

RESEARCH ARTICLE

Divergent responses of functional diversity to an elevational gradient for vascular plants, bryophytes and lichens

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Abstract

Question: Cold environments are stressful for vascular plants, and stress-tolerant non-vascular photoautotrophs, e.g. bryophytes and lichens, become relatively more important as competition from vascular plants decreases towards higher elevations. Under increasingly stressful climatic conditions, species assembly of vascular plants is commonly driven more by environmental filtering, and abiotic constraints may lead to increased similarity between species and thus low functional diversity. Because bryophytes and lichens are less constrained by harsh environments, environmental filtering may be less strong. Instead, reduced competition from vascular plants can potentially free up niche space for non-vascular vegetation. Therefore, we hypothesized that functional diversity of vascular plants, bryophytes and lichens are likely to show contrasting responses to elevation.

Location: Finse Alpine Research Centre, Southern Norway.

Methods: We utilized measurements of species abundance and functional traits of the three groups along a 500-m elevational gradient in alpine southern Norway and calculated multi-trait and single-trait functional dispersion.

Results: Functional diversity of vascular plants declined with elevation, indicating increased environmental filtering. By contrast, functional diversity of lichens and bryophytes increased along the same gradient, suggesting they are less exposed to environmental filtering, in line with our hypothesis. Instead, they likely benefit from the lower abundance of vascular plants at higher elevation.

Conclusions: Our findings suggest that different photoautotroph groups vary in how they respond to the same environmental gradient, which may contribute to contrasting community assembly processes across groups. These divergent responses likely occur because non-vascular vegetation differs from vascular plants in terms of nutrient acquisition and water economy strategies, meaning that they respond differently to the same factors. This highlights the need to explicitly consider bryophytes and lichens in community-level studies whenever these groups are abundant.

KEYWORDS

alpine ecology, bryophytes, community assembly, functional dispersion, functional diversity, functional traits, lichens, stress gradient, vascular plants

1 | INTRODUCTION

In an ecological community, each species is represented by a group of individuals with a specific set of traits that regulate where they can exist and how they interact with the environment and other organisms (McGill et al., 2006). Further, the assemblages of traits of all the constituent species can determine community and ecosystem processes (Grime, 2001; Wardle, 2002), and for this reason, functional trait diversity can be a stronger predictor than species diversity of ecosystem functioning (Tilman et al., 1997; Díaz & Cabido, 2001). To understand the ecological consequences of functional diversity, several community-level indices have been proposed to quantify the degree of similarities and differences of traits among and within species, and how these are distributed (Mouchet et al., 2010; Pla et al., 2012). Such indices have been widely used for vascular plants to characterize variation in functional diversity among ecosystems and across environmental gradients (Pakeman, 2011; Spasojevic & Suding, 2012). However, few studies have considered functional diversity of lichens and bryophytes (Ah-Peng et al., 2014; Bässler et al., 2016; Henriques et al., 2017), despite them being important components of many ecosystems, especially at high latitudes and elevations (Lindo & Gonzalez, 2010; Asplund & Wardle, 2017).

Extreme environments in terms of low temperatures or moisture availability are stressful for vascular plants, and stress-tolerant non-vascular bryophytes and lichens become relatively more important as competition from vascular plants decreases (Cornelissen et al., 2001; Elmendorf et al., 2012). Under such stressful climatic conditions, species assembly of vascular plants is commonly driven by environmental filtering, and abiotic constraints may lead to increased similarity between species and thus to low functional diversity (Weiher & Keddy, 1995; de Bello et al., 2013). Because many alpine bryophytes and lichens are less constrained by climatically harsh environments than are vascular plants, the forces of environmental filtering may be less strong in these groups. Instead, reduced competition from vascular plants can potentially free up niche space for non-vascular vegetation and thereby increase their functional diversity. As such, functional diversity of vascular plants, bryophytes and lichens could be expected to respond in contrasting ways to environmental stress, although to our knowledge there are no empirical tests of this across natural environmental stress gradients.

