Evolution of sexual systems, dispersal strategies and habitat selection in the liverwort genus *Radula*

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Received: 7 March 2011
Accepted: 26 April 2011


**Key words:** bryophyte, comparative methods, epiphytism, life-history theory, liverwort, *Radula*, sexual system, trade-off.

### Summary

- Shifts in sexual systems are among the most common and important transitions in plants and are correlated with a suite of life-history traits. The evolution of sexual systems and their relationships to gametophyte size, sexual and asexual reproduction, and epiphytism are examined here in the liverwort genus *Radula*.
- The sequence of trait acquisition and the phylogenetic correlations between those traits was investigated using comparative methods.
- Shifts in sexual systems recurrently occurred from dioecy to monoecy within facultative epiphyte lineages. Production of specialized asexual gemmae was correlated to neither dioecy nor strict epiphytism.
- The significant correlations among life-history traits related to sexual systems and habitat conditions suggest the existence of evolutionary trade-offs. Obligate epiphytes do not produce gemmae more frequently than facultative epiphytes and disperse by whole gametophyte fragments, presumably to avoid the sensitive protonemal stage in a habitat prone to rapid changes in moisture availability. As dispersal ranges correlate with diaspore size, this reinforces the notion that epiphytes experience strong dispersal limitations. Our results thus provide the evolutionary complement to metapopulation, metacommunity and experimental studies demonstrating trade-offs between dispersal distance, establishment ability, and life-history strategy, which may be central to the evolution of reproductive strategies in bryophytes.

### Introduction

For more than two centuries, the diversity of plant sexual systems has captured the curiosity and imagination of biologists and stimulated fruitful research by both ecologists and population geneticists (Cheptou & Schoen, 2007). In angiosperms, only 6% of species are dioecious, but their scattered taxonomic positions within the group suggest that shifts in sexual systems, mostly towards dioecy from monoecious ancestors, occurred independently multiple times (Renner & Ricklefs, 1995). The evolutionary transition from sexual monomorphism to dimorphism is governed by three factors, which are the optimal allocation of resources to female and male function, the genetic control of sex expression, and the fitness consequences of selfing and outcrossing (Barrett, 2002).

Dioecious species may benefit from reduced inbreeding depression, but, as only females produce seeds, dioecious females must produce more or better seeds than their hermaphrodite or monoeccious counterparts and/or disperse those seeds to an equivalent number of suitable sites to ensure an equivalent number of progeny (Charlesworth & Charlesworth, 1978). In fact, theoretical work suggests that, in order for dioecy to persist, dioecious individuals need a substantial fitness and/or dispersal advantage over cosexuals, even when the number of seeds per female is twice that of cosexuals (Heilbuth et al., 2001).

In bryophytes, where sexual reproduction depends on sperm swimming to eggs via free water, separation of sexes can present serious problems for successful sexual fusion and dioecious species therefore often fail to reproduce sexually (Vanderpoorten & Goffinet, 2009). In a study on the
reproductive biology of British mosses, Longton (1997) found that 87% of the species for which sporophytes are unknown are dioecious, whereas sporophytes are commonly found in 83% of the monoecious species. Despite this, c. 70% of liverworts and 60% of mosses are dioecious (Vanderpoorten & Goffinet, 2009). Along with the frequent independent evolution of dioecy among angiosperm lineages and other major groups of land plants (Renner & Rickles, 1995; Sakai et al., 1995), this suggests that separation of sexes is not necessarily associated with increased extinction risks. In fact, the uncertainty of sexual reproduction in dioecious bryophyte species is thought to have selected for a series of life-history traits that promote dispersal (Wilson & Harder, 2003; During, 2007).

