Range size heritability and diversification patterns in the liverwort genus *Radula*

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ABSTRACT

Why some species exhibit larger geographical ranges than others, and to what extent does variation in range size affect diversification rates, remains a fundamental, but largely unanswered question in ecology and evolution. Here, we implement phylogenetic comparative analyses and ancestral area estimations in *Radula*, a liverwort genus of Cretaceous origin, to investigate the mechanisms that explain differences in geographical range size and diversification rates among lineages. Range size was phylogenetically constrained in the two sub-genera characterized by their almost complete Australasian and Neotropical endemism, respectively. The congruence between the divergence time of these lineages and continental split suggests that plate tectonics could have played a major role in their present distribution, suggesting that a strong imprint of vicariance can still be found in extant distribution patterns in these highly mobile organisms. *Amentuloradula*, *Volutoradula* and *Metaradula* species did not appear to exhibit losses of dispersal capacities in terms of dispersal life-history traits, but evidence for significant phylogenetic signal in macroecological niche traits suggests that niche conservatism accounts for their restricted geographic ranges. Despite their greatly restricted distribution to Australasia and Neotropics respectively, *Amentuloradula* and *Volutoradula* did not exhibit significantly lower diversification rates than more widespread lineages, in contrast with the hypothesis that the probability of speciation increases with range size by promoting geographic isolation and increasing the rate at which novel habitats are encountered. We suggest that that stochastic long-distance dispersal events may balance allele frequencies across large spatial scales, leading to low genetic structure among geographically distant areas or even continents, ultimately decreasing the speciation rates in highly mobile, widespread lineages.

1. Introduction

Geographical ranges tremendously vary among species (Lester et al., 2007; Abellán and Ribera, 2011; Laube et al., 2013a, b), but in fact, also vary during the lifespan of a species depending on intrinsic (the proportion of the ancestor's range inheritance) and extrinsic (geological and climatic history) factors until decline and extinction (Jones et al., 2005; Sheth et al., 2014; Fine, 2015). Four main models of range size transformations have been proposed (Gaston, 1996, 1998). In the 'age and area' and 'stasis' models, species lifespans and range sizes are correlated, but the two models differ by the cause-and-effect relationship between these two factors: species with long lifespans are expected to exhibit larger ranges than short-lived species in the former, whereas species with large range sizes are expected to have longer lifespans than species with small ranges in the latter. Under the 'random' model, conversely, range sizes continuously vary depending on environmental factors. In the 'cyclical model', there is a rapid range size increase post-speciation, followed by a steady decline to extinction.

If, as the 'stasis model' implies, geographic range determines the probability of persistence of lineages, we expect that, following Jablonski's hypothesis (Jablonski, 1987, but see Webb and Gaston, 2003) based on geographic range reconstructions of Cretaceous mollusks, range size is under selection and is heritable. Furthermore, under the 'age and area model', we expect to observe a trend towards progressive increases of range size with lineage age. Trait heritability over a phylogeny can be measured through several estimators, such as Pagel's lambda (Pagel, 1999b), which reveals whether the tree correctly predicts the character states observed in present taxa. If range size globally tends to increase or decrease as the 'age and area' models suggest, one would further

expect that a directional random-walk model, which includes a parameter measuring the regression of trait values across species against total path length from the root of the tree to the tips (Pagel, 1999a), describes the data significantly better than a constant-variance random walk model.

Measures of phylogenetic signal are, however, based on the distribution of traits observed in species and then ‘evolved’ along the phylogeny, assuming that the relationship between the traits of ancestors and descendants can be inferred from the distribution of traits among descendants. This may, however, be a problematic assumption in the context of geographic range-size heritability (e.g. Gaston, 1998; Hunt et al., 2005). In fact, species-level heritability of range sizes may result from two mechanisms, namely phylogenetic conservatism of ecological traits such as species niche (Sheth et al., 2014), dispersal ability (Lester et al., 2007) and mating systems (Randle et al., 2009), and direct inheritance of ranges (vicariance) (Borregaard et al., 2012). In the first case, the sharing of traits that are strong determinants of range size is expected to lead closely related species to exhibit more similar range sizes than distantly related ones, indeed resulting in significant lambda statistics. In the second case, conversely, the asymmetric division of an ancestral range (vicariance) will tend to make the range sizes of sister species more dissimilar (Waldron, 2007). As a result, direct range inheritance cannot be detected using lambda estimators.