Natural environmental gradients enable exploration of ecological drivers over large spatial and temporal scales in a manner that is not achievable through manipulative experiments, and when they are used carefully may have considerable potential for understanding how environmental changes impact on community and ecosystem processes (Fukami & Wardle, 2005; Walker et al., 2010). For example, studies along elevational gradients have provided insights about how macroclimate regulates community assembly and functioning of vascular plant communities (Sundqvist et al., 2013). Further, natural gradients may be particularly valuable when studying ecological responses of slow-growing organisms such as bryophytes and lichens, for which responses to short-term manipulative experiments may be too slow. A few studies have measured the response of vascular

plant functional diversity to elevational gradients, with contrasting conclusions. While de Bello et al. (2013) found decreasing functional diversity with elevation, Pescador et al. (2015) found higher trait convergence at low elevations which was explained by greater water shortage with decreasing elevation. To our knowledge, no studies to date have looked at how changes in the functional diversity of lichens or bryophytes compares with those of vascular plant functional diversity across the same environmental gradient.

In this study, we used trait and species community composition data of vascular plants, bryophytes and lichens collected by Roos et al. (2019b), along an elevational gradient spanning 500 m in alpine southern Norway. For each of these three groups across the gradient, we calculated functional dispersion (i.e., the average abundance-weighted distance of individual species to the centroid in a multivariate trait space) as a measure of multi-trait and single-trait functional diversity (Laliberté & Legendre, 2010). We used these data to test the hypothesis that functional diversity of vascular plants decreases with elevation while functional diversity of bryophytes and lichens shows the opposite response. For vascular plants, we base our hypothesis on the expectation that only stress-tolerant species will persist at higher elevation, leading to lower functional diversity (Weiher & Keddy, 1995; de Bello et al., 2013). Meanwhile, for the more stress-tolerant lichens and bryophytes, our hypothesis is based on the expectation that these groups will be less negatively affected by environmental stress at higher elevations than vascular plants and will instead benefit and have a wider range of habitat space available through less vegetation cover by vascular plants. By testing these hypotheses, we aim to advance our understanding of community assembly processes involving contrasting groups of photoautotrophs across environmental gradients or among ecosystems.

2 | METHODS

We used five sites along an elevational gradient spanning 500 m in Finse in southern Norway (60°33'–60°38' N, 7°34'–7°42' E) that were positioned at approximately 1,120, 1,240, 1,360, 1,480 and 1,600 m a.s.l. on a south-facing slope on acidic granite and gneiss bedrock, as described in Roos et al. (2019b), van Zuijlen et al. (2020) and Asplund et al. (2021). The lowest elevation had a growing season that was 54 days longer than at the highest elevation, and the average July temperature decreased with 0.9°C with each level (120 m) of increasing elevation (Roos et al., 2019b; Appendix S1). The lowest site was situated approximately 150 m above the nearest tree line (*Betula pubescens* ssp. *czerepanovii*). The plant communities are relatively species-poor with *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana* dominating the lowest two elevations, and *Carex bigelowii* and *Salix herbacea* being more common at the higher elevations. Abundant lichen species are *Cladonia arbuscula* s. lat., *Cladonia rangiferina* and *Flavocetraria nivalis*. Common bryophyte species are *Pleurozium schreberi* and *Dicranum acutifolium* at lower elevations, and *Polytrichum hyperboreum*, *Polytrichum alpinum* and *Racomitrium lanuginosum* at higher elevations (Appendix S2). Changes in species

composition of the three communities across elevation are presented in ordination plots using non-metric multi-dimensional scaling by Roos et al. (2019b).