In particular, a strong association between dioecy and the ability to produce specialized asexual propagules has long been known to exist (Longton & Schuster, 1983; Hedderon & Longton, 1995; During, 2007). Crawford et al. (2009), however, failed to find support for a phylogenetic correlation between the production of specialized propagules and separate sexes in a recent comparative study across mosses. That study revealed that organisms with separate sexes tend to be significantly larger than monoecious ones and characterized by strong, competitive vegetative growth. This correlation, also observed in angiosperms (de Jong, 2000), is consistent with the hypothesis that dioecious taxa compensate for the low production of spores or seeds by increased size and life expectancy.

These trade-offs between sexual systems and other life-history traits have led to the concept of life-history strategies, which can be defined as a recurrent combination of life-history traits that are predicted to occur in response to particular ecological conditions (During, 1992). For example, given the presumed ephemeral nature of their substrates, and the importance of dispersal and colonization (Snäll et al., 2005), epiphytes are typically hermaphroditic (van Dulmen, 2001) and expected to undergo substantial inbreeding to ensure reproductive success (Hooper & Haufler, 1997; Chiou et al., 2002). In fact, a survey of 15 vascular montane cloud forest epiphytes in Costa Rica showed that all were self-compatible, which represents the highest proportion of self-compatible species documented within any life form at any tropical site (Bush & Beach, 1995).

A number of studies have employed phylogenies to investigate evolutionary transitions in plant sexual systems (see Case et al., 2008 for a review). The aims of those studies were primarily to estimate the number of times particular traits arose, to identify their life-history trait correlates, and to determine the local direction of changes. In practice, however, mapping traits onto trees is not necessarily straightforward, particularly for those with a high degree of lability that erodes phylogenetic signal (Weller & Sakai, 1999). Maximum parsimony has been the most widely used principle for inferring character-state transformations from a phylogenetic tree (Smith, 2010). Under the parsimony criterion, which implicitly involves transition rates being equal among states, the solution requiring the minimum amount of changes on a tree is singled out, regardless of branch lengths. A range of alternative reconstructions on the same tree, however, exists, creating a source of error known as ‘within-tree uncertainty’ (Pagel et al., 2004).

Model-based methods, by contrast, directly use branch lengths to determine the probability of change along a branch, allow transition rates between states to vary, and enable an assessment of the accuracy of reconstructions. Because they implement actual transition rates, model-based methods further enable one to make and test hypotheses regarding evolutionary processes (Pagel, 1994). Looking across multiple shifts, it is, in particular, possible to test for significant correlations among traits and determine the contingency and order of acquisition of those traits independently from the ancestral state reconstructions themselves (Pagel, 1994). Most recently, Markov chain Monte Carlo methods have offered a formal framework to sample model parameters and phylogenies according to their posterior probabilities, thereby taking both within-tree and among-tree uncertainty into account and increasing the statistical power as compared with single-tree approaches (Pagel & Lutzoni, 2002).

In the present study, we take advantage of the leafy liverwort genus *Radula* to investigate the evolution of sexual systems and explore trade-offs in life-history traits involved in those transitions. The genus includes c. 200 species (Yamada, 2003) and has an almost world-wide distribution, with the majority of the species occurring in humid, tropical or warm-temperate regions. The species usually grow as epiphytes on bark or living leaves, and less commonly on rock, in a variety of habitats varying from rainforest to alpine tundra, and from sea level to over 4000 m in elevation. Phylogenetically, *Radula* has a rather isolated position within the leafy liverworts and is classified in its own family and order (Crandall-Stotler et al., 2009). Morphologically, the genus stands out by virtue of its unique, *Radula*-type branching system, rhizoids being produced on leaf lobules rather than on stems, the total absence of underleaves, the possession of very large, often single, brown oil bodies in leaf cells, and the development of a tubular or trumpet-like, dorsiventrally flattened perianth which surrounds and protects the developing sporophyte. The genus exhibits a wide range of reproductive characteristics in terms of sexual condition and production of asexual propagules. The genus has both obligate and facultative epiphytes and therefore allows the unique opportunity to investigate possible correlations between this particular trait and sexual systems.

