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Comparing the responses of bryophytes and short-statured vascular plants to climate shifts and eutrophication

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35 **Summary**

36 1. Few experimental studies have tested how abundance and diversity of grassland bryophytes
37 respond to global environmental changes such as climate shifts and eutrophication. Because
38 bryophytes in grasslands are low-statured, and because plant height is a key functional trait
39 governing plant responses to resource gradients, their responses to these factors could resemble
40 those of better-studied small vascular plants. Alternatively, traits unique to bryophytes could
41 lead to qualitatively different responses than those of small vascular plants.

42 2. In a **semiarid Californian grassland system, where bryophytes are at relatively low abundance**
43 **and their ecology has been little studied**, we compared changes in cover and species richness of
44 bryophytes and short-statured vascular plants in response to five years of experimental
45 fertilization, springtime watering, and fertilization + watering, which produced strong gradients
46 in vascular plant biomass.

47 3. Supporting our hypotheses, the cover and richness of both bryophytes and short vascular
48 plants were negatively related to total community biomass and tall vascular plant cover, and
49 declined in response to the fertilization + watering treatment, in which the cover of tall vascular
50 plants most strongly increased.

51 4. Two divergent responses were also observed: watering alone increased the cover of
52 bryophytes but not short vascular plants, while fertilization alone reduced the cover of short
53 vascular plants but not bryophytes.

54 5. Bryophytes and short-statured vascular plants in grasslands both may be expected to **decline**
55 **under projected global changes in climate and nutrient deposition that enhance total community**
56 **biomass and competitive pressure**. However, shifts in either precipitation or eutrophication
57 regimes alone may have differential effects on bryophytes and short vascular plants in
58 grasslands, and organism-specific plant functional traits must also be considered.

59

60 *Keywords:* climate change, grasslands, nutrients, plant height, precipitation, productivity, semi-
61 arid ecosystems

62 Introduction

63 Climatic shifts and anthropogenic eutrophication are anticipated to cause profound changes in
64 most of the world's grassland plant communities, and a rapidly growing literature has identified
65 some relatively predictable aspects of these changes. Nutrient enrichment typically shifts plant
66 community composition toward greater dominance by tall-statured species and lower species
67 richness and diversity (Bobbink *et al.*, 1998; Stevens *et al.*, 2004; Harpole & Tilman, 2007), and
68 even relatively small levels of nutrients have been found to exert persistent effects (Isbell *et al.*,
69 2013; Street *et al.*, 2015). Climatic shifts and their effects are intrinsically more variable, but
70 some evidence indicates that increasing precipitation exert positive direct effects on plant
71 productivity, while shifts towards more arid conditions have opposite effects (Heisler-White *et al.*,
72 2008; Mowll *et al.*, 2015). Climatic shifts may also exert competitively-mediated indirect
73 effects; for example, increased rainfall in a water-limited climate may lead to greater competitive
74 dominance and thereby to lower species richness (Suttle *et al.*, 2007), similarly to the effects of
75 nutrient enrichment. Finally, the effects of climate change may synergize with those of nutrient
76 enrichment, and may be strongest in communities on fertile soils, where the dominant plant
77 species have high capacities for rapid growth and low tolerances for resource scarcity (Grime *et al.*,
78 2000, 2008; Eskelinen & Harrison, 2014, 2015; Harrison *et al.*, 2015).

79 While ever-increasing attention has led to these emergent generalizations about
80 vascular plants, there is much less understanding of the direct, indirect, and interactive effects of
81 global change on the abundance and diversity of the non-vascular bryophyte component of
82 grassland plant communities. Bryophytes **may** form a substantial fraction of the plant diversity of
83 semi-arid grasslands (e.g., Eldridge & Tozer, 1997; Löbel *et al.*, 2006), **and even at low**
84 **abundances**, they can play critical roles in nutrient retention and water cycling as well as
85 vascular plant regeneration (Turetsky, 2003; Freestone, 2006; Elbert *et al.*, 2012; Reed *et al.*,
86 2012; Doxford *et al.*, 2013; Michel *et al.*, 2013; Voortman *et al.*, 2014). A handful of existing
87 experimental studies highlight the idiosyncratic and even surprising nature of bryophyte
88 responses to environmental changes. For example, in calcareous grasslands in the UK, bryophyte
89 utilization of dewfall as a water source evidently mitigated the effects of a drought treatment
90 (Bates *et al.*, 2005), while in deserts of the western US, a dominant moss responded negatively to
91 the imposition of small rainfall events in summer due to negative effects on moss carbon balance
92 (Reed *et al.*, 2012), as well as to the interaction of N addition and increased summer rainfall
93 (Stark *et al.*, 2011).

94 Plant functional attributes have been thought to have considerable power to predict
95 community patterns and processes across geographically and phylogenetically disparate groups

96 (Grime, 1977; Westoby, 1998), including community responses to eutrophication and climatic
97 changes (Suding *et al.*, 2005; Soudzilovskaia *et al.*, 2013; Eskelinen & Harrison, 2015). Plant
98 height is a particularly important trait because it responds strongly to water and nutrient
99 enhancement (Suding *et al.*, 2005; Dickson *et al.*, 2014; Eskelinen & Harrison, 2015) and plays a
100 significant role in determining competitive hierarchies (Keddy & Shipley, 1989). Increased
101 nutrient availability leads to intensified competition (Bonser & Reader, 1995), favoring taller
102 over shorter-statured vascular plants and reducing vascular diversity (Hautier *et al.*, 2009; Gough
103 *et al.*, 2012; Dickson *et al.*, 2014; Borer *et al.*, 2014; Humbert *et al.*, 2016).