Finally, if range size is indeed heritable and controls for lineage persistence through time, we expect that range size also impacts on diversification patterns (Jablonsky and Roy, 2003). Under Jablonski’s hypothesis (Jablonski, 1987), widely distributed species, persisting for longer, are expected to exhibit lower extinction rates. In turn, larger areas

are expected to provide greater opportunities for genetic isolation due to a higher incidence of dispersal barriers and/or greater habitat heterogeneity for ecological speciation (Kisel and Barraclough, 2010; Losos and Alder, 1996; Rabosky and Lovette, 2008; Rosenzweig, 1995). Following long-distance dispersal, similarly, either founder effects or exposure to new habitats and selective pressures can trigger speciation (Wessel et al., 2013). Conversely, the combination of geographical boundaries limiting clade distributions and restricted availability of ecological opportunities is expected to lead to a decrease in diversification rates. Therefore, if, as theory predicts (Goldberg et al., 2011; Wagner and Erwin, 1995), the probabilities of speciation are dependent on the geographical extent of the species, variations in the rates of diversification over time and among lineages are expected (Losos and Alder, 1996).

In the present study, we focused on *Radula*, a leafy liverwort genus that, with its Cretaceous origin (Cooper et al., 2012; Laenen et al., 2014) and *ca.* 200 species with diverse geographic ranges, appears as an ideal model to investigate the evolution of range sizes through time and their impact of diversification patterns. Indeed, earlier phylogenies for the genus (Devos et al., 2011a; Devos et al., 2011b; Patiño et al., 2013b; Renner et al., 2014; Renner et al., 2013) resolved a mixture of nearly cosmopolitan lineages (subgenera *Radula* and *Cladoradula*) and more geographically restricted lineages (*Amentuloradula* and *Odontoradula*, with a concentration of species in Australia and New Zealand, *Metaradula* in the paleotropics, and *Volutoradula* in Central and South America). More precisely, we addressed the following questions: (i) Is range size phylogenetically constrained? If so, is there a trend across the tree so that geographic ranges progressively become larger or smaller with the taxon age? (ii) What are the mechanisms accounting

for range size heritability? In particular, are macroecological niche traits also phylogenetically constrained, and/or does heritability correlate with variation in dispersal life-history traits? And (iii) to what extent does variation in geographic range correlate with shifts in diversification rates?

2. Materials and methods

2.1. Taxon sampling and molecular protocols

Building on previous work focusing on the infra-generic classification of *Radula* (Devos et al., 2011a; Devos et al., 2011b; Patiño et al., 2013b; Renner et al., 2013), we sequenced six plastid loci, including *atpB-rbcL*, *psbT-psbH*, *psbA-trnH*, *rps4*, *trnG* and *trnL-F*, for another 25 species (see Devos et al., 2011a, for details on the molecular protocols). With 108 species, our sampling includes *ca.* 50% of the currently recognized species in the genus (Devos et al., 2011b; Yamada, 2003). Devos et al. (2011b) proposed an infrageneric classification for *Radula* with a total of seven subgenera. Two of these subgenera, *Amentuloradula* (which encompasses *ca.* 16 % of the total species diversity in *Radula*) and *Odontoradula* (*ca.* 12 %), are mostly restricted to Australasia, *Volutoradula* (*ca.* 23 %) is mostly restricted to Central and South America, *Metaradula* (*ca.* 17 %) is Pan-tropical but largely restricted to the Paleotropics, and both *Radula* (*ca.* 26 %) and *Cladoradula* (*ca.* 6 %) are nearly cosmopolitan. The last subgenus, *Dactyloradula*, includes a single species, the northern amphi-Pacific disjunct *R. brunnea* Steph. *Diplophyllum obtusifolium*, *Frullania moniliata*, *Jubulopsis novaezealandiae*, *Jungermannia atrovirens*, *Lejeunea tuberculosa*, *Lepidolaena clavigera*, *Mylia taylorii* and *Porella navicularis* were employed as outgroups based on Laenen et al. (2014).

Herbarium voucher numbers and GenBank accession numbers are provided in the Supporting Information (Tables S1 and S2).

2.2. Character scoring

The range size of each species was described by its number of occurrences among the twenty world floristic regions defined by van der Wijk et al. (1959) with subsequent refinements by Tan and Pócs (2000). Dispersal life-history traits (Table S3) included both variation in sexual condition (monoecious vs dioecious), which controls spore production, and the ability to produce specialized asexual diaspores, which were recently shown to complement sexual spores in enhancing the long-distance dispersal capacities of bryophytes (Laenen et al., 2016). Elevation, substrate, and biome ranges were used to describe the amplitude of the macro- and microecological niche for each *Radula* species (Table S3). To determine the elevation range, we considered five categories, which were defined according to the breadth of the altitudinal range that *Radula* species occupy, as follows: (1) very narrow range [< 500 m]; (2) narrow range [< 1000 m]; (3) medium range [< 2000 m]; (4) large range [< 3000 m]; and very large range [> 3000 m]. We defined substrate range as the number of substrates (as a proxy of microecological conditions) where the species occurs. We considered: (1) rocks; (2) barks including trunks and canopies; (3) leaves; and (4) soils. Biome range was based on the number of biomes (defined according to Olson et al., 2001) occupied by each species, which were grouped as follows: (1) Tundra; (2) Boreal forest and Taiga; (2) Montane grasslands and shrublands; (3) Temperate coniferous forests and Temperate broadleaf and mixed forests; (4) Tropical and sub-tropical dry, coniferous and moist broadleaf forests; (5)

Mediterranean forests, woodlands and scrublands; (6) Tropical and sub-tropical grasslands, savannas and shrublands; (7) Temperate grasslands, savannas and shrublands; and (8) Flooded grasslands and savannas. We gathered the dataset for these ecological attributes from the sources listed in Table S3.