Using a molecular species-level phylogeny of the genus, we studied the evolution of its sexual systems in relation to four life-history traits (reproductive effort, asexual repro-
duction, gametophyte size and facultative vs obligate epiphytism), implementing competing explicit models of trait evolution (Barker et al., 2007). We then tested phylogenetic correlations among those traits and addressed the following questions. What is the ancestral sexual system in Radula? Are shifts from one sexual system to another random or directional, thereby suggesting their adaptive potential? To what extent are shifts in sexual system correlated with shifts from a facultative to an obligate epiphytic condition; that is, is monoecy favoured in strictly epiphytic lineages in response to the necessity to disperse in a dynamic environment? Do dioecious species compensate for the reduced levels of sporophyte production by increasing life-span and the production of asexual gemmae?

Materials and Methods

Taxon sampling, DNA extraction, PCR, and sequencing

Ninety-three of the c. 200 species of Radula were sampled, depending on the availability of suitable material for DNA studies (see Supporting Information, Table S1 for voucher information). Our sampling covered the entire distribution range of the genus, with samples from Asia, Australia, New Zealand, Africa, Europe, and North and South America as well as various islands and archipelagos such as Reunion, Madagascar, Madeira, the Azores and the Canary Islands. It also included representatives from the four subgenera and major sections recognized within Radula. Frullania montiliata, F. pennisylvanica and Porella pinnata were employed as outgroups based upon the results of a genus-level molecular phylogenies of liverworts (Heinrichs et al., 2005; Forrest et al., 2006).

Total genomic DNA was isolated using a Cetyltrimethylammonium Bromide (CTAB) extraction protocol (Doyle & Doyle, 1987) without RNase treatment and purified using the GeneClean® III Kit (MP Biomedicals, Solon, OH, USA). The chloroplast atpB-rbcL, psbT-psbH, psbA-

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Phylogenetic analyses

The nucleotide data matrix, available from TreeBASE at http://www.treebase.org under study number S11286, was submitted to a Bayesian phylogenetic inference using MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). The six individual data sets were first analysed separately in order to identify possible incongruence between them. 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 an Hasegawa, Kishino and Yano (HKY) model with gamma-distributed rate variation across sites and a proportion of invariable sites was selected for psbT-psbH. These models were implemented using four independent Markov chain Monte Carlo (MCMC) simulations run for 20 000 000
generations and sampled every 10 000th generation. Burn-in length and convergence between the four runs were confirmed by comparing the trace files of each run using TRACER 1.4 (Rambaut & Drummond, 2007). After discarding the burn-in, outputs from the four runs were combined for final inference of posterior probabilities of both trees and model parameters.

No taxon was resolved as part of two distinct clades supported each by > 70% posterior probabilities in analyses of the individual data sets. These partitions were therefore combined into a single matrix that was submitted to a heterogeneous Bayesian analysis using the settings and implementing, for each partition, the best-fitting substitution model detailed in the previous paragraph. Model parameters (with the exception of branch lengths and topology) were unlinked using the ‘unlink’ command in MrBayes such that each partition had its own set of parameters.

Evolution and correlated evolution in life-history traits

The sexual system (dioecious (0) or monoecious (1)) of each species was scored from the literature (See Table S2 for a list of the references consulted). Nine monoecious species were sampled, and this reflected the 10% rate of monoecy (16 species) within the genus (S. R. Gradstein, unpublished observations). In order to determine the correlation between sexual systems, sexual and asexual reproduction, habitat conditions, and life expectancy, the following four traits were also scored from the same sources: presence (1) or absence (0) of specialized asexual propagules (gemmae or caducous leaf lobes); obligate (1) or facultative epiphytes occurring on a wide range of substrates (0); gametophyte size: shoot width < 2.0 mm (0) or > 2.0 mm (1); sexual reproduction: perianth never or very rarely produced (0) or occasionally to frequently present (1). The absence of perianth formation was used here as a proxy for the absence of sporophytes and, as a consequence, of sexual reproduction. With the exceptions of Plagiocladia and Gymnolea, perianths in liverworts only develop when sporophytes are initiated after sexual reproduction (Schuster, 1966; Vanderpoorten & Goffinet, 2009). Obligate vs facultative epiphytism was similarly taken as a proxy for habitat stability. In fact, all Radula species are restricted to hard surfaces, basically living bark (or leaves) or rocks (Gradstein et al., 2001). Given the longer duration of the latter habitat (Söderström & Herben, 1997) coupled with the high turnover rate of cryptogamic communities on a tree (Barkman, 1958), this means that an individual of a facultative epiphytic Radula species has theoretically a longer life expectancy than an individual of an obligate one.

