Functional diversity and composition of bryophyte water-related traits in Azorean native vegetation

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Background: Functional trait-based approaches link species diversity patterns to ecosystem functioning. In the context of global change, understanding these links is vital for developing holistic biodiversity management strategies. Bryophytes, important ecosystem components owing to their biogeochemical functions, have not been the focus of many functional studies.

Aims: This is the first assessment of bryophyte functional diversity in the Azores archipelago, aiming to uncover multivariate trait richness and composition patterns along the elevational gradient on Terceira Island.

Methods: Based on five water acquisition and retention traits of leafy liverworts and mosses, we calculated functional diversity metrics within and among six bryophyte communities sampled along a 1021-m elevational transect.

Results: Trait composition differed significantly between coastal and mountain communities. Mosses presented inrolled leaves and ornamented leaf cells at low elevation but not at high elevation. These patterns were associated with an uphill shift from drier and warmer conditions to a moister and cooler environment.

Conclusions: Future climatic changes might affect bryophyte functional diversity patterns in Terceira Island, particularly for mosses. These results can be directly compared with those obtained for other archipelagos where the same protocol has been applied, allowing a joint assessment of insular vegetation functional diversity patterns.

Keywords: elevation gradient; environmental filtering; liverworts; mosses; Terceira Island

Introduction

It is widely accepted nowadays that the concept of biodiversity, despite being commonly associated with taxonomic richness (Swingland 2001), is in fact multidimensional, encompassing not only taxonomic information but also phylogenetic and functional data (Devictor et al. 2010; Pavoine and Bonsall 2011; Willig and Presley 2013; Jarzyna and Jetz 2016). Awareness of this multidimensionality, along with a growing concern to identify the ecological impacts of global changes, is shifting the focus of biodiversity studies to functional diversity (Laureto et al. 2015), which is determined based on the value and range of species functional traits (Tilman 2001; Pavoine et al. 2009). Such traits are any morphological, biochemical, physiological, structural, phenological, ecological or behavioural features that are potentially relevant to growth or fitness (Violle et al. 2007). Their distribution in a community is, by and large, limited by habitat filtering, often varying predictably along environmental gradients such as along elevation (Michel and Knouft 2014; Pescador et al. 2015). In turn, functional traits are associated with the ecological tolerance of species and their habitat requirements, which determine where a species can and cannot live, how it interacts with other species and also how it contributes to ecosystem functioning (Cadotte

et al. 2011). Thus, trait-based approaches, by focusing on how function is linked with variability in distribution and abundance of species (Garnier and Navas 2012), are instrumental in any attempt to provide a sound ecological understanding of ecosystem processes and determine how these can be affected by environmental changes (Petchey and Gaston 2006; Pavoine et al. 2009).

Present in various biomes worldwide, bryophytes can reach cover and abundance levels that can influence ecosystem processes (Michel et al. 2013). For instance, they contribute to above-ground biomass, prevent erosion by creating biological crusts on bare substrates, affect the hydrological cycle of ecosystems (Michel et al. 2013), soil temperature and chemistry; they host nitrogen-fixing bacteria (Cornelissen et al. 2007). Having no vascular tissues, bryophytes satisfy their moisture requirements by taking up water directly through the entire surface of their gametophytes (Vanderpoorten and Goffinet 2009) and, in doing so, enhance the interception and retention of water from rain, dew and fog, later redistributed to the surrounding vegetation (Belnap 2006). Bryophyte water-holding capacities can reach 1400% of their dry mass (Glime 2015) and supply up to 5 mm precipitation equivalent of storage in forest ecosystems (Michel et al. 2013).

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Given these characteristics, bryophytes are a prominent and ecologically important component of most forested habitats (Raabe et al. 2010). Such is the case with Azorean native vegetation, mostly moist and shaded formations with relatively short (up to 10 m) and uniformly spaced trees (less than 3 m apart) and a rich shrub and fern understorey layer, which provide an ample range of bryophyte microhabitats and substrata (Gabriel and Bates 2005). Nonetheless, there have been to date no functional studies of the Azorean bryophyte diversity and ecosystemic interactions, despite recent research pointing to the future local loss of climate space and range shifts for some endemic and native species, based on projected climate change studies (Ferreira et al. 2016; Patiño et al. 2016). Given these possible scenarios, it is important to determine if and how changes in bryophyte taxonomic diversity in the Azores will translate to loss or gain in functions, which could carry potential implications for the resilience of ecosystem processes on which humans depend, such as the interception and storage of water.

The objective of this study was to explore changes in bryophyte functional diversity and composition along an elevation and climatic gradient in a small island (Terceira Island, Azores, Portugal), focusing on water-related functional traits that link these plants to their important role in ecosystem hydrological processes. In doing so, this study contributes to the "Mapping and Assessment of Ecosystems and their Services" initiative (Layke et al. 2012) and establishes a baseline of the bryophyte trait–environment relationships in the Azores, allowing future assessments of climate change impacts on the functional diversity of the archipelago.

Previous work has shown that bryophytes on Terceira Island have their maximum richness at mid to high elevations (500–800 m a.sl.) where average temperatures are lower (13°C vs. 25°C at sea level) and there is higher rainfall (mean annual of more than 2800 mm) and air humidity (80–100%) (Henriques et al. 2016). Assuming that optimum as opposed to suboptimum climate conditions can support a wider range of functional strategies (Spasojevic et al. 2014), we built on some of the general patterns of differences in multivariate trait composition between two communities suggested by Boersma et al. (2016), adapting them to accommodate multiple samples along an elevational/climatic gradient. Our hypotheses were:

(i) Trait diversity and composition do not differ between communities along an elevation gradient (H_0). This means that communities are exposed to similar structuring processes reflecting an absence of environmental filtering along the climatic gradient; communities contain either the same species or distinct species but with the same trait combinations, creating complete functional overlap (functional alpha diversity is stable along the gradient and functional turnover is absent).

(ii) Trait composition changes among communities along the gradient as a result of environmental filtering, but trait diversity remains unchanged. There is a shift in trait composition along the gradient but functional alpha diversity is stable (Functional turnover hypothesis, H_1).

