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12   **Comparing the responses of bryophytes and short-statured vascular plants to**

13   **climate shifts and eutrophication**

14

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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

Introduction

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

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

Plant functional attributes have been thought to have considerable power to predict 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 Hejcman *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

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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 $\times$ 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 (10^1-10^2 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.

Results

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

There were significant plant group-biomass interactions in the LME models for both cover and species richness (Table 1), indicating that the cover and richness of bryophytes, short vascular plants and tall vascular plants all were differently related to biomass (Table 1, Fig. 1). The cover of both short vascular plants and bryophytes were negatively associated with total community biomass, while the cover of tall vascular plants showed a strong positive relationship and the richness of tall vascular plants a weak negative relationship to community biomass (Fig. 1). These results supported our first prediction. However, the LME model without tall plants showed that biomass-cover and biomass-richness relationships of bryophytes and short vascular plants also significantly differed (Table 1), and regression analyses indicated that the negative relationships were generally stronger (steeper negative slopes) for short vascular than for bryophytes (Fig. 1c,e)).

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

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

For species richness, the lack of a significant plant group-fertilization-watering interaction term indicated similarity in the responses of all three plant groups to treatments. Fertilization alone or in combination with watering decreased species richness, while watering 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).

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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 (Boulangeat *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   Combined watering and fertilization, although not either treatment alone, led to

310 consistent increase in the cover of tall vascular plants and decreases in the cover and richness of

311 bryophytes and short vascular plants. This result agrees with previous findings that water and

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

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

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

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

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

379

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Author contributions

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

390

Data accessibility

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

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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

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" $P > 0.05$.

582

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584

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: "***" $P < 0.001$,
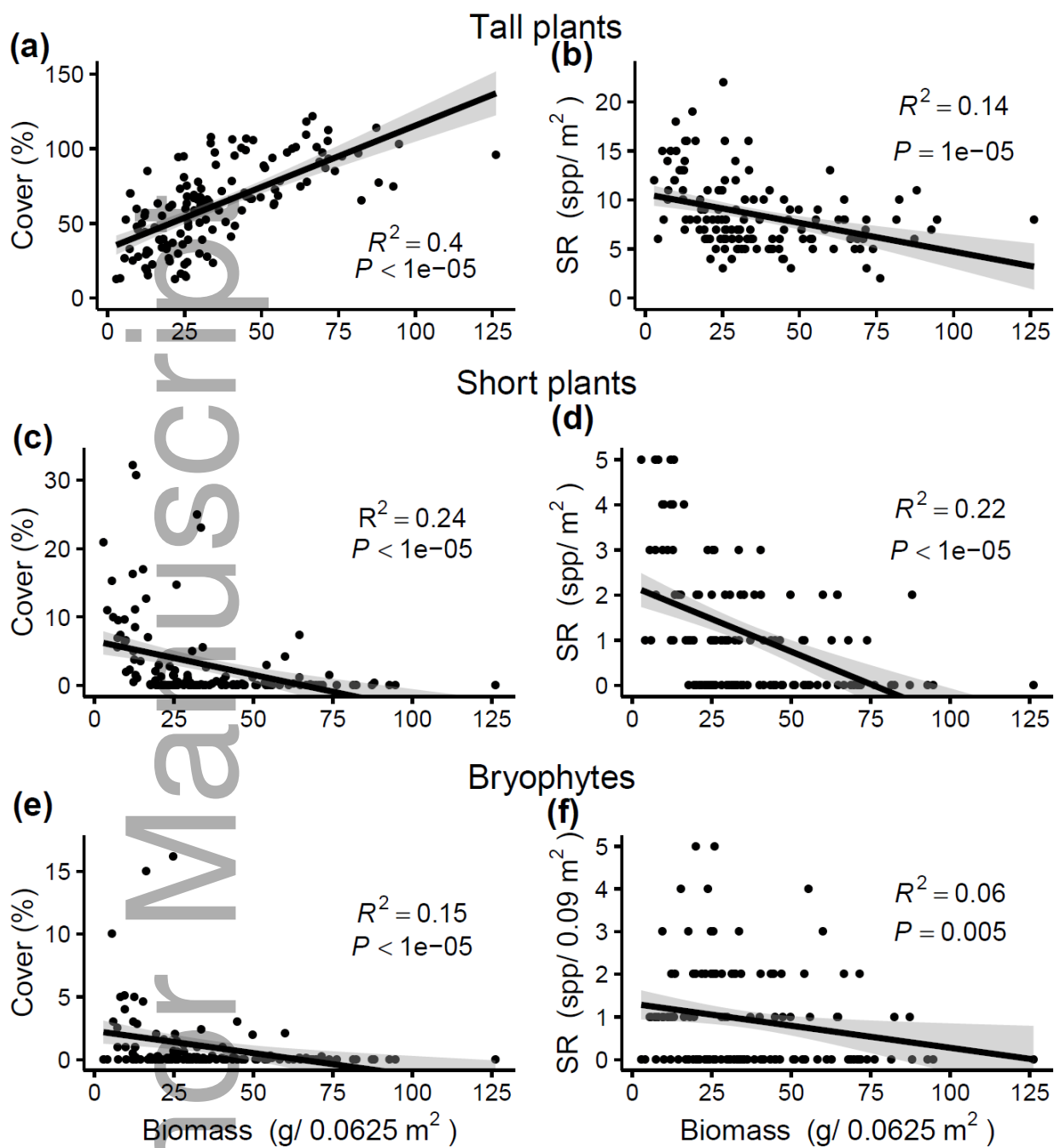
590   "**", $P < 0.01$, and "*" $P < 0.05$.

