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

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27

28 **Abstract**

29 *Question*

30 Cold environments are stressful for vascular plants, and stress-tolerant non-vascular

31 photoautotrophs, e.g. bryophytes and lichens, become relatively more important as competition

32 from vascular plants decreases towards higher elevations. Under increasingly stressful climatic

33 conditions, species assembly of vascular plants is commonly driven more by environmental

34 filtering, and abiotic constraints may lead to increased similarity between species and thus low

35 functional diversity. Because bryophytes and lichens are less constrained by harsh environments,

36 environmental filtering may be less strong. Instead, reduced competition from vascular plants can

37 potentially free up niche space for non-vascular vegetation. Therefore, we hypothesized that

38 functional diversity of vascular plants, bryophytes and lichens are likely to show contrasting

39 responses to elevation.

40 *Location*

41 Finse Alpine Research Centre, Southern Norway.

42 *Methods*

43 We utilized measurements of species abundance and functional traits of the three groups along a

44 500m elevational gradient in alpine southern Norway and calculated multi-trait and single-trait

45 functional dispersion.

46 *Results*

47 Functional diversity of vascular plants declined with elevation, indicating increased environmental

48 filtering. By contrast, functional diversity of lichens and bryophytes increased along the same

49 gradient, suggesting they are less exposed to environmental filtering, in line with our hypothesis.

50 Instead, they likely benefit from the lower abundance of vascular plants at higher elevation,

51 leading to a negative relationship between lichen and bryophyte functional diversity and vascular

52 plant cover.

53 *Conclusions*

54 Our findings suggest that different photoautotroph groups vary in how they respond to the same

55 environmental gradient, which may contribute to contrasting community assembly processes

56 across groups. These divergent responses likely occur because non-vascular vegetation differs

57 from vascular plants in terms of nutrient acquisition and water economy strategies, meaning that

58 they respond differently to the same factors. This highlights the need to explicitly consider

59 bryophytes and lichens in community-level studies whenever these groups are abundant.

60 **Keywords:** Alpine ecology; Bryophytes; Community assembly; Functional traits; Functional

61 dispersion; Functional diversity, Lichens, Stress-gradient; Vascular plants

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

93 environmental changes impact on community and ecosystem processes (Fukami & Wardle 2005;

94 Walker et al. 2010). For example, studies along elevational gradients have provided insights about

95 how macroclimate regulates community assembly and functioning of vascular plant communities

96 (Sundqvist et al. 2013). Further, natural gradients may be particularly valuable when studying

97 ecological responses of slow-growing organisms such as bryophytes and lichens, for which

98 responses to short-term manipulative experiments may be too slow. A few studies have measured

99 the response of vascular plant functional diversity to elevational gradients, with contrasting

100 conclusions. While de Bello et al. (2013) found decreasing functional diversity with elevation,

101 Pescador et al. (2015) found higher trait convergence at low elevations which was explained by

102 greater water shortage with decreasing elevation. To our knowledge, no studies to date have

103 looked at how changes in the functional diversity of lichens or bryophytes compares with those of

104 vascular plant functional diversity across the same environmental gradient.

105 In this study, we used trait and species community composition data of vascular plants,

106 bryophytes and lichens collected by Roos et al. (2019b), along an elevational gradient spanning

107 500 m in alpine southern Norway. For each of these three groups across the gradient, we

108 calculated functional dispersion (i.e., the average abundance-weighted distance of individual

109 species to the centroid in a multivariate trait-space) as a measure of multi-trait and single-trait

110 functional diversity (Laliberté & Legendre 2010). We used this data to test the hypothesis that

111 functional diversity of vascular plants decreases with elevation while functional diversity of

112 bryophytes and lichens shows the opposite response. For vascular plants, we base our hypothesis

113 on the expectation that only stress-tolerant species will persist at higher elevation, leading to lower

114 functional diversity (Weiher & Keddy 1995; de Bello et al. 2013). Meanwhile, for the more stress-

115 tolerant lichens and bryophytes, our hypothesis is based on the expectation that these groups will

116 be less negatively affected by environmental stress at higher elevations than vascular plants and

117 will instead benefit and have a wider range of habitat space available through less vegetation cover

118 by vascular plants. By testing these hypotheses, we aim to advance our understanding of

119 community assembly processes involving contrasting groups of photoautotrophs across

120 environmental gradients or among ecosystems.

