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ARTICLE

Geographical range in liverworts: does sex really matter?

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ABSTRACT

Aim Why some species exhibit larger geographical ranges than others remains a fundamental, but largely unanswered, question in ecology and biogeography. In plants, a relationship between range size and mating system was proposed over a century ago and subsequently formalized in Baker's Law. Here, we take advantage of the extensive variation in sexual systems of liverworts to test the hypothesis that dioecious species compensate for limited fertilization by producing vegetative propagules more commonly than monoecious species. As spores are assumed to contribute to random long-distance dispersal, whereas vegetative propagules contribute to colony maintenance and frequent short-distance dispersal, we further test the hypothesis that monoecious species exhibit larger geographical ranges than dioecious ones.

Location Worldwide.

Methods We used comparative phylogenetic methods to assess the correlation between range size and life history traits related to dispersal, including mating systems, spore size and production of specialized vegetative propagules.

Results No significant correlation was found between dioecy and production of vegetative propagules. However, production of vegetative propagules is correlated with the size of geographical ranges across the liverwort tree of life, whereas sexuality and spores size are not. Moreover, variation in sexual systems did not have an influence on the correlation between geographical range and production of asexual propagules.

Main conclusions Our results challenge the long-held notion that spores, and not vegetative propagules, are involved in long-distance dispersal. Asexual reproduction seems to play a major role in shaping the global distribution patterns of liverworts, so that monoecious species do not tend to display, on average, broader distribution ranges than dioecious ones. Our results call for further investigation on the spatial genetic structure of bryophyte populations at different geographical scales depending on their mating systems to assess the dispersal capacities of spores and asexual propagules and determine their contribution in shaping species distribution ranges.

Keywords

Baker's law, bryophytes, clonal reproduction, dispersal, phylogeny, range size, sexual systems, spores, vegetative propagules

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INTRODUCTION

Why some species exhibit larger geographical ranges than others remains a fundamental, but largely unanswered, question in ecology and biogeography (Lester *et al.*, 2007; Laube

et al., 2013a,b). Differences in the distribution of species have been attributed to a variety of factors including local and regional habitat conditions, species age, dispersal capacities, fecundity, niche breadth, local abundance, physiological tolerance linked to adaptation at the molecular level and

ploidy, and mating systems (Randle *et al.*, 2009; Slatyer *et al.*, 2013). In plants, reproduction and dispersal are intrinsically linked, as the primary mode of dispersal occurs via the dissemination of the products of sexual reproduction in the form of spores or seeds (Cheptou, 2012). Over a century ago, Henslow (1879), noting that most weedy plant species are self-fertilizing and that the most widely distributed plants in Great Britain were also self-fertilizing, was the first to suggest a relation between mating system, high colonization rates, and large range size. Baker (1955) subsequently formalized this relationship and proposed a model linking colonizing ability and mating system. Baker's Law predicts that, in flowering plants, '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, 1967). Unlike self-incompatible species, long-range dispersing self-compatible species can readily establish new geographically isolated populations. This prediction has led support to the idea that self-compatible species, as well as species producing seeds asexually (Johnson *et al.*, 2010), can more easily establish new populations, facilitating range expansion and leading to larger ranges than those of self-incompatible species (Lowry & Lester, 2006; Randle *et al.*, 2009; Vamosi & Vamosi, 2012; De Waal *et al.*, 2014; Pannell, 2015). As Randle *et al.* (2009) concluded, however, further studies exploring the relationships between mating system and range size in a variety of other taxa are necessary to determine the generality of this pattern.

Bryophytes (liverworts, mosses and hornworts) are especially well suited to investigate the impact of variation in mating systems on range size for several reasons. First, bryophytes exhibit an unparalleled evolutionary lability in their sexual systems (see McDaniel *et al.*, 2013 for mosses and Villarreal & Renner, 2013 for hornworts). This offers many independent observations of the potential link between shifts in sexual systems and geographical range, which is a key issue in the context of increasing concern for pseudo-replication in analyses of phylogenetic correlation (Maddison & Fitzjohn, 2015).

