DETECTING THE PHYLOGENETIC SIGNAL OF GLACIAL REFUGIA IN A BRYODIVERSITY HOTSPOT OUTSIDE THE TROPICS

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Abstract

Glacial refugia have likely been important in shaping diversity gradients outside the tropics. However, the biogeographical histories of most species within glacial refugia remain unclear. In this thesis, I examine the geographic range structure and phylogenetic attributes of the mosses of Haida Gwaii, a putative glacial refugium and 'hotspot' of moss diversity off the northwest coast of British Columbia. I show that many species have widespread, but disjunct distributions, typically with few close relatives on the islands. I suggest that these features reflect the imprint of glacial history, whereby species within refugia represent isolated populations of previously more widespread species that may have diversified elsewhere. The phylogenetic dispersion of species within high elevation habitats, which best match the climatic regime of the historical glacial refugium, is consistent with the filtering of evolutionarily distinct glacial relicts, and contrasts markedly with the patterns of phylogenetic clustering observed across other habitat types. My study illustrates how the present-day phylogenetic structure of species composition and diversity can reveal the signal of glacial refugia, and help explain why some taxa are more diverse outside of the tropics.

Lay Summary

About 80,000 years ago, continental North America entered the Wisconsin Glaciation, precipitating a massive loss of local diversity. However, some areas remained ice-free and provided refugia for biodiversity to persist. Today, these refugia still retain distinct species assemblages, different from previously glaciated areas. Haida Gwaii, an archipelago and glacial refugium off the coast of British Columbia, Canada, hosts a remarkable moss diversity, both in species richness and evolutionary history. Using data on present-day species distributions, I show that many of the species on Haida Gwaii have highly disjunct distributions and co-occur with few close relatives. I suggest that these mosses on Haida Gwaii represent relictual populations of once more diverse and widespread lineages that contracted dramatically during the last glaciation. My study illustrates how glaciation has left a signature on the regional flora, and helps explain why some taxa are able to maintain high diversity outside of the tropics.

Preface

This thesis is based on research questions I have developed with J. Davies. Under the supervision of J. Davies, I established appropriate experimental design, data collection protocol, and statistical methodology. I conducted fieldwork with assistance from an undergraduate research assistant, Caitlin Laidlaw. I conducted the DNA extraction and phylogenetic reconstruction with Dr. Yang Liu, at the Key State Laboratory of Southern Subtropical Plant Diversity, Fairy Lake Botanical Garden, Chinese Academy of Sciences. J. Davies further assisted with the subsequent phylogenetic analysis. I wrote this manuscript with editorial input from J. Davies. The dataframe of species habitat and traits generated in this thesis is available on Dryad Digital Repository: <<u>https://doi.org/10.5063/F1RN367K</u>> (Wu 2020).

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1. General Introduction

The present day distribution of plant biodiversity has been shaped by species' biogeographical and evolutionary histories. Understanding the processes driving biodiversity patterns of major clades is critical for effective conservation strategies, and may help guide management action to support and maintain ecosystem function and ecological resilience. Bryophytes are an important aspect of terrestrial plant diversity, playing key roles in primary succession, carbon sequestration, water retention, and nutrient cycling (Geffert et al. 2013). Yet the biogeographical histories of most bryophyte lineages are still poorly understood compared to vascular plants. Today there are some 20,000 described bryophyte species (Shaw et al. 2011; ~9000 liverworts, ~300 hornworts, and over 12,000 mosses). This diversity, however, is much lower than historically, and the ecological role of bryophytes is likely reduced to just a shadow of what it once was – *c.f.* sequential replacement hypothesis (Laenen et al. 2014). Nevertheless, present day biodiversity patterns of extant bryophytes can shed light on the macroevolutionary history of early land plants.

Bryophytes are generally slow evolving with an average net diversification rate ~30% that of angiosperms (Laenen et al. 2014). However, bryophytes went through major bursts of diversification in the mid-Mesozoic, and by the Cenozoic bryophyte diversification rates were comparable to angiosperms. It is likely that subsequent changes in climate alongside major extinction events, such as glaciation, contributed to much reduced diversification (Crisp et al. 2011). The variable rates of bryophyte diversification through space and time (Shaw et al. 2003b) resulted in distinct patterns of diversity and distribution. During the Carboniferous, plate tectonic movements and desertification fragmented a diverse bryoflora, subjecting it to strong selective pressure and different evolutionary trajectories. The cool, mesic climate of southern

Gondwana and northern Laurasia provided a refugium for temperate bryophytes, while the warmer and drier regions of central Laurasia favored more drought-adapted and niche-specific groups, creating major systematic discontinuities (Miller 2008). Strong phylogenetic niche conservatism within bryophytes likely restricted the diversification of some clades, and may have prevented bryophytes from radiating into open, disturbed environments, for example the South African fynbos, where several of the most spectacular angiosperm radiations took place (Patiño et al. 2014).

Perhaps more so than in any other taxa, phylogenetic niche conservatism is the dictating factor in the species distribution of mosses, with species retaining the ancestral traits adapted to the climate of their region of diversification (Stephens and Wiens 2003, Wiens and Donoghue 2004). Nonetheless, through long distance dispersal, many species are able to track suitable climates, even across great distances (Biersma et al. 2017), with single extreme long dispersal events from spores thought more likely than multiple stepping-stone dispersal events (Crisp et al. 2011). As a consequence, many Holarctic species have extremely widespread and disjunct, and in some cases even bi-polar distributions (Schofield 1974). For example, *Polytrichum juniperinum*, a common Holarctic species, diversified in the Antarctic, and subsequently dispersed to colonize both the Holarctic and Southern Hemisphere regions (Biersma et al. 2017).

The strong niche conservatism exhibited by mosses helps explain departures from more general biodiversity distributional patterns. For example, the geographic distribution of mosses does not generally follow Rapoport's rule of species range size – the tendency for range sizes to increase at higher latitudes – as there is no evidence that species have larger ranges at higher elevations or altitudes (Garu et al. 2007). Although mosses typically have broad, widespread

areas of occurrence at higher latitudes, their geographic distributions are frequently interrupted or disjunct in the Holartic (Shaw 2001). Mosses also depart from global latitudinal diversity gradients, with moss diversity in temperate regions, where many species have persisted in refugia, being equal to or higher than in the tropics (Gefferts et al. 2013, Möls et al. 2013, Shaw et al. 2015, Mateo et al. 2016).

Globally, several hotspots of moss diversity are found at higher latitudes outside the tropics, including in British Columbia, the northern Andes, Japan, Madagascar, the East African Highlands, the Himalayan region, central Europe, and Scandinavia (Geffert et al. 2013). These biodiversity hotspots not only support high taxonomic diversity, but may also encompass high phylogenetic diversity, depending on the clade in question and its origin (Shaw et al. 2011). Within some early diverging lineages, such as *Sphagnum*, taxonomic richness is high in the neotropics, but phylogenetic diversity is highest in temperate and boreal regions (Shaw et al. 2003a). Most phylogenetic analyses have placed *Takakia* and *Sphagnum* as sister groups to all other mosses, and both lineages likely have a temperate origin. *Takakia* is strictly a northern temperate lineage, while the high richness but low phylogenetic diversity of *Sphagnum* in the Southern Hemisphere suggests a northern temperate origin with later colonization and rapid radiation in the South. In contrast, within the more recently evolved pleurocarpous lineages, for example, Hookeriales, a tropical clade, and Hypnales, a temperate clade, phylogenetic diversity is higher than predicted (by the number of genera) in the tropics (Shaw et al. 2011).