121

122 **Materials and Methods**

123 We used five sites along elevational gradient spanning 500 m in Finse in southern Norway

124 (60°33'N–60°38'N, 7°34'E–7°42'E) that were positioned at approximately 1120, 1240, 1360, 1480

125 and 1600 m a.s.l. on a south-facing slope on acidic granite and gneiss bedrock, as described in

126 Roos et al (2019b), van Zuijlen et al. (2020) and Asplund (2021). The lowest elevation had a

127 growing season that was 54 days longer than the highest elevation, and the average July

128 temperature decreased with 0.9 °C with each level (120 m) of increasing elevation (Roos et al.

129 2019b; Appendix S1). The lowest site was situated approximately 150 m above the nearest tree

130 line (*Betula pubescens* ssp. *czerepanovii*). The plant communities are relatively species poor with

131 *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana* dominating the lowest two elevations,

132 and *Carex bigelowii* and *Salix herbacea* being more common at the higher elevations. Abundant

133 lichen species are *Cladonia arbuscula* s. lat., *C. rangiferina* and *Flavocetraria nivalis*. Common

134 bryophyte species are *Pleurozium schreberi* and *Dicranum acutifolium* at lower elevations, and

135 *Polytrichum hyperboreum*, *P. alpinum* and *Racomitrium lanuginosum* at higher elevations

136 (Appendix S2). Changes in species composition of the three communities across elevation are

137 presented in ordination plots using non-metric multidimensional scaling by Roos et al. (2019b).

138 We used data on percent cover and functional traits of vascular plants, bryophytes and

139 lichens from this gradient collected by Roos et al. (2019b; data deposited at 2019a). Briefly, at

140 each of the five elevations, five 1×1 m plots were randomly established on ridges that each

141 contained vascular plants, bryophytes, and lichens. The median distance between plots within

142 elevations was 43 m, which is sufficient to ensure adequate independence among plots, given the

143 high spatial heterogeneity in tundra communities (Björk et al. 2007; Opedal et al. 2015), and is in

144 line with previous studies along environmental gradients in similar environments (Sundqvist et al.

145 2011; Veen et al. 2017). There was no relationship between spatial distance of plots and the Bray-

146 Curtis dissimilarity index for any of the three communities (Appendix S3). From each plot, Roos

147 et al. (2019b) collected 30 young but fully developed (i.e. current growing season) and undamaged

148 leaves from 15 shoots (or 150 leaves for small-leaved species) for each species of vascular plant;

149 10 shoots of each species of bryophyte; and 10 thalli of each species of lichen. They used these

150 materials for measuring non-chemical traits: specific leaf area (SLA, $m^2\,g^{-1}$; vascular plants and

151 bryophytes), specific thallus area (STA, $m^2\,g^{-1}$; lichens), leaf dry matter content (LDMC, %;

152 vascular plants) and water holding capacity (WHC, $g\,g^{-1}$; bryophytes and lichens). Lichens and

153 bryophytes are poikilohydric and their dry matter contents will therefore vary with the water

154 availability in their surroundings. For this reason, unlike for vascular plants, LDMC is not a

155   relevant measure for these groups. Instead, WHC is strongly related to their water uptake and loss

156   kinetics which is why this measure is widely used for studying their moisture characteristics

157   (Gauslaa 2014; Eriksson et al. 2018; Mallen-Cooper et al. 2021). In addition, they collected 500

158   mg of leaf material from each vascular plant species, shoots from each bryophyte species and

159   thalli from each lichen species for analyses of tissue N, P and N:P. More detailed descriptions of

160   the measurements of these traits are given by Roos et al. (2019b). For two vascular plant species

161   for which we could not obtain sufficient material on a particular plot, we used the average trait

162   value for that species from the other plots.