2.3. Phylogenetic and molecular dating analyses

The phylogeny was reconstructed using BEAST 1.8.0 (Drummond et al., 2012). The best-fitting substitution model for each individual locus was selected with the Akaike information criterion using MrModelTest (Nylander, 2004) in conjunction with PAUP* (Swofford, 2002). A General Time-Reversible (GTR) model with gamma-distributed rate variation across sites and a proportion of invariable sites was selected for *psbA-trnH*, *rps4*, *trnL-F*, *atpB-rbcL*, and *trnG*, while a Hasegawa, Kishino and Yano (HKY) model with gamma distributed rate variation across sites and a proportion of invariable sites was selected for *psbT-psbH*. Since the phylogeny was used to perform diversification analyses and comparative analyses of trait evolution, and given that trait evolution is related to time, but not necessarily to the number of substitutions (Cusimano and Renner, 2014; Pellicer et al., 2014), trees were ultrametricized. Using the Akaike information criterion through Markov chain Monte Carlo (AICM; Baele et al., 2012) with 1000 bootstraps in BEAST, a strict molecular clock was rejected (AICM of 58930.8 and 58557.8 for the strict vs. lognormal relaxed, respectively) and, therefore, an uncorrelated lognormal relaxed molecular clock was employed for the subsequent dating analysis. Although two Baltic amber fossils of *Radula* have been described, their taxonomic position within the genus is uncertain, so that they represent a minimum constraint for the crown node

(Feldberg et al., 2014). Therefore, to facilitate the interpretation of the trees, we transformed branch lengths into actual time periods by using absolute nucleotide substitution rate sampled from a log-uniform prior distribution according to the results of relaxed-clock analyses across the Liverwort Tree of Life (Laenen et al., 2014), with a mean of 5.273E-4 and SD of 6.463E-6 substitutions/site/million of year. A Yule prior on branching rates was employed and four independent chains of 150,000,000 generations were sampled every 10,000 generations. Convergence and mixing of the sampled parameters were checked using Tracer 1.6 (Rambaut et al., 2014). After discarding the burn-in steps (10%), runs were combined to obtain an estimate of the posterior probability distributions for the dates of divergence.

2.4. Ancestral area estimation

To visualize the evolution of range size across a subset of 100 BEAST trees randomly sampled from the posterior probability distribution obtained from BEAST to account for phylogenetic uncertainty, we used the package BioGeoBEARS (Biogeography with Bayesian Evolutionary Analysis in R Scripts; Matzke, 2014). BioGeoBEARS calculates maximum likelihood estimates of the ancestral states at internal nodes by modeling transitions between geographical ranges along phylogenetic branches as a function of time. It allows the use of the Lagrange DEC model (Dispersal Extinction Cladogenesis) and a new model called BioGeoBEARS DEC + J model (Matzke, 2014 and references therein). Both models include two free parameters (d = dispersal and e = extinction), but DEC + J includes the additional parameter j that corresponds to founder event speciation

(Matzke, 2013). Likelihood values of these models were compared using Likelihood Ratio Test.

Since different ancestral area reconstructions are based on different assumptions and can produce conflicting results (Matzke, 2013, 2014; Pirie et al., 2012), we compared these two versions of the DEC model with a likelihood version of the Dispersal-Vicariance Analysis (DIVALIKE), and a likelihood version of the range evolution model of the Bayesian Binary Model (BAYAREA) of RASP (Yu et al., 2015). In BioGeoBEARS, founder-event speciation can be added to any of these previously described models, and its relative probability can be left as a free parameter, which is estimated from the data, also creating “DIVALIKE+J” and “BAYAREA+J” models. We used Akaike Information Criterion (AIC) to directly compare how well the different biogeography models fit the data and the best model was represented on the maximum clade credibility (MCC) tree.