The endemic bryoflora of temperate western North America combines both recently diversified and relictual lineages. For example, on the Pacific coast the relatively young genus, *Neckera,* and relictual genus *Andreaeobryum* both contribute to endemic diversity. In contrast, endemic east coast bryodiversity is mostly composed of relictual species (Carter et al. 2016). As

a consequence, endemic richness is much higher in the west than in the east, and rates of new endemic species discoveries are also higher in western North America.

Haida Gwaii, a temperate island archipelago and putative glacial refugium on the northwest coast of British Columbia (Mathewes et al. 2015), has an exceptionally high regional bryophyte diversity, with over 390 species of moss and 180 liverworts (Golumbia and Bartier 2004). While over half of these species have widespread and continuous range distributions, 14 are IUCN listed as globally threatened, one of which, Carey's Small Limestone Moss (*Seligeria careyana;* Vitt and Schofield 1976) is endemic to Haida Gwaii and has only been observed in three localities. Many others exhibit extreme disjunctions throughout their global distribution, for example, *Daltonia splachnoides, Zygodon gracilis*, and *Trichostomum recurvifolium* have their only North American occurrence on Haida Gwaii (Schofield 1989). The biogeographic histories of these disjunct and endemic species, whether they are relictual species (fortunate survivors in glacial refugia), extreme long distance dispersers from elsewhere, or recently diversified species, remains unclear.

Biogeographical scenarios can be tested using present day distributional patterns to infer historical processes (Crisp et al. 2011). Here, I evaluate evidence for the glacial refugia hypothesis – that Haida Gwaii provided a glacial refuge that allowed many moss species to persist through the last glaciation, helping explain the high present day bryodiversity of the archipelago. I reconstruct the phylogenetic tree of Haida Gwaii mosses, and use phylogenetic comparative methods to explore the correlations between species evolutionary distinctiveness, life history traits, and species geographic distributions. Cross species analysis of trait × environment relationships can be confounded by the phylogenetic non-independence of species, leading to potentially misleading statistical associations (Ackerly and Donoghue 1995). By controlling for evolutionary non-independence, phylogenetic comparative methods provide

more statistically robust analyses. Finally, I examine whether phylogenetic diversity is higher in present day habitats that resemble historic glacial refugia.

2. The phylogenetic signature of Glacial Refugia in the mosses of Haida Gwaii

2.1 Introduction

The diversity of life is unevenly distributed across the globe. Perhaps the most well-recognized biodiversity pattern is the latitudinal gradient in species richness, which describes the tendency for richness to be highest in equatorial regions and taper towards the poles (see Hawkins et al. 2003, Hewitt 2000). However, some taxa show counter gradients, for example, with highest richness at high latitudes (Kindlmann et al. 2007). Understanding these 'exceptions to the rule' can provide unique insights into the mechanisms shaping biodiversity gradients. Vascular plants demonstrate a typical latitudinal gradient in species richness, with highest diversity in the warm and moist tropics (Brown 2014). The biogeography of non-vascular plants has been less well explored; while there is some evidence that liverworts and hornworts also exhibit a general latitudinal richness gradient (Wang et al. 2016), mosses may exhibit inverse or no latitudinal diversity gradient (Shaw et al. 2015, Mateo et al. 2016). Additionally, several hotspots of moss species richness are found outside of the tropics, including in British Columbia (Geffert et al. 2013). Here, I use a regional phylogeny of extant mosses from the glacial refugium and island archipelago of Haida Gwaii (formerly known as the Queen Charlotte Islands), off the northwest coast of British Columbia, Canada, to explore the historical mechanisms that have shaped this exceptionally rich northern latitude bryophyte flora.

The moss diversity of Haida Gwaii is remarkable, with over 380 species within an area of 10,180 km₂ (Golumbia and Bartier 2004). While 172 of Haida Gwaii moss species have continuous circumpolar distributions, a further 47 species have widely interrupted distributions. It is possible that rare single long-distance dispersal events contribute to the unique diversity of

disjunct species in glacial refugia (Provan and Bennett 2008, Heinrichs et al. 2009). However, some disjunct species appear to lack the mechanisms for effective long-range dispersal, thus suggesting vicariance rather than recent dispersal may better explain their unusual distributions (Shaw 2001). The occurrence of similarly disjunct non-bryophyte plants indicate a possible common process: Eurasian origin, dispersal to North America, and subsequent western North America disjunction (Xiang et al. 1998). The presence of these disjunct and endemic species on Haida Gwaii and their absence elsewhere in north-western North America, which resembles a more boreal flora compared to the more temperate flora on Haida Gwaii (Alaback 1996), suggest a unique spatial and temporal history of the Haida Gwaii ecosystem that has sustained a rich bryoflora to the present (Heusser 1989).

One explanation for the unique bryophyte diversity of Haida Gwaii is linked to suggestions that the archipelago was a glacial refugium during the Late Wisconsin Glaciation (Matthewes and Clague 2017). Graham island, the largest island in the Haida Gwaii archipelago, was glaciated at least twice, once >52,000 years ago, then again between 27,500 and 16,000 years ago (Demboski et al. 1999; Matthewes et al. 2015), but Haida Gwaii was partially ice free as early as 16,000 years ago, when the lowland phase of the Late Wisconsin Glaciation was at its maximum. Possible locations of refugia include the Queen Charlotte Ranges, the west coast of Graham and Moresby islands, and the shelf beneath Hecate Straight, which was at various times exposed with freshwater lakes (Shafer et al. 2010). Present-day plant communities located between 900 - 1,100 m in elevation potentially represent remnants of the refugial flora (Heusser 1989), as the climate at these elevations may resemble the climatic conditions of historical refugia.

To date, the biogeographical histories of most species within glacial refugia remain unclear. Regional species diversity is determined by four factors: dispersal, speciation, extinction, and time (Cook et al. 2006). Glaciation might influence all these factors. For a few species, population studies and phylogeographic methods have allowed us to identify continental refugia and patterns of post glacial range expansion (Provan and Bennett 2008, Allen et al. 2015), for example in oaks, common beech, black alder, and silver fir in Europe (Hewitt 1999). Commonalities across relictual species can also be found, for example, as reflected in their present day genetic diversity and geographical distributions – species that survived within several large refugia have greater diversity than those which were restricted to fewer, small refugia (Roberts and Hamann 2015), and more often exhibit disjunct present day distributions. The evolutionary history of species can capture the fingerprint of these biogeographic processes, and phylogenetic approaches allow us to robustly test for correlations between species biogeographic histories, dispersal traits, and their present day distributions (Harvey and Pagel 1991).

