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

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## Summary

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

2. In a semi-arid Californian grassland system, where bryophytes are at relatively low abundance and their ecology has been little studied, we compared changes in cover and species richness of bryophytes and short-statured vascular plants in response to 5 years of experimental fertilization, springtime watering and fertilization + watering, which produced strong gradients in vascular plant biomass.

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

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

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

**Key-words:** climate change, grasslands, nutrients, plant height, precipitation, productivity, semi-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 towards greater

dominance by tall-statured species and lower species richness and diversity (Bobbink, Hornung & Roelofs 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, Burns & Woodin 2015). Climatic shifts and their effects are intrinsically more variable, but some evidence indicates that increasing precipitation exerts positive direct effects on plant productivity, while shifts towards more arid conditions have

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opposite effects (Heisler-White, Knapp & Kelly 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, Thomsen & Power 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, Gornis & Copeland 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, Dengler & Hobohm 2006), and even at low abundances, they can play critical roles in nutrient retention and water cycling as well as in vascular plant regeneration (Turetsky 2003; Freestone 2006; Elbert *et al.* 2012; Reed *et al.* 2012; Doxford, Ooi & Freckleton 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, Thompson & Grime 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, Brinda & McLetchie 2011).

Plant functional attributes have been thought to have considerable power to predict community patterns and processes across geographically and phylogenetically disparate groups (Grime 1977; Westoby 1998), including community responses to eutrophication and climatic changes (Suding *et al.* 2005; Soudzilovskaia *et al.* 2013; Eskelinen & Harrison 2015). Plant height is a particularly important trait because it responds strongly to water and nutrient enhancement (Suding *et al.* 2005; Dickson *et al.* 2014; Eskelinen & Harrison 2015) and plays a significant role in determining competitive hierarchies (Keddy & Shipley 1989). Increased nutrient availability leads to intensified competition (Bonser & Reader 1995), favouring taller over short-statured vascular plants and reducing vascular diversity (Hautier, Niklaus & Hector 2009; Gough *et al.* 2012; Borer *et al.* 2014; Dickson *et al.* 2014; Humbert *et al.* 2016).

To the extent that plant height has strong predictive power, the abundance and diversity of both bryophytes and short-statured vascular plants in grasslands may be

expected to decline in the face of global change factors that increase vascular plant biomass. Several experimental studies of bryophytes illustrate the potential for negative, competitively mediated responses to global change (Virtanen *et al.* 2000; Klanderud & Totland 2005; van der Wal, Pearce & Brooker 2005). However, bryophytes also differ from vascular plants in some critical functional respects; most importantly, they take up water and nutrients directly from rainwater and are unable to regulate their internal water status while they are photosynthetically active. Some studies have shown that bryophytes are highly sensitive to water addition (Bates, Thompson & Grime 2005; Stark, Brinda & McLetchie 2011; Reed *et al.* 2012), while others have indicated their high sensitivity to nutrient loads (Potter *et al.* 1995; Bergamini & Pauli 2001; Pearce, Woodin & van der Wal 2003; Power *et al.* 2006; Hejman *et al.* 2010; Armitage *et al.* 2012). These considerations suggest that the direct, that is not competitively mediated, effects of global change factors may be stronger in bryophytes than in small vascular plants.

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

## Materials and methods

The experiment was conducted at the Donald and Sylvia McLaughlin University of California Natural Reserve (38°51'N, 123°30'W) in the North Coast Range of California, USA. In the reserve area, climate is Mediterranean with hot, dry summers and rainy, cool winters. The rainy season normally extends from October to March, and some heavy rain can occur in April–June. The amount of annual rainfall (September–August) during the experiment ranged between 54 and 846 mm in 2010–2014.