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(a) Tall plants

(b) $R^2 = 0.14$
$P = 1e{-}05$

Short plants

(c) $R^2 = 0.24$
$P < 1e{-}05$

(d) $R^2 = 0.22$
$P < 1e{-}05$

Bryophytes

(e) $R^2 = 0.15$
$P < 1e{-}05$

(f) $R^2 = 0.06$
$P = 0.005$
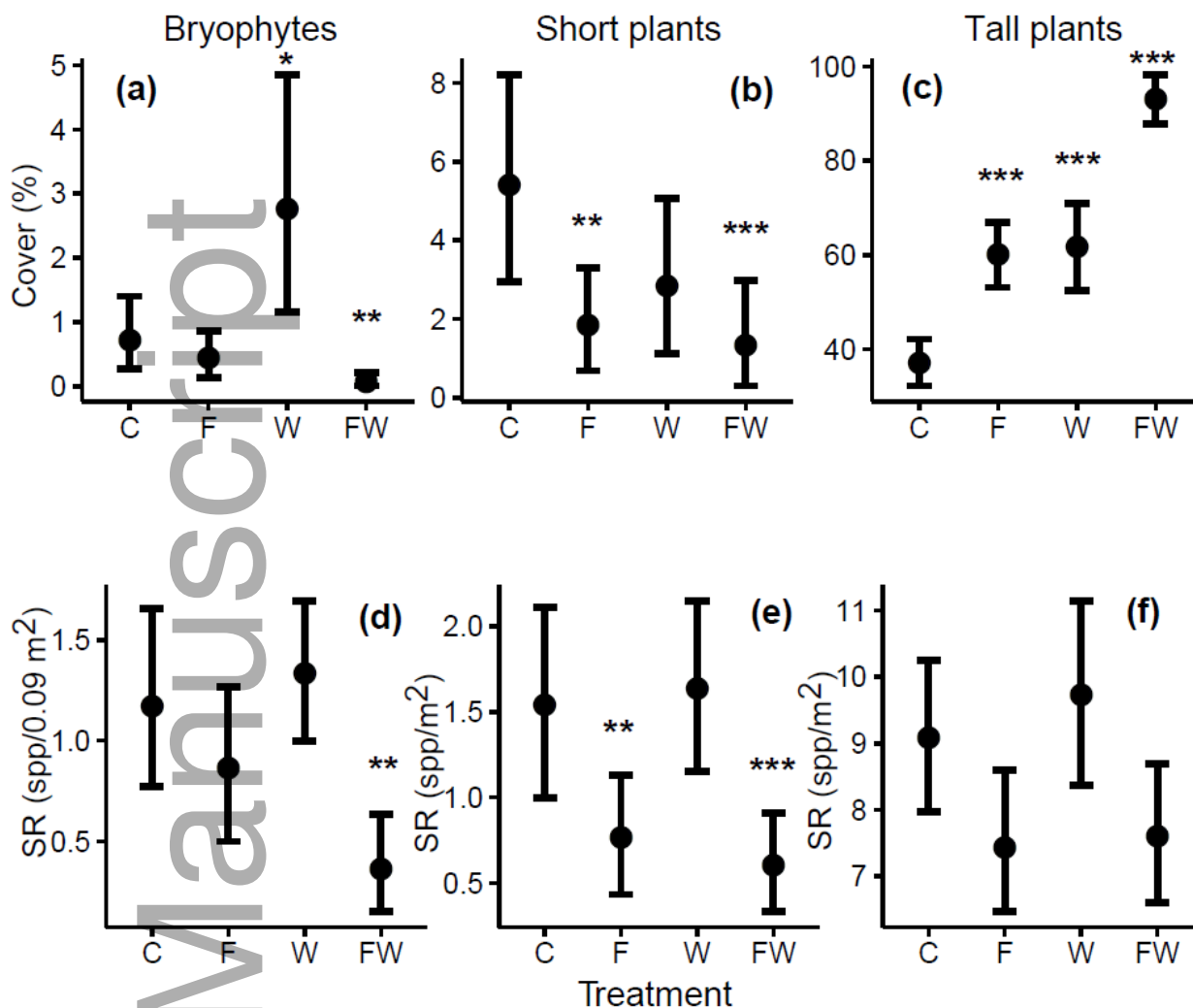
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597   Fig 1