163   For each of the three photoautotroph groups (vascular plants, bryophytes and lichens) for each

164   plot, we calculated, species richness, Pielou's evenness and functional dispersion (FDis) based on

165   all measured standardized traits and of individual traits. Pielou's evenness was calculated as the

166   Shannon diversity index divided by the natural logarithm of species richness. Functional

167   dispersion is defined as the mean distance of individual species to the abundance-weighted

168   centroid of all species in the multidimensional trait-space (Laliberté & Legendre 2010). The

169   contribution of each trait was weighted, using the R package gawdis, to make sure that each trait

170   contributed equally (i.e. had a similar correlation) to the measure of multi-trait dissimilarity (de

171   Bello et al. 2021). Traits were grouped as chemical (N, P and N:P) and non-chemical (SLA/STA

172   and LMDC/WHC), again using gawdis, to account for the fact that they contain some partially

173   overlapping and redundant information. As such, the two groups contributed equally to the

174   measure of multi-trait dissimilarity. All calculations of functional diversity were performed using

175   the R package FD (Laliberté et al. 2014).

176

177   *Statistical analysis*

178   To test for the effect of elevation (1120, 1240, 1360, 1480 and 1600 m a.s.l.) on evenness and

179   functional dispersion, we performed one-way ANOVAs for each group (vascular plants,

180   bryophytes, and lichens) separately, because the non-chemical traits are not directly comparable

181   across groups. We fitted generalized linear models, using a Poisson error distribution, to test for

182   the effect of elevation on species richness of each taxonomic group. The assumption of

183   equidispersion was tested using the dispersiontest function of the R-package AER (Kleiber &

184   Zeileis 2008). Pairwise comparisons between groups were performed with the R package

185 emmeans, using Tukey-adjusted *P*-values (Lenth 2021). We explored the composition of

186 community weighted traits (calculated and described by Roos et al. 2019b) with principal

187 component analyses (PCA) for vascular plants, bryophytes and lichens separately using the R

188 package vegan (Oksanen et al. 2016). All analyses were performed using R 4.1.1 (R Core Team

189 2021).

190

191 **Results**

192 Overall, species richness of lichens was 1.7 and 1.5 times higher than for vascular plants and

193 bryophytes, respectively, across the elevation gradient (Fig. 1a-c). Species richness peaked at 1360

194 m for vascular plants and bryophytes, and at 1480 m for lichens (Appendix S4). Vascular plant

195 evenness was 1.25 times higher overall than the evenness of the bryophyte community, with lichen

196 evenness intermediate between these two groups (Fig. 1d-f). This was mainly driven by the very

197 low bryophyte evenness at 1240 m, which was significantly lower than the evenness at 1120 m

198 and 1600 m. Lichen evenness was significantly higher at 1600 m compared with the four other

199 elevations. Meanwhile, vascular plant evenness was unaffected be elevation (Appendix S5)

200 The composition of community-weighted traits showed clear separations between the

201 highest two elevations and the lowest two elevations for all three groups along the primary

202 ordination axis (Fig. 2). These patterns were partly driven by different traits for the three groups,

203 but all groups had higher N:P at higher elevations. Vascular plant communities also had increasing

204 specific leaf area and N, and decreasing leaf dry matter content with increasing elevation.

205 Meanwhile, bryophyte communities had decreasing P, WHC and SLA with increasing elevation,

206 while lichen communities had increasing STA and decreasing WHC and P with increasing

207 elevation.

208 Functional dispersion of the vascular plant community decreased with elevation while the

209 bryophyte and lichen communities showed opposite responses (Fig. 3). As such, functional

210 dispersion of the vascular plant community was negatively correlated with bryophyte functional

211 dispersion (r = -0.545, *P* =0.006, Pearson), but not significantly with lichen functional dispersion

212 (r = -0.272, *P* = 0.188, Pearson). Bryophyte and lichen functional dispersion was not correlated (r

213 = 0.048, *P* = 0.823). When functional dispersion of individual traits was considered, we found that

214 vascular plant functional dispersion either decreased with elevation (N and P), peaked at mid

215 elevation (leaf dry matter content and specific leaf area), or showed no response (N:P ratio) (Fig. 4

216 left panels). Bryophytes had the highest functional dispersion at the highest site for all traits except

217 SLA (Fig. 4 mid panels). The functional dispersion of lichen traits was non-consistently related to

218 elevation (Fig. 4 right panels). As such, functional dispersion of STA was highest at the two

219 highest elevations. Further, functional dispersion of WHC tended to increase with elevation, but

220 the highest elevation was only significantly higher than the central elevation. Chemical lichen

221 traits were less responsive to elevation.

