Cryptogam community structure and functioning along an elevational gradient

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PREFACE

Thesis Format

This thesis has been collated in manuscript format as permitted by McGill University submission regulations. The titles of both chapters, or manuscripts, are listed below:

1. Disentangling the components of cryptogam beta diversity along an elevational gradient.
2. Diversity affects productivity along an elevational gradient in a subarctic bryophyte community.

Chapter 1 is being written up for submission to the Journal of Ecology. Chapter 2 is in preparation for submission to Proceedings of the Royal Society B, and will be complete once functional diversity measures are included in the analysis. The General Introduction to this thesis provides the background to this research, and the progression from my first to second chapter is documented in the Connecting Statement. The General Conclusions section provides a synopsis of my overall findings. Literature cited for these three general sections is found at the end of the thesis. Literature specific to Chapter 1 or 2 is to be found at the end of each, respectively.

CONTRIBUTION OF AUTHORS

This thesis is the culmination of my own independent research directed under the supervision of Dr. Jonathan Davies in the Department of Biology at McGill University. Dr. Davies provided guidance for the development of this research, as well as with the analysis and preparation of these manuscripts. He is included as a co-author for both. For Chapter 1 and 2, I carried out all field data collection, laboratory work, statistical analysis and manuscript preparation.

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This thesis is the culmination of two years of work, and would not be possible without the help of my supervisor Dr. Jonathan Davies. He has done so much work to bring this thesis to its final form and throughout has provided me with an incredible amount of patience and guidance. He has been a great role model and I hope to one day become as excellent of a mentor as he is.

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Thank you to my friends and family for their support. Dad and Mom, you never failed to remind me that I live in a fantasy world and that I cannot and should not complain about being paid to study the research I love. Thank you to my partner-in-crime, Michael, for dragging me back from the Middle East to get back into biology. You have been incredibly supportive and I wouldn’t have gone anywhere without you. And finally, thanks to my wonderful roommates. I know we all have crazy schedules and don’t see each other often (really my fault), but you guys are wonderful. I will always appreciate our early morning discussions on politics and feminism.

Funding for this research was provided by NSERC Discovery, funded to Dr. Jonathan Davies. Funding was also contributed from the Quebec Center for Biodiversity Excellence Award for our undergraduate field assistant and for presentation of this work at two conferences, as well as my own personal funding through the Sir Lougheed Award of Distinction from the Government of Alberta.

ABSTRACT

Biodiversity studies have recently focused on incorporating measures of phylogenetic and functional diversity into examinations of community ecology. Functional diversity describes those traits that influence the interaction between a species and the environment, whereas phylogenetic diversity is a more derived measure that represents the evolutionary history of species, and might incorporate information on functional identity, taking into account multiple traits. This thesis examined patterns in cryptogam (bryophyte and lichen) diversity across an elevation gradient to (i) evaluate the interplay between species, phylogenetic, and functional lichen diversity within and between habitats and (ii) link diversity (species and phylogenetic) to bryophyte productivity across environmental gradients. We found that phylogenetic and functional turnover correlate strongly, despite low signal in measured traits. Within and between habitats, different beta diversity indices are driven by different environmental factors, and as such one metric cannot be used as a surrogate for another. By establishing a link between diversity and productivity within bryophytes, we highlight the importance of diversity in regulating biomass production within stressful environments. We also highlight the use of alternative phylogenetic measures as descriptors of the diversity-productivity relationship, as they provide more information on the underlying mechanisms that drive the relationship. Cryptogams are relatively understudied in comparison to their vascular counterparts, and as such the information from this study will provide valuable insights into their community structure and turnover across space.

RÉSUMÉ

Les études sur la biodiversité ont récemment mis l'accent sur l'intégration des mesures de diversité phylogénétique et fonctionnelle dans les examens de l'écologie des communautés. La diversité fonctionnelle décrit les traits influençant l'interaction entre une espèce et l'environnement, alors que la diversité phylogénétique est une mesure dérivée représentant l’histoire de l’évolution d’une espèce et peut inclure des renseignements sur l'identité fonctionnelle d'une espèce. J'ai étudié les modèles de diversité des cryptogames (bryophytes et lichens) à travers un gradient d'altitude afin (i) d’examiner les interactions entre la diversité des espèces, la diversité phylogénétique et la diversité fonctionnelle des lichen au sein des habitats et entre eux, et (ii) de relier la diversité (des espèces et phylogénétique) à la productivité des bryophytes à travers les gradients environnementaux. Nous avons constaté que les changements de la composition phylogénétique et fonctionnelle sont fortement corrélés, malgré le faible signal dans les traits mesurés. Puisque les différents indices de diversité bêta sont entrainés par différents facteurs environnementaux au sein des habitats et entre eux, une unité de mesure ne peut être utilisée comme substitut à une autre. En établissant un lien entre la diversité et la productivité au sein des bryophytes, nous soulignons l'importance de la diversité dans la règlementation de la production de biomasse au sein d’environnements stressants. Nous appuyons également l'utilisation de mesures phylogénétiques alternatives comme descripteurs de la relation diversité-productivité, car celles-ci apportent plus d'information sur les mécanismes entrainant cette relation. Puisque les cryptogames sont relativement peu étudiés, cette étude fournit des indications précieuses sur la structure de leur communauté et leur changement de composition à travers l'espace.

GENERAL INTRODUCTION

The importance of phylogeny in elevational studies

Patterns of biotic and abiotic turnover along elevational gradients on mountain slopes are central to biogeographic theory and key to our understanding of the effects of the environment on organisms and their associated feedbacks (Stevens 1992, Brown 2001, Lomolino 2001, McCain 2005, Korner 2007). Studies along such gradients have documented how changes in environment can cause shifts in community structure over space, but there exists considerable gaps in understanding the underlying mechanisms driving these changes and how these effect different guilds of organisms in parallel (Bryant et al. 2011). Another major gap surrounds the question of scale, and how evolutionary factors that structure diversity gradients at regional scales are connected to those biotic processes acting on more local scales (Cavender-Bares et al. 2004a, Graham & Fine 2008).

Phylogenetics has recently been developed as a tool for examining community assembly in an evolutionary framework (Webb et al. 2002, Cavender-Bares et al. 2009). Because more closely related species tend to be ecologically more similar, the phylogenetic structure of communities can therefore capture information on their functional and ecological diversity (Prinzing et al. 2001, Cadotte et al. 2008). The use of phylogenetic information in studies of the evolutionary relationships between co-occurring species allows us to link local patterns to regional and global level processes (Graham & Fine 2008, Cavender-Bares et al. 2009). Community phylogenetics attempts to bridge the gap between ecology and evolution to determine how they interact to influence distribution of diversity in the form of species and traits (Webb et al. 2002). Through comparisons of the phylogenetic structure of communities, two alternative processes dictating the rules of community assembly have been proposed. The first is based upon competitive interaction, in which species that are more closely related (and thereby predicted to occupy similar niches within an environment) outcompete each other, forming communities with species evenly dispersed along the tips of the phylogeny. The second is based upon environmental filtering, in which species with similar traits are filtered into a community. These communities exhibit a clustered phylogenetic distribution, with species generally more closely related. These differences in phylogenetic structure are important, as they point to the major processes structuring communities and can provide indications of whether the environment or biotic factors are most important across spatial scales (Graham & Fine 2008).

The use of beta diversity measures in examining community turnover across gradients

Beta diversity, a measure of community turnover, has historically been interpreted as changes in species composition across space, allowing for the examination of community change along environmental gradients (Whittaker 1960,1972). Although most studies documenting this relationship have focused on taxonomic diversity metrics (Morlon et al. 2011), functional beta diversity measures have been developed in order to directly examine turnover in measured traits along a gradient (e.g. Siefert et al. 2013, Swenson et al. 2012). Phylogenetic beta diversity has recently been developed as a proxy for functional measures, as patterns that incorporate phylogenetic information will most likely provide more information on functional shifts in community structure than taxonomic diversity (Jabot & Chave 2009). Phylogenetic beta diversity measures change in phylogenetic relatedness across space (Graham & Fine 2008). As such it provides an opportunity to describe the relevant processes structuring the distribution of species and their associated traits by examining this turnover with relation to environmental gradients and spatial distance (Chave et al. 2007, Ferrier et al. 2007, Bryant et al. 2008, Graham & Fine 2008, Sander & Wardell-Johnson 2011).

Phylogenetics and ecosystem functioning

Phylogenetics has recently been proposed as a powerful metric to assess the effect of diversity on productivity (Cadotte et al. 2008, Cadotte et al. 2009). This research has focused on the return to classical experiments involving the manipulation of diversity in biomass estimates, but the importance of phylogeny to biomass production has yet to be assessed in a natural system (but see Paquette and Messier 2011). Additionally, experimental manipulations generally do not take into account the potential for changes in the strength of the diversity-productivity relationship across resource gradients, and thus might overlook facilitative interactions and their role in shaping community structure (Bruno et al. 2003, Freestone et al. 2006). For example, Callaway et al. (2002) showed that at lower elevations plant communities were dominated by competitive interactions, but at higher elevations, where abiotic stress was high, plant species interactions were more often positive. In fact, they found that globally, with increasing abiotic stress (higher elevation), there was a general shift from competition to facilitation. A theme in this research will be to attempt to document the importance of aspects of diversity along gradients in natural communities and provide information on the evolutionary processes that dictate it.

Lichen and bryophyte focal clades

Cryptogams (non-vascular plants) are important components of ecosystem functioning in polar biomes (Longton 1997) and essential contributors to biogeochemical cycling in the environment. They provide a direct link between the abiotic and biotic realms, and yet they have often been passed over in favor of research in vascular plants. Both lichen and bryophyte groups contribute to above-ground biomass, play host to nitrogen-fixing bacteria which in turn provide nitrogen input to soil, provide hydrological and temperature buffers over soil and vegetation, prevent erosion along steep slopes, provide food for caribou (lichens) and arthropods and provide a home for microarthropods (Cornelissen et al. 2007). They interact with vascular plants through facilitation of seedling establishment (Freestone 2006) or negatively act to prevent generation in closed areas (Zamfir 2000). Thus, these groups have an important effect on the abiotic environment and can act to determine vegetation success (Sedia & Ehrington 2003, Soudlizovskaia et al. 2011).

Cryptogams are considered to be particularly vulnerable to predicted global environmental change (Bates & Farmer 1992, Callaghan et al. 2004). Lichen and bryophytes groups may be sensitive to vascular plant range expansion pole-ward with projected climate change (Hobbie et al. 1999, Cornelissen et al. 2001, Van Wijk et al. 2004, Wookey et al. 2009). Temperature increases are predicted to elevate soil nitrogen and phosphorus availability through enhanced soil nutrient mineralization and anthropogenic-induced atmospheric deposition, causing differential effects on lichen and bryophytes species depending on their functional or species group (Cornelissen et al. 2007). By modeling shifts in cryptogram community structure and diversity under climate change, it may be possible to predict large-scale changes in ecosystem dynamics, including cycling in nutrients, carbon and hydrology (Chapin et al. 2000, Beringer et al. 2001, Cornelissen et al. 2007).

Mount Irony, Labrador

The proposed study site for this research is situated on the border of Western Labrador, Canada, at 54.901° N 67.147° W. The location of this project is unique in that it describes the transition between boreal forest and alpine tundra in subarctic Quebec, providing a glimpse into the northern edge of boreal species and how they interact with abiotic conditions to turnover in space. The site lies on an elevational gradient on the southwestern slope of Mount Irony, one of the few mountains in the area, with a height of 888 m above sea level. Here we set up a long-term study of 88 plots along a slope spanning 200 m in vertical elevation, with horizontal distances equaling 100 m between plots. This spacing provides more distance separating plots within elevations than between so that the estimates of community change over elevation will be conservative with respect to spatial distance. The southwestern slope was chosen as its light exposure over the course of the year was higher than the northern slope, and in addition to being more sheltered from harsher elements this side allowed for a more consistent gradient between cryptogams and vascular plants from low to high elevations. Hobo data loggers for tracking average soil temperature were buried at a depth between 5-10 cm in the northern corner of each plot and logged measurements every hour for the course of the year. Two lines of data loggers to track air temperature and humidity were also installed along elevational midpoints on either side of the southwestern slope to track hourly changes in ambient air conditions. Cryptogam sampling involved obtaining percent cover of both lichen and bryophyte species from within 0.25 m^2 circular plots, designed to reduce environmental heterogeneity within plot.

Research Objectives

We use phylogenetics, the study of evolutionary relationships in co-occurring species, to characterize plant communities and their spatial turnover in the subarctic of Canada. Specifically, this thesis examines measures of phylogenetic turnover of non-vascular plant species with spatial change along an elevational gradient on Mount Irony, Labrador, and how this measure is decoupled from that of other more traditional diversity metrics (taxonomic and functional). We will also link phylogenetic measures to productivity across an elevational gradient in order to assess the usefulness of this metric in predicting ecosystem functioning. We hope to advance our understanding of the evolutionary history of lichen and bryophyte groups as a novel contribution to phylogenetic research, and evaluate how these understudied taxa interact with the surrounding biota to structure subarctic communities.

Chapter Synopsis

Chapter 1 focuses on lichen species and examines taxonomic, phylogenetic and functional diversity and their respective turnover across an elevational gradient. Here we sought to characterize the relationship between these three diversity measures across two spatial scales (within and between two major habitat classes, forest and alpine). Percent cover of lichens across 88 plots was collected during June and July 2011/2012. Tissue samples from each species were collected for sequencing and used to construct a representative regional phylogeny. Trait measurements of all species occurred during June 2012 and were used to construct a functional cladogram. Environmental variables (ground temperature, canopy, vascular presence) were related to beta diversity measures in order to examine the drivers of change across this gradient. From this data we were able to assess the correspondence of phylogenetic and functional information, and gain further insight into the drivers of community change within two habitats.

Chapter 2 uses a similar phylogenetic approach and applies it to an assessment of the diversity-productivity relationship across an environmental gradient in a natural system. In this chapter we focus solely on bryophyte species and use phylogenetic diversity and taxonomic diversity to assess the importance of these measures to mean plot-level biomass, both as single predictors, as well as members of a multi-variable prediction with elevation included as a proxy for environmental effects. In addition, we take a focal species approach to determine the effect of species richness, phylogenetic diversity, and a focal measure of phylogenetic distance to the biomass of the abundant feathermoss, *Pleurozium schreberi*. Here we use a novel distance-based phylogenetic function to assess the effects of niche complementarity on this dominant species across our study site.