We used data on percent cover and functional traits of vascular plants, bryophytes and lichens from this gradient collected by Roos et al. (2019b; data deposited at 2019a). Briefly, at each of the five elevations, five 1 m × 1 m plots were randomly established on ridges that each contained vascular plants, bryophytes, and lichens. The median distance between plots within elevations was 43 m, which is sufficient to ensure adequate independence among plots, given the high spatial heterogeneity in tundra communities (Björk et al., 2007; Opedal et al., 2015), and is in line with previous studies along environmental gradients in similar environments (Sundqvist et al., 2011; Veen et al., 2017). There was no relationship between spatial distance of plots and the Bray–Curtis dissimilarity index for any of the three communities (Appendix S3). From each plot, Roos et al. (2019b) collected 30 young but fully developed (i.e., current growing season) and undamaged leaves from 15 shoots (or 150 leaves for small-leaved species) for each species of vascular plant; 10 shoots of each species of bryophyte; and 10 thalli of each species of lichen. They used these materials for measuring non-chemical traits: specific leaf area (SLA, $\text{m}^2 \text{g}^{-1}$; vascular plants and bryophytes), specific thallus area (STA, $\text{m}^2 \text{g}^{-1}$; lichens), leaf dry matter content (LDMC, %; vascular plants) and water-holding capacity (WHC, g g^{-1} ; bryophytes and lichens). Lichens and bryophytes are poikilohydric and their dry matter contents will therefore vary with the water availability in their surroundings. For this reason, unlike for vascular plants, LDMC is not a relevant measure for these groups. Instead, WHC is strongly related to their water uptake and loss kinetics which is why this measure is widely used for studying their moisture characteristics (Gauslaa, 2014; Eriksson et al., 2018; Mallen-Cooper et al., 2021). In addition, they collected 500 mg of leaf material from each vascular plant species, shoots from each bryophyte species and thalli from each lichen species for analyses of tissue N, P and N:P. More detailed descriptions of the measurements of these traits are given by Roos et al. (2019b). For two vascular plant species for which we could not obtain sufficient material on a particular plot, we used the average trait value for that species from the other plots.

For each of the three photoautotroph groups (vascular plants, bryophytes and lichens) for each plot, we calculated, species richness, Pielou's evenness and functional dispersion (FDs) based on all measured standardized traits and of individual traits. Pielou's evenness was calculated as the Shannon diversity index divided by the natural logarithm of species richness. Functional dispersion is defined as the mean distance of individual species to the abundance-weighted centroid of all species in the multi-dimensional trait space (Laliberté & Legendre, 2010). The contribution of each trait was weighted, using the R package *gawdis*, to make sure that each trait contributed equally (i.e. had a similar correlation) to the measure of multi-trait dissimilarity (de Bello et al., 2021). Traits were grouped as chemical (N, P and N:P) and non-chemical (SLA/STA and LDMC/WHC), again using *gawdis*, to account for the fact that they contain some partially overlapping and redundant information. As such, the

two groups contributed equally to the measure of multi-trait dissimilarity. All calculations of functional diversity were performed using the R package *FD*.

2.1 | Statistical analysis

To test for the effect of elevation (1,120, 1,240, 1,360, 1,480 and 1,600 m a.s.l.) on evenness and functional dispersion, we performed one-way ANOVAs for each group (vascular plants, bryophytes and lichens) separately, because the non-chemical traits are not directly comparable across groups. We fitted generalized linear models, using a Poisson error distribution, to test for the effect of elevation on species richness of each taxonomic group. The assumption of equidispersion was tested using the “dispersiontest” function of the R package *AER*. Pairwise comparisons between groups were performed with the R package *emmeans*, using Tukey-adjusted *p*-values. We explored the composition of community-weighted traits (calculated and described by Roos et al., 2019b) with principal components analyses (PCA) for vascular plants, bryophytes and lichens separately using the R package *vegan*. All analyses were performed using R 4.1.1.

3 | RESULTS

Overall, species richness of lichens was 1.7 and 1.5 times higher than for vascular plants and bryophytes, respectively, across the elevation gradient (Fig 1a–c). Species richness peaked at 1,360 m for vascular plants and bryophytes, and at 1,480 m for lichens (Appendix S4). Vascular plant evenness was 1.25 times higher overall than the evenness of the bryophyte community, with lichen evenness intermediate between these two groups (Figure 1d–f). This was mainly driven by the very low bryophyte evenness at 1,240 m, which was significantly lower than the evenness at 1,120 m and 1,600 m. Lichen evenness was significantly higher at 1,600 m compared with the four other elevations. Meanwhile, vascular plant evenness was unaffected by elevation (Appendix S5).