104 To the extent that plant height has strong predictive power, the abundance and
105 diversity of both bryophytes and short-statured vascular plants in grasslands may be expected to
106 decline in the face of global change factors that increase vascular plant biomass. Several
107 experimental studies of bryophytes illustrate the potential for negative, competitively-mediated
108 responses to global change (Virtanen *et al.*, 2000; van der Wal *et al.*, 2005; Klanderud &
109 Totland, 2005). However, bryophytes also differ from vascular plants in some critical functional
110 respects; most importantly, they take up water and nutrients directly from rainwater and are
111 unable to regulate their internal water status while they are photosynthetically active. Some
112 studies have shown that bryophytes are highly sensitive to water addition (Bates *et al.* 2005;
113 Stark *et al.* 2015, Reed *et al.* 2012), while others have indicated their high sensitivity to nutrient
114 loads (Potter *et al.*, 1995; Bergamini & Pauli, 2001; Pearce *et al.*, 2003; Power *et al.*, 2006;
115 Hejzman *et al.*, 2010; Armitage *et al.* 2012). These considerations suggest that the direct, i.e.,
116 not competitively mediated, effects of global change factors may be stronger in bryophytes than
117 in small vascular plants.

118 In a heterogeneous Californian grassland, we compared the community-level
119 responses of bryophytes and short-statured vascular plants to factorial rainfall and nutrient
120 additions. Our first set of predictions was that, across the range of natural and experimental
121 variation, the cover and diversity of both bryophytes and short vascular plants would be
122 negatively related to total community biomass and tall vascular plant cover. Our second set of
123 predictions, was that the cover and diversity of both bryophytes and short vascular plants would
124 be reduced by the rainfall and nutrient additions leading to increases in tall vascular plant cover.
125 Our third set of predictions was that increased community biomass would mediate the responses
126 of both bryophytes and short vascular plants to the rainfall and nutrient additions. Alternatively,
127 bryophyte responses could inherently differ from those of short vascular plants, and mainly
128 reflect their greater sensitivity to direct impacts of global change factors.

129

130

131 **Materials and methods**

132

133 The experiment was conducted at the Donald and Sylvia McLaughlin University of California
134 Natural Reserve (38.851°N, 123.830°W) in the North Coast Range of California, USA. In the
135 reserve area, climate is Mediterranean with hot, dry summers and rainy, cool winters. The rainy
136 season normally extends from October to March and some heavy rain can occur in April–June.
137 The amount of annual rainfall (September–August) during the experiment ranged between 54
138 and 846 mm in 2010–2014.

139 The experimental area of roughly 1000 m × 500 m lies at 650–680 m elevation and
140 consists of a mixture of grasslands that vary in productivity, moss cover, vascular plant species
141 composition and height (Eskelinen & Harrison, 2014; Virtanen *et al.*, 2015). Shallow rocky
142 serpentine soils found on rocky hilltops represent the most infertile soil type and support sparse,
143 short-statured vascular plant vegetation, while deeper and finer-textured serpentine soils on
144 slopes and valley bottoms, and non-serpentine soils derived from sedimentary rocks support
145 more fertile and productive grasslands with higher nitrogen concentration, biomass, and
146 vegetation height (Eskelinen & Harrison, 2014, 2015). At our experimental site these grassland
147 productivity levels are interspersed over short distances (10¹-10² m), making it an ideal study
148 system to replicate treatments along a productivity gradient.

149

150 *Experimental design and sampling*

151

152 In early spring 2010, we established approximately equal numbers of 2 × 2 m plots in grasslands
153 on “harsh” rocky serpentine, “lush” fine-textured serpentine, and non-serpentine soils (Fig. S1).
154 Within each of these grassland types, we randomly allotted plots to watering, fertilization,
155 watering + fertilization, and control treatments. The plots were >5m apart and none were directly
156 **downslope** another. Several plots were lost when heavy equipment drove over them, resulting in
157 30–35 per treatment and 131 plots total. **Rainwater was harvested on a rooftop, stored in large**
158 **tanks, and sprayed in a 3-m radius by sprinkler heads (Mini Rotor Drip Emitters, Olson**
159 **Irrigation, Santee, CA, USA) placed 50 cm above the soil in the center of each 2 × 2 m plot.** In
160 each year, watering was started after March 15 when rainfall had ceased for at least a week and
161 none was forecast. Plots were watered weekly for 8 consecutive weeks in 2010–2014. Watering
162 occurred at night for 12 hours and provided ca. 25 mm of water, adding ca. 18 % over mean
163 annual rainfall. This amount and timing was based on previous work in Californian grasslands,

164 which found water addition has strong effects in spring when rainfall has largely ceased and soils
165 are drying rapidly, but little effect during the rainy winter season (Suttle *et al.*, 2007). Rainfall
166 addition in spring corresponds to the predictions of some though not all climate forecasts for
167 northern California (National Assessment Synthesis Team, 2000; Cayan *et al.*, 2012).

168 In the fertilized plots, we added slow-release granular NPK (10-10-10) fertilizer
169 with micronutrients (Lilly Miller Ultra Green), a total of 10 g N m⁻², 10 g P m⁻² and 10 g K m⁻²
170 per year, in equal applications in November, February, and March, 2010-2014. This treatment
171 was chosen for consistency with a protocol used in grasslands worldwide
172 (<http://www.nutnet.umn.edu/>), and the amount of added N corresponds to observed and
173 anticipated levels of N deposition near major urban and agricultural areas (Fenn *et al.*, 2003;
174 Lamarque *et al.*, 2005). **In our most nutrient-poor habitat, harsh serpentine, this fertilization
175 treatment increased total soil available N by approximately threefold (Eskelinen & Harrison,
176 2014, Appendix A).**

177 We sampled bryophytes by visually estimating percent cover by each species in 30
178 × 30 cm subplots in the center of the vascular plant subplots (see below). We used classes of
179 0.01, 0.05, 0.1, 0.2, 0.5, 1, 2, 3, 8, and 10 % (where 1% corresponded to a colony area of 3 × 3
180 cm), and >10 % values were estimated 5% increment classes within each subplot. We sampled in
181 April 2014 when the rains had just ended and all species were clearly visible. Bryophytes were
182 identified to species if possible, but some species of Bryaceae and Pottiaceae had to be treated
183 collectively at genus level. In total, we found 15 taxa of which most common were *Didymodon*
184 *vinealis* and *Fissidens sublimbatus* (Table S1). The majority of bryophyte colonies were < 1 cm
185 tall (R. Virtanen, personal observations). From published sources, we found that the shoot length
186 of these taxa is 0.3–5 cm (Hill *et al.*, 2007).

