

Evolutionary Trends in Endemic Mosses of the Hawaiian Islands

What is the pattern and potential explanations for moss endemism on the Hawaiian islands? Are endemics the products of single or multiple dispersal events followed by differentiation or is there evidence of radiation?

Introduction

Though oceanic islands have been shown to have high levels of angiosperm endemism (probably through adaptive radiation due to island isolation and environmental heterogeneity), moss endemism is distinctly lower (Vanderpoorten *et al.* 2008). Possible explanations for lower endemism in mosses include higher gene flow by long-distance dispersal and slower evolution in bryophytes compared to angiosperms (Vanderpoorten and Goffinet 2009, Shaw 2009). Long-distance dispersal in mosses is by spores, which may be carried by air currents over oceans separating continents and islands (Vanderpoorten and Goffinet 2009). Variability in sexual reproduction and spore viability under desiccation and freezing conditions affect this long-distance dispersal ability of moss species (Vanderpoorten and Goffinet 2009). Though Mosses show widespread geographic distributions, they can exhibit a high degree of morphological and sometimes genetic similarity across intercontinental disjunctions (Shaw 2009). The two explanations for this (long-distance dispersal and slow substitution rates) seem unlikely, and studying moss speciation is confounded by the difficulty in extricating current gene flow from historic effects (Shaw 2009). A further difficulty lies in moss cryptic speciation, which can hide genetic differences through similar morphology (Shaw 2001). This cryptic speciation indicates that mosses are genetically complex, so phylogenetic studies could be important in exploring biogeographic patterns (Shaw 2001).

In order to evaluate three explanations for low bryophyte radiation (cryptic speciation, long-distance gene flow and slow evolution), Vanderpoorten *et al.* (2008) undertook a phylogenetic study of the globally distributed moss *Grimmia montana*. They sequenced chloroplast regions and identified haplotypes to create a network. They also measured F_{st} and N_{st} values to test the phylogeography ($N_{st} > F_{st}$ suggests alleles within populations are more similar phylogenetically than between populations). Their results suggest that intercontinental gene flow is not as important as mutation in explaining global genetic variation. This does not mean that long-distance dispersal is not involved, since their results also indicate some level of intercontinental gene flow and multiple long-distance dispersals. Multiple colonizations were especially evident on islands, since almost none of the island groups were monophyletic. They hypothesize that high gene flow and niche pre-emption prevent island radiation in mosses with high dispersal ability.

Endemic moss species on the Hawaiian islands constitute about 31% of the indigenous moss species (Staples *et al.* 2004) compared with about 90% endemism among angiosperms (Sakai *et al.* 2002). Hoe (1979) suggested that almost all

Hawaiian mosses came from single dispersal events and have undergone little differentiation, with sources in both the Paleotropical and Boreal regions. For example, Frahm (1991) suggested that Hawaiian species in the genus *Campylopus* came from separate species in southeast Asia with different geographic distributions, though the endemics were of uncertain origin. In order to better understand moss endemism on the Hawaiian islands (and moss evolution in general), I propose a phylogenetic study similar to the one by Vanderpoorten *et al.* (2008) to assess the relative contributions of long-distance dispersal and radiation.

Experimental System

I would like to focus the phylogenetic study on Hawaiian endemic mosses with congeneric relatives on Hawaii and in North America, especially those whose relatives on Hawaii have conspecific relatives in North America. Some of the species satisfying these requirements are shown below in Table 1.

Table 1. Some Hawaiian endemics and their relatives on Hawaii and in North America. I have listed the genera once per entry, the species following and separated by commas. Information from Staples *et al.* (2004) and Anderson *et al.* (1990) and Anderson (1990).

Hawaiian Endemics	Congeneric Relatives on Hawaii	Conspecifics in N. A. (# species in genus in N. A.)
<i>Bartramia baldwinii</i>	<i>Bartramia halleriana</i>	<i>Bartramia halleriana</i> (2)
<i>Brachythecium hawaiiicum</i>	<i>Brachythecium lamprocarpum</i> , <i>plumosum</i> , <i>rutabulum</i>	<i>Brachythecium plumosum</i> , <i>rutabulum</i> (34)
<i>Bryum baldwinii</i> , <i>hawaiiicum</i>	<i>Bryum argenteum</i> , <i>atrovirens</i> , <i>caespitium</i> , <i>chrysonuron</i> , <i>conicum</i> , <i>mildeanum</i>	<i>Bryum argenteum</i> , <i>caespitium</i> (66)
<i>Dicranodontium falcatum</i> var. <i>atrovirens</i>	<i>Dicranodontium denudatum</i> , <i>porodictyon</i>	<i>Dicranodontium denudatum</i> (4)
<i>Fissidens delicatulus</i> , <i>hoei</i> , <i>kilaueae</i> , <i>lancifolius</i> , <i>nothotaxifolius</i> , <i>pacificus</i>	<i>Fissidens aphelotaxifolius</i> , <i>bryoides</i> , <i>elegans</i> , <i>submarginatus</i> , <i>taxifolius</i>	<i>Fissidens aphelotaxifolius</i> , <i>bryoides</i> , <i>taxifolius</i> (36)
<i>Grimmia mauiense</i> , <i>maunakeaense</i>	<i>Grimmia anodon</i> , <i>laevigata</i> , <i>longirostris</i> , <i>pulvinata</i> , <i>trichophylla</i>	<i>Grimmia anodon</i> , <i>laevigata</i> , <i>pulvinata</i> , <i>trichophylla</i> (34)
<i>Orthotrichum alpestre</i> , <i>hawaiiicum</i> , <i>incrassatum</i>	<i>Orthotrichum diaphanum</i> , <i>lyellii</i> , <i>rupestre</i>	<i>Orthotrichum diaphanum</i> , <i>lyellii</i> , <i>rupestre</i> (37)
<i>Plagiothecium mauiense</i>	<i>Plagiothecium cavifolium</i> , <i>denticulatum</i>	<i>Plagiothecium cavifolium</i> , <i>denticulatum</i> (7)
<i>Pohlia baldwinii</i> , <i>mauiensis</i>	<i>Pohlia cruda</i> , <i>flexuosa</i>	<i>Pohlia cruda</i> (30)
<i>Racomitrium fasciculare</i>	<i>Racomitrium crispulum</i> , <i>lanuginosum</i> var. <i>lanuginosum</i> , <i>lanuginosum</i> var. <i>pruinatum</i>	<i>Racomitrium lanuginosum</i> (24)
<i>Sphagnum wheeleri</i>	<i>Sphagnum palustre</i>	<i>Sphagnum palustre</i> (~72)
<i>Weissia ovalis</i>	<i>Weissia controversa</i>	<i>Weissia controversa</i> (8)
<i>Zygodon rubrigemmius</i>	<i>Zygodon reinwardtii</i> , <i>tetragonostomus</i>	<i>Zygodon reinwardtii</i> (5)