(iii) Trait composition changes among communities along the gradient as a result of differences in niche availability, with communities occupying increasingly larger quantities of trait space. Functional alpha diversity increases as conditions become optimal for bryophytes, and the smaller range of trait values at low elevation may be a subset of those found at high elevation (Functional convergence hypothesis, H_2).

Materials and methods

Study site and sampling

Terceira Island is one of the nine volcanic islands that constitute the mid-Atlantic Azores Archipelago. Its temperate oceanic climate, characterised by high relative humidity, regular precipitation and mild temperatures (Forjaz 2004), fosters the development of a lush bryoflora, despite the small size (402 km^2) of the island and its isolation (Gabriel and Bates 2005; Aranda 2013). The bryophyte flora of Terceira Island contains 354 taxa (species and subspecies), of which 207 are mosses, 143 are liverworts and four are hornworts (Gabriel et al. 2010; updated by Aranda et al. 2014; Ellis et al. 2015).

The island has an elevational gradient of 1021 m, which provides variation in a number of climatic variables (e.g. temperature, precipitation, relative humidity) that are related to the occurrence of species within a manageable distance (Henriques et al. 2016). We established an elevation transect in the remaining native vegetation at the western side of the island, aiming to encompass native vegetation areas. At each 200 m interval, from 40 m to 1000 m a.s.l., two plots of 10 m × 10 m were established in homogeneous vegetation, at a maximum of 20 m distance between them, resulting in a total of 12 permanent plots. The plots were sampled in late September 2012, following the BRYOLAT sampling protocol (Ah-Peng et al. 2012; adapted by Gabriel et al. 2014), a multiscale hierarchical sampling procedure for bryophytes along environmental gradients. Each plot was divided into 25 2 m × 2 m quadrats and, within each plot, three quadrats were randomly selected to be sampled. From each quadrat, three 50-cm^2 microplots were collected from available substrates (rock, soil, humus, decomposing wood and leaves). For tree trunks, nine replicates were made, three up to 50 cm height, three from 51 cm to 100 cm and three above 100 cm, when possible. This resulted in the collection of 636 microplot samples.

Abundance values for each species at each site were calculated as the number of microplots in which the species was present.

Climatic variables associated with the elevation gradient (temperature, rainfall, relative humidity) were acquired at a 100 m resolution from the CIELO Model (Azevedo et al. 1999). All these variables were highly correlated among them and, in turn, with elevation (Pearson product-moment correlation coefficient $r > 0.9$, $\alpha = 0.005$): temperature decreased linearly along the gradient and both rainfall and relative air humidity increased. Therefore, for simplicity, we use elevation as a proxy predictor (Körner 2007).

Trait data

Trait data were extracted from the BRYOTRAIT-AZO database (available online at http://islandlab.uac.pt/software/ver.php?id=26), a comprehensive trait data set for the Azorean bryoflora, based on published morphological information. As most water-related traits in the literature for bryophytes pertain to leaf architecture, we used leaf traits in this study. As for number of traits, we followed the recommendations by Laughlin (2014) to avoid using correlated traits and limited our trait set to five traits which are thought to be connected with water uptake, flow and/or retention on bryophytes (Table 1).

Leaf length in bryophytes is connected with water loss in the sense that, being in permanent hydric equilibrium with the surrounding atmosphere (Proctor and Tuba 2002), bigger leaves, despite being able to absorb more water, are also more prone to losing it when exposed to dry conditions. Leaf bases which are decurrent (extending below the leaf insertion) or sheathing (surrounding and clasping the stem) facilitate water movement and can store small amounts of water between the stem and the sheathing leaf portion (Watson 1914a). In papillose and mamillose leaves, cell surfaces present minute protuberances in a variety of forms which expedite water transport, acting as capillaries without disturbing gaseous exchanges, hastening leaf rewetting (Guerra et al. 1992; Vitt et al. 2012). As for margin rolling, incurved margins form sacciform structures which reduce evaporation (Watson 1914b; Guerra et al. 1992). Liverwort leaves are nerveless, but in some moss taxa the leaves can be costate, that is, presenting a nerve or costa. Leaf nerves that extend across

the entire length of the leaf (percurrent nerves) or even surpass it (excurrent nerves) are thought to offer increased structural support to the leaf during desiccation, as well as providing an avenue for water transport (Guerra et al. 1992; Waite and Sack 2010). Moreover, some excurrent nerves can project into hyaline hairpoints, thin hair-like structures which appear to be very effective captors of dew (Watson 1914a; Ah-Peng et al. 2014).

We measured the correlations for each pair of traits in order to estimate the level of redundancy in our functional information following the methodology developed by Pavoine et al. (2009). We first computed the squared pair-wise distance matrices for each trait and then we calculated the Pearson correlations between every possible pair of distance matrices. Here we used Gower's distance (Gower 1971), a metric that accommodates different types of variables. As correlation values were all close to zero (all $r < 0.3$), we ascertained that the traits were not correlated and thus should provide independent functional information.

Functional diversity metrics

According to Mason et al. (2005), functional diversity within a community can be decomposed in three facets which, together, describe the distribution of species in niche space: (1) functional richness, which refers to the amount of niche space occupied by all the species; (2) functional evenness, concerning the evenness of the distribution of abundance in the occupied niche space; and (3) functional divergence, quantifying the degree to which abundance distribution in niche space maximises divergence in functional traits. To quantify these three functional components to characterise alpha diversity we employed the multidimensional indices of Villéger et al. (2008), namely FRic (functional richness), FEve (functional evenness) and FDiv (functional divergence). We standardised FRic, so that all indices varied between 0 and 1. We tested both linear and quadratic regressions to account for potential relationships between elevation and functional diversity measures. The significance of the models was assessed using the correlation coefficient (R^2) and the small sample size-corrected Akaike index (AICc), and only the best fit was considered.

For beta diversity, we used the partition method proposed by Carvalho et al. (2012), in which functional beta

Table 1. Bryophyte water-related leaf traits used in our functional diversity analyses, with information on variable type and possible trait values.