The experimental area of roughly 1000 × 500 m lies at 650–680 m elevation and consists of a mixture of grasslands that vary in productivity, moss cover, vascular plant species composition and height (Eskelinen & Harrison 2014; Virtanen, Eskelinen & Harrison 2015). Shallow rocky serpentine soils found on rocky hilltops represent the most infertile soil type and support sparse, short-statured vascular plant vegetation, while deeper and fine-textured serpentine soils on slopes and valley bottoms, and non-serpentine soils derived from sedimentary rocks support more fertile and productive grasslands with higher nitrogen concentration, biomass and vegetation height (Eskelinen & Harrison 2014, 2015). At

our experimental site, these grassland productivity levels are interspersed over short distances ( $10^1$ – $10^2$  m), making it an ideal study system to replicate treatments along a productivity gradient.

#### EXPERIMENTAL DESIGN AND SAMPLING

In early spring 2010, we established approximately equal numbers of  $2 \times 2$  m plots in grasslands on 'harsh' rocky serpentine, 'lush' fine-textured serpentine and non-serpentine soils (Fig. S1, Supporting Information). Within each of these grassland types, we randomly allotted plots to watering, fertilization, watering + fertilization and control treatments. The plots were  $>5$  m apart, and none were directly downslope another. Several plots were lost when heavy equipment drove over them, resulting in 30–35 per treatment and 131 plots total. Rainwater was harvested on a rooftop, stored in large tanks and sprayed in a 3 m radius by sprinkler heads (Mini Rotor Drip Emitters, Olson Irrigation, Santee, CA, USA) placed 50 cm above the soil in the centre of each  $2 \times 2$  m plot. In each year, watering was started after March 15 when rainfall had ceased for at least a week and none was forecast. Plots were watered weekly for eight consecutive weeks in 2010–2014. Watering occurred at night for 12 h and provided c. 25 mm of water, adding c. 18% over mean annual rainfall. This amount and timing was based on previous work in Californian grasslands, which found water addition has strong effects in spring when rainfall has largely ceased and soils are drying rapidly, but little effect during the rainy winter season (Suttle, Thomsen & Power 2007). Rainfall addition in spring corresponds to the predictions of some though not all climate forecasts for northern California (National Assessment Synthesis Team 2000; Cayan *et al.* 2012).

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

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

We sampled vascular plants by visually estimating per cent areal cover by each species in  $1 \times 1$  m subplots within each  $2 \times 2$  m experimental plot. We used a minimum estimate threshold of 0.1%. To account for few vascular species that reach their peak sizes in summer, we conducted sampling three times annually (in April, June and August) and combined the three surveys using the largest cover value for each species in 2014. (We note that bryophyte richness and abundance peaked strongly in spring, making repeated sampling unnecessary.) We found 96 vascular species. We measured heights from 10 individuals per species from the study area around the experimental plots; species mean heights

were 0.85–160.1 cm (Spasojevic, Damschen & Harrison 2014; Table S1). We harvested vascular plant biomass (live and litter) from  $25 \times 25$  cm subplots in April 2014, oven-dried it for 24 h at  $60^\circ\text{C}$  and weighed it.

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

#### STATISTICAL ANALYSIS

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

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

Secondly, to ask whether the cover and/or richness of bryophytes and short vascular plants both responded negatively to water and nutrient addition (prediction 2), we tested for interactions among plant type and the experimental treatments. As above (prediction 1), to assess more specifically whether bryophytes differed from short vascular plants, we repeated this model using only data on bryophytes and short vascular plants and again asked whether plant type interacted with treatments. Thereafter, we performed Dunnett's contrast analysis for the respective LME models [function 'glht' of the package 'MULTCOMP' of R (Hothorn, Bretz & Westfall 2008)]. The Dunnett's contrasts compared the means of cover and richness between fertilization and watering treatments and controls.