The composition of community-weighted traits showed clear separations between the highest two elevations and the lowest two elevations for all three groups along the primary ordination axis (Fig 2). These patterns were partly driven by different traits for the three groups, but all groups had higher N:P at higher elevations. Vascular plant communities also had increasing SLA and N, and decreasing LDMC with increasing elevation. Meanwhile, bryophyte communities had decreasing P, WHC and SLA with increasing elevation, while lichen communities had increasing STA and decreasing WHC and P with increasing elevation.

Functional dispersion of the vascular plant community decreased with elevation while the bryophyte and lichen communities showed opposite responses (Fig 3). As such, functional dispersion of the vascular plant community was negatively correlated with bryophyte functional dispersion ($r = -0.545$, $p = 0.006$, Pearson),

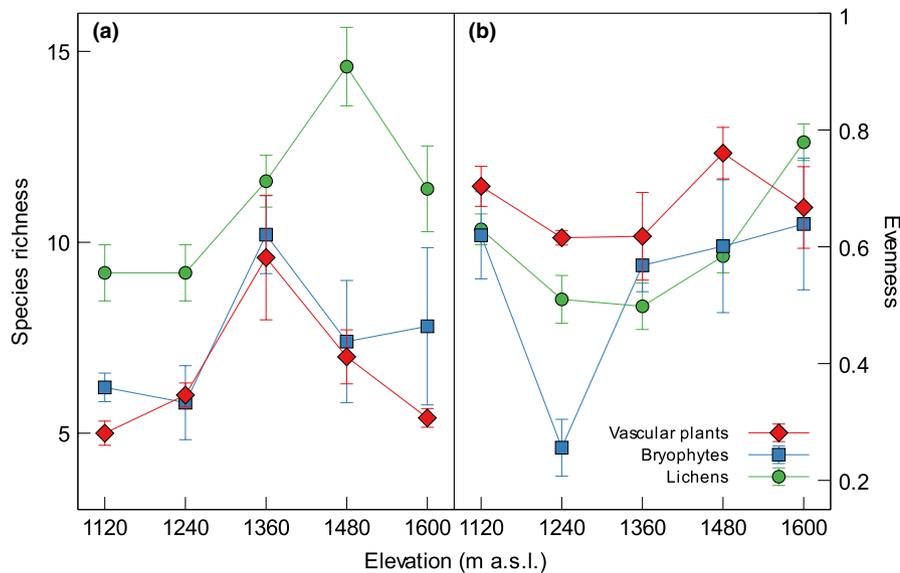


FIGURE 1 (a) Species richness and (b) evenness (mean \pm SE) of communities of vascular plants, bryophytes and lichens along an elevational gradient spanning from 1,120 to 1,600 m a.s.l. Estimates of the generalized linear model (species richness) and the one-way ANOVA (evenness) are given in Appendices S4 and S5

but not significantly with lichen functional dispersion ($r = -0.272$, $p = 0.188$, Pearson). Bryophyte and lichen functional dispersion was not correlated ($r = 0.048$, $p = 0.823$). When functional dispersion of individual traits was considered, we found that vascular plant functional dispersion either decreased with elevation (N and P), peaked at mid-elevation (LDMC and SLA), or showed no response (N:P ratio; Fig 4 left panels). Bryophytes had the highest functional dispersion at the highest site for all traits except SLA (Fig 4 mid-panels). The functional dispersion of lichen traits was non-consistently related to elevation (Fig 4 right panels). As such, functional dispersion of STA was highest at the two highest elevations. Further, functional dispersion of WHC tended to increase with elevation, but the highest elevation was only significantly higher than the central elevation. Chemical lichen traits were less responsive to elevation.

4 | DISCUSSION

Our finding that increased functional similarity (decreased functional dispersion) of the vascular plant community increased with increasing elevation is in line with our hypothesis. As such, it indicates a higher degree of environmental filtering under colder and harsher conditions, and selection from the species pool for species with a narrower range of ecological tolerance (Grime, 2006; Garnier et al., 2007). Temperature acts as a key environmental filter that drives changes in vascular plant community composition, and this commonly leads to convergence of functional leaf traits to those associated with stress tolerance (Read et al., 2014).