For the reconstruction of ancestral range areas, we considered eight world geographical areas by merging some of van der Wijk et al.’s original regions, following criteria provided by Sanmartín and Ronquist (2004), but with a few modifications from Chacón and Renner (2014) to accommodate the Northern Hemisphere regions. For the definition of these eight geographical areas, we also considered the evidence available for floristic relationships in liverworts (Vanderpoorten et al., 2010) and the distribution of strongly restricted *Radula* subgenera (Devos et al., 2011b). Specifically, we scored occurrences in: Asia, including western Indonesia (S); sub-Saharan Africa (F); North America (N); South and Central America including Mexico and southern California (A); European, Mediterranean and Irano-Turanian regions, including Europe, northern Africa,

Anatolia, and parts of Jordan (E); New Zealand (Z); Australia, including New Guinea (T); and Pacific archipelagos (O) (Table S4).

2.5. Phylogenetic constraints in range size and macro-ecological niche traits

Phylogenetic signal in for geographic range size, elevational range, substrate range, and biome range, was quantified in terms of Pagel's λ (Pagel, 1999b) and Blomberg's K (Blomberg et al., 2003) using ML estimators implemented in the R package phytools (Revell, 2012) on the 100 randomly sampled BEAST trees. To obtain statistical significance (P value) for Blomberg's K, we randomly shuffled the character states among taxa 100 times. Because the calculation of Pagel's λ is computationally demanding for large-scale phylogenies, we followed Münkemüller et al. (2012) in contrasting the fit of a model with $\lambda = 0$ (no phylogenetic signal) to a model where λ is not constrained. Significance of the difference of fit between the two models was assessed by a likelihood ratio test (LRT). The phylogenetic and non-phylogenetic models include the same number of parameters, and thus their likelihood values were directly comparable, with a difference of 2.0 being considered significant (Mooers and Schluter, 1999). However, the presence of phylogenetic signal can vary depending on the taxonomic level because antagonistic patterns at different levels can obscure one another when the analysis of phylogenetic signal is conducted simultaneously across the entire phylogeny (Machac et al., 2011). The analyses were therefore run individually for each subgenus (except for *Dactyloradula* and *Cladoradula* due to their small size) across the 100 randomly sampled BEAST trees to account for phylogenetic uncertainty and the results were summarized on the MCC tree.

We further determined, if variation in geographic range is phylogenetically constrained, whether it varies with age by comparing the fit of two models to the data, as implemented by the Continuous function of BAYESTRAITS 2.0 (Pagel et al., 2004). Model A is a constant-variance random-walk model, whereas model B is a directional random-walk model measuring the regression of trait values (here, range size) across species against total path length (Pagel, 1999b). These two models were fitted by ML onto the 100 randomly sampled trees and their goodness-of-fit compared with a likelihood ratio test.

2.6. Phylogenetic correlation between range size and dispersal traits

The correlation between range size and dispersal life-history traits was investigated by comparing the fit of two nested models to the observed data as implemented by the Continuous function of BAYESTRAITS. 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 on each of the 100 trees sampled from the posterior probability distribution of the BEAST analysis. Although Continuous is primarily designed for the analyses of continuous characters, correlations between continuous and discrete variables are computed using the same formulas as correlations between continuous variables. A justification for the use of the same statistics for mixtures of binary and continuous variables is that, according to Wright (1934) threshold model for discrete traits, an unobserved quantitative character, termed the liability, determines the state of discrete characters based on whether the liability exceeds a threshold value.

Under the threshold model, underlying liabilities of discrete traits and continuous characters are assumed to evolve through covarying Brownian motion, allowing correlation between discrete and continuous characters (Lambert and Wiens, 2013).

2.7. Diversification analyses

We used BAMM 1.0 (Bayesian Analysis of Macroevolutionary Mixtures; Rabosky, 2014; Rabosky et al., 2014b) to look for shifts in speciation and net diversification rates (speciation minus extinction) in *Radula* based on the MCC tree produced by BEAST. The general model assumes that phylogenetic trees have been shaped by a heterogeneous mixture of distinct evolutionary regimes of speciation and extinction. We assumed that the extinction rate is constant through time within regimes. However, we avoid interpreting extinction rates because of substantial controversy over the meaning of this parameter as estimated from molecular phylogenies (e.g., Quental and Marshall, 2009, 2010; Rabosky et al., 2014a; Rabosky et al., 2014b). We accounted for incomplete taxon sampling using the analytical correction, as implemented in BAMM (Rabosky, 2014; Rabosky et al., 2013). We estimated that our sampling included between 30% and 100% of the species diversity depending on the subgenus (Table S5). All visualization was performed using R and C++ codes available at www.bamm-project.org (Rabosky et al., 2014b).

To summarize diversification histories and avoid some of the challenges associated with interpreting all distinct shift configurations (Rabosky et al., 2014a), as well as to display marginal probabilities for all rate shifts, we used macroevolutionary cohort analysis, which depicts the pairwise probability that any two lineages or clades

share a common set of macroevolutionary rate parameters. For a given sample from the posterior distribution simulated with BAMM, a pair of species is assigned a value of 1 if they inherit a common rate dynamic and a value of 0 if they have different rate dynamics. A mean value is then computed over the full set of sampled shift configurations in the posterior distribution. A value of 0.5 implies that 50% of the samples in the posterior distribution include the focal species within a common macroevolutionary rate regime.