Chapter 1

Disentangling the components of cryptogam beta diversity along an elevational gradient

Chelsea L. Chisholm and T. Jonathan Davies

ABSTRACT

The use of beta diversity in community ecology has allowed for an examination of the processes dictating community composition and structure across space. Phylogenetic and functional diversity have been used as complimentary measures to assess the relative importance of environmental filtering and competition for community assembly in this regard. In this study we use these approaches to compare the taxonomic, phylogenetic and functional diversity of lichens (non-vascular plants) along an elevational gradient in subarctic Canada. We examine the correspondence of these metrics within and between habitats, and with respect to space and various environmental predictors. Lichen show strong correlations between phylogenetic and functional beta diversity, suggesting that phylogeny is capturing turnover in traits across space. Both of these measures correlate with taxonomic beta diversity, but the relationship is relatively weak. Phylogeny appears to correspond better to functional diversity in the form of multiple traits, and poorly with regard to single trait diversity measures. Importantly, we find that there are different environmental drivers of turnover metrics both within and between habitats, and as such one measure cannot be considered as a surrogate for another.

INTRODUCTION

The use of beta diversity in community ecology has allowed for the examination of processes dictating community composition and structure across space (e.g. Condit et al. 2002, Bryant et al. 2008, Kraft et al. 2008, Chase 2010, Vellend 2010, Kraft et al. 2011, Stegen & Hurlbert 2011, Myers et al. 2013). Although the definition of beta diversity has recently been debated (e.g. see Anderson et al. 2011), studies have commonly used it in the sense of examining patterns of diversity, or turnover, along environmental gradients and at different scales (Brown 1984, Rahbek 1995, Cayley & Schluter 1997). Recent work has highlighted the limited information conveyed by taxonomic diversity alone and expanded beta diversity to include phylogenetic and functional components of species assemblages (Cadotte et al. 2009, Swenson 2011a, Swenson 2011b, Stegen & Hurlbert 2011, Swenson et al. 2012).

Direct measures of functional traits have been used in the quantification of functional beta diversity (McGill et al. 2006), allowing the examination of trait conservatism across space (Petchey & Gaston 2006). Phylogenetic beta diversity quantifies the amount of shared phylogenetic history between communities (Bryant et al. 2008, Graham & Fine 2008), and is thought to provide a more integrated measure of functional diversity. These alternative beta diversity indices can provide more information on the relevant processes structuring the distribution of species than simple metrics of taxonomic diversity by allowing examination of functional or phylogenetic turnover in relation to environmental gradients and spatial distance (Bryant et al. 2008, Graham & Fine 2008, Kraft & Ackerly 2010, Sander & Wardell-Johnson 2011). However there exist considerable gaps in our understanding of how these diversity measures relate to each other and to the environment (Swenson et al. 2012), and how these patterns change with spatial scale (Lessard et al. 2012).

Patterns of community assembly have been found to be highly scale-dependent (Swenson et al. 2006, Cavender-bares et al. 2006, Kraft et al. 2007, Vamosi et al. 2009, Kraft & Ackerly 2010). Recent studies by Kraft et al. (2011) and Myers et al. (2013) have attempted to tackle the problem of scale in beta diversity indices, and have shown that observed beta diversity is often influenced by the defined species pool. Differences in observations due to sampling among species pools can be accounted for by employing a null model approach to determine a standardized effect size of beta diversity (β-deviation). Myers et al. (2013) noted that while similar patterns in β-deviation could be driven by different processes, such as environmental filtering or dispersal limitation, these processes might be disentangled by exploring beta diversity at different scales. We propose the use of a similar approach, incorporating the various components of beta diversity, to evaluate environmental filtering by comparing communities within and between habitats, assuming regional and local habitat species pool definitions based upon environmental definitions of scale. To date, only a few studies have attempted to examine phylogenetic or functional turnover with respect to scale (e.g. Kembel & Hubbell 2006, Fine & Kembel 2011, Hardy et al. 2012), with even fewer evaluating parallel changes in the various components of beta diversity (e.g. Devictor et al. 2010).

Here we examine the taxonomic, phylogenetic, and functional turnover of lichen communities along an elevational gradient on Mount Irony, Labrador, Canada. Cryptograms, or non-vascular plants, are important components of ecosystem functioning and essential contributors to biogeochemical cycling in the arctic biome (Longton et al. 1997). They provide a direct link between the abiotic and biotic realms through their effects on the evapotranspiration rate of soils, thermal and hydrological buffering and seedling establishment (Cornelissen et al. 2007), yet they have often been passed over in favor of research in vascular plants. The use of elevational gradients in this respect provides an ideal system in which to examine shifts of lichen community structure with external factors, both abiotic (e.g. temperature, humidity) and biotic (e.g. vascular abundance, canopy cover). Cryptogams are considered to be particularly vulnerable to global climate change (Bates & Farmer 1992, Callaghan et al. 2004), with predicted sensitivity to vascular plant range expansion pole ward (Hobbie et al. 1999, Cornelissen et al. 2001, Van Wijk et al. 2004, Wookey et al. 2009). Through a better understanding of how the distribution of cryptogams relates to the environment and the projected impacts of climate change on their biodiversity, we may be able to more accurately predict large-scale changes to biotic communities and abiotic environmental cycling in nutrients, carbon and hydrology due to shifts in cryptogram community structure and abundance (Chapin et al. 2000, Callaghan et al. 2004, Cornelissen et al. 2007).

We examine the turnover of lichen communities with respect to elevation, space and various environmental predictors. Using beta diversity metrics of taxonomic, phylogenetic and functional community composition we (i) quantify the relationship between different components of beta diversity, (ii) examine turnover in community composition within and between habitats (low elevation forest versus high elevation tundra), and (iii) relate community dissimilarity to environmental gradients. Overall, the three measures of biodiversity are expected to be somewhat auto correlated, such that dissimilarity in taxonomic membership between communities will be reflected in a parallel turnover in functional and phylogenetic diversity. However, we predict differences in the magnitude of turnover, depending upon the factors shaping community composition and the evolutionary structure of relevant traits.

If most traits are evolutionarily conserved, we expect that phylogenetic beta diversity will be more strongly correlated with functional beta diversity than taxonomic beta diversity. Further, because species within habitats may have already passed through an abiotic filter, the correlation between functional and phylogenetic turnover is predicted to be stronger between versus within habitats. However, if there is large microsite variation, it is possible that a strong relationship between phylogenetic and functional beta diversity will remain even within habitats. In addition, if functional information is evolutionarily conserved, both phylogenetic and functional beta diversity should be driven by similar environmental factors. But at within-habitat scales, the effect of environment may be removed (or lessened) and the factors important in driving turnover might vary based upon the relative strength of assembly processes associated with that habitat (e.g. competition versus environmental filtering). We expect that within a competitively structured environment, phylogenetic and functional turnover will show a weaker relationship with environmental drivers, and a stronger relationship when environmental filtering is important.

METHODS

Study Site

Field sampling was conducted in the summer of 2011 and 2012 along an elevational gradient on the southwestern slope of Mount Irony, bordering Quebec and Western Labrador, Canada (54.901 N 67.147 W). The study site represents a transition zone between boreal forest and subarctic alpine tundra, with dominant spruce-moss or spruce-lichen woodland in lowland areas shifting to alpine tundra at higher elevation.

Data Collection

Transects were set out along eight elevation bands and sampled using 0.25m^2 plots at 100 meter intervals (n= 88). A plot size of 0.25 m^2 was chosen to best capture the local diversity of cryptogams while reducing within plot environmental heterogeneity. Hobo data loggers for soil temperature were buried under 5-10 cm of soil at the northern edge of each plot and temperatures were tracked over a one year period preceding collection of community composition data. Presence/absence and percent cover of cryptogam species were estimated visually at each plot, with measures of elevation, slope, and aspect recorded using a GPS and clinometer. In addition, percent canopy cover and percent abundance of lower shrubs and vascular plant cover were estimated for each plot. Lichen species identification followed Brodo et al. (2001), and was confirmed directly by Irwin Brodo and through the use of DNA barcoding (see below).

Phylogeny Estimation

Tissue samples were collected from each identified species, and submitted to the Barcode of Life Datasystem (BOLD) for sequencing. Voucher specimens are deposited in the MacDonald Herbarium at McGill University and sequence-associated information is accessible on Genbank (see Appendix S1 for associated species information). A molecular phylogeny was constructed using *ITS* sequences for the fungal component of lichens. Sequences were aligned using MAFFT ver. 7 (Katoh 2013) and MacClade (Maddison and Maddison 2000). Phylogenetic tree estimation was conducted using the *phanghorn* (Schliep 2011) and *ape* (Paradis et al. 2004) packages in R. We constructed two phylogenies for lichen molecular data, using maximum likelihood (ML) and parsimony methods on the aligned data matrix and using a neighbor joining starting tree. For the ML analysis, the best-fit model of evolution (GTR+G+I) was determined using the function *modelTest* in the *phanghorn* package. Internal support was assessed using 100 bootstrap iterations. Bootstrap values were compared between trees to evaluate congruence across well-supported nodes (bootstrap values >75%). Using the AIC criterion for model searches and the function *pml* in *phanghorn*, the maximum likelihood tree was the best model fit for the sequence data. We use this tree topology for all subsequent analysis (the ML tree and associated bootstrap values is reported in Appendix S2).

Functional Trait Estimation

Traits that captured cryptogam functional diversity were chosen from Cornelissen et al. (2007), and relate to cryptogram life history (form and habitat association), competition (height, biomass [dry matter content]), and nutrient content (N and P tissue concentrations). Because lichens are colonial, we followed a standardized sampling protocol to ensure that each species sample constituted a sufficiently distinct set of homogenous individuals (following Waite & Sack 2010). Species sampling targeted terricolous macro-lichens, which produce a fruiting body for which trait data can be obtained. Common species were sampled in five plots randomly selected from across the study site, with a single core three cm in diameter collected from within 1 m^2 of each chosen plot. For some rare species sample size was limited by necessity to one or two specimens per species. Each core was incubated in the dark overnight in a towel saturated in 10 mL of distilled water and measured for wet weight, height and core area. Samples were subsequently oven dried for 48 hours at 60 degrees Celsius and re-weighed to obtain a measure of dry matter content (dry weight/wet weight x 100%). Last, core samples were ground for tissue nutrient analysis. Plant tissue was extracted using the micro-Kjeldahl method (Bremner & Mulvaney 1982) and relative N and P nutrient content was analyzed colorimetrically.

A functional dendrogram was estimated using methods from Petchey & Gaston (2002). For each trait in turn, a species-level measure was derived by averaging sample values. A dissimilarity matrix was generated using the combined set of species-level traits with the function *gowdis* in the package *FD* in R (Laliberté & Legendre 2010, Laliberté & Shipley 2011), which allows for both continuous and categorical data. This distance matrix was then transformed into a dendrogram to give a functional tree with branch lengths denoting trait similarity between species using hierarchical clustering. Single trait dendrograms were also produced using this method to compare environmental correlations between trait types.

Statistical Analysis

Taxonomic beta diversity was estimated using Bray-Curtis pairwise distances. Beta diversity indices for both phylogenetic and functional data were generated using three separate functions: *unifrac* (Lozupone 2005), *phylosor* (Bryant et al. 2008) and *PCD* (Ives 2010). Patterns generated by each function were not significantly different and for the purposes of this analysis we have chosen to report results using *unifrac*, which describes the unshared branch lengths between two communities and is most comparable to the Bray-Curtis distances generated for taxonomic diversity (for other results see Appendix S3).

To compare beta diversity between habitat types at different scales, we evaluated correlations based on Mantel tests (using Pearson's r) between beta diversity indices across all plots combined and then separately within major habitat classes. We grouped plots into three major classes: alpine, forest and 'other'. Alpine and forest represent the two dominant habitat types at the site, and differ obviously in community membership, functional types and abiotic environment, and we therefore focus on the contrast between them here. Beta diversity values within both alpine and forest were calculated separately and explored using Mantel tests. Due to differences in sample pool size between forest (n=14) and alpine (n=21), mean turnover could not be compared between sites. Therefore we developed a null model for each habitat, in which mean beta diversity values were generated from 1000 null communities by randomly sampling species membership within plots from a habitat species pool (constrained to those species able to establish within habitat), while maintaining per plot diversity and abundance. A standardized effect size ($SES=[[mean(\beta_{obs)}-mean(\beta_{null})]/SD(\beta_{null})]$) was calculated based on this distribution, with values >0 suggesting greater overall turnover than expected by random sampling, whilst values <0 indicate less turnover than expected by random sampling. Significant differences in SES beta diversity values between plots in both alpine and forest were evaluated using a one-sample t-test to evaluate significant differences from zero.

The phylogenetic and functional values of alpha diversity for plots within each habitat class were calculated using the net relatedness index (NRI) and nearest taxon index (NTI) from Webb et al. (2002). Both are standardized effect sizes of the observed mean pairwise phylogenetic distance between species (MPD) and the observed mean nearest phylogenetic neighbor distance (MNND) respectively. Thus NRI gives an estimate of the clustering or over-dispersion of a community, while NTI considers nearest neighbors, and is a better indicator of the fine scale structure of the community representing interactions between close relatives and functionally similar taxa. Identical functional NRI and NTI values were calculated for traits by substituting the trait dendrogram in place of the phylogenetic tree. Evidence for significant structure in per plot NRI and NTI values was evaluated using a one-sample t-test, with values >0 suggesting species present were clustering within clades, whilst values <0 indicate over-dispersion across the trait dendrogram/phylogeny.

Finally, we compared taxonomic, phylogenetic and functional beta diversity indices to Euclidian distance-based measures of spatial (distance, elevation) and environmental variables (soil temperature, canopy cover, vegetation cover) using Mantel tests. Additionally, we evaluated functional beta diversity for individual traits to examine more closely the effect of the external environment on the turnover of single traits.

All statistical analysis was performed using R v. 2.15 (R Development Core Team, 2012).