Here, I reconstruct the regional phylogeny of the Haida Gwaii bryoflora – focusing on mosses – using *rbcL* and *trnL-F* DNA barcode markers extracted from field samples and herbarium specimens. I use this phylogeny to explore the macroevolutionary and macroecological imprint of glacial history on the moss flora of Haida Gwaii by examining the relationship between evolutionary distinctiveness, dispersal traits (i.e. spore size and sexuality), and range continuity in their present-day distributions. I also examine whether species with more disjunct distributions are more phylogenetically isolated, and if habitats associated with glacial refugia support more phylogenetically dispersed bryophyte communities.

2.2 Materials and Methods:

2.2.1 Plant material and molecular sequencing

I used the two molecular barcode markers, *rbcL* and *trnL-F*, to reconstruct the regional phylogeny of the mosses of Haida Gwaii, as they currently have the best taxonomic coverage within bryophytes. Using the species list (with corrections to conform to current nomenclature conventions) provided in Golumbia and Bartier (2004) — a comprehensive baseline inventory report for the bryophytes of Haida Gwaii — I downloaded the available *rcbL* and *trnL-F* sequences from the GenBank database (https://www.ncbi.nlm.nih.gov/genbank/) for each species. Species that did not have either existing *rbcL* or *trnL-F* sequences were targeted for field collection and sequencing.

During July and August 2019, I collected voucher specimens representing 109 species from Haida Gwaii using standard field collection methods, as outlined in Schofield (1992). The 21 collection sites (Figure 1), consisting of two alpine locations, four hyper-oceanic locations, eleven low to mid elevation forest locations (four of which are along creeks), and four low elevation open wetlands, were selected to encompass as many as possible of the different habitat types described by Golumbia and Bartier (2004). All microhabitat and substrate types within each site (e.g. hummocks, rock faces, forest floor, coarse woody debris, ruts, and crevices) were targeted for collection. Location description, latitude and longitude, microhabitat, and other environmental characteristics were recorded for each voucher. Each specimen was photographed in situ, and accessioned at the University of British Columbia Herbarium (UBC). Occasionally a voucher specimen would consist of more than one species. Taxonomic identification and nomenclature of the specimens conform to the information in volumes 27 and 28 of the Flora of North America (Flora of North America Bryophyte Editorial Committee 2007 and 2014).



Figure 1 – Sampling locations on Haida Gwaii. Topographical map of Haida Gwaii, BC.Red symbols indicate sampling locations.

In total 99 field samples and an additional 86 species previously vouchered at the UBC were sampled and sequenced for both molecular barcode regions. Samples were ground at 60 Hz for 60 seconds using Tissuelyser – 24 (Shanghai Jinxin Industrial Development Co. Ltd., China), and total genomic DNA for each sample was extracted using the HP Plant DNA Kit (Omega Bio-Tek, GA, USA) following the manufacture's protocol. A nested PCR reaction system was optimized based on the recommended protocol from Hentschel et al. (2006) and Feldberg and Heinriches (2006), using the primers in Feldberg et al. (2016): *rbcL*1F and *rbcL*1390R for the first round, and *rbcL*210F and *rbcL*1200R for the second round of PCR for *rbcL*; and *trnLF* and *trnLR* for the one round of PCR for *trnL-F*. The amplification products were sequenced at the Beijing Genomic Institute (BGI, China). The generated sequences for each species, it was only possible to sequence one of the two barcode genes.

2.2.2 Phylogenetic reconstruction

I reconstructed a dated molecular phylogeny of the 319 moss species using a combined dataset of the newly generated *rbcL* and *trnL-F* sequences and sequences downloaded from GenBank. Sequences were aligned using Geneious Prime (v. 2020.0.3 Biomatters Ltd., Auckland, New Zealand; Kearse et al. 2012). For new barcode sequences, ambiguous ends were trimmed, and consensus sequence was generated using forward and reverse reads. I aligned *rbcL* and *trnL-F* sequences separately using MUSCLE v3.8.13 (Edgar 2004) and optimized using Gblocks Server (Castresana 2002) to eliminate poorly aligned regions. The aligned genes were then concatenated into a single matrix.

I reconstructed the phylogeny using RAxML v8.2.12 (Stamatakis 2014), with the GTR+GAMMA+I model for both *rbcL* and *trnL-F* genes, as selected by J Model Test v2.1.10 (Darriba et al. 2012). Bootstrap analyses were implemented by GTR+CAT approximation for 100 replicates. I rooted the resulting topology with *Takakia lepidozioides* as the outgroup. Because the phylogenetic signal within barcode regions is limited, I enforced topological constraints at the family level, assigning genera to families using the topology reflecting the ordinal relationships of mosses proposed by Liu et al. (2019). Branch lengths were made proportional to time using the penalized likelihood method, as implemented in r8s v1.8.1 (Sanderson 2003). Calibration points were assigned for different nodes on the phylogeny based on the minimum age of dated clades. The age for the most recent common ancestor for mosses, 380.4 mya, as estimated using Bayesian inference by Newton and Tangney (2007), was fixed at the split between the basal moss genus Takakia and other mosses. Subsequent calibration points were set based on fossil records for Sphagnaceae, 330.0 mya (Nuberg 1958, Ignatov 1990, Hübers and Kerp 2012, Maslova et al. 2012, Hübers et al. 2013); Polytrichales, 83.6 mya (Konopka et al. 1997, Konopka et al. 1998); Dicranidae, 152.0 mya (Heinrichs et al. 2014); and Bryidae, 136.0 mya (Shelton et al. 2015).

2.2.3 Species life history traits, evolutionary distinctiveness, and distribution data

I used the habitat and distributional information from Golumbia and Bartier (2004) as well as life history strategies from the bryological literature (Söderström and During 2005) to generate a matrix of species distribution and habitat types on Haida Gwaii, species sexuality, and spore size (minimum, maximum and mean). I also calculated evolutionary distinctiveness (ED) for each species on the phylogeny using the evol.distinct function in the R package picante (Kembel et al. 2010) and the 'equal splits' method (Redding and Moores 2006).

I recorded spore size as a continuous variable, and species sexuality as a discrete variable (0 = monoicous, 1 = dioicous) using data from volumes 27 and 28 of the Flora of North America (Flora of North America Bryophyte Editorial Committee 2007 and 2014) augmented with information from the California moss eflora (2020).

I classified species geographic distributions using information from Appendix A of Golumbia and Bartier (2004), which presents a continuum of 10 categories (indicated in parentheses, below). First, I broadly classified species from widespread to local on a scale of 1 to 6: 1 (Widespread in Northern hemisphere), 2 (Amphipacific), 3 (Western European – Western North American), 4 (Western European – Western North American showing a widely interrupted pattern in the northern hemisphere and Eastern North American disjuncts), 5 (tropical subtropical disjuncts and species for which Haida Gwaii contains the only known Canadian population), and 6 (Western North America and Pacific coast). Second, I generated a discrete classification scheme distinguishing species with continuous distributions (grouping distribution codes 1 and 2), disjunct distributions (grouping distribution codes 3, 4, and 5), and localized distributions (distribution code 6). Third, I used a binary classification to distinguish between species with continuous (distribution codes 1, 2, and 6) versus disjunct distributions (distribution codes 3, 4, and 5). Where possible, species missing distribution data from Golumbia and Bartier (2004) were classified based on the available distribution information in volumes 27 and 28 of the Flora of North America (Flora of North America Bryophyte Editorial Committee 2007 and 2014). Taxa without distribution data (N = 40) were excluded from subsequent analyses. Finally, I coded the presence of species within each of the 16 habitat and vegetation types (hereon

referred to as habitat types) in Appendix A of Golumbia and Bartier (2004), which broadly describes species habitat preferences summarized in Schofield and Hong (2002). In some cases, these habitat types are not discrete, and species can occur in multiple habitats. For example, *Dicranum scoparium* can occur in the following habitat types: forest floor, epiphytic habitats, sand dunes, and siliceous rock.