187 We sampled vascular plants by visually estimating percent areal cover by each
188 species in 1 × 1 m subplots within each 2 × 2 m experimental plot. We used a minimum estimate
189 threshold of 0.1%. **To account for few vascular species that reach their peak sizes in summer, we
190 conducted sampling three times annually (in April, June, and August), and combined the three
191 surveys by using the largest cover value for each species in 2014. (We note that bryophyte
192 richness and abundance peaked strongly in spring, making repeated sampling unnecessary.)** We
193 found 96 vascular species. We measured heights from 10 individuals per species from the study
194 area around the experimental plots; species mean heights were 0.85–160.1 cm (Spasojevic *et al.*,
195 2014; Table S1). We harvested vascular plant biomass (live and litter) from 25 × 25 cm subplots
196 in April 2014, oven dried it for 24 hours at 60°C, and weighed it.

197 For comparison with the 15 bryophyte taxa, we selected the 15 shortest vascular
198 plant species (all forbs), which had mean heights < 7.3 cm (Table S1, Fig. S2). We also
199 experimented with altering the height threshold to 15 cm and found our results to be qualitatively
200 unaffected, but preferred 7.3 cm because it equalized the sample size of bryophyte and small
201 vascular species. The remaining “tall” vascular plants included abundant annual grasses (e.g.
202 *Avena fatua* and *Lolium multiflorum*) as well as annual forbs (e.g. *Centaurea solstitialis*,
203 *Hemizonia congesta*, and *Vicia villosa*). For the analyses, we calculated the total cover and
204 species richness per plot for these three plant types (bryophytes, short plants and tall plants).

205

206 *Statistical analysis*

207

208 To analyze the relationships of cover and richness of the three plant types (bryophytes and short
209 and tall vascular plants) to biomass and treatment levels, we fitted a series of multivariate LME
210 models (Pinheiro & Bates, 2000; function ‘lme’ of the package ‘nlme’; R Core Team, 2015) with
211 cover or richness as the dependent variable (in separate models), and various combinations of
212 predictors including biomass and treatments. In LMEs, we used plots in close proximity to each
213 other and similar in soils and vegetation (i.e. “habitat patches”), and nested within watering lines,
214 as a random ‘block’ factor (14 in total). This specification adequately controlled for spatial
215 autocorrelation in residuals (tested using function ‘ACF’ of the package ‘nlme’, R Core Team,
216 2015). We tested the significance of model terms using function ‘anova.lme’ (Crawley, 2011; R
217 Core Team, 2015). We also examined residuals to ensure the assumptions of normality and
218 homogeneity of variances were met, after double square-root transforming ($x^{0.25}$) cover and
219 square-root transforming species richness.

220 First, to ask whether the cover and/or richness of bryophytes and short vascular
221 plants responded negatively to variation in biomass and whether their response differed from that
222 of tall plants (prediction 1), we tested for interactions among plant type (three levels) and
223 community biomass. This analysis revealed overall differences in the responses among three
224 plant groups. To test more specifically whether bryophytes differed from short vascular plants,
225 we repeated this analysis using only data on bryophytes and short vascular plants, and again
226 asked whether plant type interacted with biomass. We also used simple regressions to test the
227 relationships of biomass to richness and cover separately for each three plant types (function
228 ‘lm’, R Core Team, 2015).

229 Second, to ask whether the cover and/or richness of bryophytes and short vascular
230 plants both responded negatively to water and nutrient addition (prediction 2), we tested for

231 interactions among plant type and the experimental treatments. As above (prediction 1), to assess
232 more specifically whether bryophytes differed from short vascular plants, we repeated this model
233 using only data on bryophytes and short vascular plants, and again asked whether plant type
234 interacted with treatments. Thereafter, we performed Dunnett's contrast analysis for the
235 respective LME models (function 'glht' of the package 'multcomp' of R (Hothorn *et al.*, 2008)).
236 The Dunnett's contrasts compared the means of cover and richness between fertilization and
237 watering treatments and controls.

238 Third, to ask whether biomass mediated the effects of fertilization and watering
239 treatments on both bryophytes and short plants (prediction 3), we added biomass into models
240 with either the pooled cover or pooled richness of bryophytes and short vascular plants as
241 response variables, and fertilization and watering treatments as explanatory variables. We then
242 examined whether this addition resulted in a loss of significance in the fertilization and watering
243 treatment effects.

244 **Results**

245

246 *Are bryophyte and short vascular plant relationships with biomass similar to each other?*

247

248 There were significant plant group-biomass interactions in the LME models for both cover and
249 species richness (Table 1), indicating that the cover and richness of bryophytes, short vascular
250 plants and tall vascular plants all were differently related to biomass (Table 1, Fig. 1). The cover
251 of both short vascular plants and bryophytes were negatively associated with total community
252 biomass, while the cover of tall vascular plants showed a strong positive relationship and the
253 richness of tall vascular plants a weak negative relationship to community biomass (Fig. 1).

254 These results supported our first prediction. However, the LME model without tall plants showed
255 that biomass-cover and biomass-richness relationships of bryophytes and short vascular plants
256 also significantly differed (Table 1), and regression analyses indicated that the negative
257 relationships were generally stronger (steeper negative slopes) for short vascular than for
258 bryophytes (Fig. 1c,e)).

259

260

261 *Do bryophytes and short vascular plants respond negatively to watering and fertilization?*

262

263 There was a significant plant group-fertilization-watering interaction in the LME for cover,
264 indicating that the cover of bryophytes, short vascular plants and tall vascular plants responded
265 differently to the treatments (Table 2). The interaction for cover remained significant when only
266 bryophytes and short vascular plants were considered, indicating that these two groups
267 responded differently to fertilization and watering treatments (Table 2). Watering increased the
268 cover of bryophytes, but did not significantly affect short vascular plant cover; fertilization
269 decreased the cover of short vascular plants, but did not significantly affect bryophyte cover
270 (Fig. 2a,b). However, in agreement with our second prediction, fertilization plus watering caused
271 a similar decline in the cover of both bryophytes and short vascular plants (Fig. 2a,b).