RESULTS

This study identified a regional pool of 54 lichen species across the southwest slope of Mount Irony, with an average of 3.966 ±13.425 species per plot. In general lichen communities showed increasing taxonomic diversity (r^2=0.372, p<0.001), phylogenetic diversity (r^2=0.306, p<0.001) and functional diversity (r^2=0.423, p<0.001) with elevation. There was no significant relationship between measures of phylogenetic net-relatedness index (NRI) and elevation at the plot level (r^2=-0.010, p=0.590), and only marginal significance between phylogenetic nearest-taxon index (NTI) and elevation (r^2=0.040, p=0.045). However, when plots were grouped by elevation band, NRI and NTI both showed a significant linear decrease with elevation (r^2=0.850, p<0.001 and r^2=0.699, p<0.001, respectively), with significantly positive values denoting phylogenetic under-dispersion at low elevations.

Partitioning Beta Diversity Components

Comparisons of tree topology and structure between the functional diversity dendrogram and molecular phylogeny showed that both phylogenetic and functional information cluster similarly (Penny & Hendy (1985) test=81, p>0.05 for values lower than those obtained from a null distribution of randomly generated trees; see Figure 1). Some exceptions occur; for example, the genus Cladonia groups on the functional tree, however certain fruticose species, such as *Bryocaulon divergens* and *Alectoria ochrolechia* are added as sister species, but are phylogenetically distant relatives. Nonetheless, overall structure was similar between the two types of trees, and this is reflected in the results from Figure 2, with functional turnover showing a significant parallel increase with phylogenetic turnover between plots (Pearson's r [r]=0.874, p<0.001). In addition, functional and phylogenetic turnover demonstrated a comparable significant positive relationship with taxonomic turnover (r=0.438 and 0.439 respectively, with p<0.001). Notably, the strength of the correlation between functional and phylogenetic diversity was stronger than that observed for either with taxonomic diversity.

Environment was a strong predictor for all measures of beta diversity; however, different aspects of the environment were found to correlate more strongly with different beta diversity indices. Functional and phylogenetic beta diversity most strongly correlated with differences in temperature (r=0.376 and 0.286 respectively; see Table 1). Taxonomic beta diversity correlated significantly with all variables (except distance), but the strength of correlations did not match those found for either phylogenetic beta diversity or functional beta diversity (e.g. r=0.136 for correlations with temperature), and with vegetation cover within plots the strongest correlate ($r=0.236$, $p<0.001$). Additionally, comparisons of beta diversity indices were made using both a multi- and single trait approach. All traits (exempting form) showed low phylogenetic signal across the phylogeny (Table 2) and generally weaker correlations with phylogenetic and taxonomic beta diversity (Table 3). Multi-trait functional diversity correlated significantly with distance and temperature, whereas single-trait diversity measures differed in type and strength of environmental predictors (Table 3). All traits apart from dry matter content correlated strongly with elevation ($p<0.001$).

Beta Diversity Within and Between Habitat Types

The two habitat types (alpine and forest) differed significantly in temperature, canopy cover and vegetation presence. Variation in minimum ground temperature was significant across the alpine habitat, ranging from -3.1° to -30.3°C ($\mu=-15.1 \pm 6.2$°C), with the forest plots being relatively invariant ($\mu=-4.2 \pm 3.3$°C). In contrast, canopy cover showed a much larger variance between plots in forest environments, ranging from 0% in some plots to a maximum of 70% ($\mu=23.4 \pm 19.8\%$). Canopy cover in the alpine was minimal, however the presence of krumholtz (low lying juniper and spruce) allowed for some canopy and microhabitat differences among plot sites ($\mu=3.8 \pm 13.3\%$). Both alpine and forest habitat types demonstrated significant positive clustering in mean pairwise distance values for phylogenetic diversity at the plot level (mean $NRI_{PD}=1.485$, $p<0.001$ and mean $NRI_{PD}=1.085$, $p<0.001$, for forest and alpine plots respectively); however, functional diversity was only significantly structured in the forest habitat (mean $NRI_{FD}=1.085$, $p<0.001$, and mean $NRI_{FD}=0.432$, $p=0.077$, for forest and alpine respectively). Values of

NTI for both PD and FD were significantly structured in alpine habitat (mean $NTI_{PD}=1.523$, $p<0.001$ and mean $NTI_{FD}=1.010$, $p<0.001$) and forest habitat (mean $NTI_{PD}=1.240$, $p<0.001$ and mean $NTI_{PD}=0.858$, $p=0.007$).

To remove the effect of filtering into habitats, we compared the relationship of the different beta diversity indices to one another within each of the habitat types separately. Phylogenetic beta diversity was more strongly correlated with functional beta diversity in forest habitat than in alpine habitat ($r=0.901$, $p<0.001$ and $r=0.729$, $p<0.001$ for forest and alpine communities respectively; see Figure 3), and the correlation strength in forest was stronger than observed across habitats. In addition, the mean phylogenetic turnover in the forest environment was higher than alpine (standard effect size [SES]=1.952 and 1.547 respectively, $p<0.001$, from a null model randomizing species membership between plots within habitats). However, functional (SES=1.713 in alpine and 1.891 in forest, $p=0.0590$) and taxonomic (SES=1.523 in alpine and 1.521 in forest, $p=0.982$) turnover were not significantly different between the two environments. Importantly, at the within-habitat scale we show shifts in both strength and significance in the environmental drivers of beta diversity (see Table 4). Within forest habitat, canopy cover and to a lesser extent temperature drive phylogenetic turnover between plots, whereas temperature and percent cover of shrubs and low-lying vegetation are more significantly correlated with functional beta diversity. Taxonomic turnover is correlated solely to changes in canopy cover, and not temperature or vegetation cover. In alpine habitat, canopy cover is significantly correlated with both phylogenetic and functional turnover. Both canopy cover and vegetation cover significantly correlate to taxonomic beta diversity, but distance and temperature do not.

DISCUSSION

We explored the distribution of cryptogam diversity along an elevational gradient across which communities are strongly structured at a relatively small spatial scale. Recent studies have contrasted different indices of beta diversity at a large scale (Kraft et al. 2011, Cáceres et al. 2012), but it is not clear what drives the similarities and differences between them (Swenson et al. 2012). Myers et al. (2013) showed that although similar trends in beta diversity exist between temperate and tropical forest regions, these patterns are not necessarily generated by the same ecological processes. Here we show that even at the local scale, taxonomic, phylogenetic and functional beta diversity are affected by different environmental drivers and may be sensitive to alternative community assembly mechanisms. Additionally, by deconstructing functional diversity into single-trait components, we were able to not only evaluate general trends in cryptogam functional diversity, but also examine how specific environmental variables drive beta diversity in individual traits.

Cryptogams (mosses and lichens) are poikilohydric, meaning that they rely on their environment for access to water and nutrients (Green & Lange 1994). Physiologically lichens are particularly adept at thriving in harsh conditions due to a tolerance to desiccation (Robinson et al. 1989). Their reproductive systems are adapted to a dry environment, as their gametes are not motile and are wind-dispersed through spores.

Additionally, their photobiont (photosynthetic algae or bacteria) is protected from environmental extremes by the mycobiont (fungal component). Lichens thrive in drier conditions, with an optimal photosynthetic rate at below-saturation water levels (Robinson et al. 1989). However, lichens contain less chlorophyll per biomass than other cryptogams, such as mosses, and as such do less well in low-light conditions. We might, therefore, expect lichens to do poorly in habitats with moist conditions and dense canopy, and flourish in more extreme environments. Supporting this prediction, we find lichen communities strongly structured within lower elevation bands, with increasing taxonomic diversity and phylogenetic diversity at higher elevations across both plots and elevation bands. Lichen communities are phylogenetically and functionally clustered within forest habitat, which might reflect sensitivity to small changes in microclimatic factors in the boreal, such as shade or temperature (Robinson et al. 1989, Vitt et al. 1990). Interestingly, we also observe strong clustering in phylogenetic diversity within the alpine habitat (but no functional clustering), suggesting that the traits we measured are not corresponding to changes in phylogenetic community structure between these plots. This is the first study to examine community phylogenetic structure and functional indices based upon measured traits in cryptogams (see Rapai et al. 2011 for an alternate analysis using traits recorded from the literature).

Overall comparisons of turnover varied between beta diversity indices. Taxonomic beta diversity did not correlate overly strongly with either phylogenetic or functional diversity, however there was a strong match between phylogenetic and functional beta diversity. The significant correlation between phylogeny and function was surprising considering that all measured traits (excluding the categorical trait 'form') showed no significant phylogenetic signal. In general, turnover across elevation reflects variation in ground temperature, but the alternative beta diversity metrics are sensitive to different environmental drivers. Phylogenetic and functional beta diversity (both considered to be related to the function of a species in its environment) appear to be driven more by abiotic and spatial variables, whereas taxonomic diversity is more influenced by non-abiotic variables, such as canopy and vegetation cover. It is clear that these diversity measures differ in their response to external factors, but that phylogenetic and functional diversity nonetheless appear to respond similarly across the elevational gradient.

By restricting our analysis to within-habitat, we hoped to remove the filtering effect of environment on each habitat type. We then re-examined the relationship between turnover and environment. One prediction is that we may remove evidence of environmental filtering (e.g. due to temperature); alternatively, we might detect stronger correlations with environment in one habitat compared to the other. At high elevations, the alpine zone has been found to represent a strong environmental filter for many taxa groups due to the harsh conditions of the environment (e.g. Graham et al. 2009, Hoiss et al. 2012). However, for lichens high elevations might provide a respite from competition with higher plants (Bruun et al. 2009), and thus represent a more benign environment. Within this zone, we find that lichen communities cluster with phylogeny but not function (in terms of NRI), and phylogenetic turnover under-predicts functional turnover, such that communities with very different phylogenetic compositions are not necessarily equally functionally distinct. This suggests that the traits important for filtering into the alpine zone are not necessarily the same as those determining species coexistence within the alpine zone. The difference in turnover amongst environmental variables and beta diversity metrics further demonstrates this disjunction. All metrics are significantly correlated to canopy cover, but functional beta diversity is also driven by temperature, and taxonomic beta diversity by vegetation cover.

In contrast to the alpine zone, we observe strong clustering and larger than expected turnover in both functional and phylogenetic diversity in the forest environment. The phylogenetic and functional components of beta diversity in the forest zone are significantly correlated with environment; however, the identity and strength of environmental predictors differs somewhat between the two indices. Strong clustering might indicate filtering in the forest at the microhabitat scale, with differences in habitat type driving both functional and phylogenetic turnover. The boreal forest exhibits large variation in both canopy and moisture availability across a relatively small scale (Vitt et al. 1990), which could explain the correlation of these diversity measures with canopy and temperature. As we found in the alpine environment, differences in response to the abiotic and biotic factors indicate that these metrics may be driven by different components of the environment within the forest plots.

The results of our study indicate that the choice of trait type is critical to patterns of functional diversity, and that important traits may vary depending on the assembly rules driving community membership in different environments. In some cases, such as when there is an easily identified (and measureable) trait linking species function and environment, a single trait approach may be optimal (e.g. Butterfield & Suding 2013), but more generally we might expect the process of competition or filtering would operate on multiple traits. In our study system, phylogeny may more accurately track functional patterns derived from multiple traits, as predominantly neutral markers from molecular data used to reconstruct phylogenetic history may better represent the evolutionary history of selection on multiple traits, each with separate evolutionary trajectories, or an aggregate trait value. This finding parallels Felsenstein's (1988) observation that covariance in traits is due to a correlation in their selective pressures. We show that phylogeny can provide a useful proxy for functional trait data in the examination of community assembly mechanisms, even when singular traits show low phylogenetic signal. However, we find some differences in the environmental predictors of turnover between the two metrics, indicating that they are not completely interchangeable.

Meynard et al. (2011) concluded that overall patterns of taxonomic diversity could be extended to both phylogenetic and functional diversity and provide insights on the ecological processes occurring at macroecological scales. Our study has shown differences in community assembly patterns emerge even at local scales and demonstrates an incongruity between taxonomic, phylogenetic and functional diversity among cryptogrammic lichen communities. We suggest that one dimension of diversity, for example, taxonomic richness, will not necessarily capture other dimensions of diversity, such as functional or phylogenetic information. Attention must be given to the differences between these diversity measures, especially when evaluating patterns between scales. Devictor et al. (2010) emphasized spatial differences in hotspots between taxonomic, phylogenetic and functional turnover at the regional scale, and recommended that any biodiversity assessment should consist of an integrated approach that takes into account all three aspects of biodiversity. We extend this argument, and recommend that multiple dimensions of diversity must be considered to fully understand community structure and assembly at both the local and regional scale.

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FIGURES

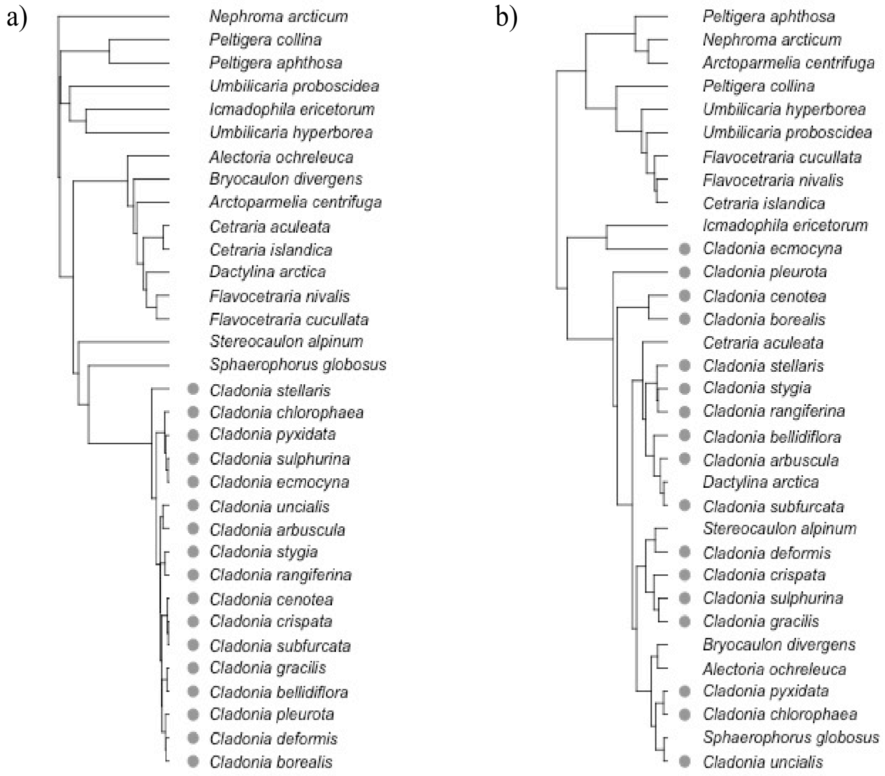

Figure 1. A comparison of the phylogeny and functional dendrogram, with members of the genus *Cladonia* highlighted. The tree on the left (a) is constructed using maximum likelihood analyses of genetic sequences from the *ITS* region. The tree on the right (b) uses the functional diversity methodology of constructing dendrograms based on multiple traits (Petchey & Gaston 2002).