2.2.4 Analysis of species distribution and evolutionary history

To explore the composition of mosses across the 16 habitat types listed in Golumbia and Bartier (2004), I first summarised the phylogenetic diversity (PD) and species richness (SR) (Faith 1992) within each habitat type. Next, I calculated the standard effect size of phylogenetic diversity (ses.PD) for bryophyte assemblages associated with each of the habitats, using the 'tip-swap' algorithm and 1000 randomizations. This metric of phylogenetic diversity evaluates whether the observed PD differ from a null expectation derived from sampling species at random from the species pool. Last, I calculated the mean evolutionary distinctiveness (mED) of the different habitat types by taking the mean of the species evolutionary distinctiveness (ED) estimated on the reconstructed regional phylogeny.

I used three approaches (phylogenetic generalized least squares, phylogenetic ANOVA, and phylogenetic generalized linear model) to test the relationship between species distribution, life history traits, and evolutionary distinctiveness.

First, I used a phylogenetic generalized least squares regression to model trait correlations in the R package caper (Orme et al. 2012). For purposes of model fitting, zero length branches were assigned a nominal unit length. The phylogenetic variance covariance matrix was included to model phylogenetic non-independence in the data, and the model was then fit with species sexuality, spore size, and evolutionary distinctiveness as predictors, and species distribution, coded on a continuous scale from 1 to 6 (see above), as the response, fitting the maximum likelihood value of λ .

Second, to further explore the relationship between ED and distribution, I compared differences in ED between the three distribution classes: continuous, disjunct, and regional (see above) with a phylogenetic ANOVA using the phylANOVA function from the R package phytools (Revell 2012). Because the ANOVA could not be fitted to an incompletely resolved phylogenetic tree, I removed polytomies by randomly dropping all except one taxon per terminal clade using the function thin_terminal_polytomies (Davies et al. 2012), and fit the model on this reduced dataset. P-values for the posthoc tests were adjusted using Holm's correction for multiple comparisons. I then repeated this thinning procedure 1000 times to generate a distribution of test results.

Third, I compared ED between species with continuous versus disjunct distributions using phylogenetic logistic regression fit on the full tree using the function phyloglm from the R package phylolm (Ho and Ane 2014), and with 100 independent bootstrap replications. Here, species distribution was modelled as a binary response with ED as the explanatory variable.

2.3 Results:

2.3.1 Phylogenetic reconstruction of Haida Gwaii moss species

The regional phylogeny of Haida Gwaii mosses (Figure 2) was constructed using 264 *trnL-F* sequences (145 newly generated sequences and 119 from GenBank; Table S1) and 324 *rbcL* sequences (127 newly generated sequences and 195 from GenBank; Table S1), and includes 319 out of the total 380 species present on the islands. Major clades were constrained to agree with

the topology proposed by Liu et al. (2019), and therefore our reconstruction matches to their ordinal relationships. Following calibration, some short branches were collapsed to polytomies, resulting in a few unresolved clades within the Hypnales, including in Campyliaceae, Calliergonaceae, and Leskeaceae, and also in the Orthotrichales between the genera *Ulota* and *Orthotrichum*. The overall topology is 65.5% resolved (with bootstrap supports > 50).



Campylium stellatum Campyliadelphus chrysophyllus Cratoneuron filicinum Palustriella falcata Amblystegium serpens Drepanocladus aduncus Leptodictya riperium Calliergonella cuspidata Hygrohypnum luridum Hygrohypnum bestii Sanionia symmetrica Sanionia uncinata Hygrohypnum smithii Hygrohypnum ochraceum Campylophyllum halleri Brotherella canadensis Wiikia carlottae Schofieldiella micans Entodon concinnus Iwatsukiella leucotricha Myurella julacea Abietinella abietina Pseudoleskea atricha Pseudoleskea stenophylla Pseudoleskea patens Pseudoleskea baileyi Straminergon stramineum Warnstorfia sarmentosa Claopodium whippleanum Scorpidium scorpioides Sarmentypnum exannulatum Warnstorfia fluitans Hamatocaulis vernicosus Loeskypnum badium Calliergon cordifolium Calliergon giganteum Pleuroziopsis ruthenica Climacium dendroides Scorpidium revolvens Brachythecium plumosum Brachythecium velutinum Brachythecium albicans Brachythecium rivulare Brachythecium frigidum Brachythecium leibergii Kindbergia oregana Eurhynchium praelongum Eurhynchium pulchellum Homalothecium nuttallii Homalothecium fulgescens Homalothecium aeneum Scleropodium cespitans Scleropodium obtusifolia Sciuro-hypnum reflexum Antitrichia californica Antitrichia curtipendula Rhytidiadelphus loreus Rhytidiadelphus squarrosus Rhytidiadelphus triquetrus Hylocomium splendens Pleurozium schreberi Hylocomiastrum pyrenaicum Hylocomiastrum umbratum Porotrichum bigelovi - Neckera douglasii - Metaneckera menziesii Thamnobryum neckeroides Isothecium cardotii Isothecium stoloniferum Bryolawtonia vancouverensis Hypnum plicatulum Hypnum lindbergii Hypnum dieckii Hypnales Hypnum vaucheri Hypnum cupressiforme Hypnum callichroum Hypnum revolutum Hypnum recurvatum Hypnum circinale Hypnum pallescens Ptilium crista-castrensis Ctenidium schofieldii Herzogiella adscendens Herzogiella striatella Plagiothecium denticulatum Plagiothecium cavifolium Plagiothecium laetum Plagiothecium undulatum Isopterygiopsis pulchella Plagiothecium piliferum Heterocladium dimorphum Heterocladium procurrens Rhytidium rugosum Pseudotaxiphyllum elegans Platydictya jungermannoides 150 100 50 0



Figure 2 – **Phylogenetic reconstruction of Haida Gwaii mosses.** Reconstructed maximum likelihood, dated phylogeny of 304 Haida Gwaii moss species based on rbcL and trnL-F sequence barcodes. Scale bar in millions of years.

2.3.2 Phylogenetic attributes and species range structure across habitats

Species with widespread northern hemisphere, amphipacific, and contiguous North American -European distributions dominate across all habitat types. Following the habitat classification of Schofield and Hong (2002), calcareous rock, siliceous rocks and water body margins have the highest overall species richness. Open forests of fen slopes, peatland bogs, and fens have the highest proportion of species with continuous distributions relative to the total number of species within each of these habitat types (Table 1); epiphytes, seaside outcrops, disturbed soil, and high elevation habitats have the highest proportion of species with disjunct distributions; while forest floor, epiphytes, aquatic, and high elevation habitats have the highest proportion of species with localized western North American distributions (Table 1). Interestingly, both epiphytes and high elevation habitats have both a high proportion of disjunct and localized species relative to other habitat types.