Leaf trait	Type	Values	Associated function
Leaf length	Continuous	From 0.15 mm to 13 mm	Water uptake
Decurrent/sheathing base	Binary	0 – absent; 1 – present	Water movement and storage
Cell ornamentation	Binary	0 – absent; 1 – present	Water movement and storage
Margin rolling	Binary	0 – plane; 1 – rolled	Reduction of evapotranspiration
Nerve extension	Ordinal	1 – absent; 2 – short; 3 – long; 4 – excurrent; 5 – with hairpoint	Water interception and movement

diversity between sites is decomposed into replacement or turnover (the substitution of traits by other traits) and richness differences (loss or gain of traits between sites), allowing us to determine which process is originating the functional dissimilarities among sites (see also Cardoso et al. 2014). According to the typology of beta diversity measures proposed by Anderson et al. (2011), Carvalho's framework was appropriate since it allowed the measurement of a directional turnover in assemblage structure (e.g. through time or along an environmental gradient). Mantel regressions were applied to determine the existence of significant correlations between beta diversity patterns and site dissimilarity matrices created based on elevation.

To determine if our observed alpha and beta diversity values arose by chance or were associated with site-specific factors of community assembly, we compared the observed functional alpha and beta values to a random distribution under the null hypothesis of no association between elevation and traits. Our null model resulted from 10,000 permutations of the site x species abundance matrix, using the "independent swap" algorithm (Gotelli and Entsminger 2001, 2003), which randomises species occurrence values without changing the total richness of each sample or species frequency. To quantify the deviation from the null expectations, we computed the standardised effect size (SES), using the formula:

SES = (Obs – μ null) /σ null,

where Obs is the observed functional alpha/beta value, μ null is the mean functional alpha/beta value of the simulated communities and σ null is the associated standard deviation (Gotelli and McCabe 2002). We considered that there was a significant deviation from the null expectation when SES < 2 (diversity lower than expected) and when SES > 2 (diversity higher than expected). Finally, for each site, community-weighted mean (CWM) values were calculated for each trait. These were the mean trait values weighted by the relative abundance of the species displaying them. Plotting CWM values against elevation allowed

us to determine which traits were creating the functional diversity patterns observed.

Liverworts and mosses are known to show different diversity patterns along ecological gradients (Mateo et al. 2016). In Terceira Island, liverwort taxonomic richness is more closely related to environmental variables than moss taxonomic richness (Gabriel and Bates 2005; Henriques et al. 2016), which is why separate analyses were carried out for liverworts and mosses. All calculations were made by in R 3.3.1 (R Core Development Team 2014) by using the ade4, BAT, vegan and FD packages.

Results

The 636 samples yielded a total of 3680 bryophyte records, corresponding to 89 leafy bryophyte taxa, plus three thallose taxa that were not considered in this study since they do not possess leaves. Of the 89 taxa, 55 were liverworts and 34 were mosses. Taxonomic richness increased with elevation, peaking at 600 m ($N = 52$) and stabilising above ($N = 47$); abundance peaked at 800 m (Figure 1). The same elevational pattern was observed in both mosses and liverworts, but with liverworts being constantly more species-rich and abundant than mosses, representing on average 58% of the taxa at all sites.

Functional alpha diversity

Functional richness followed a non-linear pattern with a maximum at 600 m, both for mosses and all bryophytes combined, while for liverworts it increases linearly with elevation ($R^2 = 0.89$, $P < 0.01$) (Figure 2(a)). However, this increase in occupied functional space for liverworts did not differ from random expectations, while the maximum at 600 m for mosses was significantly higher than would be expected by chance (Figure 2(b)). Functional evenness decreases significantly with elevation for the three groups (all bryophytes: $R^2 = 0.93$, $P < 0.01$;
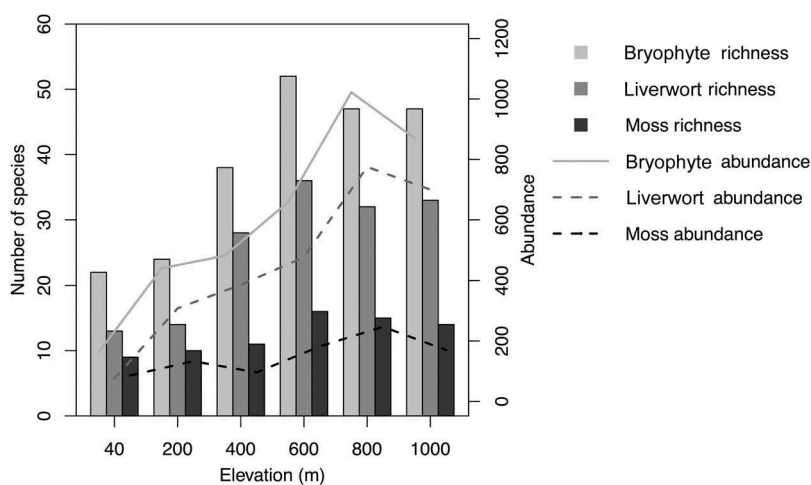