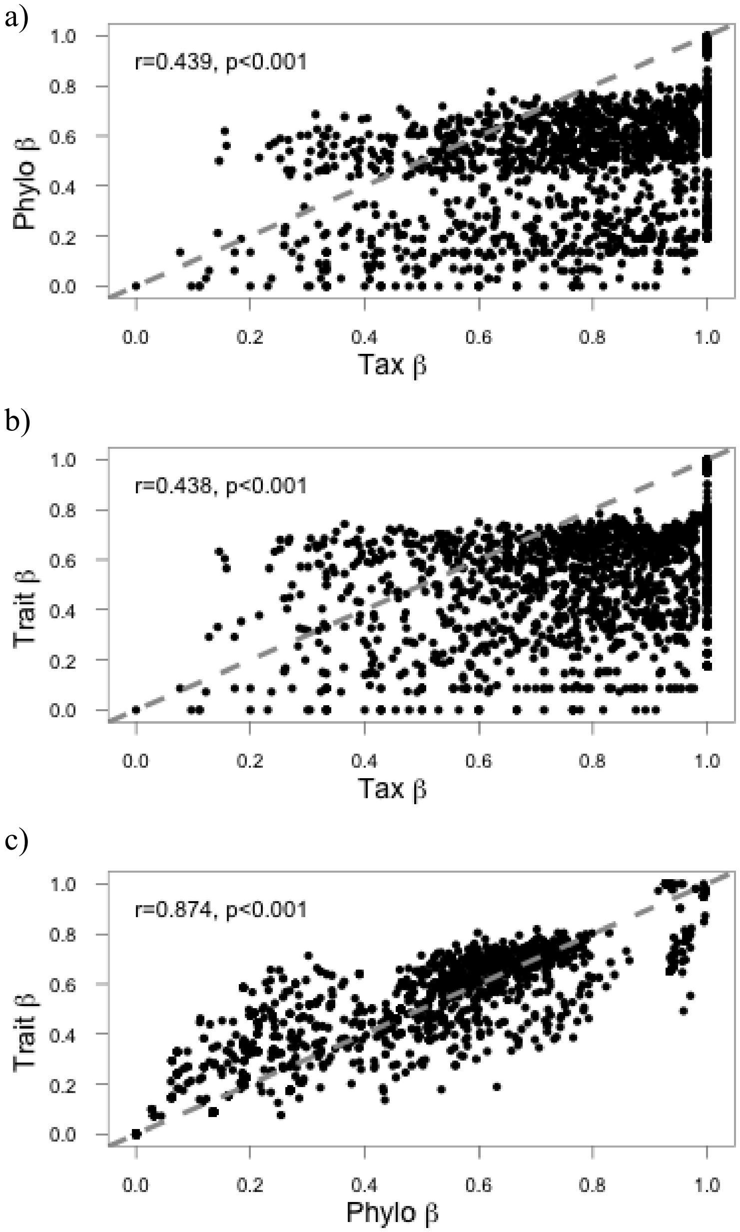

Figure 2. Correlation of taxonomic beta diversity with both a) phylogenetic and b) functional beta diversity measures, as well as phylogenetic and functional correlations (c). Statistics displayed are Pearson's r statistics from Mantel tests, with associated significance values. A 1:1 reference line is plotted in grey to show over- and under-prediction of each correlation.

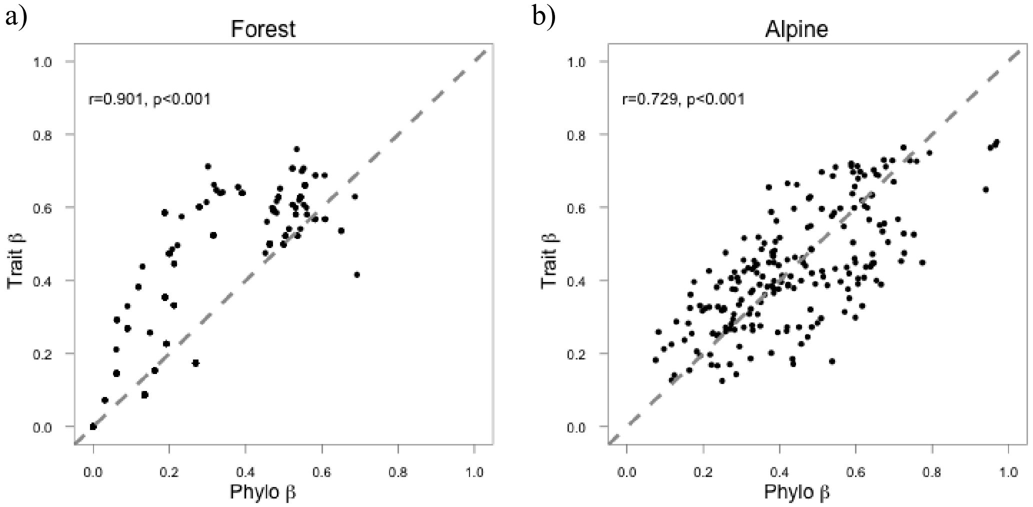

Figure 3. Comparison of beta diversity measures within two habitat types, (a) forest and (b) alpine. The graphs show the correspondence of phylogenetic and functional beta diversity across plots within these habitats, with Mantel test-statistics reported (Pearson's r and associated significance values).

TABLES

Table 1. The results of the Mantel tests correlating beta diversity measures with spatial and environmental variables. Pearson's r values are displayed with associated significance from permutation tests.

	Taxonomic Beta diversity	Phylogenetic Beta diversity	Functional Beta diversity
Distance	0.054	0.054	0.097*
Slope	-0.006	0.062	0.096
Elevation	0.148**	0.284***	0.300***
Temperature	0.136**	0.376***	0.286***
Canopy Cover	0.136**	0.051	0.077
Vegetation Cover	0.236***	0.130	0.071

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 2. Phylogenetic signal calculated using Blomberg's K for trait values measured across the regional phylogeny of lichens. [Form- Thallus formation type, DMC- Dry Matter Content, N- Total nitrogen tissue content, P- Total phosphorus tissue content]

Trait	Mean	K Value	Significance
Multitrait	---	0.080	0.490
Form	---	0.994	0.01
Wet Weight (g)	1.421	0.113	0.113
Dry Weight (g)	0.479	0.040	0.887
DMC	0.413	0.054	0.670
Maximum Height (cm)	5.944	0.101	0.802
N (µg /g)	0.522	0.035	0.869
P (µg /g)	5.697	0.103	0.320
N:P	0.106	0.038	0.924

Table 3. The results of the Mantel test correlating multi- and single-trait functional beta diversity measures with geographic and environmental variables. Pearson's r values are displayed with associated significance from permutation tests. [TBD- Taxonomic beta diversity, PBD- Phylogenetic beta diversity, Form- Thallus formation type, DMC- Dry Matter Content, N- Total nitrogen tissue content, P- Total phosphorus tissue content]

	TBD	PBD	Distance	Elevation	Temperature	Canopy	Veg.
Multitrait	0.438***	0.874***	0.090*	0.300***	0.286***	0.077	0.071
Form	0.241***	0.712***	0.096*	0.257***	0.205***	0.059	0.032
Wet (g)	0.369***	0.683***	0.096*	0.265***	0.241***	0.063	0.106*
Dry (g)	0.556***	0.355***	0.028	0.150**	0.027	0.23***	0.029
DMC	0.357***	0.560***	0.069	0.036	0	0.111	0.068
H (cm)	0.359***	0.560***	0.021	0.297***	0.167**	0.162**	0.136*
N (µg /g)	0.420***	0.398***	0.035	0.221***	0.135*	0.168*	-0.035
P (µg /g)	0.287***	0.364***	0.020	0.162***	0.280**	0.102	-0.019
N:P	0.347***	0.513***	0.035	0.320***	0.153*	0.127*	0.024

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 4. The results of the Mantel test correlating beta diversity measures with spatial and environmental variables within alpine and forest habitat. Pearson's r values are displayed with associated significance from permutation tests.

		Taxonomic Beta diversity	Phylogenetic Beta diversity	Functional Beta diversity
Forest	Distance	-0.017	-0.053	-0.023
	Slope	0.011	-0.051	0.072
	Elevation	-0.011	0.072	0
	Temperature	0.066	0.256*	0.245*
	Canopy Cover	0.201**	0.357***	0.202
	Vegetation Cover	0.104	0.152	0.214*
Alpine	Distance	-0.070	-0.039	0.135
	Slope	0.131	0.092	0.363
	Elevation	-0.090	-0.097	-0.045
	Temperature	0.059	0.193	0.205*
	Canopy Cover	0.293**	0.403*	0.521**
	Vegetation Cover	0.331**	0.143	0.070

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

CONNECTING STATEMENT

Chapter 1 makes use of both phylogenetic and functional information to characterize turnover of lichen species across a steep environmental gradient. These findings suggest that phylogenetic information captures trait information, even if traits are not conserved across the phylogeny.

1. Comparisons of beta diversity indices across elevational gradients show a strong relationship between phylogenetic and functional turnover. However, the different diversity indices are driven by different environmental predictors, with varying strengths.
2. By examining turnover between plots within the two major habitat types, alpine and forest, we see marked differences in both strength and type of predictor for these beta diversity measures. We also show that the sample pool matters even at the local scale, and demonstrate a stronger turnover within forest when standardized by a null model.

Phylogenetic and functional measures have recently been used to examine turnover among communities (e.g. Devictor et al. 2010, Swenson et al. 2011b), but only within select clades. The aim of Chapter 2 is to extend this research to relate these measures to ecosystem functioning in another cryptogam group. Here we use phylogenetic diversity to examine the diversity-productivity relationship in bryophyte communities along an elevation gradient. With increasing environmental stress, diversity is thought to become an increasingly strong predictor of productivity. We will additionally explore measures of focal species biomass, using a derived measure of phylogenetic distance, to assess the important of complementarity effects across the elevation gradient.

Chapter 2

Diversity affects productivity along an elevational gradient in a subarctic bryophyte community

Chelsea L. Chisholm and T. Jonathan Davies

ABSTRACT

The diversity-productivity relationship has been tested in numerous study systems in both experimental and natural settings. Most such studies have quantified diversity as simply the number or relative abundance of different species; only recently have studies expanded their definition of diversity and taken into account other measures such as phylogenetic diversity. Phylogeny is thought to capture more information on the ecological processes occurring in communities, such as environmental filtering and competitive exclusion. As such phylogeny might provide more insights into the relationship between biomass production and diversity than traditional metrics of taxonomic richness. In this study we examine the effect of multiple diversity measures (both taxonomic and phylogenetic) on biomass of bryophyte communities along an elevational gradient in the subarctic of Canada. We find that biomass decreases with diversity, with both species richness and the net-relatedness index being the best predictors. Further, we find that the explanatory power of diversity is greater when accounting for variation in elevation, but remains negative. Results differed when considering a single focal species, the red stem feathermoss, *Pleurozium schreberi.* We find that the relationship between biomass and diversity was positive for *P. schreberi*, with greater production along an elevational gradient when it grew with less closely related neighbors.

INTRODUCTION

The past few decades have seen a burgeoning of studies documenting the effects of diversity loss on ecosystem functioning (Hooper et al. 2005). Historically, diversity has been thought to be contingent on the resource availability of a given environment (Currie 1991, Rosenzweig & Abramsky 1993, Abrams 1995, Waide et al. 1999). A number of seminal studies (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999) demonstrated that diversity influences productivity at smaller spatial scales (e.g. within community). This diversity-productivity relationship is based on the hypothesis that that a more diverse community is able to capitalize on a wider variety of resources (Chapin III et al. 2000, Tilman et al. 2001, Naeem 2002, Hooper et al. 2005, Ruijven & Berendse 2005). These studies and others have established that diversity can influence productivity positively in an experimental setting, however the underlying mechanism driving this relationship remains up for debate (Cardinal et al. 2006).

Two classes of mechanisms have been proposed to explain the increase in productivity with diversity (Loreau 2010). First, increased diversity may lead to the increased probability that a more productive and dominant species is sampled from the species pool, referred to as the “selection effect” (Huston 1997, Loreau & Hector 2001). Second, increasing species diversity may concurrently increase functional diversity, allowing communities to sample a wider breadth of resources. Resource breadth might be increased either due to reduced interspecific competition in comparison to intraspecific competition (Cardinal et al. 2009), or to an increase in overall complementarity of nutrient uptake in space and time (Ruijven & Berendse 2005). Facilitation may also lead to increased productivity, with a number of experiments demonstrating positive interactions between species (see Callaway 1995). A greater understanding of the phenotypic attributes of species relating to resource use is important if we are to fully understand how diversity drives productivity (Cadotte et al. 2009).

Species richness has been used as a proxy for functional diversity, however simple richness counts do not contain information on how species partition resources (Diaz & Cabido 2001, Cadotte et al. 2009). Phylogenetic and functional diversity have been proposed as alternate, more direct, predictors of productivity, as they might provide better indicators of the way in which species use resources in their environment (Petchey & Gaston 2006, Cadotte et al. 2008, Cadotte et al. 2009, Flynn et al. 2011). For example, richness gives no indication of the redundancy of species within a community with regards to their traits. The removal or addition of a single species can potentially have far reaching effects on the productivity of that community, and depending on the identity of that species can vastly increase overall resource use and niche breadth (Tilman et al. 2001, Mulder et al. 2002, Hooper et al. 2004, Lambers et al. 2004).

Researchers have argued that linking productivity with functional diversity is the best approach to account for species-level differences (Cadotte et al. 2009, Roscher et al. 2012), yet assessing which functional traits are more associated with limiting resources is difficult at best (Petchey & Gaston 2006). Functional diversity is a direct measure of phenotypic variation, however, it is not straightforward to identify the key traits associated with resource use and productivity. In addition, the type and number of these traits may change between species group, and quantifying these traits is an arduous task. Recently, Cadotte et al. (2008 and 2009) proposed the use of phylogenetic information in examining the links between diversity and productivity. Cadotte et al. (2008) argued that evolutionary history acts as a proxy for functional diversity, with more distantly related species able to make use of different resources. Phylogenetic diversity may be better able to capture the integrated effects of multiple traits (Felsenstein 1988), and as such may provide a fundamentally superior diversity measure taking into account multiple trait-function relationships that collectively drive productivity. It also offers a relatively convenient measure for evaluating the link between diversity and productivity when little functional information is available.