272 Fertilization, watering, and fertilization plus watering all increased the cover of tall vascular
273 plants (Fig. 2c).

274 For species richness, the lack of a significant plant group-fertilization-watering
275 interaction term indicated similarity in the responses of all three plant groups to treatments.
276 Fertilization alone or in combination with watering decreased species richness, while watering
277 alone had little effect (Fig. 2d-f). The plant group-fertilization-watering interaction for richness

278 remained non-significant when only bryophytes and short vascular plants were considered (Table
279 2). However, the Dunnett's contrast analyses showed that bryophyte richness decreased only in
280 response to the combined watering and fertilization treatment (Fig. 2d), whereas both
281 fertilization alone and fertilization together with watering decreased richness of short vascular
282 plants (Fig. 2e).

283

284 *Does biomass mediate the effects of watering and fertilization on richness and cover of short*
285 *vascular plants and bryophytes?*

286

287 Consistent with our third prediction, the addition of community biomass to our models largely
288 negated the significant effects of fertilization, watering and their interactions on the cover and
289 richness of bryophytes and short vascular plants (Table 3).

290

291

292

293

294 **Discussion**

295

296 Productivity exacerbates competition for light and space and favors tall-statured plants over
297 short-statured ones (Hautier *et al.*, 2009; Gough *et al.*, 2012; Dickson *et al.*, 2014; Borer *et al.*,
298 2014). Under the premise that biotic constraints will drive phylogenetically unrelated plant
299 groups to have similar responses dependent on their functional traits (Boulangéat *et al.*, 2012),
300 we expected bryophytes to resemble short vascular plants, and to differ from tall vascular plants,
301 in their responses to natural and experimental variation in community productivity. Our results
302 largely support this premise, with both bryophytes and short vascular plants – but not tall
303 vascular plants – decreasing in cover and/or richness in response to the natural biomass gradient
304 in our study system and also in response to the combined watering and fertilization treatment.
305 We also found that the effects of watering and fertilization treatments on short-statured plants
306 were largely explainable by changes in community biomass, supporting the broad importance of
307 biomass as a mediator of global changes on the diversity and composition of plant communities
308 (Bobbink *et al.*, 1998; Stevens *et al.*, 2004).

309

310 Combined watering and fertilization, although not either treatment alone, led to
311 consistent increase in the cover of tall vascular plants and decreases in the cover and richness of
bryophytes and short vascular plants. This result agrees with previous findings that water and

312 nutrients are often jointly limiting to plant productivity, and that relaxation of this co-limitation
313 shifts communities toward greater dominance by tall vascular plants, increase in community
314 biomass and the loss of diversity of short-statured plants (Eskelinen & Harrison, 2015). Our
315 finding suggests that bryophytes as well as short vascular plants will be net 'losers' under the
316 combination of wetter precipitation regimes and high levels of anthropogenic nutrient
317 enrichment. These results also underscore the importance of considering multiple simultaneously
318 acting global change factors, as their joint impact may greatly deviate from single-factor impacts.

319 Despite the broad consistencies of our results with trait-based expectations, we also
320 found some divergent environmental responses of bryophytes and short vascular plants.
321 Watering led to 3.5-fold increase in the cover of bryophytes but did not affect the cover of short
322 vascular plants. In other experimental studies, bryophytes have likewise been shown to respond
323 to the amount and seasonal timing of precipitation, although the direction and strength of the
324 response varies among climatic regions and among taxa with varying levels of drought tolerance
325 (Bates *et al.*, 2005; Stark *et al.*, 2011; Reed *et al.*, 2012). The strong increase of bryophytes in
326 our semi-arid system following the enhancement of spring rainfall suggests that bryophytes in
327 these systems are moisture-limited, and that lengthening of the rainy season may lead to
328 increases in bryophyte cover. We find it possible that such increases could play a role in
329 regulating important grassland properties and functions such as carbon and nutrient cycling,
330 moisture retention and buffering against temperature fluctuations. Dominant bryophytes of semi-
331 arid grasslands (such as *Didymodon*) absorb water with all surfaces, and their perennial cushions
332 are able to rapidly enlarge and shrink under water fluctuations which may further increase their
333 survival and growth-potential under variation of cool-wet and dry-hot seasons. The lack of
334 response in short vascular plants to watering alone suggests that they are generally better
335 buffered against precipitation shifts than bryophytes, as expected on the basis of annual life-
336 cycle and other structures improving drought-tolerance. Our results also suggest that short
337 vascular plants experience more competition from tall vascular plants than bryophytes,
338 potentially because they are unable to escape competition.

339 We also found that fertilization alone did not significantly affect bryophyte cover and richness,
340 whereas it decreased the cover of short vascular plants, as has been found in many previous
341 studies (Bobbink *et al.*, 1998, 2010; Stevens *et al.*, 2004; Hautier *et al.*, 2009). In contrast, our
342 findings deviate from many studies reporting negative effects of fertilization on bryophytes
343 (Potter *et al.*, 1995; Bergamini & Pauli, 2001; Pearce *et al.*, 2003; Power *et al.*, 2006; Hejman *et al.*, 2010).
344 It is possible that the relatively low abundance of bryophytes in these grasslands
345 contributed to the weak effects of fertilization compared with other studies. Also, fertilizer may

