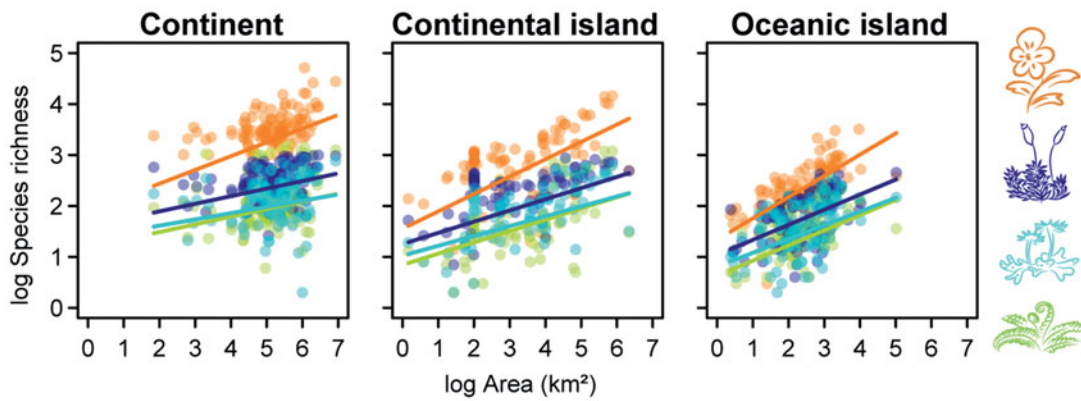
Figure 5. Relationships between species richness [log(SR)] and area [log(AREA), km^2] in spermatophytes (orange), pteridophytes (violet), liverworts (blue), and mosses (green) on continents, continental islands, and oceanic islands. The regression lines are derived from linear mixed-effects models accounting for variation among geological contexts (GEO), lineages of land plants (TAXON), biomes (BIOME), and realms (REALM) (reproduced with permission from Wiley from Patiño *et al.* (2014b)).

bryophyte communities. This illustrates one of the central predictions of metapopulation theory: maintaining a regional equilibrium between extinction and colonization requires an area sufficiently large for the preservation of both inhabited and potentially inhabitable patches (Zartman and Nascimento, 2006).

B. The general dynamic model of island biogeography

MacArthur and Wilson's (1967) theory of island biogeography relies on the assumption of an equilibrium between rates of immigration and extinction. Oceanic islands are, however, dynamic systems, building to a high cone-shaped form of maximal area and elevation, followed by a period of increased erosion and maximal topographic complexity, decrease in elevation and size, and eventually, complete subsidence into the sea (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016; Whittaker *et al.*, 2017). This specific island life cycle and the idea that island species richness is also affected by diversity-dependent dynamics is not explicitly taken into account in MacArthur and Wilson's model. Based on the premise that oceanic islands are relatively short-lived landmasses whose physical properties (e.g. area, altitude, and environmental complexity) change through their ontogeny, the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016) adds this new dimension into MacArthur and Wilson's model and predicts a hump-shaped variation of species richness as a function of island area through time. This hump-shaped relationship characterizes the colonization, speciation, and extinction process as well as the carrying capacity of islands.

In bryophytes, a growing body of evidence indicates that ecological factors largely prevail over historical ones in determining patterns of species richness. In a survey of the factors accounting for bryophyte species richness in 67 oceanic islands, Patiño *et al.* (2013b) reported that 67% of the competing models included time elapsed since island emergence as an explanatory factor. Time, however, contributed substantially less to explain the observed species richness patterns as compared to other factors, such as area and elevation, which were included in all of the competing models. Time, furthermore, accounts for both historical factors (dispersal limitations) and the changing area and topographic complexity during the ontogeny of oceanic islands. In fact, other factors associated with dispersal limitations, such as distance from the mainland and distance among islands within archipelagos, were not selected in the best models of species richness. Sundberg *et al.* (2006) also found that island species richness correlated positively with island area and with degree of shelter by surrounding islands, while distance from the mainland, connectivity, or time did not add to the model. Aranda *et al.* (2014) further showed that a purely ecological model including habitat diversity and climate accounted for only slightly less variation in moss and liverwort richness than a model including both historical and ecological factors (area, island age, and climate). Investigating the relative importance of time since disturbance and habitat variables in creating diversity in old-growth forests, Fenton and Bergeron (2008) similarly suggested that mosses and forest liverworts were primarily influenced by habitat variables and concluded that time since disturbance was not the primary factor limiting species richness.