Studies examining the diversity-productivity relationship have often focused on experimentally manipulating communities, yet these do not resemble natural communities where environmental effects also play a critical role in biomass production. For example, species might have been filtered into natural communities, such that some species combinations are more or less likely to co-occur than those found in an artificial setting. Idiosyncratic results have been found in systems other than the seminal grassland experiments (e.g. Cedar Creek LTER and BIODEPTH) that first attempted to explore the diversity-productivity relationship (Cardinal et al. 2007). Despite the abundance of experiments and natural manipulations examining the diversity-productivity relationship, few have considered either phylogeny or cryptic species, such as bryophytes, that are a major contributor to productivity in many ecosystems.

Here we examine the diversity-productivity relationship in natural bryophyte communities of the boreal forest using information on taxonomic richness and phylogeny. Bryophytes are considered an important sink of carbon in peatland and boreal forest (DeLucia et al. 2003), with sphagnum moss containing more biomass globally than any other plant taxa (Clymo & Hayward 1982). The dominant feather mosses, such as *Pleurozium schreberi* and *Hylocomium splendens*, play host to nitrogen fixing bacteria that provide the largest source of nitrogen inputs to the boreal ecosystem (Turetsky 2003, Zackrisson et al. 2004, DeLucia et al. 2007, Zackrisson et al. 2009). Overall bryophyte productivity is equivalent to or exceeds the productivity of trees in the boreal forest (Vasander 1982, Oechel & Van Cleave 1986). This productivity is vital to the boreal, functioning to insulate soils against temperature change and regulate surface processes such as nutrient flux and carbon cycling (Lindo & Gonzalez 2010). However, bryophyte communities are predicted to be particularly vulnerable to climate change due to a strong coupling between growth and water availability (Brisbee et al. 2001).

Our study examines variation in productivity of bryophyte communities along an elevational gradient at the ecotone between the boreal forest and tundra, where tree growth becomes limited by permafrost. Previous work on bryophytes suggested that diversity becomes increasingly important to productivity with environmental stress in experimental communities (Mulder et al. 2001), but few studies have assessed the diversity-productivity relationship along an environmental gradient in natural systems (but see Korhonen et al. 2011, Zuo et al. 2012) or simultaneously considered phylogenetic information. Although elevation is predicted to be the major driver of biomass change across environmental scales, coupling this with information on diversity may help explain variation in community productivity between and within communities. We compare alternative indices of diversity, and evaluate whether phylogeny provides a better explanation of changes in biomass with elevation. We also examine an ecologically dominant focal species, *Pleurozium schreberi*, to explore more directly the effect of phylogenetic relatedness on intraspecific biomass along the same elevational gradient. If phylogenetic distance captures functional differences between species, we predict that focal species biomass will increase with increased phylogenetic distance to coexisting community members due to increased intraspecific niche space availability.

METHODS

Study Site

Bryophyte communities were sampled along an elevational gradient on the southwestern slope of Mount Irony, at the border of Labrador and northern Quebec (54.901 N 61.147 W) in the summer of 2012. The mountain (888 m) is characterized by a strong vegetation gradient from low elevation spruce-moss boreal forest to high elevation alpine tundra. Plots were established in 2011 along 11 transects at 8 elevation bands, spanning 200 meters in altitude. Plot size (0.25 m^2 in diameter) was chosen to minimize within plot environmental heterogeneity. Temperature loggers were placed in the northern corner of each plot to obtain mean annual temperature. In addition we recorded key environmental variables including slope, aspect, and canopy cover. Each plot was sampled for bryophyte presence/absence and abundance using percent cover.

Biomass

Because it is difficult to estimate biomass per individual for colonial species, productivity was measured as a species-level average for each bryophyte species present in the species pool. This allows a species-level assessment of productivity with a mean and range associated with each species, and can be combined to provide an overall estimate of mean biomass at the plot level. For each species, five cores of 3 cm^2 diameter were collected from randomly sampled plots across the elevational gradient (following Waite and Sack 2010). Cores were dried in an oven for 48 hours at 60°C and weighed for an estimate of total dry matter (g/cm^2). Dry matter provides a direct measure of total productivity in the form of tissue weight, or the amount of total fixed carbon. Focal species biomass was estimated for *Pleurozium schreberi* using a similar methodology, sampling five cores from within $1m^2$ of each plot in which *Pleurozium schreberi* was present. In this manner we were able to obtain intraspecific values of core biomass from the majority of the plots (n=47) along the elevational gradient.

Plot level biomass was estimated as a community weighted mean (CWM) for dry weight. Community weighted means are calculated as the mean trait value weighted by relative species abundances in a community. This measure provides a measure of biomass that accounts for bryophyte abundances at each plot. Weighted means were based on average values per species.

$\bar{z}_i = \{\sum_{j=1}^{m} y_{ij} z_j\}/\{\sum_{j=1}^{m} y_{ij}\}$

This formula calculates the sum of each trait ($\bar{z}_i$) at site *i* by multiplying the value of the trait (z_j) for each species *j* with the species abundance y_{ij}. Community-weighted means were estimated for dry weight at each plot using the function *dbFD* in the package *FD* (Laliberté & Shipley 2011).

Phylogeny Construction

Tissue samples were collected from the 28 species of bryophytes found on Mount Irony and submitted to Barcode of Life Data systems (BOLD) at Guelph, Ontario, for sequencing (see Appendix S4 for species information). Sequences for *rbcla* were obtained for each species and aligned using MAFFT v. 7 (Katoh 2013). A regional phylogeny was constructed using the packages *phanghorn* (Schliep 2011) and *ape* (Paradis et al. 2004) in R v. 2.15 (R Development Core Team, www.R-project.org). We selected the best-fit model of nucleotide substitution using the function *modelTest* in the *phanghorn* package, and reconstructed the phylogeny using maximum likelihood methods. We report the maximum likelihood tree along with associated bootstrap values in Figure 1. Voucher specimens for each sample are deposited in the MacDonald Herbarium at McGill University.

Calculating Diversity and Productivity

Species richness and phylogenetic diversity were recorded for each plot. For our purposes, phylogenetic diversity was defined as the total shared branch lengths between each community member per plot (Faith 1992). Two indices of phylogenetic clustering were also calculated from the phylogeny: net-relatedness index (NRI) and nearest-taxon index (NTI). Both are standardized measures obtained from a null model which takes into account differences in diversity between plots. NRI is based on the mean phylogenetic distance between community members (MPD) and provides a measure of spread of species across the phylogeny, while NTI is obtained from an estimate of mean nearest phylogenetic neighbor distance (MNND) and gives an indication of finer scale clustering of species at the tips of phylogenies. Plots with species falling within different phylogenetic clades would have a lower NRI and NTI value, following convention, we refer to this pattern as over-dispersed or evenly-dispersed. Plots with species that are more closely related (cluster in the phylogeny) have higher NRI and NTI values, and are referred to as under-dispersed.

Additionally, we calculated the phylogenetic distance between our focal species (*Pleurozium schreberi*) and its neighbors. Pairwise distances of each plot sub-tree were calculated using the *cophenetic.phylo* function in the package *ape* (Paradis 2013). Distance from *P. schreberi* to each of its neighbors was calculated by excluding the distance to itself and taking the average of all distances to every other species in the plot to generate a mean focal pairwise distance (MFPD). We also calculated the nearest-neighbor distance (NND), considering only the distance from *P. schreberi* to its nearest neighbor. These measures differ from previous phylogenetic assessments of mean pairwise distance (MPD) or mean nearest-neighbor distance values (MNND) in that they no longer assess values between all species in each plot, but only that between the focal species and co-occuring species. In this way we can obtain a direct measure of the intraspecific distance between *P. schreberi* and its neighbors.

Statistical Analysis

We used a linear regression framework to assess the diversity-productivity relationship across our bryophyte communities. Using the community weighted mean of dry matter content of each plot, we assessed the influence of alternative measures of diversity and the environment. Several predictors were included for each regression, including elevation, species richness, phylogenetic diversity, NRI, abundance-weighted NRI (NRIa), NTI and abundance-weighted NTI (NTIa). First, for each predictor variable we assessed a single variable linear regression in the form:

$$y_i = \beta_o + \beta_1 x_1 + \varepsilon_i$$

Where y_i is the community-weighted biomass average, β_o is the intercept, and β_1 is the slope associated with the effect variable x_1. Individual models were compared using Akaike Information Criterion (AIC) and the Akaike weight (Johnson & Omland 2004). Second, as we were interested in the combined effect of both the environment and individual diversity measures (either SR, PD, NRI, NRIa, NTI or NTIa), we included both environment and diversity measures within a multiple regression analysis. This regression took the form of:

$$y_i = \beta_o + \beta_{env} x_{env} + \beta_1 x_1 + \varepsilon_i$$

Where $\beta_{env} x_{env}$ is a measure of the environment (elevation, ground temperature, canopy cover) and $\beta_1 x_1$ is each single measure of biodiversity (SR, PD, NRI, NRIa, NTI or NTIa). Since we *a priori* expected strong variation in productivity due to the surrounding environment, this framework allowed the examination of the added effects of diversity in addition to environmental drivers, adopting a more hypothesis-driven approach. This avoids common issues of stepwise multiple regression such as parameter estimation bias, multiple hypothesis testing problems and focus on a single best model (Whittingham et al. 2006).

The regression analyses (both single- and multi-variable approaches) were repeated for the biomass of the focal species at each plot, with MFPD and NND included as response variables in addition to species richness and phylogenetic diversity.

All analyses were conducted in R v. 2.15 (R Development Core Team, www.R-project.org).

RESULTS

We documented a total of 28 species in our plots across the elevational gradient. Overall, there was no strong gradient in any of the biodiversity variables at the plot level, and neither species richness nor phylogenetic diversity was significantly correlated with elevation. However, when plots were aggregated within elevational bands we found significant differences in diversity and structure along the gradient, likely due to this scale providing a more accurate measure of overall elevation filters vs. micro-habitat differences. Phylogenetic diversity significantly increases at higher elevations (r^2=0.604, $p<0.05$) whilst species richness remains insignificant across the gradient (r^2=0.035, $p=0.306$). Both metrics of phylogenetic community structure, NRI and NTI, show a significant trend of under-dispersion at aggregated low elevation communities to even-dispersion at higher elevations (r^2=0.850, $p<0.001$ and r^2=0.699, $p<0.01$, respectively). Here we use elevation as a proxy for variation in abiotic environment as it is highly correlated with other measured variables, including mean (r^2=0.461, p<0.001) and minimum (r^2=0.517, p<0.001) ground temperature, as well as canopy cover (r^2=0.157, p<0.001). Model results were similar using all three variables (see Appendix S5 for temperature and canopy model results).

Total plot biomass correlated significantly to plot diversity, but again elevation was not significant (Figure 2). Species richness was the best single predictor of biomass, strongly favored over phylogenetic diversity (AIC=-187.697 and -177.291 for species richness and phylogenetic diversity, respectively) as well as other measures of phylogeny such as NRI and NTI (AIC=-181.721 and -177.382 respectively; see Table 1). Interestingly the relationships of diversity with biomass were negative, such that biomass was greater in plots with lower richness and PD and more closely related neighbors. Abundance weighting of NRI and NTI values only weakened the relationship with both variables. To explore the interplay between abiotic and biotic drivers of productivity, we used multiple regression models with and without interaction effects. We found that the inclusion of the interaction and additive effects of both elevation and species richness were the best predictor models (AIC=-190.334 and -186.932, respectively), with the additive effect of elevation and NRI slightly less favored (AIC=-180.967; see Table 2). Again these predictors show a negative relationship with biomass, with the interaction of species richness and elevation explaining 35.3% of the model variance and the additive effects explaining 29.0%. The interaction and additive effects of NRI and elevation explaining 18.4% and 19.1% of biomass, respectively.

The above results were obtained after the removal of three outliers (plots 45, 47 and 49), which all contained one alpine-associated species (*Racomitrium lanuginosum*) which contributed to higher plot-level biomass. Models fitted to the original data showed some differences, with single variable models showing similar results, however, multi-variable models showed the interaction between elevation and NRI to be the best predictor overall (AIC=-43.762; see Figure 3 and Appendix S6 for results including outliers). PD predicted this data with the lowest AIC scores in both the single and multiple regression models (AIC=-31.365 and -32.733 respectively). Because models were sensitive to outliers, we are hesitant to infer support for one model over the other (i.e. species richness plus elevation versus NRI plus elevation). Since NRI and species richness capture different aspects of diversity and are not correlated, we conducted a *post hoc* test on our data on the additive and interaction effects of all three variables (elevation, SR and NRI), removing outliers. We found that overall the additive and interaction versions of this model explained our data to the same degree as the best multi-variable models with two terms and were equally favored by AIC, but the additive model including elevation, species richness and NRI explained more variation in plot biomass than the model with only species richness and elevation (43.5% vs. 35.3%). Table 3 details full model results of the interaction and additive NRI/SR and elevation models, as well as the post hoc interaction and additive combination of elevation, SR and NRI.

To further explore the relationship between community structure and productivity, we evaluated variation in biomass for the focal species *Pleurozium schreberi*, which was widespread across the elevation gradient. First we calculated an index of per plot individual biomass using observed abundance and mean values based upon the five cores obtained from each plot in which *P. schreberi* was present. Second, we determined effective measures of trait space using a focal component of the traditional MPD and MNTD values, an index of the branch length distances to other species within the plot calculated as both a mean (MFPD) and a minimum (NND). We then used these values as predictors in multi-variable and single variable models of mean biomass. The best fit model was the interaction of elevation with MFPD (AIC=382.030; see Table 4), and could explain 23.8% of the variation in biomass. Interestingly, the interaction models of focal diversity showed a negative relationship with biomass, whereas the additive models showed a weak but positive relationship. The interaction model of elevation and NND also correlated with biomass, but was less favored by AIC (AIC=389.449). Interestingly, the additive models of elevation and diversity measures, as well as the single predictors of these measures did not explain much of the variation in biomass and were mostly non-significant. Interaction effects within linear regression models are difficult to interpret, and we were particularly interested in changes in the importance of diversity on focal biomass along the elevational gradient. Thus as a *post hoc* test we performed an ANCOVA to examine the slope of the diversity-biomass relationship across each elevation band separately (as a factor). We found that in general, the relationship between focal biomass and MFPD/NND was negative at low elevation and positive at higher elevations (r^2=0.311, $p<0.05$ and r^2=0.265, $p<0.05$ respectively).