Figure 1.   Species richness and abundance (number of presences in 50-cm² field samples) of leafy bryophytes (liverworts, mosses and both combined) along an elevation gradient, Terceira Island, Azores, Portugal.
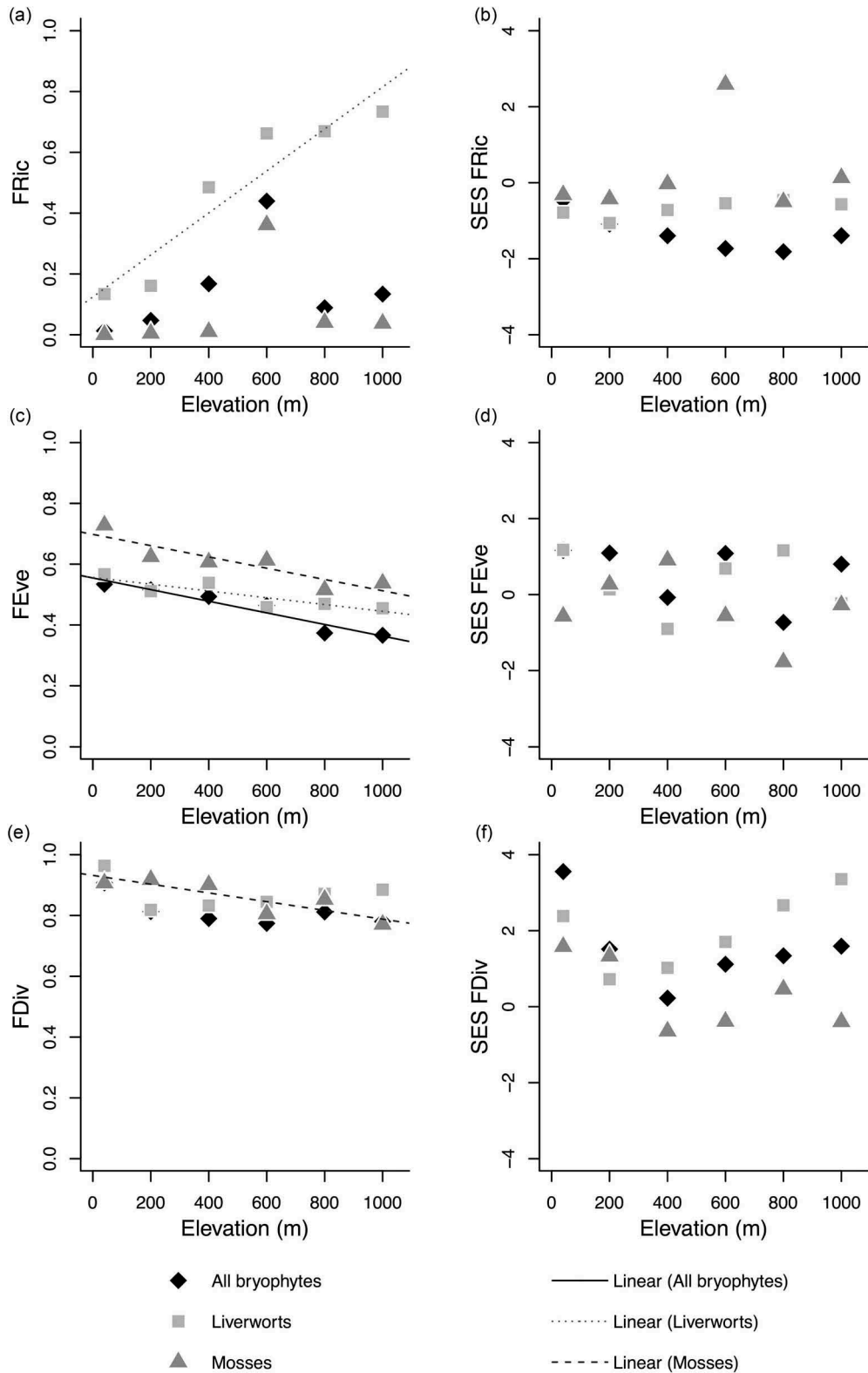
Figure 2. Functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and respective standardised effect sizes (b, d and f) for all bryophytes, liverworts and mosses along an elevation gradient, Terceira Island, Azores, Portugal. Note: Only significant correlations ($P < 0.05$) are shown as trend lines.

liverworts: $R^2 = 0.77$, $P < 0.05$; mosses: $R^2 = 0.80$, $P = 0.01$) (Figure 2(c)), but without deviating from null model predictions (Figure 2(d)). As for functional

divergence, it was quite high for all groups along the gradient and decreased significantly with elevation only for mosses ($R^2 = 0.75$, $P < 0.05$) (Figure 2(e)).

Nonetheless, FDiv values for all bryophytes and liverworts at the 40 m site were significantly higher than expected by chance. The same applied to liverworts at the 800 m and 1000 m sites (Figure 2(f)).

Functional beta diversity

Overall bryophyte functional beta diversity among sites increased with elevation ($r = 0.83$, $P < 0.01$), mostly due to an increase in replacement ($r = 0.79$, $P < 0.01$) (Figure 3(a)). Mosses were the main contributors to this pattern, showing an even steeper increase in both overall beta diversity ($r = 0.86$, $P < 0.01$) and its replacement component ($r = 0.81$, $P < 0.01$) (Figure 3(c)), a pattern which differs significantly from null model expectations for the three most distant pairs of sites. As for liverworts, the most important process at work along the gradient was the difference in richness among sites ($r = 0.53$, $P < 0.05$) (Figure 3(b)), as expected, given the linear increase in liverwort functional richness with elevation. Nonetheless, this trend did not differ from null model expectations.

Community-weighted means

Three of the five traits used in our index calculations correlated significantly with elevation: leaf length, leaf rolling and cell ornamentation. Leaf length decreased along the gradient for liverworts and mosses together ($R^2 = 0.69$, $P < 0.05$), but not for liverworts or mosses alone (Figure 4(a)). The abundance of species with cell ornamentations decreased with elevation (all bryophytes: $R^2 = 0.81$, $P = 0.01$; liverworts: $R^2 = 0.92$, $P < 0.01$; mosses: $R^2 = 0.60$, $P < 0.05$) (Figure 4(c)), as did the abundance of species with inrolled margins, both for mosses ($R^2 = 0.90$, $P < 0.01$) and all bryophytes combined ($R^2 = 0.80$, $P = 0.01$) (Figure 4(e)). Neither the presence of decurrent leaf bases or nerve extension was related to elevation (Figure 4(b,d)), despite the latter presenting its maximum value at 40 m, both for mosses and all bryophytes.