This choice of system may provide a distinction between endemics that result from multiple dispersals and those that have radiated from relatives on the island. This focus is limited, however, in that the source of dispersal may not be clear for the species above (e.g. dispersal from Asia to Hawaii and independently from Asia to North America). Without knowledge of the global patterns of distribution, the findings of the study may have limited explanatory power. Ideally, this phylogenetic study would include all members (world-wide) of the genera/species listed for comparison.

Experimental Design

Samples taken from all species in the study (either from herbaria or field sampling) will be used for DNA extraction. Nuclear ribosomal ITS regions could be used for comparison and to construct phylogenetic relationships between the species from each area. Comparing phylogenetic trees will allow inferences as to the sources of endemics and how they are related to the Hawaiian and North American species.

For intraspecific resolution of population relationships, and in cases where island endemics are closely related to their congeners, chloroplast DNA (possibly the *trnL-trnF* sequence mentioned in Vanderpoorten *et al.* (2008)) could be amplified and sequenced to identify haplotypes. This might allow a comparison of *Nst* and *Fst* values as was done in the Vanderpoorten *et al.* (2008) study.

In addition to the genetic analysis, karyotypic observations could point to one mechanism of speciation on the islands. Hybridization and allopolyploidy (as described in Shaw 2009) between descendants of multiple dispersals might explain some of the endemic species.

Ecogeographic observations for species and populations could provide insight into another mechanism of speciation and the origin of endemics.

Possible Outcomes

Results indicating that the island endemics are most closely related to one of their congeneric relatives in Hawaii provide support for the hypothesis that the Hawaiian endemics are the result of radiations from colonizing moss species. Since there are often more than one congeneric species, there is the potential that endemics are single diversifications from each dispersal event. This may show up in the phylogenetic trees if there is enough resolution.

Alternatively, endemics may be more closely related to their North American congeneric relatives (though this seems less likely). This would provide support for the hypothesis that endemics are the products of multiple dispersal events. A limitation to this is that ongoing gene flow between descendants of multiple dispersals in the past could make it difficult to resolve evolutionary relationships. This might be evident in very low *Fst* values between the species/populations.

Another possible outcome is finding that relationships are not clear between the species studied. This could indicate that dispersals are coming from a region which was not included.

Ecological observations could provide support for adaptive radiations or limitations to speciation. Differentiation of habitat between endemics and their nearest relatives (if on Hawaii) might provide support to adaptive speciation. Alternatively, common habitat preferences between species in Hawaii and North America might suggest the niche pre-emption mentioned by Vanderpoorten *et al.* (2008).

Finally, it might be revealing to compare the genetic patterns found with those of known angiosperm radiations such as the Hawaiian silversword alliance.

References

Anderson, L., Crum, H. and Buck, W. 1990. List of the mosses of North America north of Mexico. *The Bryologist* **93**: 448-499.

Anderson, L. 1990. A checklist of *Sphagnum* in North America north of Mexico. *The Bryologist* **93**: 500-501.

Hoe, W. 1979. The phytogeographical relationships of Hawaiian mosses. (Abstract from a Ph.D. thesis only). University of Hawaii.

Frahm, J. 1991. A survey of the *Campylopus* flora of Hawaii. *The Bryologist* **94**: 60-66.

Sakai, A., Wagner, W. and Mehrhoff, L. 2002. Patterns of endangerment in the Hawaiian flora. *Systematic Biology* **51**: 276-302.

Shaw, A. 2001. Biogeographic patterns and cryptic speciation in bryophytes. *Journal of Biogeography* **28**: 253-261.

Shaw, A. 2009. Bryophyte species and speciation. Chapter 11 in *Bryophyte Biology*, 2nd ed. Goffinet, B. and Shaw, A., eds. Cambridge University Press, New York.

Staples, G., Imada, C., Hoe, W., and Smith, C. 2004. A revised checklist of Hawaiian mosses. *Tropical Bryology* **25**: 35-69.

Vanderpoorten, A., Devos, N., Goffinet, B., Hardy, O., and Shaw, A. 2008. The barriers to oceanic island radiation in bryophytes: insights from the phylogeography of the moss *Grimmia montana*. *Journal of Biogeography* **35**: 654-663.

Vanderpoorten, A. and Goffinet, B, eds. 2009. *Introduction to Bryophytes*. Cambridge University Press, New York. pp. 124-159.