DISCUSSION

Here we have evaluated the relationship between productivity, phylogeny and the abiotic environment in a natural system. Previous studies have reported a positive link between phylogenetic diversity and biomass in experimental communities (Cadotte et al. 2008, Cadotte et al. 2009, Flynn et al. 2011). We have shown that both species richness and phylogeny are highly significant predictors of bryophyte community biomass production. However, the general relationship found between biomass and species richness is negative, such that there is greater biomass in less diverse plots. Further, we note that for correlations with phylogeny, it is not the total phylogenetic diversity that is most important, but rather the structure of phylogenetic relationships amongst community members. Our results have important ramifications for efforts incorporating phylogenetics into the expanding literature on biodiversity and ecosystem function. First, the inclusion of diversity in assessments of productivity can provide a better estimate of biomass, especially along stress gradients in which species membership becomes more important. Second, phylogenetic community structure, for example, as indexed by metrics that measure the phylogenetic dispersion of co-occurring taxa, may be better at capturing species interactions in the form of community wide and individual-level responses with productivity than the summed branch lengths on the phylogeny (i.e. Faith's PD; Faith 1992).

Community ecology of bryophytes has historically defined diversity in terms of species richness (e.g. Wolf 1993, Vitt et al. 1995, Robinson et al. 1989), especially with regards to linkages to productivity (e.g. Mulder et al. 2001, Rixen & Mulder 2005). This research has particular application to the boreal system, which is considered to be an essential carbon sink in northern latitudes (Dixon et al. 1994) and has strong links to the global temperature regime (Bonan 2008). Ma et al. (2012) proposed that the current trend of increased drought conditions in the boreal could substantially reduce vegetative biomass and turn this system from a net carbon sink to a carbon source. Bryophytes are a major contributor to nitrogen and carbon cycling in the boreal (Turetesky 2003). In addition bryophytes are also thought to influence post-fire trajectories (Johnstone et al. 2010) and permafrost stability (Jorgenson et al. 2010). It is essential that we gain a better understanding on the effects of climate change on these dominant understory communities, and how this will in turn affect ecosystem functioning within the boreal forest.

Due to the tight coupling between environmental variables such as temperature and canopy (and thus moisture availability), we expected to detect a significant correlation between biomass and elevation as reported for epiphytic bryophytes by Wolf et al. (1993). However, we found that bryophyte biomass is largely determined by community diversity, with species richness being the best single predictor, and elevation (which best captured general variation in abiotic environment) was only important when diversity was also included among the model predictors. Our best model could explain 43.5% of the variation in community biomass, and included elevation, species richness and a metric of community phylogenetic structure (NRI). This suggests that both abiotic and biotic predictors are important for ecosystem functioning in these communities, and that biotic factors become more important once accounting for variation in the abiotic environment.

Contrary to expectations from literature, we found that biomass was greater in species-poor plots. Theoretically, a negative relationship between biomass and species richness might arise if the most highly productive species are impacted negatively by competition (e.g. through increased competition for light with increased shoot density; Pederson et al. 2001). It is also possible that both richness and productivity co-vary with environment, however the results of additive models showed the relationship with SR remains negative when accounting for elevation. Potentially there are positive interactions occurring in our study system, which have been suggested to be common in bryophyte communities (Mulder et al. 2001). If this is the case, facilitation across this gradient may occur more regularly between closely related individuals, thereby elevating biomass in communities comprised of close relatives.

In contrast to previous studies (Cadotte et al. 2009, Flynn et al. 2011), we did not find a significant relationship with PD in our study systems. Nonetheless, phylogeny is still a significant predictor, but it is the evolutionary distances separating taxa (NRI and NTI) that are important. Because both metrics represent standardized effect sizes, they could be a better measure of relative phylogenetic distance due to their comparability across plots. In addition, they more directly capture information related to niche space within a community – which is important if community productivity is driven by species complementarity. The importance of evolutionary relationships is further emphasized in our focal species example, *Pleurozium schreberi*. The two best (and only significant) models included the interaction between focal phylogenetic distance (MFPD and NND) and elevation, emphasizing the importance of evolutionary structure of the community in determining productivity. Furthermore, we find that it is not just the distance to the nearest neighbor that matters, but more importantly the distance to every other species in the community.

The diversity-productivity relationship does not act in a single direction, and studies have documented differing effects of productivity on diversity, dependent on drivers such as the availability of resources affecting the number of species (e.g. Waide et al. 1999, Mittelbach et al. 2001) and the natural disturbance regime (e.g. Cardinale et al. 2005). Researchers have attempted to create a more comprehensive framework of the causality of diversity and productivity (e.g. Fridley 2002, Schmid 2002, Cardinale et al. 2005), and the use of elevational gradients would be particularly pertinent to teasing apart the directionality of this relationship across resource gradients. In an examination of the relationship of MNFD and NND and biomass across each slope using an ANCOVA framework, our results suggest that within the boreal forest, communities containing more closely related species are more productive. This could be due to a greater availability of resources for some highly productive lineages able to capitalize on this environment. We find an opposite relationship at higher elevations, suggesting that in the tundra/alpine environment the more phylogenetically distant the neighbors, the greater the biomass. These results lend evidence to the existence of a complimentary effect at high elevations, where community productivity is a function of niche complementarity and reduced functional redundancy among more distantly related species. This is consistent with a previous experiment by Mulder et al. (2001), who found no relationship between productivity and diversity in bryophytes under constant conditions, but a strong positive relationship in stressed environments.

We suggest that community phylogenetic structure might be a better predictor of community productivity than simple measures of total phylogenetic diversity (e.g. Faith's PD) because it provides an indication of niche spacing within the community, conditional upon the assumption that evolutionary history can represent differences in multi-variable trait space. Niche complementarity is thought to be the primary mechanistic explanation driving the diversity-productivity relationship (Cardinale et al. 2011), yet most current diversity metrics fail to capture this information. We suggest indices of community phylogenetic structure, such as NRI and NTI, might help fill this gap and may provide valuable new insights into the diversity-productivity debate at both the community and focal scale. These measures can be particularly useful when teasing apart positive effects along environmental gradients, as we have seen in our focal biomass results. We recommend that NRI and NTI indices be considered in future diversity-productivity assessments along with more traditional diversity metrics. In addition, our study also employed a focal measure of phylogenetic diversity, and, as far as we are aware, is the first to use this approach in biodiversity research. The focal species approach may be particularly relevant to boreal bryophyte communities, as these communities are frequently dominated by one or a few species of feather mosses, which likely contribute a large proportion of biomass to the boreal understory (Nilsson & Wardle 2005).

Limitations and Future Directions

One limitation to this work is inherent in the measures of MFPD and NND and their comparison across plots. Traditional metrics of clustering or over-dispersion use a standardized effect value, or z-score, generated from a null model that randomly samples the species pool to take into account a sampling effect at higher richness values at the plot level. However, estimating standardized effect sizes is not straightforward in our study because MFPD and NFND were estimated within plots where community richness varied, and thus effects sizes might not be comparable; it is our intention to explore this issue further prior to publication of this manuscript. For now, we cautiously interpret these results as focal measures of NRI and NTI, however we expect that with standardization these results will remain strongly significant. A second limitation to this study is the use of trait averages of biomass at the community level. Plot level values will change across stress gradients, and as such this is a coarse estimate of community biomass means. However, we did not observe any significant relationship between biomass and elevation, and because our sampling design included cores from across the mountainside, we should have a mean that is at least representative of that species' biomass along this gradient. In the future, we hope to also include functional diversity measures such as dry matter content (DMC) and height to evaluate the connections between biomass production, relative growth rate and competitive ability in these species. This has previously been examined in an experimental setting (see Mulder et al. 2001) and evaluated using a structural equation model to determine not only the effect size but also directionality of these interconnected measures.

The role of facilitation is increasingly being recognized as a driving factor of productivity (Bertness & Callaway 1994, Hacker & Gaines 1997, Bruno et al. 2003, Michalet et al. 2006, Brooker et al. 2008, Chu et al. 2008), and is thought to play a stronger role under stressful conditions (e.g. Forey et al. 2010, Bakker et al. 2013, Le Bagousse-Pinguet et al. 2013). Although we do not directly test for facilitation in our study, the existence of facilitative interactions in addition to niche complementarity across stress gradients has also been demonstrated in previous studies on bryophyte communities. Økland (1994) and Pederson et al. (2001) suggested that this positive effect of density-dependent facilitation could arise from increased relative humidity from the transpiration of plants of different architectures, as well as reduced photoinhibition in shorter plants through the protection of taller plants. Interspecific interactions which increase overall community or species biomass are difficult to tease apart mechanistically; however, It appears that there is some evidence for this in our own natural study system, as the relationship between biomass and mean phylogenetic diversity of our focal species to others in the community becomes increasingly positive with elevation. We may be able to provide more insight into this hypothesis by evaluating the effect of plant height on both community and focal biomass, to see if this explains additional variation in productivity along the gradient.

Conclusions

We tested the predictive power of species richness and phylogenetic metrics with regards to bryophyte productivity across an elevational gradient. We find that productivity is greater in species poor communities, and that phylogeny, but not Faith's Phylogenetic Diversity, can explain more of the variance in community productivity than richness alone (see also Cadotte et al. 2009, Flynn et al. 2011, etc.). We also assessed the importance of community diversity on a single focal species, *Pleurozium schreberi*, to gain insight into the underlying mechanism driving the diversity-productivity relationship. We find that biomass is enhanced when *Pleurozium schreberi* co-occurs with less closely related species at high elevations, and more closely related species at low elevations, suggesting evidence for the increased importance of niche conservatism and niche complementarity along stress gradients in bryophytes. Our findings emphasize the importance of including more nuanced diversity metrics, in particular measures of phylogenetic structure, in models predicting biomass production by bryophytes. This research has important implications for the projection of future impacts on productivity within the boreal forest, as well as the development of objectives for much needed management of carbon stores in the boreal forest (Bradshaw et al. 2009, Pimm et al. 2009).

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FIGURES

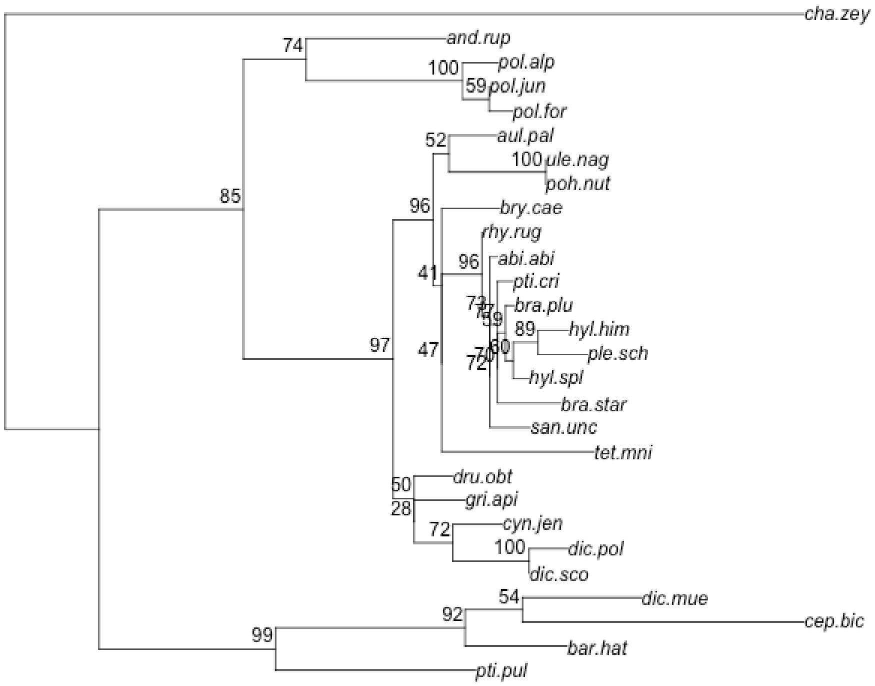

Figure 1. Maximum likelihood phylogeny of bryophyte community constructed using *rbcla* sequences. Associated bootstrap values are listed as node labels.

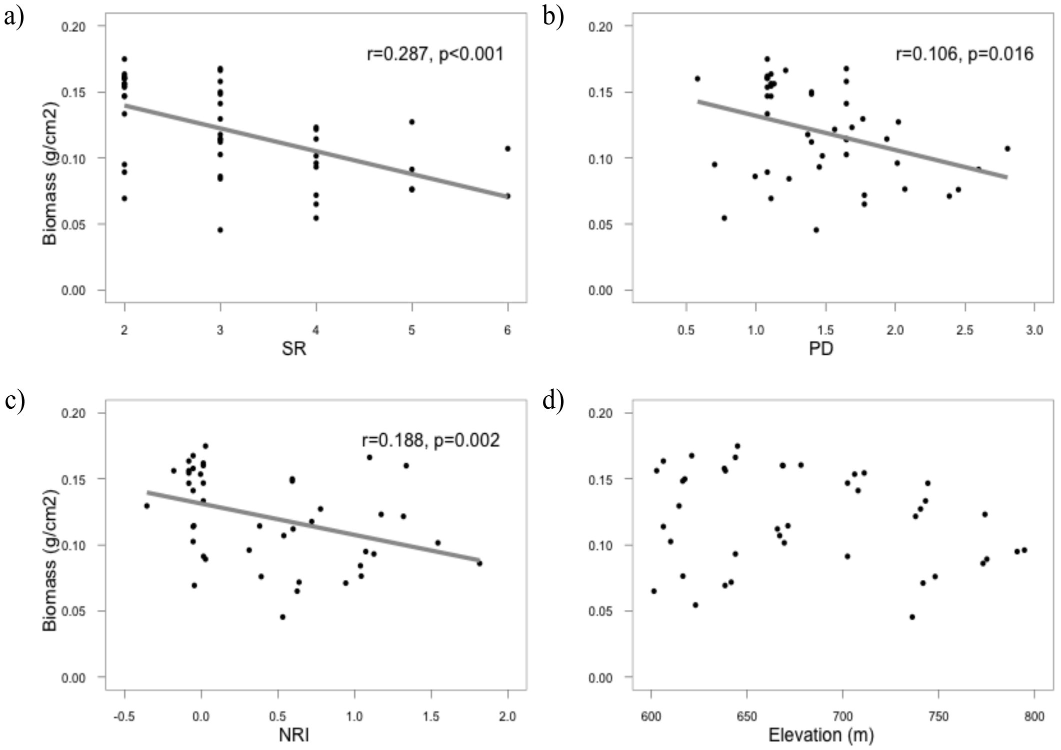

Figure 2. Single variable results of linear model fits of diversity and elevation estimates to mean plot-level biomass of bryophytes. Diversity estimates compared are (a) SR- species richness, (b) PD- phylogenetic diversity, (c) NRI- net-relatedness index, and (d) elevation (m). Significant linear regression statistics are reported with a fitted line.