The higher functional diversity at lower elevation in part emerged because these sites were dominated by ericaceous shrubs which have high interspecific trait variability relative to the regional species pool (Roos et al., 2019b). These species are scarce above 1,500 m a.s.l. in Fennoscandia (Heegaard, 2002), and in our study they were largely absent from the highest elevations. Instead, the highest elevation was dominated by *Salix herbacea* and *Carex*

bigelowii, species with low interspecific trait variability (both showing similarly high N concentrations and SLA), which are less sensitive to low temperatures (Beerling, 1998; Brooker et al., 2001). The decreasing functional diversity was most pronounced for the chemical traits, while non-chemical traits peaked at mid-elevations. Trait divergence at lower elevations could have emerged because higher competition under more favourable environments limits the level of co-occurrence of similar species (MacArthur & Wilson, 1967). The stress gradient hypothesis suggests increasing positive plant-plant interactions with increasing physical stress (Bertness & Callaway, 1994), which could cause a relaxation of the environmental filtering at higher elevations (Schöb et al., 2012). The lack of such response in our data, could be due to the absence of typical foundation species in the communities, such as distinct cushion plants like *Silene acaulis* (Antonsson et al., 2009).

In contrast to the vascular plant community and in line with our hypothesis, functional trait diversity of the lichen and bryophyte communities increased with increasing elevation and lower temperatures. As such, the lichen and bryophyte communities showed evidence for a lower degree of environmental filtering with increasing elevation. This pattern could have arisen because lichens and bryophytes, when dry, are far more freeze-tolerant than are vascular plants (Kappen, 2000). The latter may also suffer from frost drought if snow cover is not sufficient and from wind abrasion, which is more critical for vascular plant tissue than for bryophytes and lichens (Körner, 2003). Also, some lichens are capable of net photosynthesis at temperatures below -10°C , thus being able to extend their growing season at higher elevations (Kappen, 1993) leading to a competitive advantage over vascular plants. The greater trait dispersion at higher elevations, which is indicative of greater niche differentiation, likely arose because with increasing elevation the competition from vascular plants decreases, thus allowing lichen and bryophyte species to occupy a greater diversity of niches. This suggests that competition from vascular plants at lower elevations results in a greater filtering of the lichen