222

223 **Discussion**

224 Our finding that increased functional similarity (decreased functional dispersion) of the vascular

225 plant community increased with increasing elevation is in line with our hypothesis. As such, it

226 indicates a higher degree of environmental filtering under colder and harsher conditions, and

227 selection from the species pool for species with a narrower range of ecological tolerance (Grime

228 2006; Garnier et al. 2007). Temperature acts as a key environmental filter that drives changes in

229 vascular plant community composition, and this commonly leads to convergence of functional leaf

230 traits to those associated with stress tolerance (Read et al. 2014).

231   The higher functional diversity at lower elevation in part emerged because these sites were

232 dominated by ericaceous shrubs which have high interspecific trait variability relative to the

233 regional species pool (Roos et al. 2019b). These species are scarce above 1500 m a.s.l. in

234 Fennoscandia (Heegaard 2002), and in our study they were largely absent from the highest

235 elevations. Instead, the highest elevation was dominated by *Salix herbacea* and *Carex bigolowii*,

236 species with low interspecific trait variability (both showing similarly high N concentrations and

237 SLA), which are less sensitive to low temperatures (Beerling 1998; Brooker et al. 2001). The

238 decreasing functional diversity was most pronounced for the chemical traits, while non-chemical

239 traits peaked at mid-elevations. Trait divergence at lower elevations could have emerged because

240 higher competition under more favourable environments limits the level of co-occurrence of

241 similar species (MacArthur & Wilson 1967). The stress gradient hypothesis suggests increasing

242 positive plant-plant interactions with increasing physical stress (Bertness & Callaway 1994),

243 which could cause a relaxation of the environmental filtering at higher elevations (Schöb et al.

244 2012). The lack of such response in our data, could be due to the absence of typical foundation

245 species in the communities, such as distinct cushion plants like *Silene acaulis* (Antonsson et al.
246 2009).

247   In contrast to the vascular plant community and in line with our hypothesis, functional trait
248 diversity of the lichen and bryophyte communities increased with increasing elevation and lower
249 temperatures. As such, the lichen and bryophyte communities showed evidence for a lower degree
250 of environmental filtering with increasing elevation. This pattern could have arisen because
251 lichens and bryophytes, when dry, are far more freeze tolerant than are vascular plants (Kappen
252 2000). The latter may also suffer from frost drought if snow cover is not sufficient and from wind
253 abrasion, which is more critical for vascular plant tissue than for bryophytes and lichens (Körner
254 2003). Also, some lichens are capable of net photosynthesis at temperatures below -10°C, thus
255 being able to extend their growing season at higher elevations (Kappen 1993) leading to a
256 competitive advantage over vascular plants. The greater trait dispersion at higher elevations, which
257 is indicative of greater niche differentiation, likely arose because with increasing elevation the
258 competition from vascular plants decreases, thus allowing lichen and bryophyte species to occupy
259 a greater diversity of niches. This suggests that competition from vascular plants at lower
260 elevations results in a greater filtering of the lichen community than does the harsher environment
261 at high elevations. In support of this explanation, increasing lichen functional diversity were only
262 found for STA and WHC, which are known to be responsive to changes in microclimate (Gauslaa
263 2014) that in turn are affected by changes in vegetation cover. Meanwhile, functional diversity of
264 thallus nutrients did not increase with elevation. This is not surprising given that mat-forming
265 lichens commonly thrive on N and P deficient substrates, and lichens as well as bryophytes
266 primarily acquire nutrients from wet and dry atmospheric deposition rather than from the soil
267 (Crittenden 2000; Glime 2017).

268   Bryophyte communities at lower elevations were dominated by two mosses, the shade-
269 tolerant *Hylocomium splendens* and *Pleurozium schreberi* (Roos et al. 2019b) which are similar in
270 their functional traits (both have high SLA and P); thus, the combination of their dominance and
271 similarity in functional traits leading to an overall decrease in bryophyte functional diversity. At
272 1240 m, *P. schreberi* had a relative cover of 90%, which explains the low evenness. Contrary to
273 our results, Henriques (2017) found decreasing functional diversity of bryophyte communities
274 with elevation along an Azorean gradient. However, this gradient showed strong changes in
275 moisture conditions, not only elevation, and the structural traits studied were associated with water

276 acquisition and retention, reflecting mild and moist conditions at sea level to warm and dry

277 conditions at higher elevations.