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

## Results

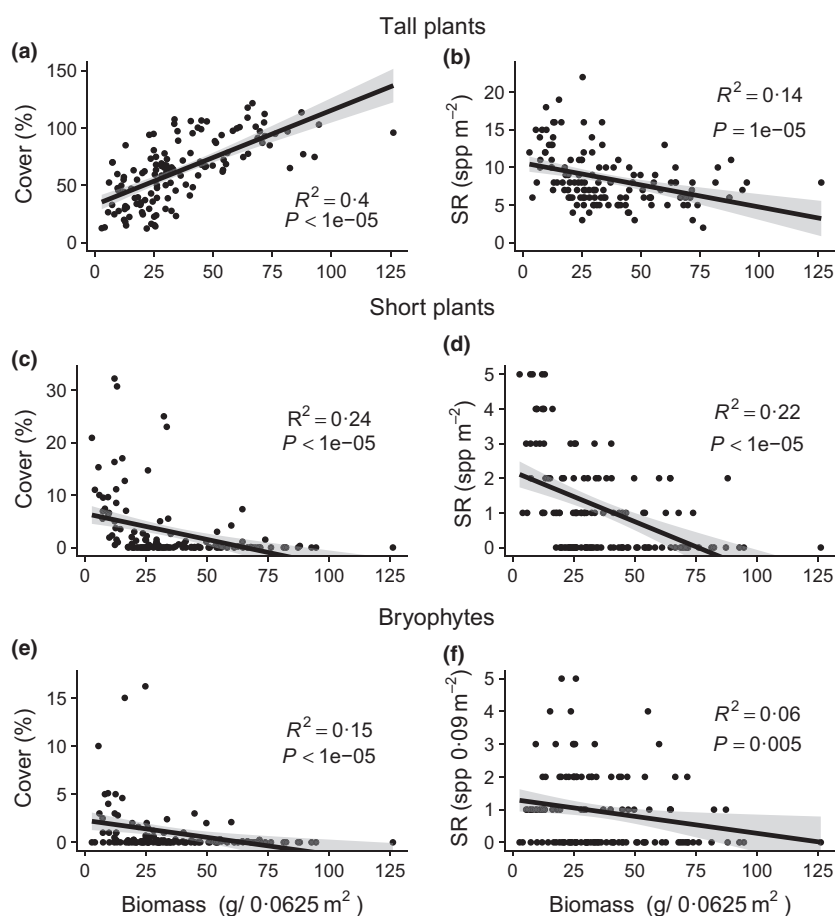
### ARE BRYOPHYTE AND SHORT VASCULAR PLANT RELATIONSHIPS WITH BIOMASS SIMILAR TO EACH OTHER?

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 was 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

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

	Cover				Species richness			
	numDF	denDF	$F$	$P$	numDF	denDF	$F$	$P$
All three plant groups								
(Intercept)	1	374	49.522	<0.0001	1	374	49.166	<0.0001
Plant group	2	374	127.16	<0.0001	2	374	160.249	<0.0001
Biomass	1	374	10.619	0.001	1	374	3.032	0.083
Plant group:Biomass	2	374	61.022	<0.0001	2	374	3.587	0.029
Short vascular plants and bryophytes only								
(Intercept)	1	245	28.732	<0.0001	1	245	50.369	<0.0001
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



**Fig. 1.** The cover and species richness (SR) of (a, b) tall vascular plants, (c, d) short vascular plants and (e, f) bryophytes in relation to biomass (biomass plus litter) across 131 experimental plots. Fitted regression lines are based on ordinary linear regression models (grey shadings indicate approximate 95% confidence intervals).

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).