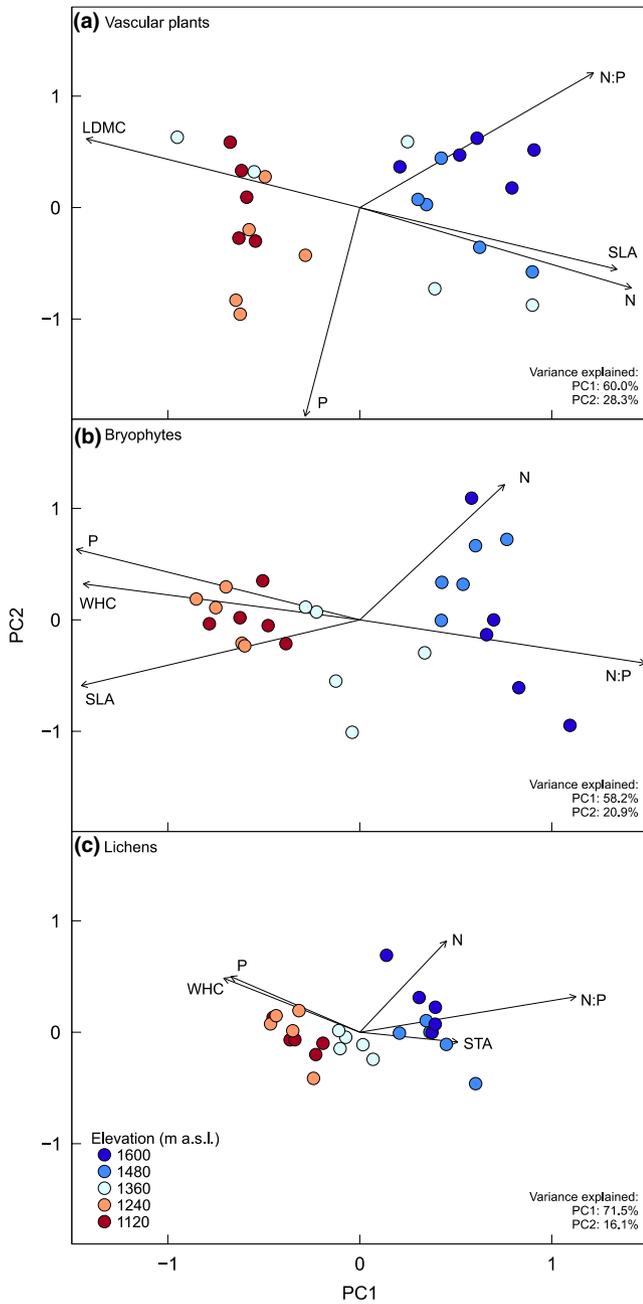


FIGURE 2 Principal component analyses of functional traits at the community level for (a) vascular plants, (b) bryophytes and (c) lichen communities. Arrows indicate direction and weighing of vectors representing the six traits considered. Dots indicate individual plots and colours denote their elevation. The six considered traits are nitrogen (N), phosphorous (P), nitrogen to phosphorous ratio (N:P), specific leaf (thallus for lichens) area (SLA or STA), leaf dry matter content (LDMC; vascular plants only), water-holding capacity (WHC; bryophytes and lichens only)

community than does the harsher environment at high elevations. In support of this explanation, increasing lichen functional diversity was only found for STA and WHC, which are known to be responsive to changes in microclimate (Gauslaa, 2014) that in turn are affected by changes in vegetation cover. Meanwhile, functional diversity of thallus nutrients did not increase with elevation. This