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601 Fig 2

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603 **Tables**

604

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.

		Cover				Species richness			
	numDF	*denDF*	*F*	*P*		*numDF*	*denDF*	*F*	*P*

	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).

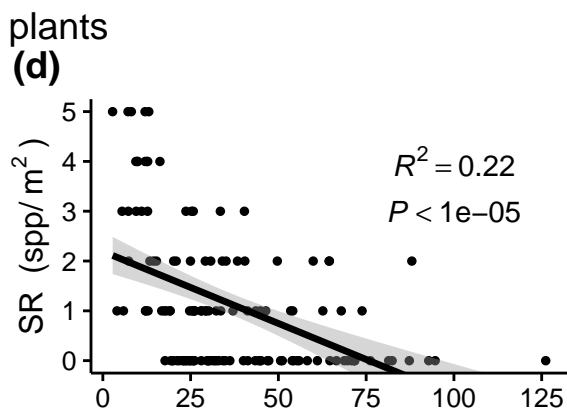|	Cover				Species richness			
	numDF	denDF	F	P	numDF	denDF	F	P
All three plant groups								
(Intercept)	1	368	13.164	0.0003	1	368	22.408	<.0001
Plant group	2	368	246.693	<.0001	2	368	133.202	<.0001
Fertilization	1	368	1.508	0.22	1	368	1.421	0.234
Watering	1	368	3.831	0.051	1	368	5.006	0.026
Plant 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

619

620

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

624

Tall plants

(a)
Cover (%)
$R^2 = 0.4$
$P < 1e{-}05$

(b)
SR (spp/ m^2)
$R^2 = 0.14$
$P = 1e{-}05$

Short plants

(c)
Cover (%)
R$^2 = 0.24$
$P < 1e{-}05$

(d)
SR (spp/ m^2)
$R^2 = 0.22$
$P < 1e{-}05$

Bryophytes

(e)
Cover (%)
$R^2 = 0.15$
$P < 1e{-}05$

(f)
SR (spp/ 0.09 m^2)
$R^2 = 0.06$
$P = 0.005$

Biomass (g/ 0.0625 m^2) Biomass (g/ 0.0625 m^2)

Bryophytes (a)

fec_ShootSplants

Tall plants (c)