Discussion

Gathering data on how functional traits change along environmental gradients can provide useful insights about
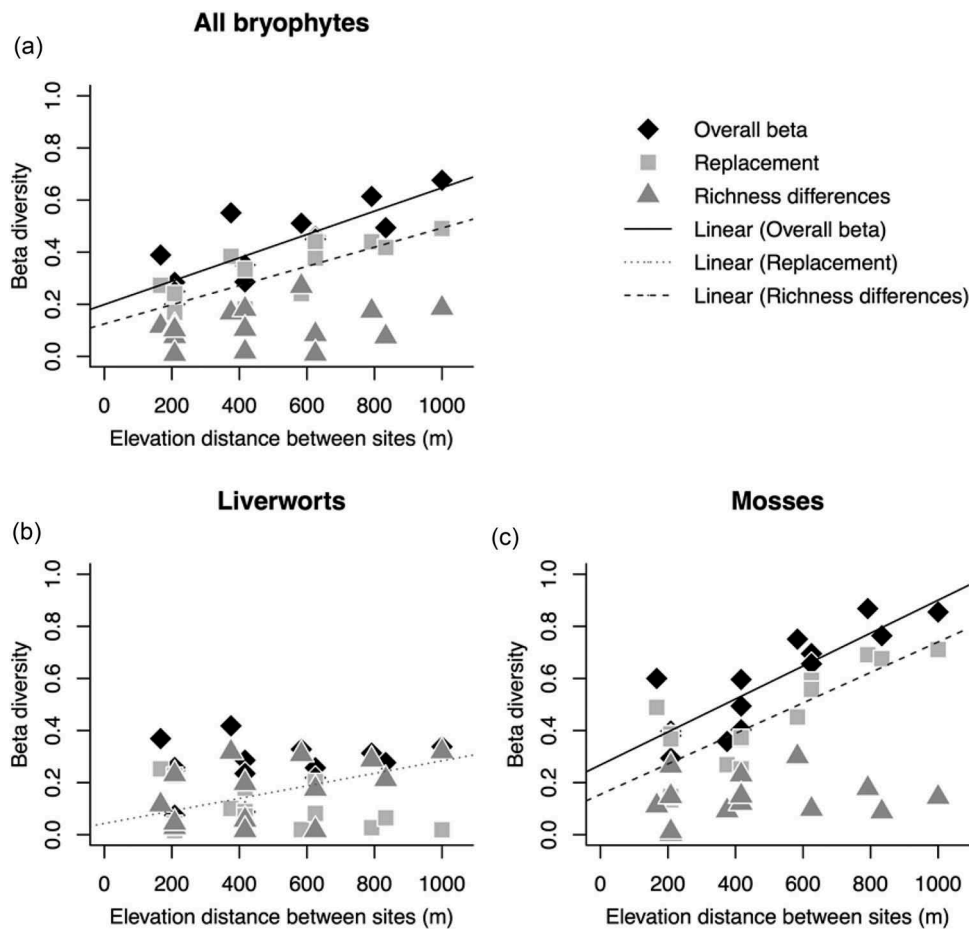

Figure 3.   Functional overall beta diversity divided into its two components, richness differences and species replacement for each possible pair of sites along an elevation gradient, Terceira Island, Azores, Portugal, plotted against elevational distance between sites for (a) all bryophytes, (b) liverworts and (c) mosses. Note: Only significant Mantel correlations ($P < 0.05$) are shown as trend lines.
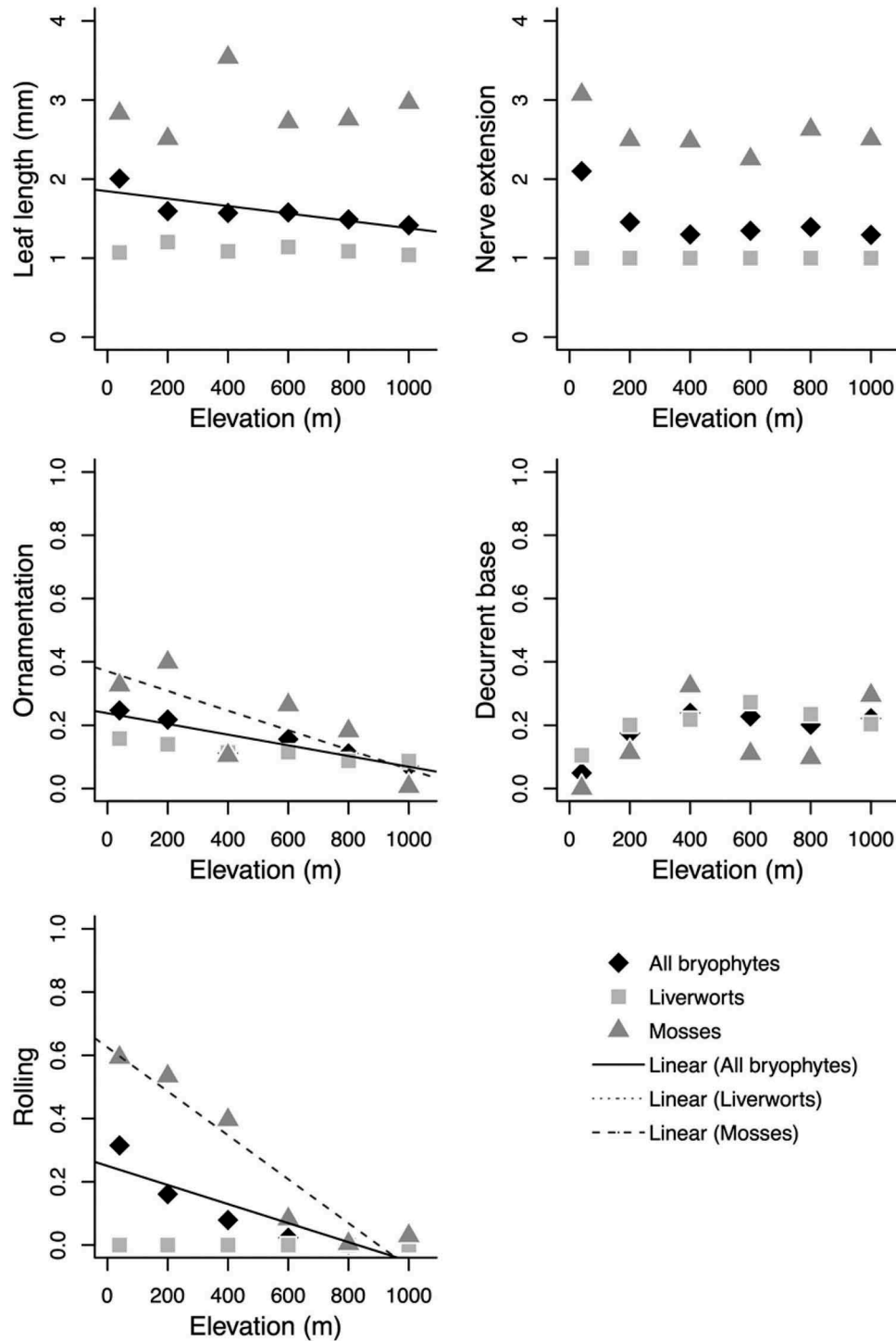
Figure 4. Community-weighted means of trait values plotted against elevation for each of the three studied groups along an elevation gradient, Terceira Island, Azores, Portugal. Note: Only significant correlations (*P* < 0.05) are shown as trend lines.