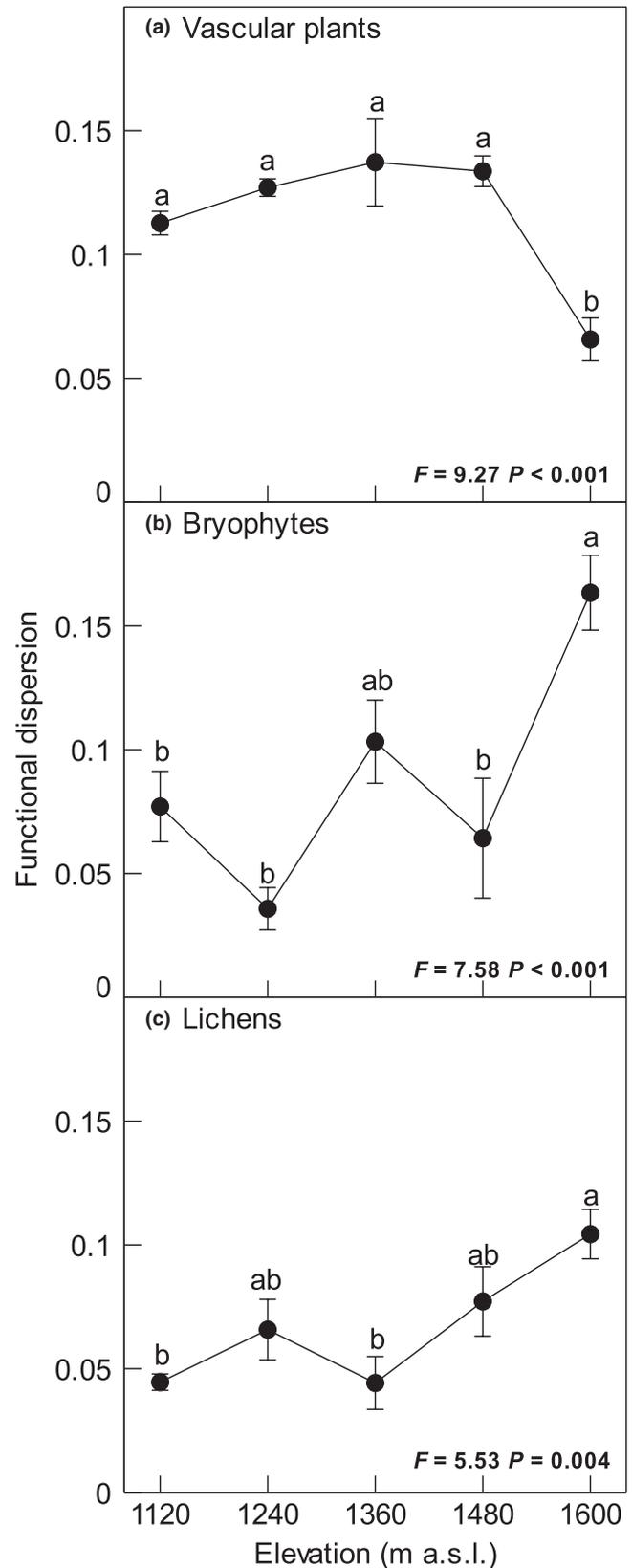


FIGURE 3 Mean (\pm SE) functional dispersion (FDi) of vascular plants (a), bryophytes (b) and lichens (c) at five different elevations. *F*- and *p*-values are derived from one-way ANOVAs. Bold values indicate significant effects at $p < 0.05$. Within panels, dots not topped with the same letter are significantly different at $p < 0.05$ according to Tukey's test