Phylogenetic structure and species diversity of bryophytes also varied across the different habitat types. Broad evidence for phylogenetic clustering (as indexed by ses.PD) indicates that most habitats capture less phylogenetic diversity (PD) than predicted from their species richness (Table 1). Epiphytes have the lowest ses.PD, indicating that epiphytic taxa are the most phylogenetically clustered. The mean evolutionary distinctiveness of species (mED) is also lower for epiphytes than for other habitat types (Table 1). In contrast, high elevation habitats capture somewhat more PD than expected from their species richness (positive ses.PD), and mean species evolutionary distinctiveness is higher than in other habitats (mED = 140.19). Overall, there was a general positive correlation between ses.PD and mED (Pearson's r = 0.66), while the relationship between ses.PD and total PD or SR was somewhat weaker and negative (Pearson's r = -0.11 and -0.38, respectively). Thus, while habitats with a less phylogenetically constrained moss flora tended to be less species rich, the species within them were more evolutionarily

distinct. However, I did not observe any strong relationship between ses.PD and the proportion of species with disjunct distributions within habitats.

2.3.3 Relationship between species distributions and evolutionary distinctiveness

In our phylogenetic generalized least squares regressions, I found no significant relationship between either dispersal traits (i.e. spore size and sexuality) or evolutionary distinctiveness and species distribution when modelled as a continuous variable assuming six distribution classes. Although there appeared to be some weak evidence for a relationship between sexuality and distribution (slope = 0.66, p = 0.04), the overall model was not significant (p > 0.05, model $R^2 <$ 0.03; Table 2). Furthermore, in the single trait model, this relationship was not supported (all p > 0.05, model $R^2 < 0.02$; Table 2).

		PD	SR	Continuous	Disjunct	Localized	Ses.PD	mED
1.	Forest floor	3142.87	17	0.71	0.06	0.24	-0.42	94.59
2.	Large woody debris	1818.91	9	0.67	0.11	0.22	-0.72	124.73
3.	Epiphytes	3894.15	35	0.51	0.20	0.29	-4.85	79.36
4.	Open forest of fen slopes	2744.39	17	0.88	0.06	0.06	-1.46	97.20
5.	Swamp forests	2171.65	13	0.75	0.08	0.17	-1.92	75.77
6.	Peatland bogs	3625.48	23	0.83	0.09	0.09	-1.63	106.13
7.	Peatland fens	3066.18	20	0.85	0.05	0.10	-2.33	103.77
8.	Seaside outcrops	924.91	4	0.75	0.25	0.00	-0.87	95.06
9.	Sand dunes	2492.91	13	0.69	0.15	0.15	-0.52	89.45
10	. Blowdown	1664.90	8	1.00	0.00	0.00	-0.66	119.34
11	. Disturbed soil	3009.38	17	0.63	0.25	0.13	-0.96	111.26
12	. Aquatic habitats	1822.90	11	0.55	0.18	0.27	-2.19	111.98
13	. Water body margins	4143.07	28	0.78	0.15	0.07	-2.08	100.69
14	. Calcareous rock	6654.45	47	0.63	0.19	0.19	-1.41	105.54
15	. Siliceous rock	5973.79	45	0.80	0.05	0.15	-2.50	94.64
16	. High elevations	5028.98	26	0.56	0.20	0.24	1.41	140.19

Table 1 – Distribution and phylogenetic attributes of 16 habitat types on Haida Gwaii. Comparison between

phylogenetic diversity (PD), species richness (SR), standard effect size of phylogenetic diversity (ses.PD), mean evolutionary distinctiveness (mED), and the proportion of species with continuous, disjunct, and localized distributions to the total number of species across the 16 habitat types.

Model	Predictor(s)	Coef.	Std. Error	T value	P (> t)	λ	F stat.	R ²	df
1	Spore size	0.01	0.02	0.48	0.63	0.33	0.23	<0.01	253
2	Evolutionary distinctiveness	0.002	0.002	1.08	0.28	0.25	0.63	<0.01	291
3	Sexuality	0.51	0.26	1.97	0.05	0.35	3.88	0.01	254
4	Spore size	0.02	0.02	0.93	0.35	0.42	2.09	0.01	231
	Evolutionary distinctiveness	0.04	0.003	1.54	0.12				
	Sexuality	0.55	0.27	2.02	0.04				

Table 2 – Phylogenetic generalized least squares analysis. Phylogenetic generalized least squares regressions assuming acontinuous classification of range size on a scale of 1-6 (where 1 = Northern hemisphere, 2 = Amphipacific, 3 = western European –western North American, 4 = northern hemisphere disjuncts, 5 = tropical – subtropical disjuncts, and 6 = localized in western NorthAmerica) as response variables, and with spore size, evolutionary distinctiveness, and sexuality as predictors. Models 1-3 showsingle trait relationship, model 4 shows the same traits in the multivariate analysis.

Reclassifying distributions into three discrete classes: localized, disjunct and continuous, revealed strong and significant differences in the evolutionary distinctiveness of species with different distributions (p < 0.05 from the phylogenetic ANOVA, Table S2). The corrected post hoc pairwise comparisons using the Holm adjustment, indicates that species with disjunct distributions are more evolutionarily distinct than species with continuous or localized distributions, but that there was no significant difference between species with continuous and regional distributions (Figure 3).

I further examined the difference in evolutionary distinctiveness between species with disjunct distribution and those with continuous or regional distributions (Figure 4) using a phylogenetic generalized linear model on binary data. Here, I again found a significant positive relationship between evolutionary distinctiveness and disjunct distribution ($\propto = 0.003$, p < 0.05; Figure S1).



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Figure 4 – **Character traits mapped on phylogeny.** Visual comparison of evolutionary distinctiveness and distribution mapped on the reconstructed bryophyte phylogeny. Evolutionary distinctiveness, based on the dated phylogeny in millions of years, is shown on the left, mapped as a continuous variable under assumptions of Brownian motion using the contMap function from phytools R library (Revell, 2012). Blue indicates lower evolutionary distinctiveness and red indicates higher evolutionary distinctiveness. The figure on the right shows species distributions classified as a binary trait (continuous vs disjunct) and mapped onto the phylogeny using stochastic character mapping using the make.simmap and densityMap functions from the phytools R library (Revell, 2012). Species at the tips of blue branches have continuous distributions while species at the tips of red branches have disjunct distributions.