Altogether, these studies suggest, in agreement with Borges and Hortal (2009), that simple models

including island area and elevation as a surrogate of habitat diversity perform equally well or even better than the favored mathematical expression of the general dynamic model (i.e. [log]Area + Time − Time^2) and its variants in explaining diversity patterns of highly mobile organisms across oceanic archipelagos. The weak contribution of historical factors to global patterns of species richness is in line with another prediction of Sundberg (2005), that is, that the inverse isolation effect could partly explain the weak relationship between latitude and diversity in bryophytes (Tan and Pócs, 2000).

C. Latitudinal species diversity gradients

1. Evidence for a latitudinal gradient of diversity

A latitudinal diversity gradient toward the tropics appears as one of the few laws in ecology (Mittelbach *et al.*, 2007), with a remarkable consistency across space, habitat, and taxonomic groups (Cox *et al.*, 2016). There are, however, some notable exceptions to these patterns, as groups originating during warmer periods of earth's history display a steeper latitudinal gradient, whereas groups originating during colder periods display a shallower diversity gradient due to a weak affinity or no affinity for lower latitudes (Romdal *et al.*, 2013). For example grasses are among the relatively few higher-order lineages that exhibit a shallow, atypical latitudinal gradient due to the climatic specialization of particular lineages to cold and arid environments (Visser *et al.*, 2012). Similarly, although approximately 50% of extant gymnosperm species occur primarily between the tropics, the diversity of gymnosperms decreases at equatorial latitudes (Fragnière *et al.*, 2015).

In bryophytes, the existence of a latitudinal diversity gradient has, due to the lack of a worldwide list of accepted names and actual data on worldwide species distribution patterns, long been an area of controversy. In fact, tropical areas, and especially lowland ones, may not be necessarily species-rich, leading the famous British botanist Richard Spruce (1908, cited by Schuster (1983a)) to write, following a several-month field trip along the Rio Negro: 'I have not gathered more mosses than I could have gathered in a month in the space of 50 miles diameter in any part of Europe'. In their review of bryophyte biogeography, Tan and Pócs (2000, p. 407) estimated, similarly, that 'the magnitude of diversity of temperate bryophytes rivals with the acclaimed high diversity of tropical bryophytes'. von Konrat *et al.* (2008) and Geffert *et al.* (2013) were the first to document worldwide liverwort and moss species richness patterns, respectively, and showed that, while some of the world's diversity hotspots are located in

the tropics, others, such as northwestern North America and New Zealand (Figure 2), are extra-tropical. Bryophyte species richness even increases toward high (rather than low) latitudes in some areas of the world, such as Europe (Mateo *et al.*, 2016) and southern South America (Rozzi *et al.*, 2008). The ability of bryophytes 'to withstand cold in the leafy state much better than their tracheophyte counterparts' (Glime, 2007) would be consistent with their higher diversity outside of tropical regions. It is worth noting that the centers of diversity of the basal lineages in mosses (e.g. *Takakia*, *Andreaea*, *Andreaeobryum*, *Tetraphis*, *Oedipodium*, and *Buxbaumia*) and liverworts (e.g. *Haplomitrium* and *Treubia*) are not located in tropical areas, and that the recent radiation of the speciose genus *Sphagnum* is associated with Miocene climatic cooling in the Northern Hemisphere (Shaw *et al.*, 2010). It is, therefore, tempting to see in such ability to withstand cold the retention of an ancestral niche.

Wang *et al.* (2017) took advantage of the most recently available checklist of liverworts and hornworts of the world to filter-out all non-accepted species names (thereby excluding taxa with 'serious doubts' or a 'knowledge problem' in Söderström *et al.* (2016)) from the most comprehensive database of species distributions available to date, which has been built in the context of the Early Land Plants Today project (http://elpt.fieldmuseum.org/). Altogether, the distributions of 3146 and 118 accepted liverwort and hornwort species names out of a total of 7271 and 215, respectively, were reported from 306 operational geographic units worldwide. Although species richness does not necessarily peak at the equator for all groups and all continents, the global species richness of tropical areas is strikingly higher than that of extra-tropical ones in both liverworts and hornworts (Figure 6). This demonstrates the existence of a latitudinal diversity gradient in hornworts and liverworts based on actual analyses of species richness distribution patterns. The existence of this pattern in liverworts and hornworts calls for a re-analysis of large-scale moss distribution patterns. Due to substantial taxonomic issues causing serious biases in estimates of species richness and distribution patterns (see Section III.B.2.1), a critical checklist of mosses comparable to that of Söderström *et al.* (2016) for liverworts and hornworts is, however, a necessary prerequisite.

The demonstration of a latitudinal diversity gradient in liverworts and hornworts reinforces the universality of this ecological pattern and suggests that inversions in the gradient previously reported at narrower spatial scales in bryophytes (for review see Mateo *et al.*, 2016) are due to regional idiosyncrasies. The intrinsic cold tolerance of bryophytes (see Section

II.C.2) and the weak contribution of historical factors to global patterns of species richness (Section IV.B) raise, however, the question of what mechanisms are responsible for the observed latitudinal diversity gradient in this group.