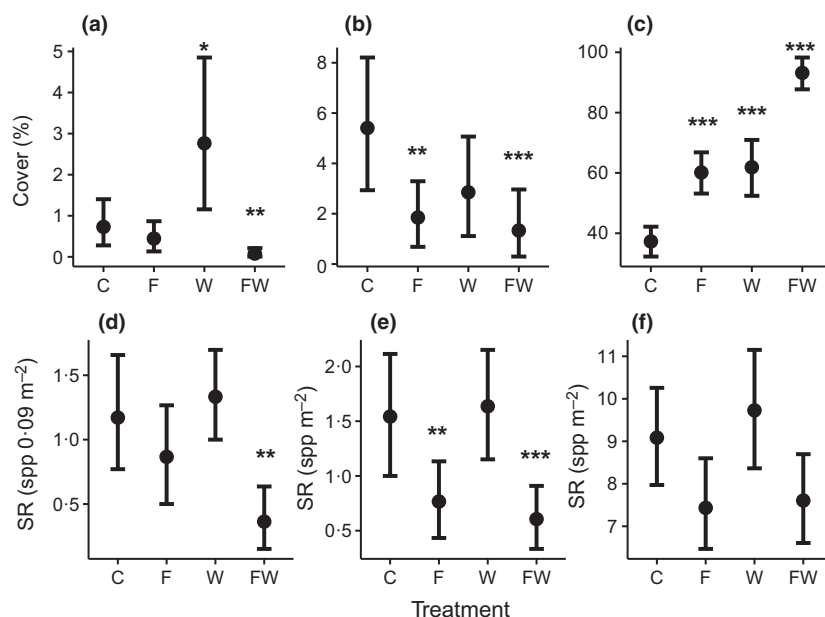
DO BRYOPHYTES AND SHORT VASCULAR PLANTS RESPOND NEGATIVELY TO WATERING AND FERTILIZATION?

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

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

	Cover				Species richness			
	numDF	denDF	<i>F</i>	<i>P</i>	numDF	denDF	<i>F</i>	<i>P</i>
All three plant groups								
(Intercept)	1	368	13.164	0.0003	1	368	22.408	<0.0001
Plant group	2	368	246.693	<0.0001	2	368	133.202	<0.0001
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	<0.0001	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	<0.0001
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



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

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

#### DOES BIOMASS MEDIATE THE EFFECTS OF WATERING AND FERTILIZATION ON RICHNESS AND COVER OF SHORT VASCULAR PLANTS AND BRYOPHYTES?

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

## Discussion

Productivity exacerbates competition for light and space and favours tall-statured plants over short-statured ones (Hautier, Niklaus & Hector 2009; Gough *et al.* 2012; Borer *et al.* 2014; Dickson *et al.* 2014). Under the premise that biotic constraints will drive phylogenetically unrelated plant groups to have similar responses dependent on their functional traits (Boulangéat *et al.* 2012), we expected

bryophytes to resemble short vascular plants, and to differ from tall vascular plants, in their responses to natural and experimental variation in community productivity. Our results largely support this premise, with both bryophytes and short vascular plants – but not tall vascular plants – decreasing in cover and/or richness in response to the natural biomass gradient in our study system and also in response to the combined watering and fertilization treatment. We also found that the effects of watering and fertilization treatments on short-statured plants were largely explainable by changes in community biomass, supporting the broad importance of biomass as a mediator of global changes on the diversity and composition of plant communities (Bobbink, Hornung & Roelofs 1998; Stevens *et al.* 2004).

Combined watering and fertilization, although not either treatment alone, led to 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 nutrients are often jointly limiting to plant productivity and that relaxation of this colimitation shifts communities towards 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.

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

	Cover				Species richness			
	numDF	denDF	<i>F</i>	<i>P</i>	numDF	denDF	<i>F</i>	<i>P</i>
Without biomass								
(Intercept)	1	114	23.374	<0.0001	1	114	43.057	<0.0001
Fertilization	1	114	21.536	<0.0001	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	<0.0001	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

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, Thompson & Grime 2005; Stark, Brinda & McLetchie 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 that 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, Hornung & Roelofs 1998; Stevens *et al.* 2004; Hautier, Niklaus & Hector 2009; Bobbink *et al.* 2010). In contrast, our findings deviate from many studies reporting negative effects of fertilization on bryophytes (Potter *et al.* 1995; Bergamini & Pauli 2001; Pearce, Woodin & van der Wal 2003; Power *et al.* 2006; Hejman *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, Pearce & Brooker 2005) and are able to rapidly photosynthesize under light pulses (Kubasek, Hájek & Glime 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, *F. 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, that is, 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.

### Authors' contributions

A.E., S.H. and R.V. planned and designed the research, performed experiments and field work and analysed data. R.V., A.E. and S.H. interpreted results and wrote the manuscript.

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### 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, Eskelinen & Harrison 2016).



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## Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

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

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

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

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