346 have less effect on bryophytes when added in granular form than when added by repeated
347 spraying that more closely simulates atmospheric deposition. On the other hand, Armitage *et al.*
348 (2012) found that moderate N deposition levels were associated with increased bryophyte
349 growth, suggesting that nutrient enrichment, even relatively high level, may not always have
350 direct toxic, counterproductive effect on bryophytes. Many bryophytes also show a marked
351 degree of shade tolerance (Marschall & Proctor, 2004; van der Wal *et al.*, 2005) and are able to
352 rapid photosynthesis under light pulses (Kubasek *et al.*, 2014), thus increasing their opportunities
353 to survive in moderately dense vascular plant understories (created by fertilization alone;
354 Eskelinen & Harrison, 2015) where competition for light is likely to be more intense. Due to
355 their small size and high colonization ability (Vanderpoorten & Goffinet, 2009), bryophytes are
356 likely to survive even in extremely small microhabitats and may be less affected by competition
357 by tall vascular plants. In our system, *Fissidens sublimbatus* is particularly common in shaded
358 microsites under dense vascular plant covers. The reasons for the negative effect of nutrient
359 enrichment on short vascular plants remain uncertain, but we propose that direct competitive
360 suppression from tall vascular plants could be involved. However, to fully understand the
361 reasons for the specific differences between bryophyte and short vascular plant responses to
362 watering and fertilization, further experiments with controlled competitive backgrounds would
363 be required to disentangle the direct from the competitively-mediated components of these
364 responses. Nonetheless, our results support the significance of phylogenetic identity as a
365 surrogate for important unmeasured traits that affect the responses of species to the biotic and
366 abiotic environment (Cadotte *et al.*, 2009).

367 In summary, our results support the idea of plant height as a key trait that broadly
368 explains negative responses of both bryophytes and short vascular plants to nutrient and
369 precipitation enhancement. Under circumstances where multiple global changes, i.e., climatic
370 shifts and nutrient enrichment, cause community biomass to increase, declines may be expected
371 in the abundance and diversity of both bryophytes and short vascular plants in grasslands.
372 However, our results also emphasize that, depending on the habitat and combination of global
373 change factors, the responses of bryophytes and short vascular plants may differ in some
374 respects. Bryophytes may react more positively to the direct effects of increased precipitation,
375 and less negatively to competition, than small vascular plants. We conclude that bryophyte
376 responses to global changes can be only partly predicted based on responses of short vascular
377 plants, and that studying both non-vascular and vascular plant responses to global changes
378 continues to be warranted.

379

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386

387 **Author contributions**

388 AE, SH, RV planned and designed the research, performed experiments, field work and analyzed
 389 data. RV, AE, SH interpreted results and wrote the manuscript.

390

391 **Data accessibility**

392 Data on bryophytes, vascular plant richness and biomass are deposited in the Dryad Digital
 393 Repository: <http://dx.doi.org/10.5061/dryad.k1g95> (Virtanen et al.2016).

394

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566 **Supporting Information**

567 Additional Supporting information may be found in the online version of this article.

568 **Appendix S1.** Comparing the responses of bryophytes and short-statured vascular plants to
569 climate shifts and eutrophication

570 **Fig. S1.** A schematic map of the experimental plots with their treatments and habitat types at
571 McLaughlin nature reserve (Inner Coastal Ranges, California).

572 **Fig. S2.** Height distribution of the 96 vascular plants included in the analyses.

573 **Table S1.** Plant taxa, height, height class and frequencies in the experimental plots.

574

575 **Figures and figure legends**

576

577 **Fig. 1.** The cover and species richness (SR) of (a,b) tall vascular plants, (c,d) short vascular
578 plants and (e,f) bryophytes in relation to biomass (biomass plus litter) across 131 experimental

579 plots. Fitted regression lines are based on ordinary linear regression models (gray shadings
580 indicate approximate 95% confidence intervals). Significance codes: “****” $P < 0.001$, “**”, $P <$
581 0.01 , “*” $P < 0.05$, “NS” $P > 0.05$.

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585 **Fig. 2.** The mean cover and species richness (SR) of (a,d) bryophytes, (b,e) short and (c,f) tall
586 plants in relation to experimental treatments. C = controls, F = fertilized plots, W = watered
587 plots, FW = fertilized and watered plots. Bars show 95% confidence intervals (based on
588 bootstrapped CIs with 5000 resamples). The asterisks denote significant differences between
589 controls and treatments based on Dunnett-type contrasts. Significance codes: “****” $P < 0.001$,
590 “**”, $P < 0.01$, and “*” $P < 0.05$.