Second, bryophytes disperse by spores whose production is tightly linked to sexuality because sexual reproduction depends on sperm being able to reach the ova by swimming through a continuous film of water. In monoecious species, this functional constraint is weak, as the distance between male and female sexual organs on the same plant is minimal. In dioecious species, conversely, the likelihood of fertilization is inversely proportional to the distance between male and female plants. Sexual reproduction in dioecious species is further complicated by several factors that hamper the chances of sexual reproduction. For example, male and female plants often exhibit contrasting phenologies (Hugonnot *et al.*, 2014). Moss and liverwort populations of dioecious species are further characterized by a strongly female-biased sex ratio (Bisang *et al.*, 2014) and populations comprised of only males or females frequently occur (Hugonnot *et al.*, 2014). This spatial segregation of the sexes at the landscape scale is potentially explained by mounting evidence that males and females exhibit different eco-physiological requirements (Stark & McLetchie, 2006). An extreme case of spacial segregation is exhibited by the moss *Syntrichia pagorum* where only male plants occur in North America while female plants are known only from Europe (Longton, 1997). As a result, sporophyte production is globally lower in dioecious than in monoecious species (Longton, 1997; Laaka-Lindberg *et al.*, 2000).

The uncertainty of successful sexual reproduction in dioecious bryophyte species has probably increased selection for a number of life history traits that promote dispersal. In particular, liverworts can readily regenerate by fragmentation of the gametophyte, but a substantial number of species (46% of the British flora, Laaka-Lindberg *et al.*, 2000) also disperse by means of specialized asexual diaspores (hereafter referred to as vegetative propagules), such as gemmae, brood bodies, modified leaves, etc., which detach from the main shoot by a wide variety of abscission mechanisms whose diversity is unparalleled among land plants (Duckett & Ligrone, 1992). A strong association between dioecy and the ability to produce vegetative propagules has long been identified (Longton & Schuster, 1983; During, 2007; but see Laaka-Lindberg *et al.*, 2000 and Crawford *et al.*, 2009). Indeed, vegetative propagules and spores are assumed to play complementary roles. Bryophyte spores contribute to random long-distance dispersal but are produced during a limited period, especially in liverworts, which have a short-lived sporophyte, although elaters in liverworts and hornworts enhance their release. In contrast, vegetative propagules are produced continuously and exhibit a larger size than spores (Schuster & Longton, 1983, but see Pohjamo *et al.*, 2006) and do not have mechanisms that promote their release. They are, therefore, thought to contribute mainly to colony maintenance and short-distance dispersal (Longton & Schuster, 1983; Kimmerer, 1991, 1994; Longton, 1997; Löbel *et al.*, 2009; Algar-Hedderson *et al.*, 2013). Consequently, if these assumptions are correct, geographical range should correlate with sexual condition and, given that long-distance dispersal depends on spores, monoecious species should have larger ranges than dioecious species (see Longton & Schuster, 1983 for review). In addition, if asexual dispersal follows a stepping-stone pattern, the geographical range of lineages dispersing by asexual diaspores but not by spores is expected to vary with their age, whereas distributional patterns resulting from long-distance dispersal of spores would not (Stebbins, 1950).

To investigate whether sexual systems and dispersal life history traits (production of vegetative propagules and spore size) correlate with geographical range in liverworts, we took advantage of the newly available data from the Liverwort Tree of Life project to address the following questions: (1) Do shifts in sexual reproductive systems correlate with the ability to produce vegetative propagules? Specifically, we investigate whether dioecious species compensate for limited fertilization by producing vegetative propagules more commonly than monoecious species (hypothesis 1); (2) Does

variation in mating system and associated life history traits correlate with geographical range size? As fertilization is severely constrained in dioecious species and spores are likely involved in random long-distance dispersal, we predict that larger geographical range size correlates with monoecy and spore size, but not with the production of vegetative propagules (hypothesis 2); (3) In lineages producing vegetative propagules, is geographical range linked to lineage age? Based on Stebbins' hypothesis, we expect this to be true, but false in species that do not produce specialized vegetative propagules (hypothesis 3).

METHODS

Data collection

In the Liverwort Tree of Life project (http://sites.biology.duke.edu/bryology/LiToL/), one species was sampled for each of 303 out of 382 liverwort genera currently recognized (Laenen et al., 2014). Life history traits (i.e. sexual systems, production of vegetative propagules and spore size) and geographical distributions of each genus were obtained based on an extensive review of published literature sources (see Appendix S2 in Supporting Information).