community structure and its relation to environmental factors, which, in turn, affect ecosystem functioning (Pescador et al. 2015). Given the general lack of such studies for island bryophytes, which play an important role in hydrological cycles, we conducted the first assessment of water-related functional diversity patterns of bryophytes in Azorean native vegetation areas. The increase in taxonomic richness with

elevation was accompanied by an increase in occupied functional space for liverworts, but without deviating from the null expectation. This reflects a seemingly random accumulation of functions, not visibly influenced by the climatic variables associated with elevation. Functional richness only surpassed null expectations for the moss community at 600 m, a site where the 16 moss species present cover a large

range of trait values. In the same community, there are moss species with small (1.2 mm), plane and non-decurrent leaves with short nerves and no cell ornamentation (i.e. *Hypnum uncinulatum*), species with long leaves (6 mm) with inrolled margins, decurrent bases and long nerves (i.e. *Leucobryum glaucum*) and species hosting several other combinations of trait values in between these. At this site, we also found the moss with the longest leaves (13 mm), *Polytrichastrum formosum*, as well as several species with excurrent nerves. These extreme trait values greatly expand the volume of the functional space. This might indicate a higher niche availability for mosses at this site, which is in fact an ecotone, corresponding to a transition area between submontane and montane forests (Elias et al. 2016).

Analysing the distribution of trait abundances, we also found that the functional divergence of liverworts at 40 m, 800 m and 1000 m elevation was significantly higher than expected by chance, meaning that the most abundant species at these sites were more dissimilar than they randomly should. This dissimilarity seems to have arisen from the wide range of leaf length values present. At 40 m, for instance, the two most abundant liverworts *Frullania tamarisci* (48% of the records) and *Cololejeunea azorica* (11%), present fivefold differences (1.5 mm and 0.3 mm, respectively). Such wide ranges are even more accentuated at 800 m, where specimens of the liverwort *Scapania gracilis* can exhibit leaves almost six times longer (2 mm) than those of an almost equally abundant liverwort species, *Drepalejeunea hamatifolia* (0.3 mm). This seemingly random distribution of liverwort species with longer and shorter leaves is corroborated by the fact that CWM values for leaf length do not show a significant variation with elevation. Small liverworts with equally tiny leaves (namely those belonging to the Family *Lejeuneaceae*) are ubiquitous and occur frequently throughout the gradient. The fact that our abundance metric is the number of 50-cm^2 microplots in which the species are present and not an actual count of individuals or cover estimation might have resulted in these smaller species to disproportionally weigh the trait mean and functional diversity indices which consider trait abundance.

Concerning patterns of beta-diversity, we found that trait composition varied between among our coastal and montane bryophyte communities. Mosses are the main contributors to a pattern of increase in bryophyte beta diversity with elevation, most of which is owing to replacement of traits by other traits along the gradient. There is a significant elevational shift from moss taxa with inrolled leaves and ornamented cells at low elevation (40 m) to moss taxa without these adaptations at high elevation (1000 m). While the correlation is not significant for nerve extension, there is also a CWM maximum for this trait in the 40 m moss community, indicating the prevalence of longer-nerved taxa at this site. This corroborates our initial trait function assumptions for these traits, in which cell ornamentation, leaf rolling and the presence of excurrent nerves were thought to provide some degree of protection against rapid water loss, delaying desiccation and/or increasing water-uptake rates and the rehydration

process when water becomes available again. As such, moss communities along the gradient conform to our functional turnover hypothesis, showing changes in trait composition along the gradient as a result of environmental filtering while functional richness remains unchanged. Liverworts, despite not deviating significantly from our null hypothesis, show an increase in functional richness along the gradient, combined with significant richness differences between low- and high-elevation communities and the lack of clear CWM elevational patterns for the studied traits. This suggests that, as these water-related traits are concerned, liverworts are less diverse and more functionally redundant than mosses, but also begs the question of if and how different combinations of traits or analysis at other spatial scales might unearth structuring deterministic processes not revealed in this study.

As the trait values used were collated from the literature and not obtained via direct measurements of our sampled specimens, it might be that intraspecific variability along the gradient was not considered. Shifts in plant functional traits have been linked both to species compositional changes (e.g. Matteodo et al. 2013; Venn et al. 2014) and species plasticity (e.g. Hulshof et al. 2013; Kichenin et al. 2013), however interspecific differences have been responsible for the largest portion of variance in trait values along elevational gradients (Auger and Shipley 2013). Additionally, the binary and ordinal traits used in this study do not display intraspecific variability along the gradient, being strongly phylogenetically conserved. Nonetheless, using trait data from European amphibians, Tsianou and Kallimanis (2016) have recently shown that trait selection can greatly impact functional diversity calculations, as focusing on different traits can produce different spatial patterns of functional diversity. As such, a thorough identification of functional hotspots must not be based solely on the study of a single organismal function, such as the hydric relations of bryophytes. This implies that further studies, focused on different traits and other axes of ecological niche variation, such as those related with photosynthesis (Chen et al. 2016) or life history and reproduction (Austrheim et al. 2005), will be required for a more complete characterisation of the bryophyte functional diversity on Terceira Island.