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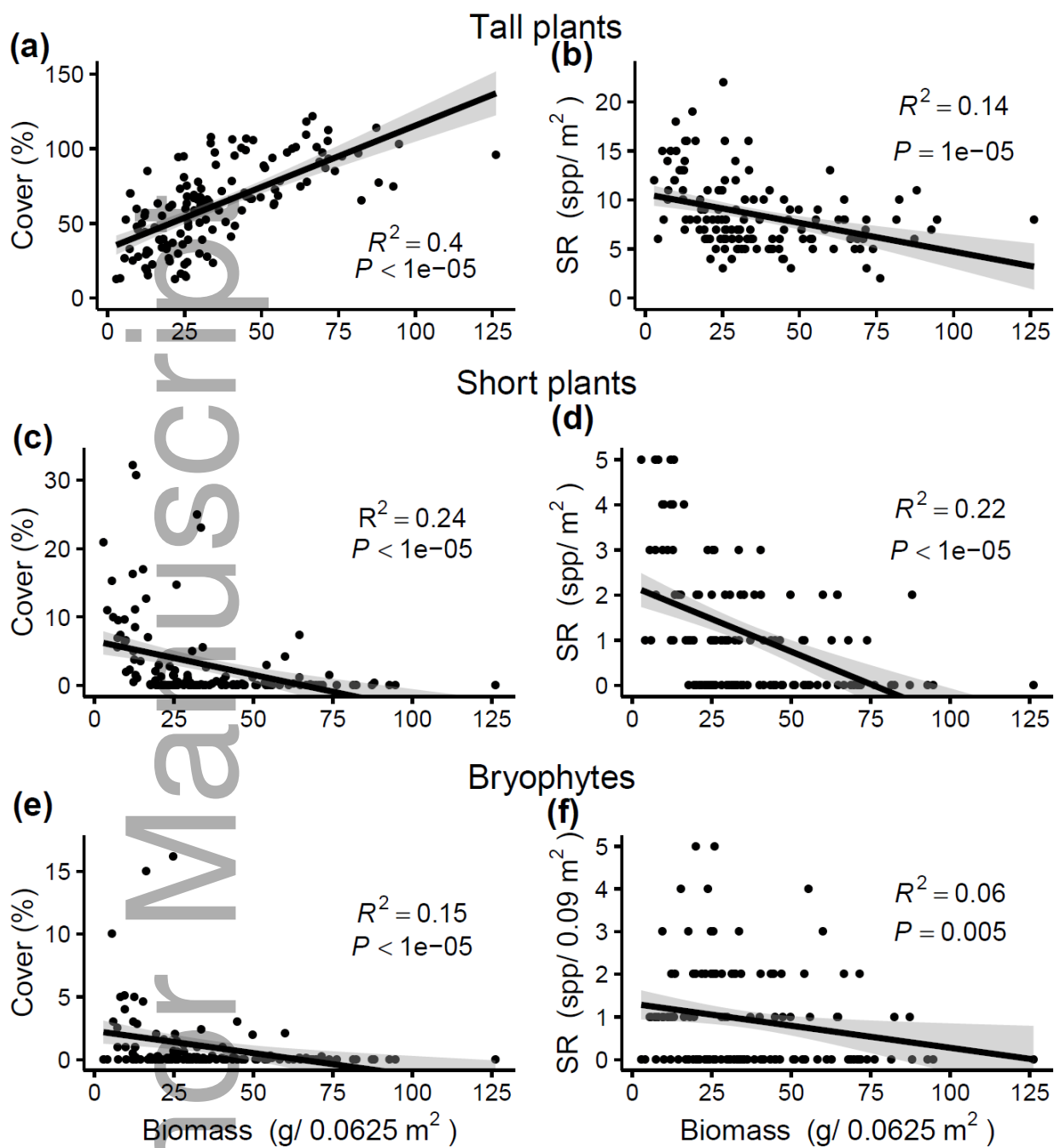
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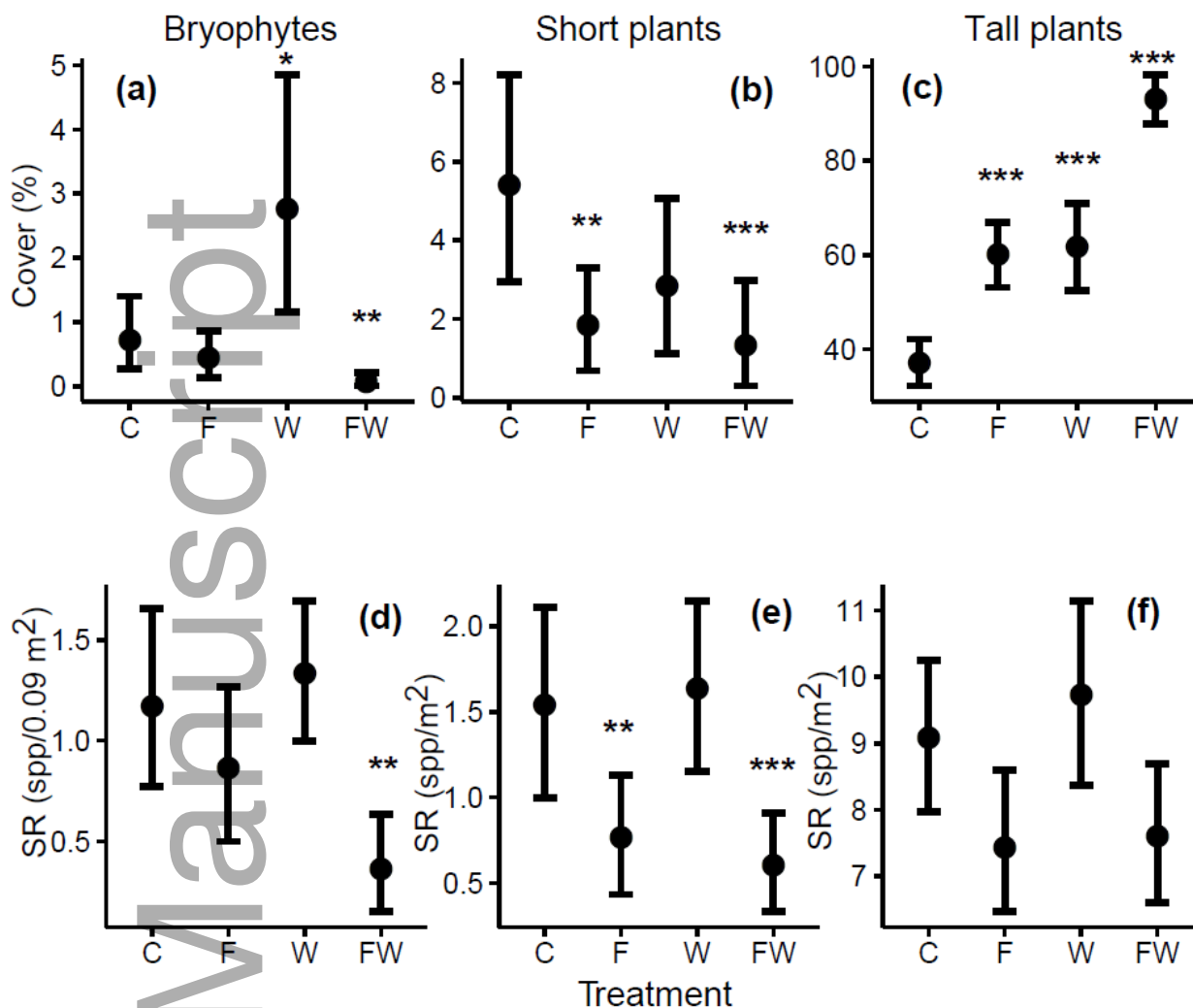
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597 Fig 1

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601 Fig 2

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603 Tables

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605 **Table 1.** Summary of the linear mixed effects models (marginal F-tests of LME models) where
 606 cover and species richness are dependent variables (both in their own models), and plant group
 607 (either three levels, i.e. bryophytes, short vascular plants and tall vascular plants, or two levels,
 608 i.e. bryophytes and short vascular plants) and community biomass as predictor variables. denDF
 609 and numDF denote denominator and numerator degrees of freedom, respectively.