278   Our findings suggest that the three different photoautotroph groups experience the same

279 environmental gradient differently, resulting in contrasting community assembly processes across

280 these groups. This may arise because these groups have different means of acquiring nutrients, and

281 differ greatly in their water economy strategies (i.e. poikilohydric vs homeohydric) and thereby

282 perceive different environmental gradients in the same physical space. Also, interactions among

283 groups are likely to play an important role; increased competition by larger faster-growing

284 vascular plants in more favourable environments limits the extent of slower-growing bryophytes

285 and lichens. Our findings suggest that climate warming might lead to trait divergence of vascular

286 plants, but that the direct effect of warming probably has a less direct impact on bryophyte and

287 lichen community assembly processes. Instead, bryophyte and lichen communities will be

288 indirectly affected through increased competition from vascular plants (Cornelissen et al. 2001;

289 Lang et al. 2012), causing trait convergence. This highlights the importance of including lichens

290 and bryophytes when aiming to understand how photoautotroph communities respond to variation

291 in environmental conditions in space or time.

292

300

Author contribution

302 J.A. designed the study in consultation with K.v.Z, R.E.R., T.B., K.K., S.I.L. and D.AW. Field and

303 laboratory work was conducted by K.v.Z. and R.E.R. with support of J.A., K.K., S.I.L. and T.B.

304 Writing and data analysis were led by J.A. All authors contributed to revisions and discussions and
305 approved the final version.

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310 **Data availability**

311 Data associated with this manuscript are deposited in the NMBU Open Research Data database
312 (https://doi.org/10.18710/FR0QNN).

313 **Literature**

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464

Appendices list

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 1×1 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.

475

476   **Figure legends**

477   **Figure 1.** (a) Species richness and (b) evenness (mean ± SE) of communities of vascular plants,

478   bryophytes and lichens along an elevational gradient spanning from 1120 to 1600 m a.s.l.

479   Estimates of the generalized linear model (species richness) and the one-way ANOVA (evennesss)

480   are given in Appendix S4-S5.

481   **Figure 2.** Principal component analyses of functional traits at the community level for (a) vascular

482   plants, (b) bryophytes and (c) lichen communities. Arrows indicate direction and weighing of

483   vectors representing the six traits considered. Dots indicate individual plots and their colour denote

484   their elevation. The six considered traits are nitrogen (N), phosphorous (P), nitrogen to

485   phosphorous ratio (N:P), specific leaf (thallus for lichens) area (SLA or STA), leaf dry matter

486   content (LDMC; vascular plants only), water holding capacity (WHC; bryophytes and lichens

487   only).

488   **Figure 3.** Mean (± SE) functional dispersion (FDis) of vascular plants (a), bryophytes (b) and

489   lichens (c) at five different elevations. *F* and *P* values are derived from one-way ANOVAs. Bold

490   values indicate significant effects at P<0.05. Within panel, dots not topped with the same letter are

491   significantly different at P<0.05 according to Tukey's test.

492   **Figure 4**. Mean (± SE) functional dispersion (FDis) of individual traits (tissue N and P

493   concentration, N to P ratio, leaf dry matter content [LDMC; vascular plants], water holding

494   capacity [WHC; bryophytes and lichens] and specific leaf/thallus area [SLA/STA] of vascular

495   plants (left panels), bryophytes (middle panels) and lichens (right panels) at five different

496   elevations. *F* and *P* values are derived from one-way ANOVAs. Bold values indicate significant