The range size of each genus was assessed by counting the number of world floristic regions (as defined by Van der Wijk et al., 1959) in which the genus occurs (Vanderpoorten et al., 2010) (see Appendix S1). These regions have traditionally been used to document bryophyte distributions (Tan & Pocs, 2000), and hence represent the best source of reliable information on range size available to date. Twenty of the regions used to score distributions correspond to the biogeographical scheme defined by Van der Wijk et al. (1959) who recognized Europe (EUR), northern Africa (AF1), continental sub-Saharan Africa (AF2), Mascarene Islands (AF3), southern Africa, (AF4), northern Asia (AS1), eastern Asia (AS2), southern Asia (AS3), south-western Asia (AS4), western Asia (AS5), North America (AM1), Central America (AM2), Caribbean islands (AM3), northern South America (AM4), Brazil (AM5), southern South America (AM6), Australia (AU1), New Zealand (AU2), Antarctica (ANT) and Oceania (OC). These regions include ecologically heterogeneous areas, but their delineation is comparable to those used in previous large-scale biogeographical analyses (e.g. Sanmartín & Ronquist, 2004; Sanmartín et al., 2007).

Spore size was averaged across congeneric species and partitioned into three classes (1–20, 20–60 and > 60 μm) that correspond to small spores assumed to exhibit the critical size for long-distance wind dispersal (Wilkinson et al., 2012), medium-sized spores and very large spores that are typically produced by annual species and rest in the bank of diaspores (Söderström & During, 2005). For the production of vegetative propagules and type of sexual system, genera were scored based on the modal condition among species (Wiens, 1998). We therefore scored genera as '0' when > 75% of the species lacked vegetative propagules and as '1' otherwise.

Genera were scored as unisexual or bisexual when they included > 75% dioecious or monoecious species, respectively, and as unknown otherwise (see Appendix S1). The threshold of 75% was set arbitrarily to reflect a marked trend in a genus and avoid the possibility that the slight dominance of one state unduly influences the analysis.

Phylogenetic correlations

Correlation analyses were conducted using the chronogram of the phylogenetic analysis performed by Laenen et al. (2014). The chronogram was the maximum clade credibility tree resulting from the relaxed-clock Bayesian analysis of 303 liverwort genera sequenced for five chloroplast genes (atpB, psbA, psbT, rbcL and rps4), two mitochondrial genes (rps3 and nad1), and the 26S nuclear ribosomal RNA gene. The chronogram was calibrated with 25 fossils, using a lognormal distribution of prior probabilities of ages centred on the fossil age estimate with a standard deviation set so that its range encompasses the upper limit of the oldest inferred estimate of the origin of land plants 815 million years (Ma) ago (Calibration III in Laenen et al., 2014).

Hypotheses of correlated evolution between sexual systems and production of vegetative propagules were tested by comparing the fit of two nested models to the observed data. For a binary character, transitions among states can be described with two rates, one for transitions between 0 and 1 and another for transitions between 1 and 0. Describing the evolution of two independent binary characters thus requires four transition rates. If traits evolve in a correlated fashion, then four additional rates that describe how variation in one trait influences evolution of the other must be included in the model. The model of correlated change is justified as a representation of the data if it fits the data significantly better then the model of independent change (Pagel, 1994). This is assessed by a likelihood ratio test (LRT) as implemented by the Discrete function in BAYESTRAITS 2.0 (http://www.evolution.rdg.ac.uk/BayesTraits.html).

The age of each genus was derived from Laenen et al. (2014) based on the molecular dating analysis described above by taking the stem age of each genus in the phylogeny. For the correlation between geographical range and genus age, we employed the 'Continuous' function of BAYESTRAITS 2.0 fitting to the data two nested models of trait evolution. In the independent model, trait covariance was set to 0; while in the dependent model, covariance was unconstrained. We used a LRT to determine whether the dependent model returned a significantly higher log-likelihood than the independent model. The same procedure was applied for the correlation between geographical range and sexual systems, production of asexual propagules and spore size.