2. Mechanisms of the latitude diversity gradient
2.1. Historical factors.
In line with the idea that temperate lineages are nested within tropical ones, the 'tropical conservatism hypothesis' postulates that most groups originated in the tropics and are adapted to a tropical climatic regime. This hypothesis, best exemplified by angiosperms (Kerkhoff et al., 2014), relies on the assumption that few species have evolved adaptations to cold, dry, or unpredictable climates (Willig et al., 2003; Wiens and Donoghue, 2004; Wiens et al., 2010). Therefore, most species would have been unable to disperse out of the tropics due to niche conservatism. In particular, dry or cold environments are specifically challenging for plants because adaptations must evolve to enable the tolerance or avoidance of extremely low water potentials (Chaves et al., 2003). This 'out of the tropics' model assumes that clades preferentially originated in the tropics but expanded poleward without losing their tropical presence. In line with this model, the 'time-for-speciation hypothesis' postulates that tropical clades, being older, have accumulated greater species richness through time than temperate clades, without necessarily having faster rates of diversification (Wiens and Donoghue, 2004; Wiens et al., 2010; Wiens, 2011).

The most straightforward way to test these hypotheses is through the paleontological record, as evidenced in angiosperms (Crane and Lidgard, 1989; Mannion et al., 2014). In bryophytes, however, the scarcity of the fossil record makes it impossible to test the hypothesis of a tropical origin of bryophyte lineages. Laenen et al. (2018), therefore, employed a different approach based on molecular dating analyses to test the hypothesis that extra-tropical liverwort lineages are younger than tropical ones. Although the analysis is weakened by the fact that there are only 20 liverwort genera that are restricted to the tropics, these genera were, on average, slightly, but significantly younger than extra-tropical ones, in strong contrast to angiosperms. In turn, the fact that the vast majority of liverwort genera are distributed across both tropical and extra-tropical regions, points to a very weak tropical niche conservatism at best. Although information on niche preference and conservatism is crucially lacking in bryophytes (Mateo et al., 2015), the sharing of many genera between tropical and extra-tropical regions, together with the younger age of tropical genera as compared to temperate ones, are also at odds with the 'out of the tropics' hypothesis.

2.2. Ecological and evolutionary factors.
Stevens (1989) associated the latitudinal diversity gradient with Rapoport's rule, which is the decrease in mean latitudinal extent of species' ranges toward the tropics. Stevens (1989) hypothesized that such a striking relationship is derived from the requirement that organisms living at high latitudes have broader environmental tolerances due to larger seasonal fluctuations. Tropical species, conversely, may have more specialized habitat requirements and narrower tolerances, permitting coexistence of more species. Šizling et al. (2009) showed, however, that the postulated decrease of species' potential range sizes toward the tropics would lead to a latitudinal gradient opposite to that observed. In contrast, an increase in the extent of potential ranges toward the tropics would lead to the observed diversity gradient.

Lowland tropical bryophytes have precisely been considered as 'highly specialized elements with higher than normal levels of monoecism' (Schuster, 1983a). Since bryophytes are primarily dispersed by spores, and given the higher spore production of monoicous species as compared to dioicous ones, it, therefore, appears that lowland tropical bryophytes, many of which are indeed pantropical (Schuster, 1983a), may exhibit larger ranges than extra-tropical ones, accounting for the observed latitudinal diversity gradient. In line with this hypothesis, niche preference rather than dispersal limitation shapes Amazonian 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 and ter Steege (2015) concluded that 'long-distance dispersal of bryophytes in the Amazon does not lead to geographical structure in species composition'. The link between monoecy and distribution range has, however, been questioned (Laenen et al., 2016b), and re-analyzing the worldwide liverwort distribution data reported by Wang et al. (2017), we failed to demonstrate that tropical species, which occurred on average in 4.82 ± 5.21 operational geographic units, have larger distribution ranges than northern (10.51 ± 16.26) and southern temperate (2.93 ± 2.54) species.