497   effects at P<0.05. Within panel, dots not topped with the same letter are significantly different at
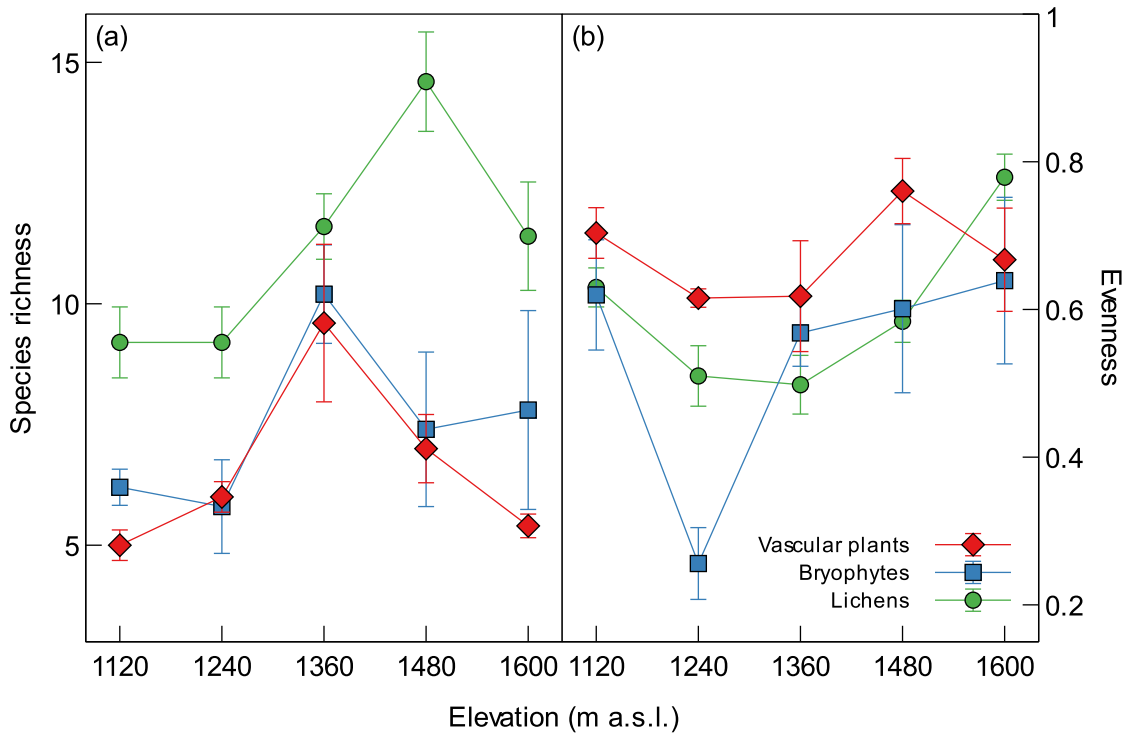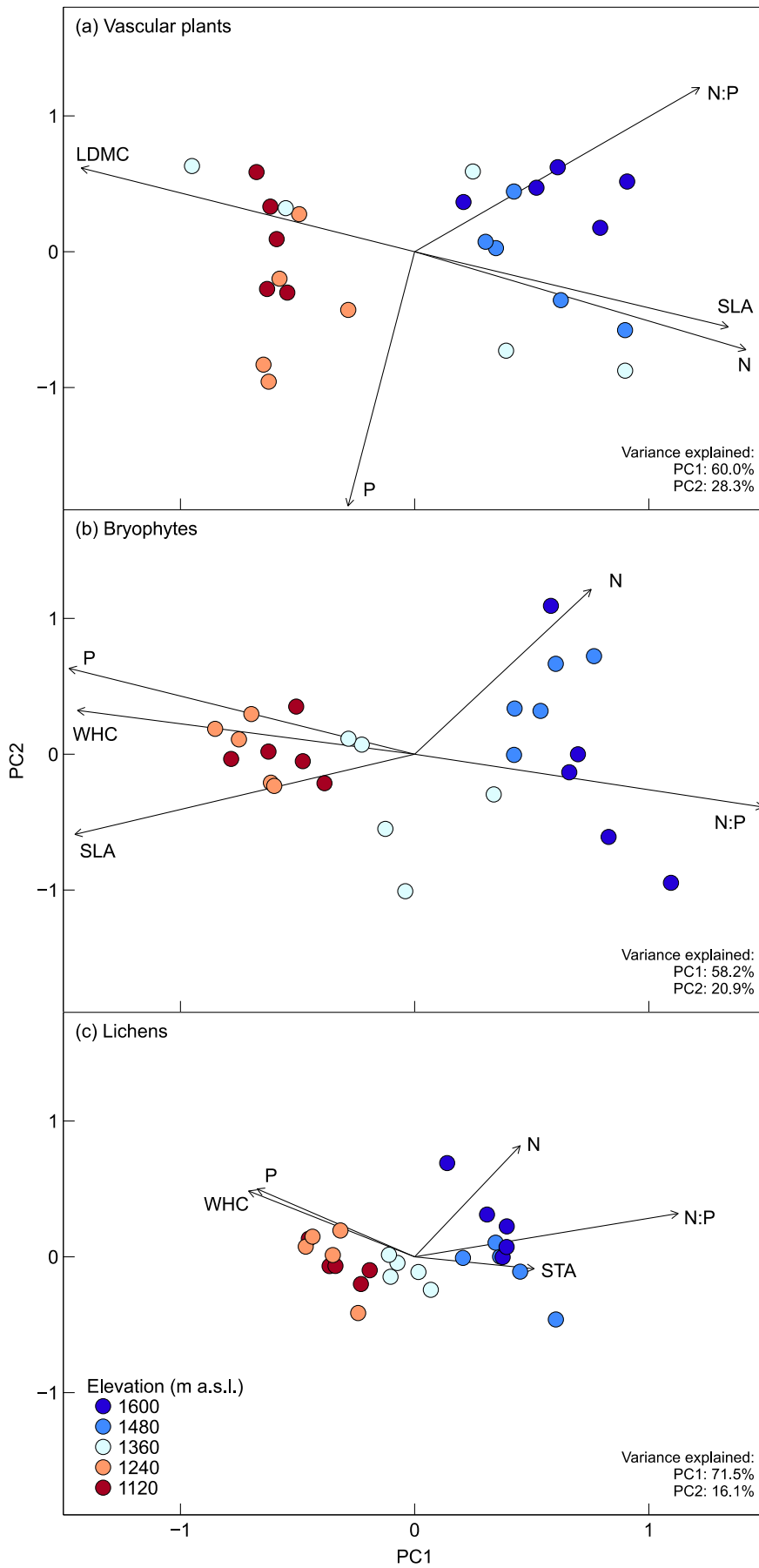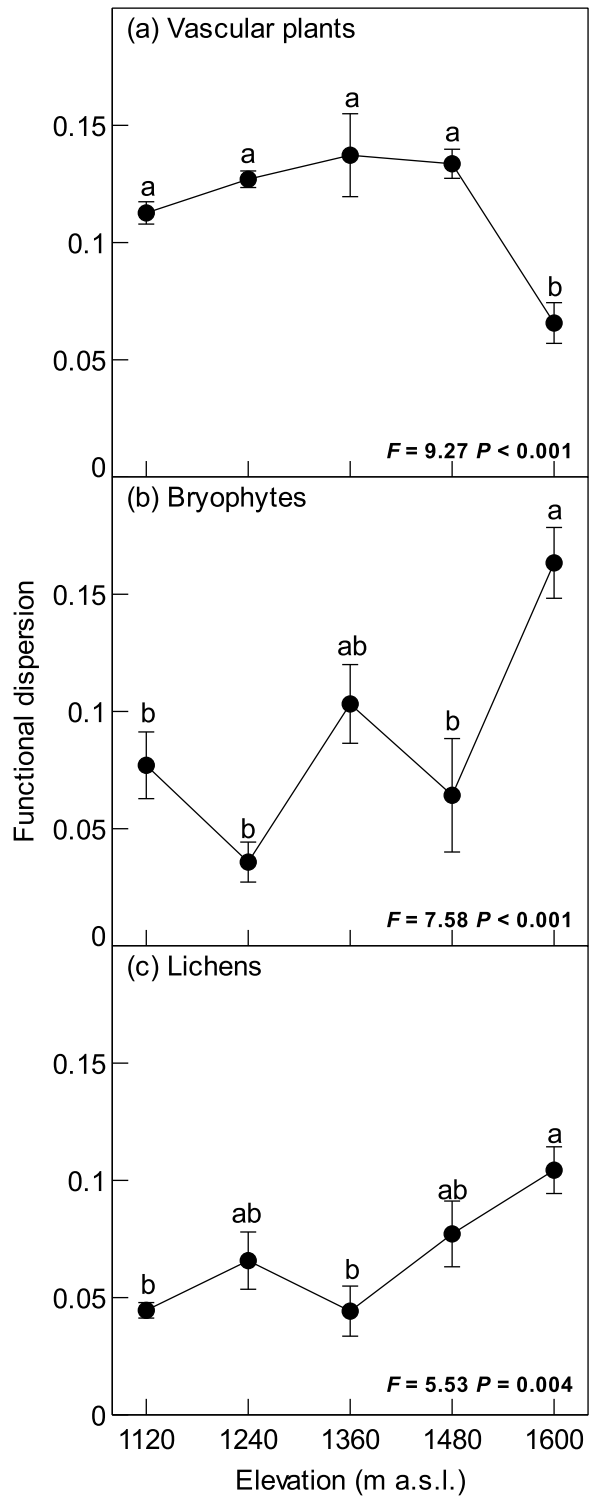