To further examine whether the sexual condition affects the potential correlation between geographical range and production of vegetative propagules, we repeated our analysis for monoecious ($n = 54$) and dioecious lineages ($n = 174$) separately, using phylogenetic generalized least squares
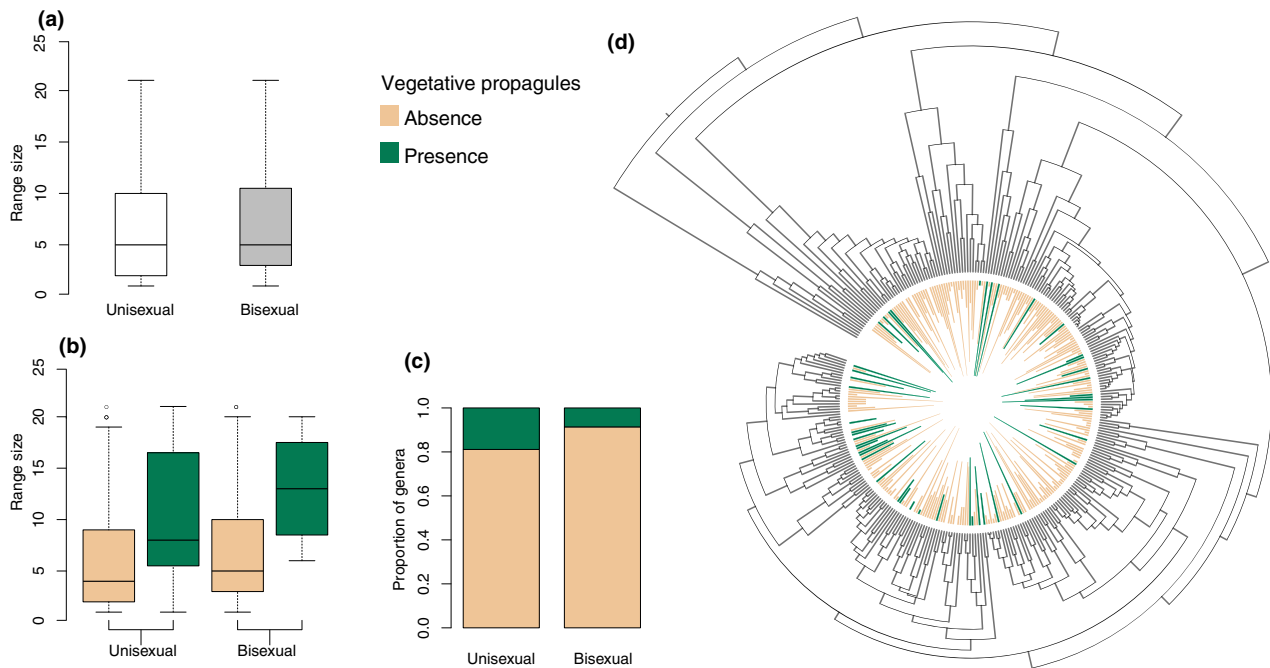
Figure 1 Geographical range, as defined by the number of biogeographical areas occupied, mating systems and production of vegetative propagules. (a) Box-and-whisker plots comparing median range size in unisexual and bisexual liverworts genera; (b) Median range size in the presence or absence of vegetative propagules in unisexual and bisexual liverwort genera, whiskers represent the interquartile range and the line, the median; (c) Proportion of liverwort genera producing vegetative propagules in unisexual and bisexual genera; (d) Variation in the production of vegetative propagules and geographical range, mapped on the liverwort tree of life. Geographical range is proportional to bar size.

(PGLS) a powerful method for analysing continuous data that has been applied to estimate the relationships among traits (see Freckleton et al., 2002; Symonds & Blomberg, 2014), implemented in the 'R' package CAPER (R Development Core Team 2015, Orme et al., 2013). This method estimates statistical correlations across the data while controlling for phylogenetic relatedness between the analysed lineages from the phylogeny. To further determine whether variation in the sexual condition affects the correlation between geographical range and production of vegetative propagules, we also applied PGLS. We fitted four models:

Model 1: Range size ~ vegetative propagules [only monoecious genera]
Model 2: Range size ~ vegetative propagules [only dioecious genera]
Model 3: Range size ~ vegetative propagules + sexual condition [whole tree]
Model 4: Range size ~ vegetative propagules + sexual condition + vegetative propagules × sexual condition [whole tree]

Models 1 and 2 include vegetative propagules as predictor for monoecious, and dioecious taxa respectively. Model 3 tests for additive effects of the mating system and model 4 additionally tests for non-additive effects (statistical interaction) between vegetative propagules and mating systems.