2.4 Discussion:

One of the most universal global diversity patterns is the latitudinal gradient in species richness. However, unlike most vascular plant taxa, mosses exhibit no general latitudinal diversity gradient, and temperate regions are equally as diverse as the tropics (Gefferts et al. 2013, Möls et al. 2013). While uncommon, several other groups of organisms also exhibit counter latitudinal gradients, including lagomorphs, arboreal ants, mollusks, and aphids (Morales-Castillia et al. 2019). Explanations for these unusual diversity gradients frequently assume that extra-tropical species richness reflects phylogenetic niche conservatism (Stephens and Wiens 2003, Wiens and Donoghue 2004) in clades with temperate or high latitude origins. Mosses may also have a temperate origin, with *Takakia*, the sister group to all other mosses (Chang and Graham 2011), being a temperate genus (first noted to occur in North America from the islands of Haida Gwaii by Persson 1958). Extra-tropical niche conservatism may thus help explain generally higher species richness for mosses in temperate environments. However, glacial history might also be part of the explanation. During glacial cycles, the distributions of many high latitude and temperate species were pushed towards the equator, reducing species richness at higher northern latitudes. Following glacial retreat, northward recolonization was generally slow (Svenning and Skov 2007). Glacial refugia allowed some areas to retain high diversity away from the tropics, and to more rapidly recolonize higher latitudes following glacial retreat (Keppel et al. 2012). Several northern hemisphere hotspots of present-day moss diversity might represent such historical refugia.

In this study, I examined the geographic range structure and phylogenetic attributes of the mosses of Haida Gwaii, a hotspot of moss diversity and putative glacial refugium off Canada's west coast. I found that many species have widely interrupted global range distributions, and

these species typically have few close relatives within the Haida Gwaii species assemblage. I suggest these features likely reflect the imprint of glacial history, where evolutionarily distinct species have persisted in isolated refugia. Our study illustrates how the present day phylogenetic structure of species composition can reveal the signal of glacial refugia, and helps explain why some taxa have higher species richness outside of the tropics.

2.4.1 Phylogenetic structure of glacial refugia

Past climate may have had as important an impact on present-day patterns of species diversity as current climatic conditions (see Jansson and Davies 2008). For example, palaeoecological studies indicate that repeated sequences of tree species range expansion and contraction, forced by glacial-interglacial cycles, reduced opportunities for habitat specialization and elevated rates of extinction, reducing diversity at higher latitudes (McGlone 1996). I suggest past climates have likely also shaped present day phylogenetic structure of regional plant assemblages. If traits associated with dispersal ability are phylogenetically conserved, then filtering of species based on dispersal during the recolonization of previously glaciated areas of species from the south (Baten et al. 2015) would lead to increased phylogenetic clustering of species towards the poles (Ma et al. 2016). However, glacial refugia would not have been subject to dispersal filtering, and we might therefore predict the species assemblages within them to be more diverse and less phylogenetically clustered. Evidence of refugia on Haida Gwaii comes from the succession of Cyperaceae captured in pond sediments from 16,830 years BP (Lacourse et al. 2005). This record suggests that the non-glaciated habitat was likely tundra, resembling present day high elevation habitats, consistent with our observation of greater phylogenetic dispersion in mosses from high elevation sites. It is difficult, however, to compare moss diversity across habitat types

because of the large variation in area encompassed by each; nonetheless, other species characteristics of the mosses on Haida Gwaii and within these high elevation habitats support the glacial refugia hypothesis.

2.4.2 Glacial history and range disjunction

The mosses of Haida Gwaii include a striking number of species with disjunct distributions – frequently with western North American populations disjunct from populations in eastern North America, western Europe, and tropical Eurasia. The global geographic extents of Haida Gwaii mosses are not easily attributable to species life history traits. In our models, traits explain little variation in species distribution. While propagule size has been commonly associated with dispersal ability (Söderström and During 2005), correlations between spore size and distribution are weak and non-significant. It is possible that, in mosses, neither small nor large spores have a dispersal advantage. Small spore species can produce higher quantities of spores, but large spore species establish more easily within a locality and have better survival (During 1997). I suggest, therefore, that these disjunct distributions are more likely a reflection of glacial history, a consequence of the process of range expansion and contraction between glacial and interglacial periods (Zhao et al. 2018).

If high elevation sites best match historical refugia, I might then also predict that they should have a higher proportion of disjunct species. While this is true to some extent, other habitat types, such as epiphytes, seaside outcrops, and disturbed soils, all have equal or higher proportions of disjunct species relative to high elevation habitats. It is possible, therefore, that species with disjunct distributions also share other traits that favour their establishment within these other habitat types, perhaps linked with their association with

frequent disturbance. The phylogenetic clustering observed within each of these alternative habitats supports this habitat filtering effect, in contrast to high elevation habitat which shows phylogenetic overdispersion.

2.4.3 Glacial refugia support more evolutionarily distinct lineages

The phylogenetic dispersion of species within high elevation habitats is also reflected in the mean evolutionary distinctness of the constituent species, which is much higher than found in any other habitat type. This high evolutionary distinctiveness suggests that species within high elevation habitats tend to have few close relatives on Haida Gwaii. It is possible that high elevation habitats encompass a larger number of vegetation types than other habitats, which could drive greater phylogenetic dispersion (there may be large differences in phylogenetic membership between vegetation types). However, such spatial structuring cannot explain why species' mean evolutionary distinctiveness is also higher.

Phylogenetic over-dispersion has often been associated with the process of competitive exclusion at small spatial scales i.e. within ecological communities (Webb et al. 2002). However, at broader regional scales, patterns of phylogenetic dispersion and evolutionary distinctiveness together are more likely to reflect historical biogeography (Davies and Buckley 2011). Here, I suggest species within refugia might have few close relatives either because their relatives were lost during previous cycles of glacial expansion, and failed to recolonize following glacial retreat, or because they represent isolated populations of previously widespread species that diversified elsewhere. Present day high elevation habitats may therefore provide a modern refuge to these glacial relicts, perhaps remnants of once more diverse cold adapted clades (Shooner et al. 2018), in today's warmer climate (Weber et al. 2014). This filtering of glacial relicts disrupts

the expected patterns of phylogenetic clustering commonly predicted in strongly filtered communities at high elevations, and contributes to the regional evolutionary distinctiveness in glacial refugia (Fryxell 1962, Brooks and Bandoni 1988, Shooner et al., 2018).

Previous work has suggested that invading tropical plant lineages contribute disproportionally to the phylogenetic diversity in northern regions. For example, in an analysis of vascular plant genera, Costion et al. (2015) suggest that forest refugia tend to capture less phylogenetic diversity than non-refugia, likely because recolonizing species in non-refugial areas represent distantly related species, perhaps with different biogeographic origins. However, it is also possible that refugia may capture greater evolutionary diversity as a result of lineages persisting within stable refugia habitats, and the preferential retention of relictual lineages in some habitats (Sundaram et al. 2019). Our results indicate that the persistence of relictual lineages within glacial refugia can contribute greater phylogenetic diversity to regional assemblages than the migration of expanding tropical lineages (Harrison and Noss 2017).

2.4.4 Evolutionary distinctiveness as a predictor for disjunct distribution

Supporting our hypotheses that glacial history shapes both the phylogenetic structure and range distribution of species, I show that evolutionary distinctiveness is a strong predictor of range disjunction, and this is highly robust to alternative classifications of range distributions. Glacial relicts are more likely to have both few close relatives and disjunct distributions. The loss of closely related species may occur if traits associated with higher extinction probability (during the last glacial maxima) are phylogenetically conserved (see Cardillo et al. 2005). Relict species might thus possess unique traits that allowed them to persist through glacial-interglacial cycles (Tang et al. 2018), or they may simply represent fortunate survivors. Furthermore, conservatism

in habitat preferences among species that persisted within glacial refugia might further reinforce the range disjunction of these relict species due to the isolated distribution of these habitat types in the present day (Lv et al. 2018).