Species

richness

Cover

*numDF**denDF**F**P**numDF**denDF**F**P*

All three plant groups									
(Intercept)	1	374	49.522	<.0001	1	374	49.166	<.0001	
Plant.group	2	374	127.16	<.0001	2	374	160.249	<.0001	
Biomass	1	374	10.619	0.001	1	374	3.032	0.083	
Plant.group:Biomass	2	374	61.022	<.0001	2	374	3.587	0.029	
Short vascular plants and bryophytes only									
(Intercept)	1	245	28.732	<.0001	1	245	50.369	<.0001	
Plant.group	1	245	16.632	0.0001	1	245	6.609	0.0107	
Biomass	1	245	5.057	0.025	1	245	3.677	0.056	
Plant.group:Biomass	1	245	6.216	0.013	1	245	5.674	0.018	

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615 **Table 2.** Summary of linear mixed effects models for cover and species richness in relation to
616 fertilization and watering treatments (marginal anova F-tests of LME models) with three plant
617 groups (bryophytes, short vascular plants and tall vascular plants) and with two groups included
618 (bryophytes and short vascular plants).

	Cover				Species richness				
	<i>numDF</i>	<i>denDF</i>	<i>F</i>	<i>P</i>	<i>numDF</i>	<i>denDF</i>	<i>F</i>	<i>P</i>	
All three plant groups									
(Intercept)	1	368	13.164	0.0003	1	368	22.408	<.0001	
Plant group	2	368	246.693	<.0001	2	368	133.202	<.0001	
Fertilization	1	368	1.508	0.22	1	368	1.421	0.234	
Watering	1	368	3.831	0.051	1	368	5.006	0.026	
Plant group:Fertilization	2	368	10.186	<.0001	2	368	0.452	0.637	
Plant group:Watering	2	368	7.184	0.0009	2	368	1.574	0.209	
Fertilization:Watering	1	368	10.705	0.0012	1	368	7.211	0.008	
Plant group:Fertilization:Watering	2	368	3.857	0.022	2	368	1.350	0.26	
Short vascular plants and bryophytes only									
(Intercept)	1	241	8.662	0.004	1	241	20.779	<.0001	
Plant group	1	241	1.927	0.17	1	241	0.122	0.73	

Fertilization	1	241	1.381	0.24	1	241	1.299	0.26
Watering	1	241	3.507	0.06	1	241	4.129	0.043
Plant group:Fertilization	1	241	2.279	0.13	1	241	0.764	0.38
Plant group:Watering	1	241	0.492	0.48	1	241	1.053	0.31
Fertilization:Watering	1	241	10.493	0.001	1	241	5.837	0.016
Plant group:Fertilization:Watering	1	241	5.318	0.022	1	241	0.938	0.33

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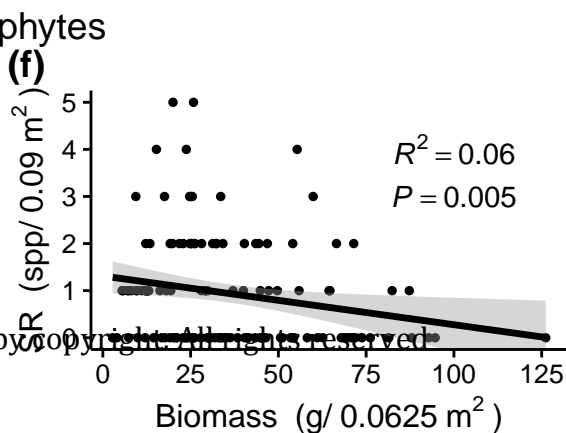
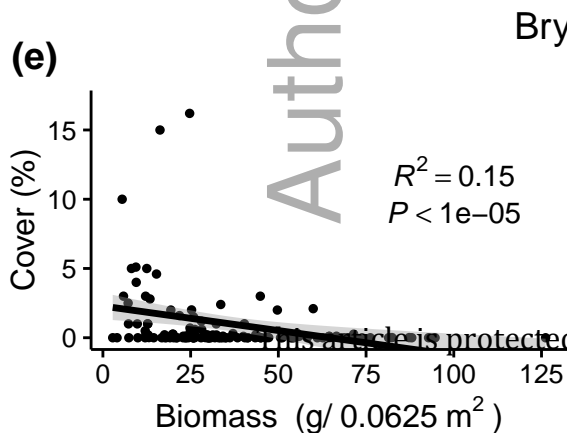
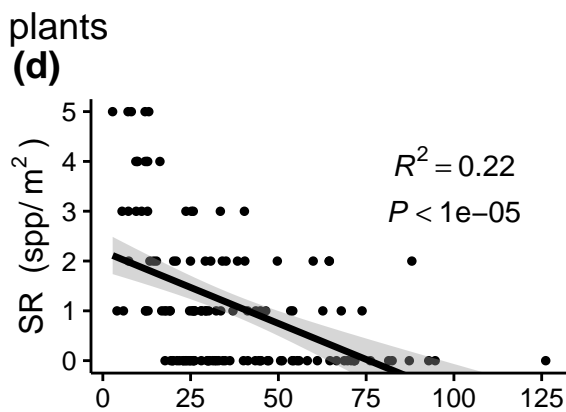
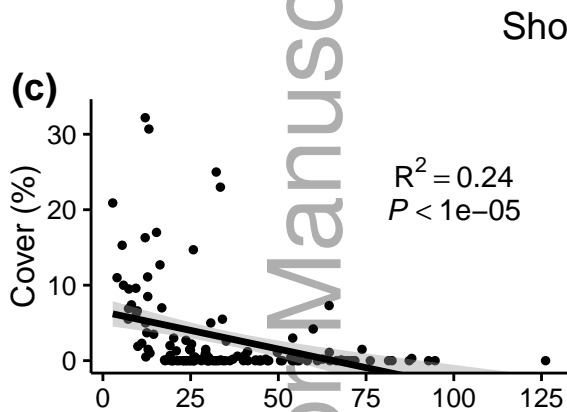
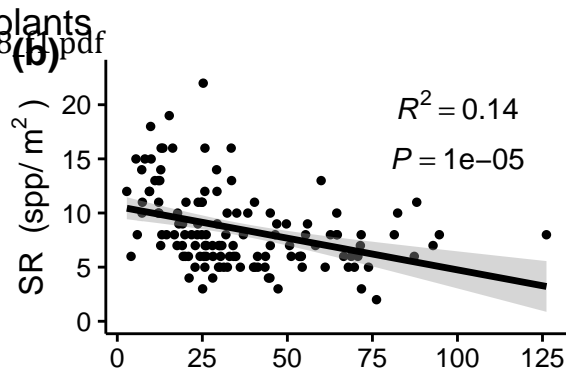
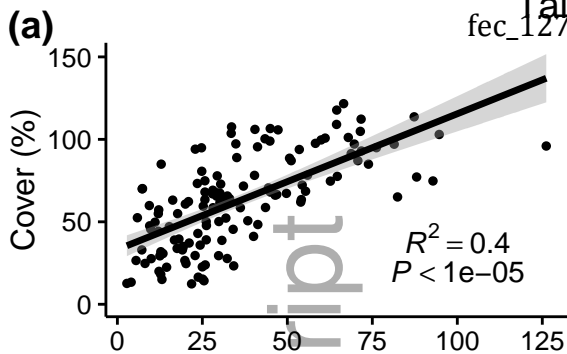
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621 **Table 3.** Summary of the linear mixed effects model for cover and species richness of all short
 622 plants (bryophytes and short vascular plants pooled) (marginal anova F-tests of LME models).