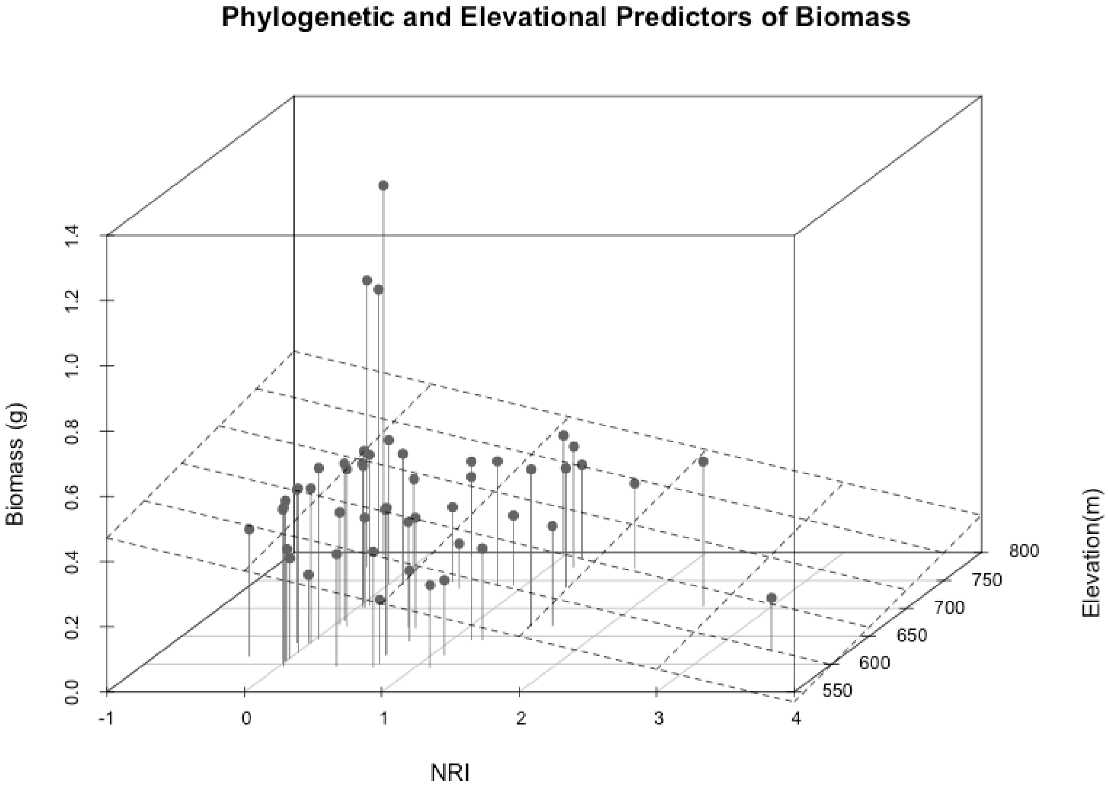

Figure 3. Multi-variable 3-dimensional plot of the additive effects of elevation and NRI (net-relatedness index) as predictors of bryophyte community biomass. A fitted slope is drawn based upon the additive terms of this model (with outliers included). Elevation and NRI significantly predicted plot-level biomass, with r^2=0.275, p<0.001 in the interaction model and r^2=0.248, p<0.001 in the additive model described here (see Appendix S6).

TABLES

Table 1. Single variable results of elevation and diversity measures as predictors of overall plot-level mean biomass. The best fit models determined by lowest AIC and highest Akaike weight are denoted in bold. [Elev- elevation (m), SR- species richness, PD- phylogenetic diversity, NRI- net-relatedness index (unweighted), NRIa- net-relatedness index (abundance weighted), NTI- nearest taxon index (unweighted), NTIa- nearest taxon index (abundance weighted)]

Predictor	*df*	*Coef*	*F*	*p*	R^2	AIC	Akaike weight
Elev	44	0.000	1.616	0.210	0.014	-172.763	0.000
SR	**44**	**-0.017**	**19.11**	**<0.001**	**0.287**	**-187.697**	**0.586**
PD	44	-0.026	6.334	0.016	0.106	-177.291	0.036
NRI	**44**	**-0.023**	**11.42**	**0.002**	**0.188**	**-181.721**	**0.251**
NRIa	44	-0.019	7.472	0.009	0.128	-178.319	0.061
NTI	44	-0.016	6.434	0.015	0.108	-177.382	0.058
NTIa	44	-0.012	3.328	0.075	0.049	-174.458	0.007

Table 2. Multi-variable results of elevation and diversity measures as predictors of overall plot-level mean biomass. Additive models are denoted by a (+), while interaction models use the (*) notation. The best fit models determined by lowest AIC and highest Akaike weight are denoted in bold. [Elev- elevation (m), SR- species richness, PD- phylogenetic diversity, NRI- net-relatedness index (unweighted), NRIa- net-relatedness index (abundance weighted), NTI- nearest taxon index (unweighted), NTIa- nearest taxon index (abundance weighted)]

Predictor	*df*	*F*	*p*	R^2	AIC	Akaike weight
Elev * SR	**42**	**9.198**	**<0.001**	**0.353**	**-190.334**	**0.390**
Elev * PD	42	2.768	0.053	0.105	-175.403	0.007
Elev * NRI	42	4.383	0.009	0.184	-179.632	0.078
Elev * NRIa	42	3.049	0.039	0.120	-176.170	0.038
Elev * NTI	42	2.995	0.041	0.117	-176.022	0.013
Elev * NTIa	42	1.846	0.154	0.053	-172.800	0.0000
Elev + SR	**43**	**10.180**	**<0.001**	**0.290**	**-186.932**	**0.198**
Elev + PD	43	3.947	0.027	0.116	-176.857	0.046
Elev + NRI	**43**	**6.325**	**0.003**	**0.191**	**-180.967**	**0.106**
Elev + NRIa	43	4.269	0.020	0.127	-177.434	0.072
Elev + NTI	43	4.063	0.024	0.120	-177.067	0.051
Elev + NTIa	43	2.494	0.094	0.062	-174.153	0.000

Table 3. Full results obtained from best interaction and additive term models for the combination effects of SR, NRI and elevation on biomass. Additive models are denoted by a (+), while interaction models use the (*) notation. [Elev- elevation (m), SR- species richness, NRI- net-relatedness index (unweighted)]

Predictor	*df*	*Coef*	SE	*t*	*p*	R^2	AIC	Akaike weight
Elev*SR*NRI	**40**				**<0.001**	**0.367**	**-187.908**	**0.009**
Intercept		0.038	0.183	2.075	0.049			
Elev		-0.000	0.000	-1.124	0.268			
SR		-0.055	0.060	-0.925	0.361			
NRI		-0.368	0.263	1.403	0.169			
Elev*SR		0.000	0.000	0.647	0.521			
Elev*NRI		0.001	0.000	-1.432	0.160			
SR*NRI		-0.117	0.073	-1.587	0.121			
Elev*SR*NRI		0.000	0.000	1.592	0.120			
Elev+SR+NRI	**42**				**<0.001**	**0.435**	**-189.052**	**0.324**
Intercept		0.221	0.049	4.543	<0.001			
Elev		-0.000	0.000	-1.080	0.286			
SR		-0.014	0.004	-3.473	0.001			
NRI		-0.009	0.005	-1.852	0.071			
Elev * SR	**42**				**<0.001**	**0.353**	**-190.334**	**0.657**
Intercept		0.571	0.158	3.615	<0.001			
Elev		-0.001	0.000	-2.524	0.015			
SR		-0.127	0.048	-2.632	0.012			
Elev*SR		0.000	0.000	2.287	0.027			
Elev * NRI	**42**				**0.009**	**0.184**	**-179.632**	**0.002**
Intercept		0.220	0.065	3.400	0.001			
Elev		-0.000	0.000	-1.443	0.156			
NRI		-0.067	0.068	-0.990	0.328			

Elev*NRI		0.000	0.001	0.769	0.446			
Elev + SR	**43**				**<0.001**	**0.290**	**-186.932**	**0.006**
Intercept		0.226	0.050	4.543	<0.001			
Elev		-0.000	0.000	-1.082	0.285			
SR		-0.017	0.004	-4.256	<0.001			
Elev + NRI	**43**				**0.003**	**0.191**	**-180.967**	**0.003**
Intercept		0.192	0.054	3.582	<0.001			
Elev		-0.000	0.000	-1.228	0.226			
NRI		-0.015	0.005	-2.891	0.006			

Table 4. Single variable and multi-variable results of the effects of diversity measures SR, PD, MFPD and NND with elevation on biomass estimates of the focal species, *Pleurozium schreberi*. Additive models are denoted by a (+), while interaction models use the (*) notation. The best fit models determined by lowest AIC and highest Akaike weight are denoted in bold. [Elev- elevation (m), SR- species richness, PD- phylogenetic diversity, MFPD- mean focal pairwise distance, NND- nearest neighbor distance]

Predictor	*df*	*Coef*	*F*	*p*	R^2	AIC	Akaike weight
Elev*MFPD	**43**	**-204.15**	**5.792**	**0.002**	**0.238**	**382.030**	**0.168**
Elev*NND	**43**	**-135.614**	**3.022**	**0.040**	**0.117**	**389.449**	**0.148**
Elev*PD	43	-95.821	1.917	0.141	0.056	392.082	0.107
Elev*SR	43	-35.961	1.560	0.213	0.035	393.125	0.062
Elev+MFPD	44	6.689	1.580	0.217	0.025	392.721	0.065
Elev+NND	44	1.333	5.612	0.274	0.014	393.217	0.062
Elev+PD	44	2.155	0.771	0.467	-0.010	394.362	0.010
Elev+SR	44	0.103	0.645	0.530	-0.016	394.634	0.000
MFPD	45	6.781	1.861	0.179	0.018	392.076	0.121
NND	45	5.579	1.314	0.258	0.007	392.628	0.080
PD	45	2.216	0.262	0.611	-0.016	393.709	0.047
SR	45	0.272	0.022	0.882	-0.022	393.958	0.047
Elev	45	0.044	1.315	0.258	0.006	392.627	0.083

GENERAL CONCLUSIONS

Phylogenetic and functional descriptions of ecological patterns are being used more frequently in ecology (e.g. Swenson et al. 2011b, Cadotte et al. 2009), and these measures have the capacity to provide additional information about the ecological processes driving community structure (Webb et al. 2002, Cavender-bares et al. 2009). However, the response of these measures to biotic and abiotic factors is not well understood, and their links to ecosystem functioning have only recently been examined (Cadotte et al. 2008, Cadotte et al. 2009). Our objective was to study these relationships in greater detail, while at the same time providing a novel application of phylogenetic and functional approaches to the relatively understudied cryptogam species group. In this thesis, we described changes in community composition using measures of phylogenetic and functional information of cryptogam species in subarctic Canada. Using a steep elevation gradient transitioning between boreal and alpine tundra, we assessed the drivers of different diversity metrics across space, and attempted to link phylogenetic diversity to productivity across an environmental gradient.

Below are listed our primary conclusions:

1. Phylogenetic and functional beta diversity within lichen communities are highly correlated across an elevational gradient, but taxonomic beta diversity does not correlate strongly with either measure. When comparing between multi- vs. single-trait functional beta diversity measures, it appears that phylogeny is strongly associated with differences in multiple traits across the elevational

gradient, but not with single trait beta diversity measures. The correlation between phylogenetic and multi-trait turnover is surprising, considering these traits generally exhibit low phylogenetic signal. Even within the categorical trait "form", which is phylogenetically conserved, we see little correspondence of functional and phylogenetic turnover. Phylogeny somehow captures information on multiple traits at the same time, and we predict it may thus provide a superior metric to direct measures of functional diversity.

2. In a comparison of turnover within habitats, we find that differences in turnover among the various diversity metrics (taxonomic, phylogenetic and functional) between plots can be explained by differences in drivers within alpine and forest zones. Additionally, our results suggest that the sample pool size is important to findings generated from these types of studies, even at the local scale. By standardizing our turnover metrics to correct for differences in pool richness, we find that an observation for greater turnover in alpine environments is driven by a sampling effect, and that turnover in the forest environment is actually higher. This is an essential finding to any study that draws comparisons between different community pools.
3. In an assessment of the relationship between diversity and productivity across an elevation gradient, we find SR and NRI to be the best predictors, but the relationship with both is negative. Interestingly, we find PD to be a poor predictor of biomass, and we provide some suggestions for reasons for this in the discussion of Chapter 2. Across the gradient, elevation is only a significant predictor of variation in biomass when other diversity metrics are accounted for, and the

additive effects between elevation, SR and NRI provides the best fit for our data.

4. An assessment of focal species (*Pleurozium schreberi*) biomass and the contribution of phylogeny to assessments of niche complementarity in stress gradients showed that evolutionary distance to neighbors becomes more important at higher elevation. In addition, it appears that the mean distance to each species in the community is a better predictor of biomass than simply nearest-neighbor distance, and both are better predictors than measures of species richness or phylogenetic diversity. Our results provide support for the niche complementarity hypothesis, and show that increased evolutionary distance from a focal species to its neighbors allows for greater biomass production. We interpret this result as indicating greater niche complementarity among less closely related species.