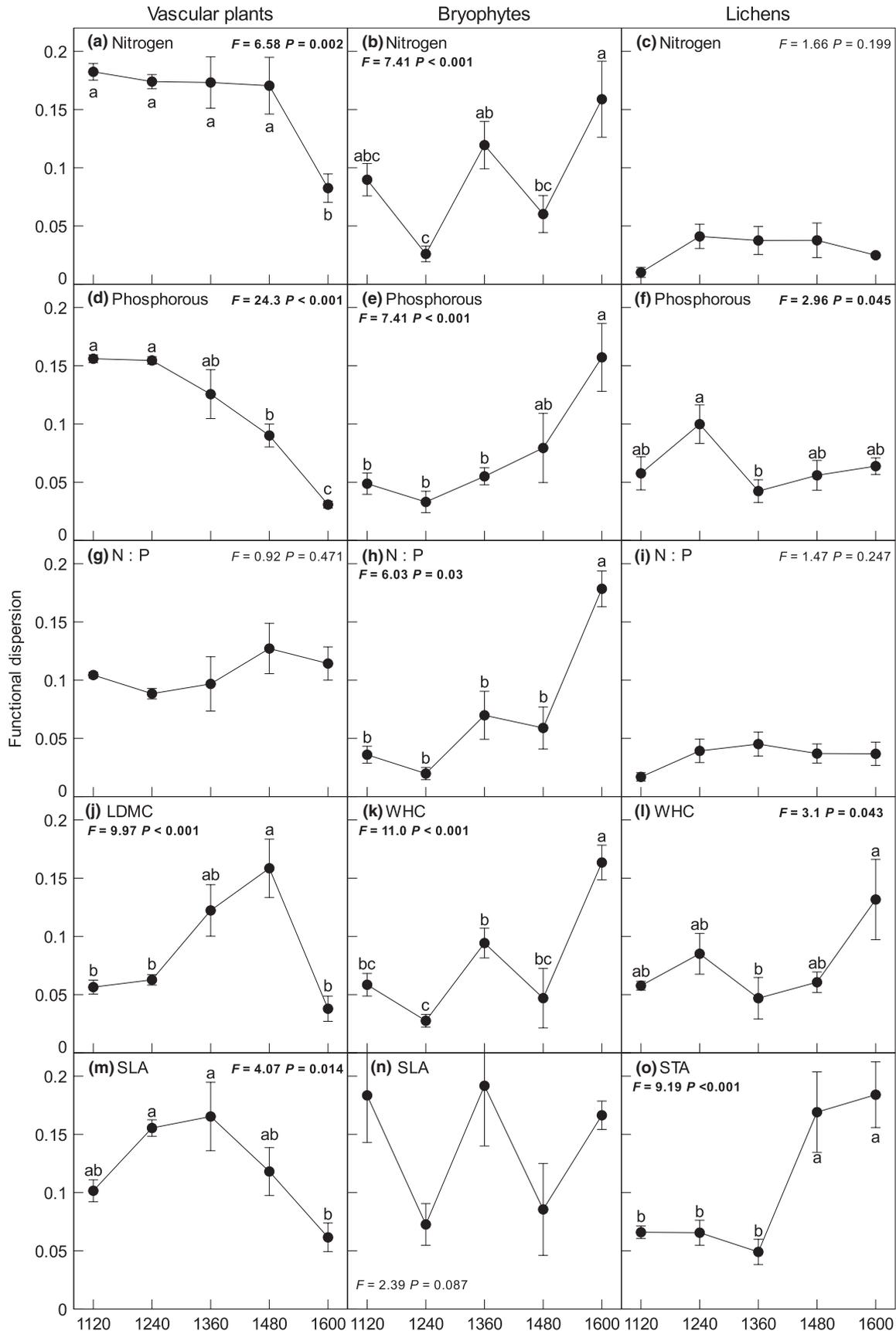


FIGURE 4 Mean (\pm SE) functional dispersion (FDi) of individual traits (tissue N and P concentration, N to P ratio, leaf dry matter content [LDMC; vascular plants], water-holding capacity [WHC; bryophytes and lichens] and specific leaf/thallus area [SLA/STA]) of vascular plants (left panels), bryophytes (middle panels) and lichens (right panels) at five different elevations. F- and p-values are derived from one-way ANOVAs. Bold values indicate significant effects at $p < 0.05$. Within panel, dots not topped with the same letter are significantly different at $p < 0.05$ according to Tukey's test

is not surprising given that mat-forming lichens commonly thrive on N- and P-deficient substrates, and lichens as well as bryophytes primarily acquire nutrients from wet and dry atmospheric deposition rather than from the soil (Crittenden, 2000; Glime, 2017).

Bryophyte communities at lower elevations were dominated by two mosses, the shade-tolerant *Hylocomium splendens* and *Pleurozium schreberi* (Roos et al., 2019b) which are similar in their functional traits (both have high SLA and P); thus, the combination of their dominance and similarity in functional traits lead to an overall decrease in bryophyte functional diversity. At 1,240 m, *Pleurozium schreberi* had a relative cover of 90%, which explains the low evenness. Contrary to our results, Henriques et al. (2017) found decreasing functional diversity of bryophyte communities with elevation along an Azorean gradient. However, this gradient showed strong changes in moisture conditions, not only temperature, and the structural traits studied were associated with water acquisition and retention, reflecting mild and moist conditions at sea level to warm and dry conditions at higher elevations.

Our findings suggest that the three different photoautotroph groups experience the same environmental gradient differently, resulting in contrasting community assembly processes across these groups. This may arise because these groups have different means of acquiring nutrients, and differ greatly in their water economy strategies (i.e. poikilohydric vs homeohydric) and thereby perceive different environmental gradients in the same physical space. Also, interactions among groups are likely to play an important role; increased competition by larger faster-growing vascular plants in more favourable environments limits the extent of slower-growing bryophytes and lichens. Our findings suggest that climate warming might lead to trait divergence of vascular plants, but that the direct effect of warming probably has a less direct impact on bryophyte and lichen community assembly processes. Instead, bryophyte and lichen communities will be indirectly affected through increased competition from vascular plants (Cornelissen et al., 2001; Lang et al., 2012), causing trait convergence. This highlights the importance of including lichens and bryophytes when aiming to understand how photoautotroph communities respond to variation in environmental conditions in space or time.

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AUTHOR CONTRIBUTIONS

JA designed the study in consultation with KvZ, RER, TB, KK, SIL and DAW. Field and laboratory work was conducted by KvZ and RER with support of JA, KK, SIL and TB. Writing and data analysis were

led by JA. All authors contributed to revisions and discussions and approved the final version.

DATA AVAILABILITY STATEMENT

Data associated with this manuscript are deposited in the NMBU Open Research Data database (<https://doi.org/10.18710/FROQNN>).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Mean July temperature and number of days above 5°C per site

Appendix S2. Abbreviations, full species names and relative cover of vascular plant, lichen and bryophyte species found in 1 m × 1 m plots along the elevational gradient

Appendix S3. Spatial distance between pairs of plots vs Bray–Curtis dissimilarity of communities of vascular plants, bryophytes and lichens

Appendix S4. Generalized linear model testing for the effect of elevation on species richness of vascular plants, bryophytes, and lichens

Appendix S5. One-way ANOVA testing for the effect of elevation on evenness of vascular plants, bryophytes and lichens

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