623

	Cover				Species richness			
	<i>numDF</i>	<i>denDF</i>	<i>F</i>	<i>P</i>	<i>numDF</i>	<i>denDF</i>	<i>F</i>	<i>P</i>
Without biomass								
(Intercept)	1	114	23.374	<.0001	1	114	43.057	<.0001
Fertilization	1	114	21.536	<.0001	1	114	11.721	0.0009
Watering	1	114	5.581	0.02	1	114	5.623	0.019
Fertilization:Watering	1	114	2.626	0.11	1	114	5.726	0.018
With biomass								
(Intercept)	1	110	22.299	<.0001	1	110	14.529	0.0002
Fertilization	1	110	2.886	0.09	1	110	4.287	0.041
Watering	1	110	0.852	0.36	1	110	0.284	0.60
Biomass	1	110	2.868	0.09	1	110	0.039	0.84
Fertilization:Watering	1	110	0.613	0.44	1	110	0.904	0.34
Fertilization:Biomass	1	110	0.011	0.92	1	110	0.777	0.38
Watering:Biomass	1	110	0.563	0.45	1	110	0.025	0.87
Fertilization:Watering:Biomass	1	110	0.067	0.80	1	110	0.008	0.93

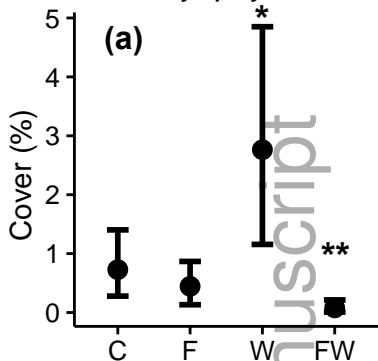
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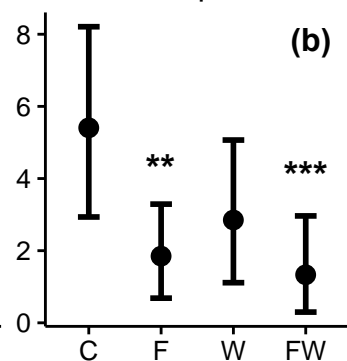
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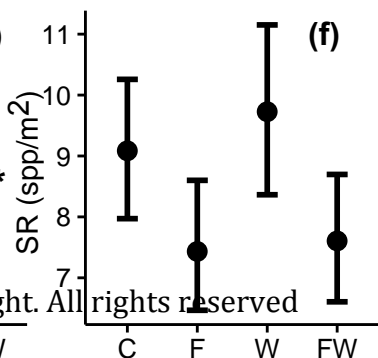
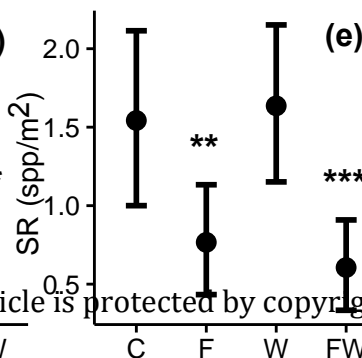
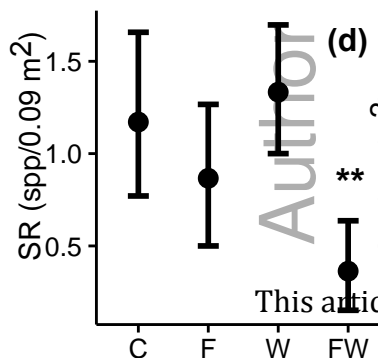
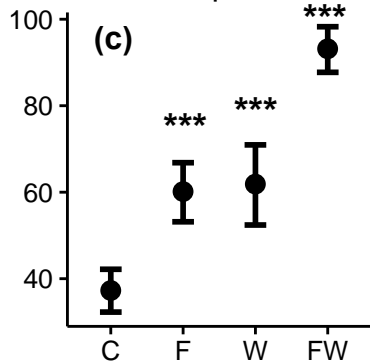
Bryophytes



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Tall plants



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Treatment