Other potentially important life-history traits, such as spore size and seta length, are sometimes implicated in trade-offs with sexual system. Those life-history traits were, however, not included in this study. In fact, only a small percentage of species have been observed with sporophytes, which hinders the scoring of those sporophytic characters and would ultimately introduce too many missing data in the data set.

For each investigated trait, ancestral states were reconstructed on the trees generated by MrBayes after pruning the outgroups. The probabilities of change on a branch were calculated by estimating the instantaneous forward ($q_{01}$) and backward ($q_{10}$) rates between the two states by implementing the ‘Multistate’ Markov model (Pagel et al., 2004) in BayesTraits 1.0 (available from http://www.evolution.rdg.ac.uk). An MCMC was used to visit, at each iteration, the space of rate parameter values and sample one of the trees generated by the MrBayes analysis. The likelihood of the new combination was calculated and this new state of the chain was accepted or rejected following evaluation by the Metropolis–Hastings term. The rate at which parameters were changed (‘ratedev’) was set at the beginning of each run so that the acceptance rate of the proposed change globally ranged between 20 and 40%. In the absence of information on rates, uniform distributions ranging from 0 to 100 were used as priors. The chain was run for 50 000 000 generations and sampled for rate parameters and state probabilities at the nodes of interest every 10 000 generations. In order to circumvent the issue associated with the fact that not all the trees necessarily contain the internal nodes of interest, reconstructions were performed using a ‘most recent common ancestor’ approach (Pagel et al., 2004).

For each trait, we compared the performances of six competing explicit evolutionary models to describe trait evolution, as advocated by Barker et al. (2007) for traits with a weak phylogenetic signal (see also Vanderpoorten et al., 2010 for a review). The first two models were the unconstrained two-rate ($q_{01} \neq q_{10}$) and single-rate ($q_{01} = q_{10}$) models, respectively, wherein $q_{01}$ and $q_{10}$ are sampled from a uniform distribution with a 0–100 range. In the third model, the forward rate $q_{01}$ was set to 0. This model, which corresponds to the ‘ML-root’ model of Barker & Pagel (2005) and Barker et al. (2007), is consistent with a scenario in which the state is already present at the root and subsequently lost in different lineages, without any possibilities of being gained again. The fourth model was used to describe a situation similar to the previous one, but low values of forward transition rates allow for rare gain events to happen. This situation was described by a model in which $q_{01}$ was forced to be very low (i.e. was sampled from a uniform distribution with a range of 0–1), whereas no constraint was imposed on $q_{10}$ (which was sampled from a uniform distribution with a range of 0–100). The fifth and sixth models are the equivalent of models 3 and 4, but with $q_{10}$ either constrained to be equal to 0 or sampled from a (0–1) uniform prior distribution. The two last models are consistent with a
scenario in which the state, once gained, can never be lost again (model 5) or has a very small probability of being lost (model 6).

Bayes factors (BFs) were used to determine which model(s) best fitted the data, and the best-fitting model was subsequently used for trait mapping. In order to contrast alternative hypotheses regarding the ancestral state at key nodes of the phylogeny, we used the ‘local’ approach, wherein the significance of the reconstruction is explicitly tested at each node of interest (Pagel, 1999). For that purpose, we successively fixed each of the latter at one of the two states it can take (0 or 1). Then, an MCMC was used to visit the sample of trees generated by the MrBayes analysis and the space of rate parameter values. A second, independent chain was run to sample rate parameters and derive overall likelihoods of the reconstructions when the node was fixed at its alternative state. BFs were then used to determine the support for alternative states.