Both continuous and PGLS were originally designed for analyses of continuous traits, but correlations between continuous and discrete traits are computed using the same formula such that they are numerically equivalent to correlations between continuous traits. Using a mixture of binary and continuous variables in analyses similar to ours has been further justified by Wright (1934) who argued that discrete traits can be perceived as functions of an unobserved 'liability function', which is continuous but switches the trait from one state to another when it crosses its threshold value. Under this model, liabilities for both discrete traits and continuous traits are assumed to evolve following the Brownian motion, allowing analysing correlations between discrete and continuous traits within a single statistical framework (e.g. Lambert & Wiens, 2013).

RESULTS

Range size in liverworts varies from 1 to 21 biogeographical regions occupied. Genera present in only 1 or 2 areas represent 22% of the data and the median range size was 6. Four per cent of the genera were present in all areas. Fifty-two genera (17.2%) showed a production of specialized asexual propagules and 250 (82.8%) did not. Fifty-eight genera were scored as bisexual (19.2%) and 195 as unisexual (64.6%). Spore size had 153 (50.6%), 67 (22.2%) and 21 (6.95%) genera classified as small, medium and large spores respectively. Median range size was identical (5 areas) for unisexual and bisexual genera (Fig. 1a), whereas

Table 1 Phylogenetic correlation between geographical range and predictors, including production of vegetative propagules, sexual systems, spore size and genus age across the liverwort phylogeny, using Continuous and Phylogenetic Generalized Least Squares (PGLS). *, **, ***, NS refer to the P-value of the model at the 0.05, 0.01, 0.001 and > 0.05 levels, respectively, and indicate in the complex PGLS models, the significance of the contribution of each variable (model 3) and their interaction (model 4) to stay in the model. R^2 as the coefficient of determination represent the percentage of variance explained.

Predictor	R^2	P-value
Continuous		
Vegetative propagules, complete tree	0.0324	0.003**
Vegetative propagules, only unisexual genera	0.0441	0.036*
Vegetative propagules, only bisexual genera	0.0400	0.002**
Sexual condition	–	0.223 NS
Spore size	–	0.802 NS
Genus age, complete tree	–	0.379 NS
Genus age, only genera with vegetative propagules	–	0.913 NS
Genus age, only genera without vegetative propagules	–	0.807 NS
PGLS		
Vegetative propagules, only unisexual genera (model 1)	–	0.124 NS
Vegetative propagules, only bisexual genera (model 2)	0.057	0.001***
Vegetative propagules** + sexual condition, complete tree (model 3)	0.0290	0.012*
Vegetative propagules** + sexual condition+ vegetative propagules x sexual condition, complete tree (model 4)	0.0260	0.030*

median range size was 5 and 12 for genera without and with presence of specialized asexual propagules respectively (Fig. 1b). Specialized vegetative propagules were present among 8.6% of unisexual genera and among 18.9% of bisexual ones (Fig. 1c).

No significant correlation was found between mating system and production of vegetative propagules (LRT = 5.76, df = 4, P > 0.05) using 'Continous'.

Phylogenetic correlations between range size and life history traits were significant only for the production of vegetative propagules even when considering unisexual or bisexual genera separately (Table 1). No significant correlation was found between lineage age and range size (Table 1).

Three out of the four PGLS models showed a significant association between range size and vegetative propagules but not with mating system or their interaction. The non-significant association with vegetative propagules was recovered only when unisexual genera were considered. We interpret the lack of significance of this correlation within unisexual genera using PGLS as a lack of statistical power in the latter analysis. Indeed, there were 195 genera with > 75% dioecious species, but only 58 with > 75% monoecious species.

DISCUSSION

The absence of association between mating system and vegetative reproduction challenges the traditional notion according to which dioecious species compensate for the lower production of sporophytes (as compared to monoecious species) by an increased production of vegetative propagules (hypothesis 1) (Longton & Schuster, 1983; During, 2007). However, Laaka-Lindberg et al. (2000) suggested that, in severe environments, fertilization constraints might also be limiting in monoecious species. Vegetative propagules enable reproduction early in the life cycle, resulting in the production of new mature adult plants at a faster rate than sexual reproduction (Mishler & Newton, 1988) and are less sensitive to habitat quality compared to vulnerable early developmental stages following spore germination (i.e. protonema) (Löbel & Rydin, 2010). Thus, production of vegetative propagules appears as a security system in response to the spatio-temporal variation in habitat quality and water supply, regardless of sexual condition.