Alternatively, the 'diversification rate hypothesis' holds that tropical regions diversify faster due to higher rates of speciation (caused by increased reproductive isolation, faster molecular evolution, short generation time or the increased importance of biotic interactions), or due to lower extinction rates (Currie et al., 2004; Wiens, 2007; Pyron, 2014). The
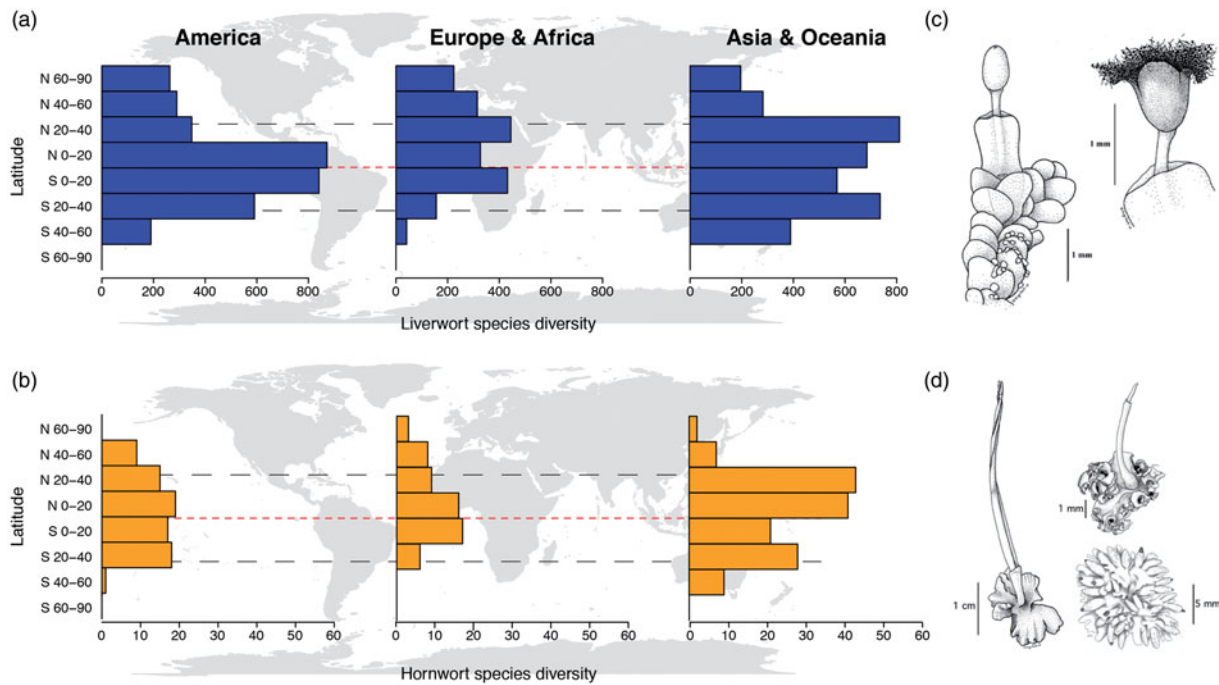
Figure 6. Latitudinal patterns of liverwort (a) and hornwort (b) species richness (reproduced with permission from Wiley from Wang *et al.* (2017)).

'diversification rate hypothesis' is linked to ecological hypotheses, whereby higher input of solar radiation in the tropics promotes productivity. This would allow larger populations to develop, reducing the risk of extinction and, over time and with further speciation, lead to higher species richness (Currie *et al.*, 2004). Although the widespread occurrence of the vast majority of liverwort genera in both tropical and extra-tropical areas complicates the comparison of diversification rates in both regions, the diversification rates observed in the 20 tropical endemic genera were significantly higher than the rates observed in the 63 genera that are restricted to extra-tropical areas (Laenen *et al.*, 2018). The apparent significant difference in diversification rates between tropical and temperate liverworts implies that tropical clades have either higher speciation rates or lower extinction rates.

While the scarcity of the fossil record in bryophytes makes it challenging to test the extinction rate hypothesis, the higher tropical speciation rate hypothesis needs to be tested before potential mechanisms accounting for it (for review see Mittelbach *et al.* (2007)) can be explored. Emerson and Kolm (2005) proposed that rates of endemism are a good reflection of speciation rates. Although the high speed at which bryophytes migrate away soon after speciation (Section III.B.2.3) results in an underestimation of speciation rates, this process is unlikely to vary from one area to another, so

that such rates could be usefully compared along a latitudinal gradient. To date, however, levels of bryophyte endemism in key areas, such as Polynesia (e.g. Hawaii and French Polynesia) or Australia crucially need to be revised based upon critical taxonomic revisions. Sub-Saharan Africa also undoubtedly remains a serious case-in-point. We, therefore, call for a continuous effort in bryophyte taxonomy and floristics. Pragmatically, a first and mandatory step further would be the production of a worldwide critical checklist of mosses in the same framework as the recently published world checklist of liverworts (Söderström *et al.*, 2016). From there, the most critical taxonomic cases, and the most poorly known geographic areas can be identified to prioritize future work, a key task in order to define the best strategies for bryophyte conservation under the ongoing global change context.

Acknowledgments

Funding

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