In order to investigate correlated evolution among traits, each pair of traits was analysed successively using two alternative models: a four-rate model describing independent evolution between traits, and an eight-rate model describing correlated evolution (Pagel, 1994) (Fig. 1a,b). Both models were implemented in a Bayesian context and BFs were used to determine whether the dependent or independent model provided a significantly better description of trait evolution. Contingency tests were then performed to detect whether evolution of trait A (sexual system in Fig. 1b) depends upon the state in trait B (epiphytism in Fig. 1b), or vice versa. For example, \( q_{13} > q_{24} \) indicates that a shift in the sexual system from 0 to 1 is more likely when epiphytism is at state 0, whereas \( q_{12} > q_{43} \) indicates that a shift in epiphytism from state 0 to 1 is more likely when the sexual condition is at state 0 (Fig. 1b). Contingency tests thus involve restricting one rate to be equal to the other, re-running the analysis, and comparing the difference of fit with the unconstrained analysis using BFs.

**Results**

**Ancestral state reconstructions**

Six thousand trees, whose 50% majority-rule consensus is presented in Fig. 2, were sampled from the MrBayes inference and used for trait mapping and comparative analyses. The unconstrained two-rate model (model 1) was systematically selected amongst the six competing models of trait evolution (Table 2) as the best-fitting model and was thus used for ancestral state reconstructions. Local ancestral state reconstructions of the sexual condition, sexual reproduction, and the presence or absence of asexual propagules (Fig. 3) showed that all shifts occurred from dioecy to monoecy; from presence to absence of sporophytes; and from absence to presence of asexual propagules, respectively. Shifts in the sexual condition and the presence or absence of asexual propagules were recurrent and occurred at very shallow nodes of the phylogeny.

At least six species of Radula evolved from being able to grow on a range of substrates to being obligate epiphytes growing on leaves and/or bark (Fig. 3; see Radula recubans, Radula reflexa, Radula fendleri, Radula quadrata, Radula physoloba and Radula gottscheana). One reversal from obligate to facultative epiphyte was reconstructed (Fig. 3; see Radula pulchella).

**Correlations among traits**

Pairwise trait comparisons revealed that the model of independent evolution was favoured over the model of correlated evolution based upon the BFs for five pairs of traits, namely sexual system and production of asexual propagules;
Three pairs of traits were significantly correlated: sexual system and epiphytism; production of gemmae and epiphytism; and production of gemmae and failure to reproduce sexually. The results of contingency tests suggest that sexual system did not influence the evolution of epiphytism but rather depended upon it (Table 3). Transitions to monoeccy were more likely within facultative epiphyte lineages than obligate ones, as indicated by a \( q_{13} \) rate of 32.22 compared with a \( q_{24} \) rate of 6.18, (Table 3).

Production of asexual propagules seemed to be favoured within facultative epiphytic lineages, as indicated by a \( q_{13} \) rate of 60.37 compared with a \( q_{24} \) rate of 14.23 (Table 3).

A significant correlation was also found between the
production of asexual diaspores and failure to reproduce sexually, but the associated contingent test was not significant \((BF = 1.22; \text{Table 3})\). The two other phylogenetic correlations (sexual system vs gametophyte size and gametophyte size vs sexual reproduction) were not significant (Table 3).