2.4.5 Conservation value of refugial habitats

The biodiversity of Haida Gwaii comprises three intertwined features: ecosystem diversity, species diversity, and genetic diversity. Maintaining genetic diversity within species is essential for sustaining healthy populations (Hughes et al. 2008). Similarly, maintaining the phylogenetic diversity of species within ecosystems contributes to sustaining ecosystem processes and integrity (Cadotte et al. 2008). Phylogenetic diversity is also a measure of evolutionary heritage with intrinsic value (Mooers et al. 2005, Faith 2015), and evolutionary distinctiveness is important when prioritizing habitats for conservation (Costion et al. 2015). On Haida Gwaii, I have shown that high elevation sites likely represent glacial refugia, and support relictual species with high evolutionary distinctiveness. These habitats therefore have high conservation value even though they may not be as species rich as other habitat types. In contrast, epiphytic habitats have high species richness, but the phylogenetic clustering of species within them captures relatively little evolutionary history. The conservation of refugial habitat, especially high elevation habitats, is increasingly important with current warming trends placing additional stress on cold-adapted species, including many northern hemisphere bryophytes (Wu et al. 2018).

3. Conclusion

By examining the imprint of range contraction and expansion during glacial cycles from a community-wide species perspective (see also Mastrogianni et al. 2019), I suggest an alternative but complementary approach to traditional population genetics and paleobiological studies, which I hope can contribute to providing a richer picture of recent biogeographic history. I examined the signature of glacial refugia using a species-level phylogenetic tree of the mosses on Haida Gwaii. I found that many species have widely interrupted global range distributions, and these species typically have few close relatives within the Haida Gwaii species assemblage. These features likely reflect the imprint of glacial history, where evolutionarily distinct species have persisted in isolated refugia. My study provides an alternative to traditional approaches that have focused on the genetic structure of populations within species (see Roberts & Hamman, 2015). The imprint of range contraction and expansion during glacial cycles can be detected both at the species level, as I show here, and at the population level (Hewitt 1999). However, the patterns of evolutionary divergence that emerge at the population level and those that emerge at the species level are distinct. Population genetics allows us to reconstruct the biogeographic pathways of post glacial recolonization, identify likely refugial populations, and is useful for targeting particular species at risk. Whereas our multi-species phylogenetic approach provides a community wide perspective, and allows us to identify habitats or areas with evolutionarily distinct species and phylogenetically diverse species assemblages. I suggest the two approaches are complementary, and when used together can provide a richer picture of recent biogeographic history.

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Appendices

Supplementary Material:

Taxon	Accession number	BOLD Process ID
Amblystegium serpens	B241814	HAIDA098-20
Amphidium lapponicum	B241764	HAIDA051-20
Amphidium mougeotii	B236145	HAIDA101-20
Andreaea rupestris	B241796	HAIDA080-20
Anomobryum concinnatum	B241788	HAIDA072-20
Antitrichia curtipendula	B241749	HAIDA037-20
Aulocomnium androgynum	B241741	HAIDA029-20
Aulocomnium palustre	B241744	HAIDA032-20
Bartramia pomiformis	B241776	HAIDA060-20
Blindia acuta	B241760	HAIDA047-20
Brachythecium albicans	B241742	HAIDA030-20
Brachythecium frigidum	B241725	HAIDA014-20
Brachythecium leibergii	B231500	HAIDA102-20
Brachythecium plumosum	B241777	HAIDA061-20
Brachythecium velutinum	B231515	HAIDA103-20
Brotherella canadensis	B237536	HAIDA104-20
Bryoerythrophyllum recurvirostrum	B241815	HAIDA099-20
Bryolawtonia vancouveriensis	B241778	HAIDA062-20
Bryum capillare	B241758	HAIDA045-20
Bryum miniatum	B236012	HAIDA105-20
Bryum pseudotriquetrum	B241791	HAIDA075-20
Calliergon cordifolium	B225775	HAIDA106-20
Calliergon giganteum	B231938	HAIDA107-20
Campylium stellatum	B241806	HAIDA090-20
Campylopus atrovirens	B241785	HAIDA069-20
Campylopus fragilis	B216485	HAIDA108-20
Claopodium whippleanum	B181999	HAIDA109-20
Codriophorus aciculare	B241800	HAIDA084-20
Codriophorus varium	B241757	HAIDA044-20
Cratoneuron filicinum	B241730	HAIDA019-20
Crumia latifolia	B218120	HAIDA110-20
Ctenidium schofieldii	B215512	HAIDA111-20
Dicranella pacifica	B240761	HAIDA112-20

Dicranella rufescens	B241805	HAIDA089-20
Dicranoweisia crispula	B241808	HAIDA092-20
Dicranum elongatum	B229609	HAIDA113-20
Dicranum fuscescens	B225401	HAIDA114-20
Dicranum groenlandicum	B212166	HAIDA115-20
Dicranum howellii	B241736	HAIDA024-20
Dicranum pallidisetum	B213059	HAIDA116-20
Dicranum scoparium	B241817	HAIDA088-20
Dicranum spadiceum	B238797	HAIDA117-20
Dicranum tauricum	B218811	HAIDA118-20
Dicranum undulatum	B241745	HAIDA033-20
Didymodon ferrugineus	B241727	HAIDA016-20
Didymodon tophaceus	B240759	HAIDA119-20
Didymodon vinealis	B241763	HAIDA050-20
Distichium capillaceum	B241787	HAIDA071-20
Ditrichum ambiguum	B241756	HAIDA043-20
Ditrichum gracile	B241789	HAIDA073-20
Ditrichum heteromallum	B241803	HAIDA086-20
Dryptodon patens	B241797	HAIDA081-20
Eurhynchium pulchellum	B218775	HAIDA120-20
Fissidens bryoides	B241775	HAIDA059-20
Fontinalis antipyretica	B241790	HAIDA074-20
Fontinalis neomexicana	B241781	HAIDA065-20
Grimmia torquata	B211665	HAIDA121-20
Grimmia trichophylla	B241734	HAIDA022-20
Gymnostomum aeruginosum	B241773	HAIDA058-20
Hamatocaulis vernicosus	B231808	HAIDA122-20
Herzogiella adscendens	B241750	HAIDA038-20
Herzogiella striatella	B218056	HAIDA123-20
Heterocladium dimorphum	B227585	HAIDA124-20
Heterocladium procurrens	B214582	HAIDA125-20
Homalothecium aeneum	B231082	HAIDA126-20
Homalothecium nuttallii	B215523	HAIDA127-20
Hookeria lucens	B241747	HAIDA035-20
Hygrohypnum bestii	B241724	HAIDA013-20
Hygrohypnum luridum	B203965	HAIDA128-20
Hygrohypnum molle	B229601	HAIDA132-20
Hygrohypnum ochraceum	B241720	HAIDA009-20
Hygrohypnum smithii	B241810	HAIDA094-20
Hylocomiastrum umbratum	B238089	HAIDA129-20