3. Results

In the MCC chronogram, all subgenera were recovered as monophyletic with high support (pp from 0.99 to 1.0; Fig. 1). The crown age of the genus was dated in the late Jurassic, with the majority of extant species originating between the Cretaceous and Eocene (Table 1).

Range size was not phylogenetically constrained at the root node but exhibited significant Pagel's λ values on 51.7% of the 100 BEAST trees in *Metaradula* and on 100% of the trees in *Amentuloradula* and *Volutoradula*, respectively (Table 2; Fig. 2). Blomberg's K values showed a similar pattern (Tables 2 and S6; Fig. S1).

In the ancestral area estimations, the DEC+J model was identified as the best-fitting model (Table 3). There was an overall high uncertainty in ancestral area estimations (Fig. 3), but the pattern of range size heritability described above precisely corresponds to subgenera that were reconstructed to be of Australasian origin, with a probability of 0.29 in *Metaradula* and 0.80 in *Amentuloradula*, and of Neotropical origin with a probability of 0.81 in *Volutoradula* (Table 1, Fig. 3).

327 None of the macroecological niche traits exhibited significant Blomberg's K and
 328 Pagel's λ values at the root node (Tables 2 and S6). Elevation range was significantly
 329 constrained in *Amentuloradula*, wherein species exhibited the lowest range as compared
 330 to species from the other subgenera (Fig. 2), with significant λ and K $\square\square\square\square\square$ in 79%
 331 and 19.5% of the 100 sampled trees, respectively (Tables 2 and S6, Figs. 2 and S1).
 332 Biome range was significantly constrained in *Odontoradula*, with significant λ and K
 333 values also observed in 69% and 1% of the 100 sampled trees, in *Volutoradula* with
 334 significant λ and K values on the in 61% and 88%, and in *Metaradula* with significant λ
 335 and K in 33% and 55%, respectively (Tables 2 and S6, Figs. 2 and S1). Substrate range
 336 showed significant λ and K values for a marginal number of the 100 sampled trees (see
 337 Tables 2 and S6).

338 The LRT for directional trends showed that the log-likelihood values of Model A
 339 (constant-variance random-walk model) mostly tended to be equally large or even
 340 significantly larger (in 11%) than those of Model B (directional random-walk model),
 341 rejecting the directional model of geographic range size evolution in 100% of the trees
 342 tested. Range size did not correlate with mating system and production of asexual
 343 diaspores in any of the trees evaluated (χ^2 distribution with one degree of freedom; $P >$
 344 0.05).

345 We found strong evidence for a shift in speciation rates in *Radula* (posterior
 346 probability of a single rate model = 0.06; posterior probability density of one rate shift =
 347 0.91). We estimated the 95% credible set of rate shift configurations, for which just these
 348 two configurations accounted for approximately 99% of the posterior (Table A7 and Fig.
 349 S2), in the form of acceleration in the rate of net diversification for subgenus *Radula* (see

diversification-through-time trajectories in Fig. 4 and Fig. S2). In the macroevolutionary cohort matrices of BAMM (Fig. 5), the color of each individual cell depicts the average correlation in rate regimes between two species averaged across the MCC tree. This plot consistently revealed a cohort of four distinct lineages that are governed by common sets of macroevolutionary rate parameters, including *Cladoradula*, *Dactyloradula*, *Radula* and for the rest of subgenera, respectively.

4. Discussion

Range size was phylogenetically constrained in *Amentuloradula* and *Volutoradula*, the two subgenera characterized by their almost complete Australasian and Neotropical endemism, respectively, and in *Metaradula*, greatly restricted to Paleotropics. The timing of diversification of those clades was difficult to assess in the absence of reliable fossil records within *Radula* (Feldberg et al., 2014), leading us to implement a secondary calibration. The accuracy of secondary calibrations has been an area of concern, some studies showing high levels of congruence between the dates obtained from primary and secondary calibrations (Aigo et al., 2009), whereas others showed otherwise (Sauquet et al., 2012). The fact that we obtained a crown age for the genus *Radula* (144.6 Ma, 109.6-197.7 HPD; Table 2) that is compatible with that found in other studies using fossil calibrations [e.g., Cooper et al. (2012) (132 Ma, 79.8-182 HPD) and Feldberg et al. (2014), with a mean age of 119.5 Ma], suggests that the time estimates obtained in the present study are robust. Furthermore, molecular dating in general (Wilf and Escapa, 2015), and the use of secondary calibrations in particular (Sauquet et al., 2012), tend to underestimate the actual age of lineages, reinforcing our vicariantist interpretation of the