**Discussion**

**Evolution of sexual systems**

Two lines of evidence suggest that evolution of sexual systems in *Radula* has been directional. First, the model corresponding to a scenario in which monoecy, once gained, has a very small probability of being lost fits the data as well as the unconstrained model. Secondly, reconstructions of sexual system evolution clearly indicate that all six inferred transitions were from dioecy to monoecy, and never the reverse between nodes with significant state assignment. In bryophytes, the monoecious transition has traditionally been viewed as a result of essentially random polyploidization events (see Crawford *et al.*, 2009 for a review). A comparative analysis across mosses in a phylogenetic framework recently failed, however, to demonstrate a significant correlation between transitions from nonpolyploid gametophytes with separated sexes to polyploid...
Secondly, monoecious species have lower sporophytic inbreeding depression than dioecious ones (Taylor et al., 2007). While dioecious species either outcross or undergo intergametophytic selfing (mating among haploid siblings from the same sporophyte), monoecious species are capable of intragametophytic selfing (merging of gametes produced by the same genetic individual), which results in a fully homozygous sporophyte generation. Monoecious species can thus rapidly purge recessive deleterious mutations through intragametophytic selfing while sporophytic inbreeding depression is assumed to occur in dioecious species (Eppl ey et al., 2007). Intragametophytic selfing inevitably leads to genetic uniformity (McDaniel et al., 2010), but low levels of genetic diversity do not necessarily hamper evolutionary success in the short term (see Karlin et al., 2011 for a review). Maintenance of selected genotypes through selfing might even prove adaptive in specialists of highly selective environments (niche-width hypothesis; Soule, 1971; but see Dubois et al., 2003). Low levels of genetic variation are, however, assumed to retard evolutionary potential, so that monoecy has commonly
been viewed in the literature as an ‘evolutionary dead-end’ (see Barrett, 2002 for a review), triggering the recurrent evolution of dioecy within unrelated lineages (e.g. Renner & Won, 2001; Miller & Venable, 2003; Ronse De Craene & Wanntorp, 2006; Renner et al., 2007; Case et al., 2008) and other mechanisms such as self-incompatibility. In this regard, the appearance of monoecy at the shallowest nodes of the Radula phylogeny could also be interpreted in terms of a recurrent evolution of monoecy followed by extinctions throughout the evolutionary history of the genus.

Sexual systems, dispersal strategies and habitat selection

Transitions to monoecy were found to be phylogenetically significantly correlated with epiphytism in Radula. However, comparison of trait acquisition rates suggests that it is not the sexual system that determines the evolution of epiphytism, but the reverse. Transitions to monoecy are, in fact, significantly more likely to occur in facultative epiphytic lineages than in obligate ones. As obligate epiphytes must necessarily disperse from one host to another within a shorter time frame than do facultative epiphytic species occurring on more stable substrates, these observations are, at first sight, counterintuitive. Unstable habitats tend indeed to favour increased reproductive effort and the production of smaller, more numerous offspring, whereas stable habitats are expected to favour increased investment in vegetative growth, reduced reproductive effort, and the production of fewer and larger offspring (Stearns, 1989; Kozlowski, 1992). In fact, Heddderson & Longton (2008) observed a trade-off between effort expended on spore production and that expended on vegetative proliferation among populations of the moss Polytrichum juniperinum from environments with contrasting habitat stability. Monoecy might not be selected for in epiphytic lineages because gravity makes sperm dispersal distances longer, potentially allowing dioecious bryophytes to reproduce sexually despite the separation in space between male and female individuals (Longton, 1997). In addition, two possible explanations may account for the lower probability of monoecious transition in obligate vs facultative epiphytes in Radula.

First, transition to epiphytism in bryophytes, and mosses in particular, is associated with a suite of gametophyte morphological transformations (see Huttunen et al., 2004 for a review) that probably competes with sporophyte production in terms of resource allocation. Sporophyte production indeed correlates with higher shoot mortality among females (Pohjamo & Laaka-Lindberg, 2003), reduced size of vegetative offshoots, and reduced branching (Rydgren & Økland, 2003; Stark et al., 2009). This hypothesis is, however, weakened in Radula because no correlation was observed between gametophyte size and the presence of sexual reproduction, and because no differences in gametophyte morphology are evident between facultative and obligate epiphytes.