No significant correlation was observed between sexual systems and geographical range (Table 1). This result negated our hypothesis 2 according to which monoecious lineages exhibit larger ranges than dioecious lineages due to the lower production of spores associated with strong fertilization constraints in dioecious species (Schuster & Longton, 1983). Indeed, a higher proportion of monoecious than dioecious species is geographically rare, and this observed rarity in monoecious species has been previously associated with a failure to produce sporophytes in the British moss (Longton, 1992) and liverwort (Laaka-Lindberg et al., 2000) floras. While, as mentioned above, monoecious species can also experience severe fertilization constraints under certain conditions, dioecious species may also develop adaptations to enhance fertilization rates. In particular, male dwarfism in mosses (Rosengren & Cronberg, 2014), dehydration tolerance in sperm cells (Shortlidge et al., 2012) and biotic sperm dispersal (Cronberg et al., 2006) potentially limit fertilization constraints in dioecious lineages. Furthermore, it should not be assumed that monoecious species are selfing simply because the male and female gametangia are simultaneously mature. Selfing could conceivably be detrimental owing to inbreeding depression from deleterious recessive alleles at loci that are predominantly or exclusively expressed in the sporophyte phase, hence mechanisms may be in place to reduce or eliminate self-fertilization. Accordingly, however, inbreeding depression does not appear to be common in bryophytes (Johnson & Shaw, 2015), monoecious species are thought to rapidly purge recessive deleterious mutations through intra-gametophytic selfing (i.e. merging of gametes produced by shoots from the same protonema and hence, originating from the same spore) (Taylor et al., 2007). Therefore, and although further research on self-compatibility in bryophytes is required, no evidence of self-incompatibility has been found to date, an observation which accords with the very high F_{is} values observed in the sporophytic

phase of monoecious species (Eppley *et al.*, 2007 ; Hutse-mekers *et al.*, 2013; Klips, 2015).

No significant correlation was found between geographical range and spore size (Table 1). However, this result does not necessarily invalidate the idea that spores are involved in long-distance dispersal and that smaller spores are more readily dispersed over long distances than large ones. Other factors, and in particular, spore viability, might indeed influence the extent of the geographical range (van Zanten, 1976, 1978; Van Zanten & Gradstein, 1988), calling for further research on spore viability under a range of environmental conditions.

Most surprisingly, however, and in contrast with our second hypothesis, production of vegetative propagules positively correlated with geographical range in all of the implemented analyses (Table 1). In agreement with the absence of a trade-off between sexual condition and production of asexual propagules, variation in sexual systems did not have an influence on the correlation between geographical range and production of asexual propagules, as the interaction between sexual systems and production of asexual propagules was not significant (model 4, Table 1). Accordingly, geographical range and vegetative propagules were significantly correlated when only monoecious and dioecious genera were considered, respectively, using the continuous analyses (Table 1). The weak but significant correlation observed was obtained although many species producing asexual propagules can also reproduce sexually, and although a range of factors potentially account for range size variation and may blur the impact of dispersal capacity. As a result, the importance of dispersal capacity in explaining range sizes has been challenged (Lester *et al.*, 2007). In the present study, the recurrent observation that genera producing vegetative propagules tend to display, on average, larger geographical ranges than genera that do not (Fig. 1), strongly suggests that the significant correlation observed is not due to pseudo-replication (Maddison & Fitzjohn, 2015).

The observed positive correlation between geographical range size and the production of vegetative propagules either suggests that asexual reproduction displays a previously unrecognized and important role in long-distance dispersal, or that the potential for production of vegetative propagules correlates with other ecological or life history characteristics that might promote broader distributions, better dispersal and/or higher rates of establishment and persistence. For instance, relictual persistence of groups that produce vegetative propagules could account for the correlation observed, without invoking long-distance dispersal of vegetative propagules. In relation to our hypothesis 3), no significant correlation was observed between geographical range and lineage age, neither globally nor within lineages with or without vegetative propagules, because comparatively young lineages can be as widespread as older ones (Table 1). This contrasts with Stebbins's (1950) stepping-stone model of vegetative propagule dispersal and with the hypothesis of a longer longevity of lineages producing vegetative propagules. Alter-

natively, vegetative propagule production might occur more frequently in species with broader ecological tolerances and hence, possibly broader geographical distributions. Although such a link between production of vegetative propagules and ecological niche has, to our knowledge, never been reported in the literature, further research on liverworts ecological niches and their potential link with life history traits would be beneficial.