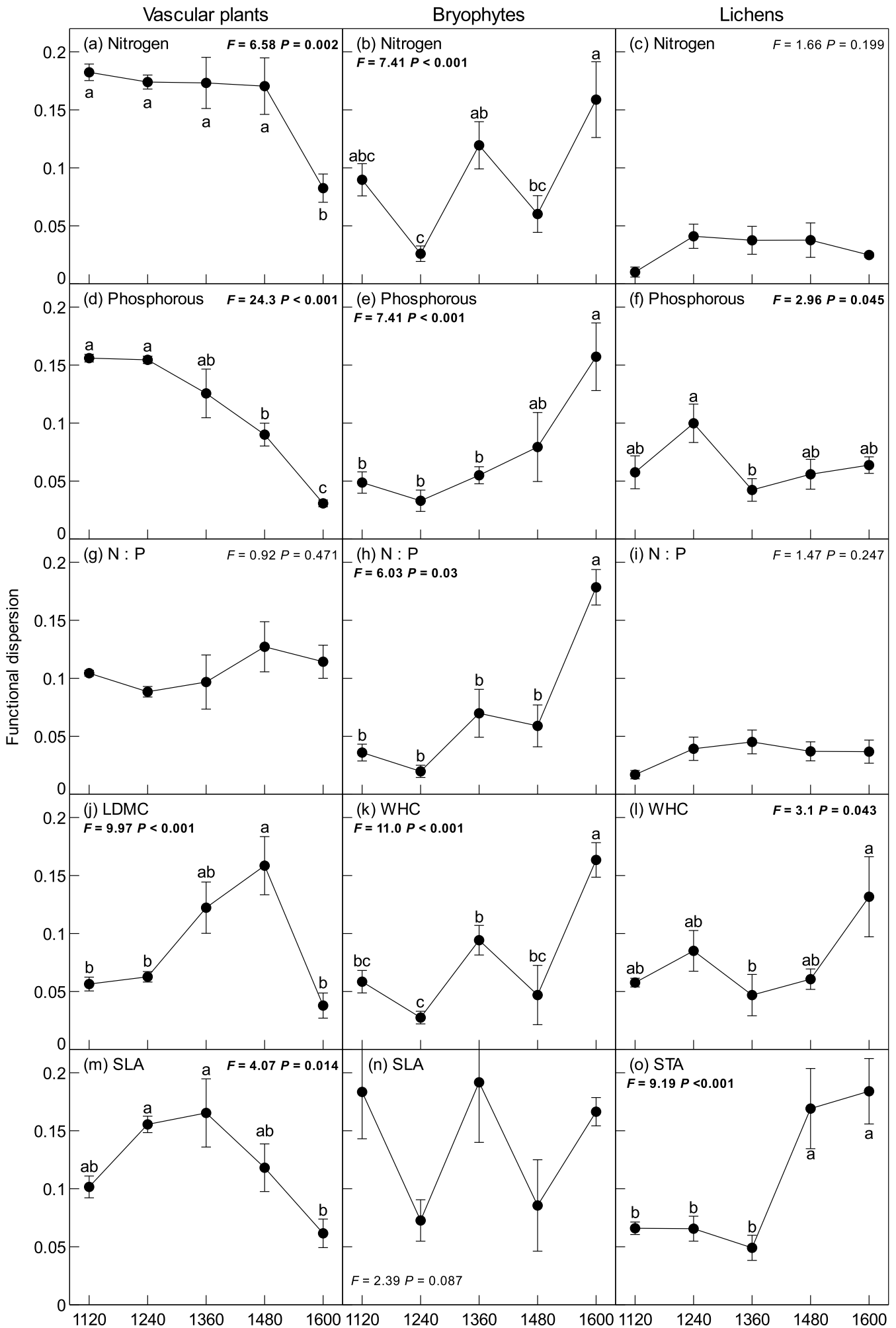
498   P<0.05 according to Tukey's test.

Figure 1

Figure 2

Figure 3

Figure 4