The trend of accelerating loss of diversity in many of the major biomes around the world has led the recent focus on diversity measures and their drivers with respect to environmental gradients (Swenson et al. 2011b). The use of phylogenetic and functional information in examining changes in community structure across gradients has gained interest due to their ability to capture more information on the interaction of species and the environment (Webb et al. 2002, McGill et al. 2006). In order to predict changes in biodiversity, we must first understand how these measures of diversity change across space and environment. An understanding of the differences between alternative diversity metrics and how they will respond to future change in anthropogenic or climate effects is essential if we are to prioritize conservation of biodiversity as a whole. A major contribution of our study is to describe patterns of community structure in two relatively understudied groups, and to highlight the differences between these with respect to spatial and environmental drivers. Our study suggests that phylogeny can be used as a proxy for functional diversity, and in some cases may be a preferable measure if trait information is not available. Additionally, phylogenetic approaches may provide more insight into the mechanistic links driving the diversity-productivity relationship.

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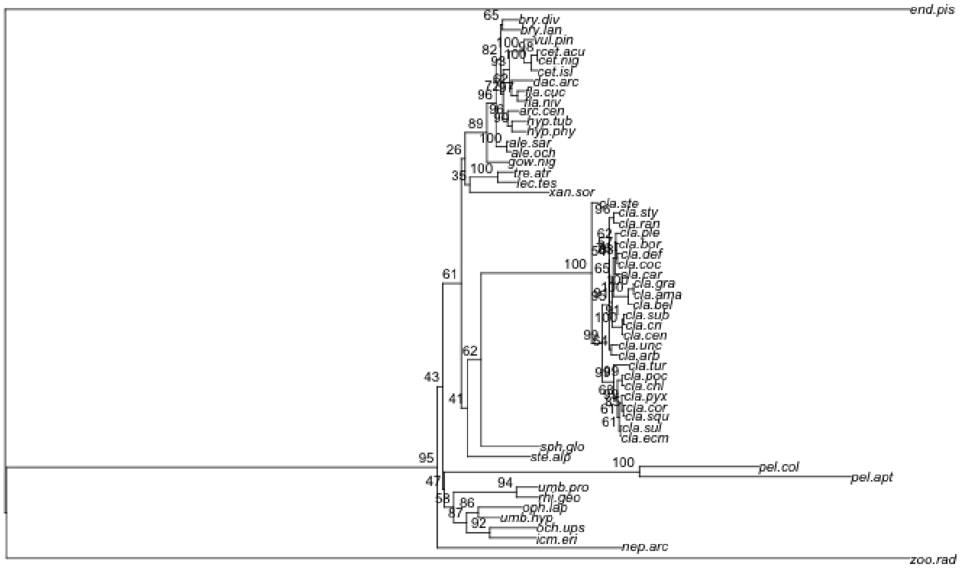
SUPPLEMENTARY INFORMATION

Appendix S1. List of lichen species within the species pool identified on Mount Irony. Included are descriptions of the form and habitat of each species.

Species Code	Family	Species Name	Form	Habitat
ale.och	Parmeliaceae	Alectoria ochroleuca	Fruticose	Ground
ale.sar	Parmeliaceae	Alectoria sarmentosa	Fruticose	Wood
arc.cen	Parmeliaceae	Arctoparmelia centrifuga	Foliose	Rock
bry.div	Parmeliaceae	Bryocaulon divergens	Fruticose	Ground
bry.lan	Parmeliaceae	Bryoria lanestris	Fruticose	Wood
cet.acu	Parmeliaceae	Cetraria aculeata	Fruticose	Ground
cet.isl	Parmeliaceae	Cetraria islandica	Fruticose	Ground
cet.nig	Parmeliaceae	Cetraria nigricans	Fruticose	Ground
cla.arb	Cladoniaceae	Cladonia arbuscula	Fruticose	Ground
cla.bel	Cladoniaceae	Cladonia bellidiflora	Fruticose	Ground
cla.bor	Cladoniaceae	Cladonia borealis	Fruticose	Ground
cla.car	Cladoniaceae	Cladonia carneola	Fruticose	Ground
cla.cen	Cladoniaceae	Cladonia cenotea	Fruticose	Ground
cla.chl	Cladoniaceae	Cladonia chlorophaea	Fruticose	Ground
cla.cri	Cladoniaceae	Cladonia crispata	Fruticose	Ground
cla.def	Cladoniaceae	Cladonia deformis	Fruticose	Ground
cla.ecm	Cladoniaceae	Cladoni ecmocyna	Fruticose	Ground
cla.gra	Cladoniaceae	Cladonia gracilis	Fruticose	Ground
cla.ple	Cladoniaceae	Cladonia pleurota	Fruticose	Ground
cla.poc	Cladoniaceae	Cladonia pocillum	Fruticose	Ground
cla.pyx	Cladoniaceae	Cladonia pyxidata	Fruticose	Ground
cla.ran	Cladoniaceae	Cladonia rangiferina	Fruticose	Ground
cla.ste	Cladoniaceae	Cladonia stellaris	Fruticose	Ground
cla.sty	Cladoniaceae	Cladonia stygia	Fruticose	Ground
cla.squ	Cladoniaceae	Cladonia squamosa	Fruticose	Ground
cla.sub	Cladoniaceae	Cladonia subfurcata	Fruticose	Ground
cla.sul	Cladoniaceae	Cladonia sulphurina	Fruticose	Ground
cla.tur	Cladoniaceae	Cladonia turgida	Fruticose	Ground
cla.unc	Cladoniaceae	Cladonia uncialis	Fruticose	Ground
dac.arc	Parmeliaceae	Dactylina arctica	Fruticose	Ground
fla.cuc	Parmeliaceae	Flavocetraria nivalis	Foliose	Ground
fla.niv	Parmeliaceae	Flavocetraria cucullata	Foliose	Ground
gow.nig	Parmeliaceae	Gowardia nigricans	Foliose	Wood
hyp.phy	Parmeliaceae	Hypogymnia physodes	Foliose	Rock

hyp.tub	Parmeliaceae	Hypogymnia tubulosa	Foliose	Rock
icm.eri	Icmadophilaceae	icmadophila ericetorum	Crustose	Wood
lec.tes	Lecideaceae	Lecidea tessellata	Crustose	Rock
nep.arc	Nephromataceae	Nephroma arcticum	Foliose	Ground
och.ups	Pertusariaceae	Ochrolechia upsaliensis	Crustose	Ground
oph.lap	Ophioparmaceae	Ophioparma lapponica	Crustose	Rock
pel.apt	Peltigeraceae	Peltigera aphthosa	Foliose	Ground
pel.col	Peltigeraceae	Peltigera collina	Foliose	Ground
rhi.geo	Rhizocarpaceae	Rhizocarpon geographicum	Crustose	Rock
sph.glo	Sphaerophoraceae	Sphaerophorus globosus	Fruticose	Ground
ste.alp	Stereocaulaceae	Stereocaulon alpinum	Fruticose	Ground
tre.atr	Hymeneliaceae	Tremolecia atrata	Crustose	Rock
umb.hyp	Umbilicariaceae	Umbilicaria hyperborea	Foliose	Rock
umb.pro	Umbilicariaceae	Umbilicaria proboscidea	Foliose	Rock
vul.pin	Parmeliaceae	Vulpicida pinastri	Crustose	Wood
xan.sor	Teloschistaceae	Xanthoria sorediata	Crustose	Rock



Appendix S2. Maximum likelihood tree constructed using *ITS* sequences of sampled lichen species, with bootstrap values identified on node labels.

Appendix S3. Results of beta diversity correlations with environmental factors using the functions *phylosor* (Bryant et al. 2008) and *PCD* (Ives 2010). Pearson's r values are displayed with associated significance of permutation tests. [TBD:PBD- correlation between taxonomic and phylogenetic beta diversity, TBD:FBD- correlation between taxonomic and functional beta diversity, PBD:FBD- correlation between phylogenetic and functional beta diversity]

	TBD:PBD	TBD:FBD	PBD:FBD
Unifrac	0.439***	0.438***	0.874***
Phylosor	-0.433	-0.405	0.860***
PCD	-0.286	-0.402	0.839***

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Appendix S4. List of all bryophyte species found within the species pool on Mount Irony. Reproductive form of pleurocary or acrocarpy is listed (with the notation "liverwort" if belonging to that group), as well as typical habitat.

Species Code	Family	Species Name	Form	Habitat
abi.abi	Thuidiaceae	Abietinella abietina	Pleurocarp	Ground
and.rup	Andreaeaceae	Andrea rupestris	Acrocarp	Rock
aul.pal	Aulacomniaceae	Aulacomnium palustre	Acrocarp	Ground
bar.hat	Anastrophyllaceae	Barbilophozia lycopodioides*	Liverwort	Ground
bra.sta	Brachytheciaceae	Brachythecium starkii	Pleurocarp	Litter
bra.plu	Brachytheciaceae	Brachythecium plumosum	Pleurocarp	Litter
bry.cae	Bryaceae	Bryum caespiticium	Acrocarp	Ground
cep.bic	Cephaloziellaceae	Cephaloza bicuspidata	Liverwort	Wood
cyn.jen	Dicranaceae	Cynodontiun jenneri	Acrocarp	Ground
dic.mue	Dicranaceae	Dicranum muehlenbeckii	Acrocarp	Ground
dic.pol	Dicranaceae	Dicranum polysetum	Acrocarp	Ground
dic.sco	Dicranaceae	Dicranum scoparium	Acrocarp	Ground
dru.obt	Orthotrichaceae	Drummondia obtusifolia	Acrocarp	Ground
gri.api	Grimmiaceae	Grimmia apiculata	Acrocarp	Rock
hyl.him	Hylocomiaceae	Hylocomiastrum himalayanum	Pleurocarp	Ground
hyl.spl	Hylocomiaceae	Hylocomium splendens	Pleurocarp	Ground
ple.sch	Hylocomiaceae	Pleurozium schreberi	Pleurocarp	Ground
poh.nut	Bryaceae	Pohlia nutans	Acrocarp	Rock
pol.alp	Polytrichaceae	Polytrichastrum alpinum	Acrocarp	Ground
pol.for	Polytrichaceae	Polytrichum formosum	Acrocarp	Ground
pol.jun	Polytrichaceae	Polytrichum juniperinum	Acrocarp	Ground
pti.cri	Hypnaceae	Ptilium crista-castrensis	Pleurocarp	Ground
pti.pul	Ptilidiaceae	Ptilidium pulcherrimumÊ	Liverwort	Ground
rac.lan	Grimmiaceae	Racomitrium lanuginosum	Acrocarp	Rock
rhy.rug	Hylocomiaceae	Rhytidium rugosum	Pleurocarp	Ground
san.unc	Amblystegiaceae	Sanionia uncinata	Pleurocarp	Ground
tet.mni	Splachnaceae	Tetraplodon mnioides	Acrocarp	Ground

* var. hatcheri

Appendix S5. Results of multi-variable diversity-biomass models including both minimum ground temperature (T) and percent canopy (C) as environmental factors. Additive models are denoted by a (+), while interaction models use the (*) notation. [Elev- elevation (m), SR- species richness, PD- phylogenetic diversity, NRI- net-relatedness index (unweighted), NRIa- net-relatedness index (abundance weighted), NTI- nearest taxon index (unweighted), NTIa- nearest taxon index (abundance weighted)]

Predictor	*df*	*F*	*p*	R^2	AIC
Ground Temp					
T * SR	42	14.380	<0.001	0.471	242.689
T * PD	42	14.990	<0.001	0.483	241.710
T * NRI	42	16.120	<0.001	0.502	239.946
T * NRIa	42	14.600	<0.001	0.476	242.332
T * NTI	42	17.39	<0.001	0.522	238.044
T * NTIa	42	15.410	<0.001	0.490	241.047
T + SR	43	21.790	<0.001	0.480	241.000
T + PD	43	23.000	<0.001	0.494	239.731
T + NRI	43	24.730	<0.001	0.513	237.972
T + NRIa	43	22.340	<0.001	0.487	240.415
T + NTI	43	26.700	<0.001	0.533	236.051
T + NTIa	43	23.22	<0.001	0.497	239.500
Canopy					
C * SR	42	5.853	0.002	0.244	400.042
C * PD	42	3.985	0.013	0.166	404.587
C * NRI	42	2.041	0.123	0.064	409.850
C * NRIa	42	2.972	0.042	0.116	407.253
C * NTI	42	2.088	0.116	0.068	409.715
C * NTIa	42	1.965	0.134	0.060	410.068
C + SR	43	4.278	0.020	0.127	405.761
C + PD	43	1.567	0.220	0.025	410.874
C + NRI	43	2.931	0.064	0.079	408.231
C + NRIa	43	4.558	0.016	0.137	405.266
C + NTI	43	2.116	0.133	0.047	409.791
C + NTIa	43	2.730	0.077	0.074	408.611

Appendix S6. Results of single and multi-variable diversity-biomass models including outlier plots 45,47 and 49. [Elev- elevation (m), SR- species richness, PD- phylogenetic diversity, NRI- net-relatedness index (unweighted), NRIa- net-relatedness index (abundance weighted), NTI- nearest taxon index (unweighted), NTIa- nearest taxon index (abundance weighted)]

Predictor	*df*	*F*	*p*	R^2	AIC	Akaike weights
Single Variable						
Elev	49	2.776	0.102	0.034	-143.047	0.004
SR	**49**	**13.07**	**<0.001**	**0.194**	**-152.294**	**0.445**
PD	49	3.159	0.082	0.041	-143.424	0.009
NRI	49	11.24	0.002	0.171	-150.767	0.369
NRIa	49	7.909	0.007	0.121	-147.868	0.040
NTI	49	7.965	0.009	0.114	-147.919	0.09
NTIa	49	6.058	0.017	0.092	-146.424	0.039
Muli-variable						
Elev*SR	47	6.09	0.004	0.234	-154.845	0.078
Elev*PD	47	2.149	0.107	0.064	-142.792	0.001
Elev*NRI	**47**	**7.259**	**<0.001**	**0.275**	**-155.654**	**0.594**
Elev*NRIa	47	5.502	0.003	0.213	-151.586	0.031
Elev*NTI	47	5.349	0.004	0.194	-151.218	0.020
Elev*NTIa	47	4.339	0.009	0.167	-148.706	0.007
Elev + SR	48	9.238	0.001	0.232	-154.845	0.218
Elev + PD	48	3.292	0.008	0.171	-144.792	0.001
Elev + NRI	48	7.611	<0.001	0.248	-152.286	0.031
Elev + NRIa	48	5.970	0.005	0.166	-149.566	0.009
Elev + NTI	48	5.446	0.008	0.151	-148.666	0.005
Elev + NTIa	48	4.413	0.017	0.120	-146.846	0.004