divergences of some of the oldest subgenera in the genus *Radula*. Thus, subgenera *Amentuloradula* and *Radula* diverged from each other during a period of time encompassing the Early Paleocene and the Early Cretaceous (62–107 Ma), in both cases slightly before or coincident with the drift of Zealandia (i.e., New Zealand and New Caledonia) from the supercontinent Gondwana. Similarly, the separation of *Metaradula* from *Volutoradula* occurred 47–85 Ma, in coincidence with the separation of Australia from Antarctica during the Late Cretaceous (Woodburne and Case, 1996). The high degree of historical association of these two clades within a single Gondwanan plate and divergence times that are contemporary with the break-up of these plates might suggest that plate tectonics could have played a major role in their present distribution. As Vanderpoorten et al. (2010) hypothesized based on analyses of worldwide distribution patterns in liverworts, our results therefore suggest that a strong imprint of vicariance can still be found in extant distribution patterns in these highly mobile organisms. Signatures of ancient vicariance have been demonstrated in amphibians (Pyron, 2014), birds (Ericson et al., 2002), and mammals (Hedges et al., 1996) but were erased in extant distribution patterns of many higher plants (but see Mao et al., 2012; Sanmartín and Ronquist, 2004) and were, indeed, unexpected in mobile spore-producing taxa like bryophytes and pteridophytes (Lewis et al., 2014; Sun et al., 2014; Wolf et al., 2001), wherein evidence for vicariance is limited (Korall and Pryer, 2014).

Although some phylogenetic constraint was present in the evolution of range size in the genus *Radula*, no significant tendency for larger or smaller ranges with age was observed. In fact, although the subgenera *Radula*, *Volutoradula* and *Metaradula* share similar crown ages, their extant distribution is almost cosmopolitan in the former,

396 pantropical in the latter, and Neotropical in *Volutoradula*. In bryophytes globally, some
397 species exhibit very old stem ages but are currently geographically very restricted, such
398 as *Alophosia azorica* in Azores and *Hedenasiatrum percurrans* in Madeira, whose stem
399 age of 100 and 40 Ma unambiguously point to a palaeoendemic origin
400 (Vanderpoorten et al., 2011), whereas others, such as *Bryoxophium norvegicum*, with a
401 stem age of 100 Ma, are widely distributed, although not necessarily common, across
402 continents (Patiño et al., 2016).

403 The mechanisms explaining such differences of range size in bryophytes globally,
404 and in *Radula* in particular, with the largely endemic in-situ diversification of
405 *Amentuloradula* and *Volutoradula* species and their almost complete failure to disperse
406 elsewhere, despite their ancient origin, are difficult to assess. *Amentuloradula* and
407 *Volutoradula* species did not appear to exhibit losses of dispersal capacities in terms of
408 dispersal life-history traits. In fact, in contrast to a previous meta-analysis of life-history
409 traits of island bryophytes that demonstrated a significant decrease in sporophyte
410 production and increase in clonal reproduction pointing to a loss of dispersal capacity
411 (Patiño et al., 2013a), range size did not correlate with any dispersal life-history trait. A
412 significant phylogenetic signal was found in variation of elevation range in
413 *Amentuloradula*, and in variation of biome range in *Volutoradula* and *Metaradula*,
414 whereas no such signal was detected within the large and widespread subgenus *Radula*.
415 Although the usefulness of metrics such as Pagel's λ in diagnosing phylogenetic niche
416 conservatism has been questioned (for review see Crisp and Cook, 2012), it is tempting to
417 interpret this pattern in terms of phylogenetic niche conservatism. A thorough
418 investigation of the evolution of ecological niches, employing actual environmental

measurements, would, however, be necessary to determine whether niche conservatism indeed constrains the ability of certain lineages to enlarge their geographic distribution ranges.

Despite their greatly restricted distribution to Australasia and the Neotropics, *Amentuloradula* and *Volutoradula* did not exhibit significantly lower diversification rates than more widespread lineages, in contrast with Rosenzweig (1995)'s prediction that the probability of speciation increases with range size by promoting geographic isolation and increasing the rate at which novel habitats are encountered. Indeed, the macroevolutionary cohort analysis implemented in BAMM suggested that subgenera *Radula* and *Cladoradula*, which exhibit a nearly cosmopolitan distribution, have a different set of macroevolutionary rate parameters with respect to the rest of clades, but also between them. In addition, subgenus *Radula* had higher net diversification rates than the clades restricted to the Neotropics and Australasia, but this pattern was not confirmed in *Cladoradula*. Rosindell and Phillimore (2011) suggested that, in highly mobile organisms, speciation rates depend on the trade-off between the number of events potentially fostering anagenesis and the intensity of migration preventing speciation through undisrupted gene flow. In this context, one potential explanation to the equivocal pattern here observed is that stochastic long-distance dispersal events are likely to balance allele frequencies across large spatial scales, leading to low genetic structure among geographically distant areas or even continents (Cronberg et al., 1997; McDaniel and Shaw, 2003; Pisa et al., 2014; Shaw et al., 2015), ultimately decreasing the speciation rates in highly mobile, widespread lineages.

