

Evolutionary significance and trade-offs in life-history traits associated to ecological specialization and mating systems in the liverwort genus *Radula* Dumort.

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✓ Introduction

Shifts in mating systems are amongst the most common and important transitions in plants and are correlated with a suite of life-history traits. The evolution of mating systems and their relationships to gametophyte size, sexual reproduction, formation of asexual diaspores, and ecological specialization, is examined here in the leafy liverwort genus *Radula*. More specifically, we attempt to answer the following questions: **(1)** What is the ancestral mating system in *Radula*? **(2)** Are shifts from one mating system to another directional or random? **(3)** How does the evolution of mating systems correlate with the evolution of other related life history traits and, in particular, the specialization to temporary habitats? **(4)** What are the contingency relationships and order of acquisition of those traits?

✓ Materials and methods

- Bayesian molecular phylogeny on 93 *Radula* species based on six chloroplast markers *atpB-rbcL*, *psbT-psbH*, *psbA-trnH*, *rps4*, *trnG* and *trnL-F* regions. (Fig1)
- Test of Explicit model of evolution for **traits reconstruction** and mapping. (Table 1, Fig3)
- Test of **correlated evolution** between traits contrasting an independent vs. a dependant model of trait acquisition. (Fig2, Table 2)
- **Test of contingency** when the dependant model is selected to determine the order of trait acquisition. e.g. when $q_{13} > q_{24}$ then change in trait X from state 0 to state 1 is more likely when the background state of Y is 1

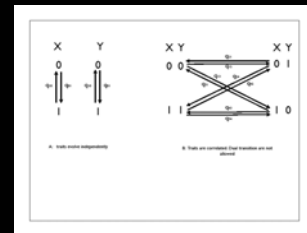


Fig2: Models of trait evolution for 2 binary discrete traits X and Y. A) Traits are evolving independently from each other on the tree. B) Traits evolve in a correlated fashion such that the rate of change in one trait depends upon the background state of the other.

✓ Results

- Shift to **monoecy** was more likely in generalists
- No relation between production of asexual gemmae and sex condition has been found.
- Production of asexual propagule seems to occur more likely in generalists.
- **Recurrent and recent** origin of monoecy.
- **Low probability of reversal** from monoecy to dioecy
- Specialisation from generalists to strict epiphyte occurred **at least eight times** on the tree

| Gender evolution and ecological specialization | | | | |
|---|---------|------------|----------------|-----------|
| Constrained evolution | L20=L25 | L01=195.47 | L20=L24 | BF = 3.98 |
| Production of vegetative gemmae and ecological specialization | L20=L25 | L01=195.56 | L20=L24 | BF = 3.98 |
| Constrained evolution | L20=L25 | L01=197.52 | L20=L24 | BF = 3.98 |
| Production of vegetative gemmae and frequency of sex | L20=L25 | L01=195.55 | L20=L24 | BF = 3.98 |
| Constrained evolution | L20=L25 | L01=195.55 | L20=L24 | BF = 3.98 |
| Production of vegetative gemmae and frequency of sex | L20=L25 | L01=195.55 | L20=L24 | BF = 3.98 |

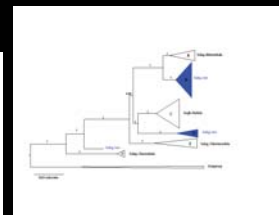


Fig1: Fifty percent majority-rule consensus of the trees sampled by a Bayesian analysis of 93 species of *Radula* as implemented in MrBayes 3.1.

Table 2: Signature of correlated evolution among pairs of traits. Each pair of characters was analyzed successively using two competitive models. Both models were implemented in a Bayesian context and Bayes factors (BF) were used to determine which of the Dependent or Independent model was a significantly better description of trait evolution (the significantly better model is in bold). BF superior or equal to 2 are considered significant. When a Dependent model was selected as the best model, tests were performed to determine if changes in trait X depends upon the state of trait Y, or vice versa.

✓ Main Conclusion

Overall, the results of the present study suggest that **habitat specialization** correlates with a suite of major life-history traits in the genus. In contrast to the traditional interpretation of ecological specialization as an evolutionary dead-end (see Futuyama & Moreno 1988 for review, but see Nosil & Mooers 2005), transitions towards strict epiphytism were not found to be irreversible, as suggested by the performance of the single-rate model, in which backward transitions are as likely as forward ones, as well as the actual inference of reversals in the evolution of the trait. **The transition towards a strictly epiphytic condition seems to have played a key role** in the diversification of leafy liverworts. Dioecy has been considered the most primitive reproductive system (Longton 1994) and the recurrent transitions from dioecy to monoecy in *Radula* is consistent with that idea. However, in contrast to the view of bryophyte dispersal strategies involving monoecy or production of asexual diaspores as alternative solutions to the problem of survival in dynamic and patchy landscapes (Longton 1994; During 2007), specialists failed to display dispersal adaptations in terms of transitions towards monoecy or production of asexual diaspores. Epiphytes experience strong dispersal limitations, as indicated by recorded colonization of trees (Snäll et al. 2005), spatial genetic structuring (Snäll et al. 2004a), and spatially segregated species distributions (Snäll et al. 2004b; Löbel et al. 2006a, b). This renders them extremely vulnerable to habitat disturbance and accounts for their wide use as indicators of forest continuity (Gradstein et al. 2001; Vanderpoorten et al. 2004; Holz & Gradstein 2005; Zartman & Nascimento 2006).

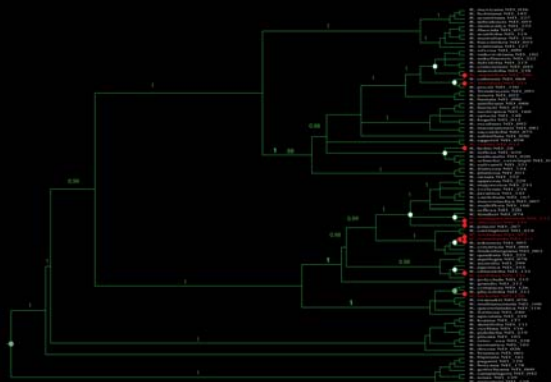


Fig3: Fifty percent majority-rule consensus of the trees (burnin removed) sampled by a Bayesian analysis of 93 species of *Radula* as implemented in MrBayes 3.1. Outgroups were removed prior to ancestral character state reconstruction. Ancestral character state for mating system (character 1; red: monoecious; white: dioecious; grey: reconstruction is ambiguous) are reconstructed for selected nodes. Species in bold are monoecious.

Table 1: Performance of six competing explicit evolutionary models of trait evolution. For each model, the harmonic mean of the loglikelihoods returned by a MCMC visiting the space of rate parameter (q) values were recorded. Bayes factors (BF) were used to determine which of the six models was a significantly better description of trait evolution (the significantly better model(s))

| Life History Trait | Models | | | | | |
|---------------------------|-----------------|--------------|-------|-----------|-------|-----------|
| | 2q Unrestricted | 1q | Q01=0 | Q01=(0-1) | Q10=0 | Q10=(0-1) |
| Ecological specialization | 60.48 | 59.82 | 94.47 | 88.58 | 72.81 | 72.91 |
| Frequency of sex | 45.42 | 49.29 | 54.49 | 54.94 | 72.64 | 66.92 |
| Gender | 66.35 | 65.68 | 87.40 | 86.41 | 98.94 | 96.40 |
| Size | 66.35 | 65.68 | 87.40 | 86.41 | 98.94 | 96.40 |
| gemmae | 57.81 | 59.28 | 76.23 | 74.31 | 77.09 | |