Conclusions

This first assessment of the functional component of the Azorean bryoflora suggests that future changes in climatic variables might particularly affect moss functional diversity. It is to expect that, as the climatic conditions change, so will the diversity patterns correlated with elevation. It is then necessary to explore how these changes will translate spatially into a loss or gain of function and the impacts those functional shifts might have on ecosystem functioning. Additionally, the application of the BRYOLAT standardised sampling protocol in Terceira will allow us to join and directly compare our results with the ones obtained for other Azorean islands and even other

archipelagos where this protocol has also been applied (i.e. the Canary Islands, the Comoros, the Lesser Antilles, the Mascarenes, French Polynesia and Madagascar) contributing to a joint assessment of insular vegetation functional diversity patterns.

Disclosure statement

Funding

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Claudine Ah-Peng is a researcher. She is interested in drivers of species diversity and distribution of non-vascular plants, specifically in insular systems.

Paulo Borges is the Leader of the Azorean Biodiversity Group. His research focuses on arthropod biodiversity, with emphasis on macroecology, biogeography and conservation.

Rosalina Gabriel is an assistant professor. Her research focuses on biodiversity studies of Azorean bryophytes, emphasising physiological, ecological, biogeographical and conservation aspects.

DSGH, RF and RG conceived and designed the study. DSGH and RG collected samples from fieldwork and identified species. DSGH analysed the data. DSGH, FR, PAVB, CAP and RG all contributed to writing the manuscript. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

References

Ah-Peng C, Flores O, Wilding N, Bardat J, Marline L, Hedderson TAJ, Strasberg D. 2014. Functional diversity of subalpine bryophyte communities in an oceanic island (la réunion). Arctic, Antarctic And Alpine Research 46:841–851.

Ah-Peng C, Wilding N, Kluge J, Descamps-Julien B, Bardat J, Chuah-Petiot M, Strasberg D, Hedderson TAJ. 2012. Bryophyte diversity and range size distribution along two altitudinal gradients: Continent vs. island. Acta Oecologica 42:58–65.

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LSDavies KF, et al. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Aranda SC 2013. Bryophyte diversity patterns in the Macaronesian region [PhD thesis]. [Alcalá, Spain]. Universidad de Alcalá.

Aranda SC, Gabriel R, Borges PAV, Santos AMC, Azevedo EB, Patiño J, Hortal J, Lobo JM. 2014. Geographical, temporal and environmental determinants of bryophyte species richness in the Macaronesian Islands. PLoS ONE 9:e101786.

Auger SShipley B. 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. Journal Of Vegetation Science. 24:419–428.

Austrheim G, Hassel K, Mysterud A. 2005. The role of life history traits for bryophyte community patterns in two contrasting alpine regions. The Bryologist 108:259–271.

Azevedo EB, Santos Pereira L, Itier B. 1999. Modelling the local climate in island environments: water balance applications. Agricultural Water Management 40:393–403.

Belnap J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrological Processes 20:3159–3178.

Boersma KS, Dee LE, Miller SJ, Bogan MT, Lytle DA, Gitelman AI. 2016. Linking multidimensional functional diversity to quantitative methods: a graphical hypothesis-evaluation framework. Ecology 97:583–593.

Cadotte MW, Carscadden K, Mirotchnick N. 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, et al. 2012. Biodiversity loss and its impact on humanity. Nature 489:326–326.

Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PAV, Podani J, Schmera D. 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. Journal of Biogeography 41:749–761.

Carvalho JC, Cardoso P, Gomes P. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography 21:760–771.

Chen X, Liu WY, Song L, Li S, Wu CS, Lu HZ. 2016. Adaptation of epiphytic bryophytes in the understorey attributing to the correlations and trade-offs between functional traits. Journal of Bryology 38:110–117.

Cornelissen JHC, Lang SI, Soudzilovskaia NA, During HJ. 2007. Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. Annals of Botany 99:987–1001.

Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. Ecology Letters 13:1030–1040.

Elias RB, Gil A, Silva L, Fernández-Palacios JM, Azevedo EB, Reis F. 2016. Natural zonal vegetation of the Azores Islands: Characterization and potential distribution. Phytocoenologia 46:107–123.

Ellis LT, Aleffi M, Bakalin VA, Bednarek-Ochyra H, Bergamini A, Beveridge P, Choi SS, Fedosov V, Gabriel R, Gallego MT, et al. 2015. New national and regional bryophyte records, 42. Journal of Bryology 37:68–85.

Ferreira MT, Cardoso P, Borges PAV, Gabriel R, Azevedo EB, Reis FV, Araújo M, Elias RB. 2016. Effects of climate change on the distribution of indigenous species on oceanic islands (Azores). Climatic Change 138:603–615.

Forjaz VH. 2004. Atlas básico dos Açores [Azores basic atlas]. Ponta Delgada: OVGA.

Gabriel R, Bates JW. 2005. Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. Plant Ecology 177:125–144.

Gabriel R, Coelho MCM, Henriques DSG, Borges PAV, Elias RB, Kluge J, Ah-Peng C. 2014. Long-term monitoring across elevational gradients to assess ecological hypothesis: A description of standardized sampling methods in oceanic islands and first results. Arquipelago, Life and Marine Sciences 31:45–67.

Gabriel R, Sjögren E, Schumacker R, Sérgio C, Sc A, Claro D, Homem N, Martins B. 2010. Lista de Briófitos (Anthocerotophyta, Marchantiophyta, Bryophyta). In Listagem dos organismos terrestres e marinhos dos Açores /A list of the terrestrial and marine biota of the Azores. Cascais: Principia. p. 99–115.

Garnier E, Navas ML. 2012. A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology. Agronomy for Sustainable Development 32:365–399.

Glime JM 2015. Water Relations: Physiological Adaptations. In Bryophyte Ecology. Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available online at www.bryoecol.mtu.edu accessed 5 May 2015.

Gotelli NJ, Entsminger GL. 2001. Swap and fill algorithms in null model analysis: Rethinking the Knight's Tour. Oecologia 129:281–291.