Hypnum circinale	B241732	HAIDA020-20
Hypnum dieckii	B241761	HAIDA048-20
Hypnum revolutum	B228198	HAIDA130-20
Hypnum vaucheri	B218773	HAIDA131-20
Isopterygiopsis pulchella	B241759	HAIDA046-20
Isothecium cardotii	B241735	HAIDA023-20
Isothecium stoloniferum	B241728	HAIDA017-20
Kiaeria blyttii	B241795	HAIDA079-20
Kiaeria starkei	B214631	HAIDA133-20
Kindbergia oregana	B241737	HAIDA025-20
Leptodictyum riparium	B231935	HAIDA134-20
Leucolepis acanthoneuron	B241712	HAIDA002-20
Loeskypnum badium	B228493	HAIDA135-20
Metaneckera menziesii	B237022	HAIDA136-20
Mnium blyttii	B240760	HAIDA137-20
Mnium lycopodioides	B173172	HAIDA138-20
Mnium marginatum	B241816	HAIDA100-20
Mnium spinulosum	B231121	HAIDA139-20
Mnium thomsonii	B241772	HAIDA057-20
Myurella julacea	B237577	HAIDA140-20
Neckera douglasii	B241783	HAIDA067-20
Niphotrichum elongatum	B241766	HAIDA053-20
Niphotrichum ericoides	B241754	HAIDA041-20
Niphotrichum muticum	B228837	HAIDA141-20
Oligotrichum aligerum	B241804	HAIDA087-20
Oncophorus virens	B210571	HAIDA142-20
Oncophorus wahlenbergii	B241752	HAIDA039-20
Orthotrichum Iyellii	B241740	HAIDA028-20
Orthotrichum pulchellum	B241802	HAIDA085-20
Palustriella falcata	B241807	HAIDA091-20
Paraleucobryum enerve	B241793	HAIDA077-20
Philonotis capillaris	B241762	HAIDA049-20
Philonotis fontana	B241809	HAIDA093-20
Plagiomnium insignii	B241746	HAIDA034-20
Plagiomnium venustum	B237042	HAIDA144-20
Plagiopus oederianus	B213345	HAIDA145-20
Plagiothecium denticulatum	B241714	HAIDA004-20
Plagiomnium insigne	B241713	HAIDA003-20
Platydictya jungermannioides	B231753	HAIDA146-20
Pleurozium schreberi	B241782	HAIDA066-20

Pogonatum contortum	B241792	HAIDA076-20
Pogonatum urnigerum	B241755	HAIDA042-20
Pohlia longibracteata	B189444	HAIDA143-20
Pohlia nutans	B241719	HAIDA008-20
Pohlia pacifica	B240763	HAIDA010-20
Polytrichastrum alpinum	B241726	HAIDA015-20
Polytrichum commune	B241743	HAIDA031-20
Polytrichum sexangulare	B217119	HAIDA147-20
Porotrichum bigelovii	B241779	HAIDA063-20
Pseudoleskea atricha	B231051	HAIDA148-20
Pseudoleskea baileyi	B228681	HAIDA149-20
Pseudoleskea patens	B239242	HAIDA150-20
Pseudoleskea stenophylla	B236173	HAIDA151-20
Ptychostomum bimum	B241768	HAIDA055-20
Racomitrium affine	B241733	HAIDA021-20
Racomitrium fasciculare	B241794	HAIDA078-20
Racomitrium heterostichum	B241769	HAIDA056-20
Racomitrium lanuginosum	B241784	HAIDA068-20
Racomitrium lawtoniae	B241721	HAIDA011-20
Racomitrium macounii	B241799	HAIDA083-20
Racomitrium occidentalis	B241812	HAIDA096-20
Racomitrium ryszardii	B241717	HAIDA007-20
Racomitrium sudeticum	B241798	HAIDA082-20
Rhabdoweisia crispata	B239007	HAIDA152-20
Rhizomnium glabrescens	B241715	HAIDA005-20
Rhizomnium magnifolium	B236745	HAIDA153-20
Rhizomnium pseudopunctatum	B238604	HAIDA154-20
Rhytidiadelphus loreus	B241738	HAIDA026-20
Rhytidiadelphus triquetrus	B241739	HAIDA027-20
Sanionia symmetrica	B213086	HAIDA155-20
Sarmentypnum exannulatum	B241767	HAIDA054-20
Schistidium rivulare	B241723	HAIDA012-20
Scleropodium cespitans	B238710	HAIDA156-20
Scleropodium obtusifolium	B241765	HAIDA052-20
Scorpidium revolvens	B228601	HAIDA157-20
Scouleria aquatica	B241780	HAIDA064-20
Sphagnum fimbriatum	B186847	HAIDA158-20
Sphagnum lindbergii	B228894	HAIDA159-20
Sphagnum mendocinum	B237691	HAIDA160-20
Sphagnum pacificum	B218803	HAIDA161-20

Sphagnum russowii	B236118	HAIDA162-20
Sphagnum tenellum	B238870	HAIDA163-20
Splachnum sphaericum	B241811	HAIDA095-20
Syntrichia norvegica	B227500	HAIDA164-20
Syntrichia princeps	B213043	HAIDA165-20
Syntrichia ruralis	B241753	HAIDA040-20
Tayloria serrata	B228303	HAIDA166-20
Tetraphis pellucida	B241716	HAIDA006-20
Thamnobryum neckeroides	B240762	HAIDA167-20
Tortella fragilis	B241813	HAIDA097-20
Tortula muralis	B213353	HAIDA168-20
Ulota megalospora	B236741	HAIDA169-20
Ulota obtusiuscula	B241729	HAIDA018-20
Ulota phyllantha	B241748	HAIDA036-20
Warnstorfia fluitans	B236740	HAIDA170-20
Wijkia carlottae	B218808	HAIDA171-20
Zygodon viridissimus	B241786	HAIDA070-20

Table S1 - Sequences submitted to Barcode of Life Database (BOLD). University of

British Columbia Herbarium accession numbers and BOLD Process ID for specimens used

for *rbcL* and *trnL-F* barcode sequencing.

	Continuous	Disjunct	Localized
Continuous	NA		
Disjunct	0.02	NA	
Localized	0.70	0.02	NA

Table S2 – **Pairwise comparison of Phylogenetic ANOVA.** Mean corrected pairwise P-values from the phylogenetic ANOVA of species evolutionary distinctiveness on species distributions (continuous, disjunct, and localized). Analyses were performed across a distribution of phylogenies randomly dropping all but one taxa from polytomies to return fully resolved trees. This procedure was simulated 1000 times. The overall phylogenetic ANOVA model was significant (P < 0.05), in 871 out of 1000 simulations, with an average P = 0.03, and F = 5.08.



Figure S1 – **Phylogenetic generalized linear model.** Phylogenetic binomial regression of species distribution (0-continuous and 1-disjunct) against evolutionary distinctiveness. The green line represents the fitted values while observed values are shown with open symbols in black. Regression model: $\infty = 0.003$, p < 0.05.