Acknowledgements

The Belgian Fund for Scientific Research (FNRS), the Leopold III Funds, and University of Liege, and the European Union's Seventh Framework Programme provided funding for this research. J.P. also acknowledges funding by Spain's Ministerio de Ciencia e Innovación (Juan de la Cierva Program - Incorporation). The work was also supported by the U.S. National Science Foundation (grant number, EF-0531730-002 to AJS). We thank three anonymous referees for constructive remarks.

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Table 1

Mean node age estimates (Ma) and 95% highest posterior density (HPD) distribution of ages for *Radula* subgenera (see Fig. 1 for the location of each node). The posterior probabilities (pp) ≥ 0.95 in BEAST and the ancestral areas inferred with a relative probability ≥ 0.25 with the best-fit model (DEC+J) in BIOGEOBEARS are also shown. An asterisk (*) indicates clades predominantly Australasian, and a hash (#) for mainly Neotropical ones (see Fig. 3). ? = not resolved. Area codes: E = Europe; F = Africa; S = Asia; N = North America; A = Central and South America; Z = New Zealand; T = Australia; O = Oceania.

Node (number)	Age (95% HPD)	pp	[Ancestral range] Relative Probability
Subgenus <i>Cladoradula</i> split (109)	144.6 (109.6-197.5)	1.00	[?]
Crown of subgenus <i>Cladoradula</i> (211)	11.6 (4.9-21.9)	1.00	[EFSa] 0.78
Subgenus <i>Dactyloradula</i> split (110)	126.1 (96.6-166.0)	0.99	[?]
Subgenus <i>Odontoradula</i> split (111)	101.2 (78.5-129.2)	1.00	[?]
Crown of subgenus <i>Odontoradula</i> (112)	68.9 (50.9-91.1)	1.00	[ATZ] 0.38
Split between subgenera <i>Metaradula</i> and <i>Volutoradula</i> (125)	64.1 (46.9-84.6)	1.00	[?]
Crown of subgenus <i>Volutoradula</i> # (126)	38.3 (25.7-54.1)	1.00	[A] 0.81
Crown of subgenus <i>Metaradula</i> * (150)	49.4 (35.2-66.2)	1.00	[TZ] 0.34
Split between subgenera <i>Radula</i> and <i>Amentuloradula</i> (167)	82.3 (61.6-107.3)	0.99	[T] 0.18
Crown of subgenus <i>Amentuloradula</i> * (168)	48.9 (35.3-65.5)	1.00	[TZ] 0.80
Crown of subgenus <i>Radula</i> (184)	45.5 (30.8-64.5)	1.00	[NZ] 0.25

692 **Table 2**

693 Phylogenetic signal in continuous characters in the liverwort genus *Radula* as evaluated by
 694 Blomberg's *K* and Pagel's λ . % *P*, percentage of significant tests; (*), in *Amentuloradula*,
 695 all the nodes immediately after the node 150 showed a strong phylogenetic signal for
 696 elevation range by using Pagel's λ (see Table S6).

	Blomberg's <i>K</i>			Pagel's lambda λ		
	Mean	Max.-Min.	% <i>P</i>	Mean	Max.-Min.	% <i>P</i>
Geographic range						
<i>Odontoradula</i> (112)	0.61	0.30-0.84	0	0	0	0
<i>Volutoradula</i> (node 126)	0.33	0.08-0.54	64	0.57	0.48-0.84	100
<i>Metaradula</i> (node 150)	0.76	0.50-1.11	3.4	0.56	0.07-1	51.7
<i>Amentuloradula</i> (node 168)	1.66	1.02-2.25	100	0.98	0.79-1	100
<i>Radula</i> (node 184)	0.08	0.20-0.01	0	0	>0.001-0.04	0
Elevation range						
<i>Odontoradula</i> (112)	0.56	0.19-0.84	0	0.01	>0.001-1	1
<i>Volutoradula</i> (node 126)	0.23	0.11-0.35	0	>0.001	>0.001	0
<i>Metaradula</i> (node 150)	0.61	0.45-0.85	0	0.12	>0.001-0.83	0
<i>Amentuloradula</i> (node 168)	0.86	0.59-1.22	19.48	0.79	>0.001-1	79 (*)
<i>Radula</i> (node 184)	0.08	0.02-0.19	0	>0.001	>0.001	0
Biome range						
<i>Odontoradula</i> (112)	0.87	0.56-1.08	1	0.85	>0.001-1	69
<i>Volutoradula</i> (node 126)	0.70	0.37-1	88	0.93	>0.001-1	61
<i>Metaradula</i> (node 150)	0.87	0.53-1.25	55	0.73	0.3-1	33
<i>Amentuloradula</i> (node 168)	0.46	0.23-0.73	0	>0.001	>0.001-0.2	0
<i>Radula</i> (node 184)	0.19	0.05-0.35	0	0.31	0.16-0.43	0
Substrate range						
<i>Odontoradula</i> (112)	0.34	0.11-0.69	0	0.03	>0.001-1.58	0
<i>Volutoradula</i> (node 126)	0.26	0.09-0.46	0	>0.001	>0.001-0.39	0
<i>Metaradula</i> (node 150)	0.59	0.29-0.84	15	0.60	0.27-0.78	0
<i>Amentuloradula</i> (node 168)	0.51	0.19-1.00	0	0.04	>0.001-0.51	2.4
<i>Radula</i> (node 184)	0.22	0.06-0.67	2.9	>0.001	>0.001	0