Gotelli NJ, Entsminger GL. 2003. Swap algorithms in null model analysis. Ecology 84:532–535.

Gotelli NJ, McCabe DJ. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. Ecology 83:2091–2096.

Gower JC. 1971. A general coefficient of similarity and some of its properties. Biometrics 27:857–874.

Guerra J, Martínez-Sánchez J, Ros RM. 1992. On the degree of adaptation of the moss flora and vegetation in gypsiferous zones of the south-east Iberian Peninsula. Journal of Bryology 17:133–142.

Henriques DSG, Borges PAV, Ah-Peng C, Gabriel R. 2016. Mosses and liverworts show contrasting elevational distribution patterns in an oceanic island (Terceira, Azores): The influence of climate and space. Journal of Bryology 38:183–194.

Hulshof C, Violle C, Spasojevic M, McGill B, Damschen E, Harrison S, Enquist BJ. 2013. Intraspecific and interspecific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity and latitude. Journal Of Vegetation Science. 24:921–931.

Jarzyna MA, Jetz W. 2016. Detecting the multiple facets of biodiversity. Trends in Ecology and Evolution 31:527–538.

Kichenin E, Wardle DA, Peltzer DA, Morse CWFreschet GT. 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. Functional Ecology. 27:1254–1261.

Körner C. 2007. The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22:569–574.

Laughlin DC. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. Journal of Ecology 102:186–193.

Laureto LMO, Cianciaruso MV, Samia DSM. 2015. Functional diversity: An overview of its history and applicability. Natureza & Conservação 13:112–116.

Layke C, Mapendembe A, Brown C, Walpole M, Winn J. 2012. Indicators from the global and sub-global Millennium Ecosystem Assessments: An analysis and next steps. Ecological Indicators 17:77–87.

Lefcheck JS, Bastazini VAG, Griffin J. 2015. Choosing and using multiple traits in functional diversity research. Environmental Conservation 42:104–107.

Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118.

Mateo RG, Broennimann O, Normand S, Petitpierre B, Araújo MB, Svenning J-C, Baselga A, Fernández-González F, Gómez-Rubio V, Muñoz J, et al. 2016. The mossy north: An inverse latitudinal diversity gradient in European bryophytes. Scientific Reports 6:25546.

Matteodo M, Wipf S, Stöckli V, Rixen C, Vittoz P. 2013. Elevation gradient of successful plant traits for colonizing alpine summits under climate change. Environmental Research Letters 8:024043.

Michel MJ, Knouft JH. 2014. The effects of environmental change on the spatial and environmental determinants of community-level traits. Landscape Ecology 29:467–477.

Michel P, Payton IJ, Lee WG, During HJ. 2013. Impact of disturbance on above-ground water storage capacity of bryophytes in New Zealand indigenous tussock grassland ecosystems. New Zealand Journal of Ecology 37:114–126.

Patiño, J, Mateo, RG, Zanatta, F, Marquet, A, Aranda, SC, Borges, PAV, Dirkse, G, Gabriel, R, Gonzalez-Mancebo, JM, Guisan, A, Muñoz, J, Sim-Sim, M, Vanderpoorten, A. 2016. Climate threat on the Macaronesian endemic bryophyte flora. Scientific Report 6:29156, 1–12.

Pavoine S, Bonsall MB. 2011. Measuring biodiversity to explain community assembly: A unified approach. Biological reviews of the Cambridge Philosophical Society 86:792–812.

Pavoine S, Vallet J, Dufour AB, Gachet S, Daniel H. 2009. On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. Oikos 118:391–402.

Pescador DS, De Bello F, Valladares F, Escudero A. 2015. Plant trait variation along an altitudinal gradient in Mediterranean high mountain grasslands: Controlling the species turnover effect. Plos One 10:e0118876.

Petchey OL, Gaston KJ. 2006. Functional diversity: Back to basics and looking forward. Ecology Letters 9:741–758.

Proctor MCF, Tuba Z. 2002. Poikilohydry and homoihydry: Antithesis or spectrum of possibilities? New Phytologist 156:327–349.

R Core Development Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raabe S, Müller J, Manthey M, Dürhammer O, Teuber U, Göttlein A, Förster B, Brandl R, Bässler C. 2010. Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. Forest Ecology and Management 260:1956–1964.

Spasojevic MJ, Grace JB, Harrison S, Damschen EI. 2014. Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. Journal of Ecology 102:447–455.

Swingland IR. 2001. Biodiversity, definition of. In: Levine S, editor. Encyclopedia of Biodiversity. Cambridge (MA): Academic Press. p. 377–391.

Tilman D. 2001. Functional diversity. In: Levine S, editor. Encyclopedia of Biodiversity. Cambridge (MA): Academic Press. p. 109–120.

Tsianou MA, Kallimanis AS. 2016. Different species traits produce diverse spatial functional diversity patterns of amphibians. Biodiversity and Conservation 25:117–132.

Vanderpoorten A, Goffinet B. 2009. Introduction to Bryophytes. Cambridge: Cambridge University Press.

Venn S, Pickering C, Green K. 2014. Spatial and temporal functional changes in alpine summit vegetation are driven by increases in shrubs and graminoids. Aob Plants 6:plu008.

Villéger SS, Mason NWH, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Vitt DH, Crandall-Stotler BJ, Wood A. 2012. Bryophytes: survival in a dry world through tolerance and avoidance. In: Rajakaruna N, Boyd RS, Harris TB, editors. Plant Ecology and Evolution in Harsh Environments. New York (NY): Nova Science. p. 267–295.

Waite M, Sack L. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. New Phytologist 185:156–172.

Watson W. 1914a. Xerophytic adaptations of bryophytes in relation to habitat. New Phytologist 13:149–169.

Watson W. 1914b. Xerophytic adaptations of bryophytes in relation to habitat (continued). New Phytologist 13:181–190.

Willig MR, Presley SJ. 2013. Latitudinal gradients of biodiversity. In: Levin S, editors. Encyclopedia of Biodiversity. Cambridge (MA): Academic Press. p. 612–626.