Secondly, epiphytes might preferentially disperse by means of asexual diaspores. Production of asexual diaspores is indeed regarded as an adaptation to the spatio-temporal variation in habitat quality and water supply because asexual propagules allow for earlier reproduction and are less sensitive to habitat quality than spores (Löbel, 2009). Asexual reproduction was further shown to result in the production of new gametophytes at a faster rate than sexual reproduction in the moss Syntrichia ruralis (Mishler & Newton, 1988). In addition, no trade-off between shoot mortality and asexual reproduction has been found to date and, as opposed to previous assumptions (Kimmerer, 1993), vegetative diaspores are also capable of long-distance dispersal (Pohjamo et al., 2006). However, as opposed to the expectations from life-history theory, the contingency test indicated that production of specialized asexual propagules is favoured within facultative epiphytic lineages of Radula.

One interpretation is that entire gametophyte fragments would be equally if not preferentially dispersed by animals in a forest environment with limited wind intensity as compared with spores or specialized gemmae. Bryophyte fragments have indeed been found on roe deer in a forest environment (Heinken et al., 2001). Accidental ingestion may also occur, so that viable fragments could potentially be dispersed via passage through the digestive tract of vertebrates such as flying foxes and birds (Parsons et al., 2007). To date, however, evidence for zoochory in bryophytes is very limited and its impact on dispersal unknown.

An alternative interpretation is that specialized gemmae necessarily germinate into a protonema that will pass through all the successive ontogenetical stages (asexual reproduction sensu Mogie (1992), although not from the embryonic state). Passage through the very sensitive early developmental stages, and especially the protonema, which is more sensitive to drought than both the diaspores and the gametophyte (Proctor et al., 2007), might be critical for epiphytes, which colonize a rather extreme habitat in terms of the temporal range of temperature, physico-chemical and humidity conditions (Leon-Vargas et al., 2006). Therefore, a perhaps more efficient strategy for epiphytic liverworts is to disperse vegetatively by means of whole plants or large gametophytic fragments, which can detach from the substrate, disperse, and resume growth from the apical meristemcal cell (asexual propagation) at a new suitable micro-site, thereby avoiding the critical protonemal phase. In fact, establishment rates in epiphytic bryophytes were experimentally shown to be higher from gametophytes than from gemmae or spores (Löbel et al., 2009). By dispersing preferentially through whole gametophyte fragments, obligate epiphytic Radula species could enhance the chances of establishment within a habitat prone to variation in quality.
and water content. In the meantime, as dispersal ranges correlate with diaspore size (Pohjamo et al., 2006), this dramatically decreases their medium and long-distance dispersal ability, reinforcing the notion that epiphytes experience substantial dispersal limitations (Snäll et al., 2004a,b, 2005; Löbel et al., 2006a,b). Our results thus provide the evolutionary complement to previous metapopulation, metacommunity and experimental studies demonstrating trade-offs between dispersal distance, establishment ability, and life-history strategy (Löbel & Rydin, 2010), which may be central to the evolution of reproductive strategies in bryophytes.

Acknowledgements

Many thanks are due to three anonymous reviewers for their constructive comments on a previous draft of this paper. A. Schäfer-Verwimp, T. Pocs, and the Helsinki (H), Liege (LG), Missouri (MO), New York (NY), Edinburgh (E), Eszterhazy Karoly College (EGR), Auckland (AK), Goettingen (GOET), and the Australian National Botanical Gardens (CBG) herbaria are gratefully acknowledged for the loan of specimens. N.D., B.L. and A.V. acknowledge financial support from the Belgian Funds for Scientific Research (FNRS) and the Fonds Léopold III. This research was also supported by NSF Grant EF-0531730-002 to A.J.S.

References


**Supporting Information**

Additional supporting information may be found in the online version of this article.

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**Table S1** List of taxa sequenced for this study, GenBank accessions numbers for the sequences produced and life-history traits scored

**Table S2** List of references consulted for the scoring of life-history traits in the genus *Radula*

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