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Table 3

Performance, as assessed by log-likelihood (lnL) and the Akaike information criterion corrected for small sample sizes (AICc), of competing models of ancestral-area estimation (dispersal–extinction–cladogenesis, DEC; dispersal–vicariance analysis, DIVA; BayArea), as well as the same three models allowing for founder-event speciation (+J) in the liverwort genus *Radula*; *n*, number of parameters; *d*, rate of dispersal; *e*, rate of extinction; *j*, relative probability of founder-event speciation. The best model is highlighted in bold.

	LnL	AIC	AICc	<i>n</i>	<i>d</i>	<i>e</i>	<i>j</i>
DEC	-336.872	677.744	677.858	2	0.0122	0.0052	0.0000
DEC+J	-316.673	639.346	639.577	3	0.0071	0.0000	0.1204
DIVALIKE	-333.106	670.212	670.326	2	0.0128	0.0030	0.0000
DIVALIKE+J	-320.588	647.176	647.407	3	0.0086	0.0000	0.0916
BAYAREALIKE	-390.233	784.466	784.580	2	0.0157	0.0363	0.0000
BAYAREALIKE+J	-327.235	660.470	660.701	3	0.0062	0.0037	0.1262

Fig. 1. Dated chronogram of the genus-level phylogenies of the genus *Radula*. Asterisks (*) show the posterior probability from BEAST analyses (pp > 0.95).

Fig. 1 (continued)

Fig. 2. Phylogenetic signal in geographic (A), elevation (B) and biome range (C) evaluated by Pagel's lambda (λ). Results using Blomberg's K are shown in Fig. S1. Pie diagrams represent the percentage of significant (green) and non-significant tests (grey) in the 100 replicates performed. The size of the pie diagrams indicates the value of λ . Bar plots represent mean values $\pm$ SD for each subgenus. Number of species here included are shown in brackets.

Fig. 3. Probabilities of ancestral area distributions under the DEC+J models in the genus *Radula*. A, South America, light blue; N, North America, light green; Z, New Zealand, violet; T, Australia, dark blue; O, Oceania, pink; E, Europe, red; F, Africa, yellow; S, Asia, green. The corner positions represent geographical ranges immediately after a speciation event. The maximum number of ancestral areas at a given node was five (parameters: $d = 0.0071$; $e = 0$; $j = 0.1204$; $\text{Ln}L = -316.99$).

Fig. 4. Inferred net diversification rates ($\lambda - \mu$; λ = speciation and μ = extinction) among lineages and over time during the evolution of the genus *Radula*. The phylogeny shows a time-calibrated maximum clade credibility tree, with branches colored by reconstructed net diversification rates (a), which are means of the marginal densities of branch-specific rates. The location of the maximum credibility rate shift configuration inferred by BAMM is also shown with a red circle indicative of a rate increase. The circle size is proportional to the marginal probability of the shift (see also Fig. S2). Net-diversification-through-time plot for several *Radula* clades (Table 1) are also included (b-g). Colour density shading illustrates the 95% confidence interval of estimated diversification rate at any point in time.

Fig. 5. Macroevolutionary cohort matrices for speciation in the liverwort genus *Radula*. Each cell in the matrix is coded by a color denoting the pairwise probability that two species share a common macroevolutionary rate regime. The maximum clade credibility trees obtained in BEAST analyses is shown for reference on the left and upper margins of each cohort matrix, but pairwise probabilities are averages from BAMM analyses conducted over a sample of trees from the posterior distribution of topologies and branch lengths. For speciation, it is evident that all species have highly correlated rate dynamics, except for the subgenera *Radula*, *Cladoradula* and *Dactyloradula*.

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Phylogenetic signal evaluated by Pagel's lambda