Finally, whereas experimental evidence suggests that asexual reproduction comes at a lower cost than sexual reproduction (Stark *et al.*, 2009), there are examples in bryophytes where this is not the case. For example, sporophyte production is correlated with higher shoot mortality among females (Pohjamo & Laaka-Lindberg, 2003), reduced size of vegetative offshoots, reduced branching (Rydgren & Okland, 2003) and reduced production of new reproductive organs (Bisang & Ehrlen, 2002). Sexual reproduction also requires specific habitat and climatic conditions, so that some species freely release spores in some areas, but not in others (Laaka-Lindberg, 2005). This raises the question of whether lineages producing asexual propagules can also better partition their resources between vegetative and sexual reproduction than species only dispersing by spores, possibly influencing their fitness and hence, their ability to disperse over greater distances. Although such hypotheses cannot be dismissed, they are not mutually exclusive of the idea that vegetative propagules have higher long-distance dispersal capacities than previously thought.

Two lines of evidence support the contribution of asexual reproduction to long-distance dispersal. First, propagules in northern temperate liverwort groups such as Lophoziaceae *s. l.*, Scapaniaceae and Cephaloziaceae p.p. are not necessarily larger than spores (Pohjamo *et al.*, 2006). In many instances, asexual propagules are single-cells with a size well below the 20 μm limit that is critical for wind-based long-distance dispersal (Wilkinson *et al.*, 2012). Vegetative propagules display, however, a much lower tolerance than spores to drought and cold conditions that prevail in high altitude air currents (Stieha *et al.*, 2014). These observations are compatible with the hypothesis that vegetative propagules travel at low rather than high altitudes, either through surface-level wind currents (Muñoz *et al.*, 2004) or bird-mediated transport (Lewis *et al.*, 2014). Second, mounting genetic evidence points to high long-distance dispersal capacities of vegetative propagules. 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 long-distance dispersal by vegetative propagules through the mathematical analysis of dioecious metapopulations. These studies, together with the results presented here, suggest that asexual reproduction plays a major role in determining the global distribution patterns of bryophytes, and raises the intriguing notion that widely disjunct bryophyte communities can function at the level of metapopulations of gigantic clonal networks.

Another consequence of the long-distance capacities of asexual propagules is that the higher proportion of species producing them on islands than on continents does not necessarily mirror a shift in mating systems to quickly invade empty ecological space (Patiño *et al.*, 2013). Rather, species producing asexual propagules may be over-represented on islands because production of asexual propagules enhances the chances of island colonization from continental source populations, following trans-oceanic long-distance dispersal.

Building on previous studies contrasting patterns of isolation-by-distance in clonal versus sexually reproducing species (Snäll *et al.*, 2004), our results therefore call for further investigation on the spatial genetic structure of bryophyte populations at different geographical scales depending on factors linked to the dispersal capacities of spores and asexual propagules and determination of their contribution in shaping species distribution ranges. The ecological importance of epiphytism in bryophytes as compared to angiosperms may also play a key role in range expansion, as it implies a suite of eco-morphological adaptations, including improved dispersal capacities to move rapidly from one host to another. In particular, it has been suggested that dispersal should be higher among species inhabiting the canopy than in ground-dwelling ones due to higher wind velocity in the canopy (Gradstein, 2006; but see Mota de Oliveira & ter Steege, 2015) and potentially, associated adaptations for long-distance wind dispersal. In this context, an area of future research would be to integrate, in a common phylogenetic framework, key factors influencing geographical range at different spatial and temporal scales.

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SUPPORTING INFORMATION

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

Appendix S1 Liverwort life history traits.
Appendix S2 References of appendix S1.

BIOSKETCH

Benjamin Laenen research interests are the evolutionary consequences of mating systems' shifts using a phylogenetic and population genomic approach in plants. He is currently a post-doctoral fellow at University of Stockholm studying the impact of mating system shifts on selection in the genus *Capsella*.

Author contributions: B.L and A.V. conceived the ideas; B.S., J.S and S.R.G collected the data; B.L. and A.M. analysed the data; all authors contributed to the writing.

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