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1 **Grassland responses to increased rainfall depend on the timescale of forcing**

2 Running head: Contrasting responses to weather and climate

3 Martin J. P. Sullivan<sup>1\*</sup>, Meredith Thomsen<sup>2</sup>, and K.B. Suttle<sup>3\*</sup>

4 1. School of Geography, University of Leeds, Leeds, LS2 9JT, UK

5 2. Department of Biology, University of Wisconsin, La Crosse, Wisconsin 54601, USA.

6 3. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064.

7 \*Corresponding authors: Martin Sullivan, tel +44 (0) 113 34 31039, email: [m.j.sullivan@leeds.ac.uk](mailto:m.j.sullivan@leeds.ac.uk);

8 Blake Suttle, email: [ksuttle@ucsc.edu](mailto:ksuttle@ucsc.edu)

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12

13 **Abstract**

14 Forecasting impacts of future climate change is an important challenge to biologists, both for  
15 understanding the consequences of different emissions trajectories and for developing adaptation  
16 measures that will minimize biodiversity loss. Existing variation provides a window into the effects  
17 of climate on species and ecosystems, but in many places does not encompass the levels or  
18 timeframes of forcing expected under directional climatic change. Experiments help us to fill in these  
19 uncertainties, simulating directional shifts to examine outcomes of new levels and sustained changes  
20 in conditions. Here we explore the translation between short-term responses to climate variability and  
21 longer-term trajectories that emerge under directional climatic change. In a decade long experiment,  
22 we compare effects of short-term and long-term forcings across three trophic levels in grassland plots  
23 subjected to natural and experimental variation in precipitation. For some biological responses (plant  
24 productivity), responses to long-term extension of the rainy season were consistent with short-term  
25 responses, while for others (plant species richness, abundance of invertebrate herbivores and  
26 predators) there was pronounced divergence of long-term trajectories from short-term responses.  
27 These differences between biological responses mean that sustained directional changes in climate  
28 can restructure ecological relationships characterizing a system. Importantly, a positive relationship  
29 between plant diversity and productivity turned negative under one scenario of climate change, with a  
30 similar change in the relationship between plant productivity and consumer biomass. Inferences from  
31 experiments such as this form an important part of wider efforts to understand the complexities of  
32 climate change responses.

33

## 34 **Introduction**

35 Understanding how species and ecosystems respond to directional environmental changes is critical to  
36 designing adaptation strategies that will maintain our ecological support systems through the current  
37 period of global climate change. A useful starting point for investigating how the functioning of  
38 ecosystems and the abundance and distribution of different species will respond to future climate  
39 change is to ask how they have responded to the changes we have already seen (e.g. Johnston *et al.*,  
40 2013, Kurz *et al.*, 2008, MacNeil *et al.*, 2010). A critical challenge is that the windows we have into  
41 these impacts—natural climatic variability and the directional forcings apparent therein, experiments  
42 simulating climate forcing, and directional changes in baseline conditions already evident—are  
43 typically short in duration or small in magnitude relative to the climatic changes expected from  
44 current emissions trajectories and resulting earth-surface energy imbalances. Ecologists must  
45 therefore grapple with how responses to pulsed or small-magnitude changes relate to responses to  
46 chronic and larger magnitude shifts (Shaver *et al.*, 2000, Smith *et al.*, 2009).

47 The translation between effects of short-term forcings and effects of sustained forcings is not always  
48 linear or straightforward. Early field experiments simulating climate change found that certain  
49 responses changed direction relative to controls through time (Chapin *et al.*, 1995, Harte & Shaw,  
50 1995), presumably owing to interactions among different species or groups of species. Changes in  
51 climate can alter the strength and nature of ecological interactions, leading to indirect effects that alter  
52 response trajectories and are often lagged relative to direct physiological responses (Forchhammer *et*  
53 *al.*, 2002, Smith *et al.*, 2009, Suttle *et al.*, 2007, Wiedermann *et al.*, 2007). Thus species interactions  
54 have been borne out as important drivers of non-linear responses to changing climate through a large  
55 body of research (reviews in Cahill *et al.*, 2012, Ockendon *et al.*, 2014, Shaver *et al.*, 2000, Walther,  
56 2010), even as they have come to be understood as one class of a suite of such drivers. Physiological  
57 thresholds and tipping points can likewise cause ecological trajectories to deviate in sudden and  
58 unexpected ways under sustained or larger-magnitude forcing that are not apparent from itinerant or  
59 smaller forcing (Grotoli *et al.*, 2014, Kirby & Beaugrand, 2009, Kortsch *et al.*, 2012, Nelson *et al.*,  
60 2013). Species may acclimate to changing climate, so that initially pronounced effects taper off with

61 repeated exposure (Donelson *et al.*, 2011, Grottooli *et al.*, 2014, McLaughlin *et al.*, 2014). Populations  
62 may also adapt to selective pressures of changing climate (Colautti & Barrett, 2013, van Asch *et al.*,  
63 2013). Each of these factors can cause long-term trajectories under sustained climate forcing to  
64 deviate from short-term effects of initial or itinerant forcing. Understanding the causes of these  
65 deviations, the urgent question becomes whether being able to identify these complexities and  
66 quantify their effects advances us toward practical improvements in predictive capability.

67 We can build biotic interactions, physiological thresholds, acclimation and adaptation into predictive  
68 models to account for their effects on target variables (e.g. Coulson *et al.*, 2011, Fordham *et al.*, 2013,  
69 Heikkinen *et al.*, 2007, Luoto *et al.*, 2007, Trainor & Schmitz, 2014, Trainor *et al.*, 2014), so much of  
70 the challenge we face is to understand when this is actually needed: under what contexts, in what  
71 ecosystem types, and for what response variables do the different factors emerge to strongly influence  
72 the shape of responses? Progress toward the development of conceptual frameworks to address these  
73 questions is already underway. Drawing on a number of field experiments in different ecosystem  
74 types around the world, Shaver and colleagues (2000) delineated the various direct and indirect effects  
75 of temperature change on ecosystem carbon budgets, illustrating how the balance among these  
76 different processes can change through time to produce multi-phase responses. The authors showed  
77 how experiments can be used to identify dominant mechanisms governing different phases of  
78 response and the transitions between them. Subsequent research has built upon these ideas to develop  
79 a general framework to organize drivers of multi-phase responses into a predictable sequence (Smith  
80 *et al.*, 2009). Smith and colleagues outline a temporal hierarchy of mechanisms governing ecosystem  
81 responses to climate change that facilitates prediction of non-linear responses through time. This  
82 hierarchical-response framework places physiological responses of individuals, reorganization of  
83 species within a community, and turnover of species across communities into a logical temporal order  
84 with respect to sustained environmental forcing. By organizing drivers of ecosystem responses to  
85 climate change into explicit sequences, both approaches focus attention around controls on non-  
86 linearity in responses and how we might generalize these according to starting conditions, response  
87 type, and ecosystem type.

88 We now well understand that responses to pulsed climatic forcings and moderate directional changes  
89 in the observed record may be poor predictors of future ecological changes under sustained global  
90 climate change, and we are making progress toward understanding how and why responses to the  
91 more chronic directional forcing may change direction through time. The possibility that we may be  
92 able to sort the complexity of such responses according to ecosystem type, species or ecosystem  
93 characteristics, or the type of response variable under focus provides a pathway to improved  
94 prediction (Shaver *et al.*, 2000, Smith *et al.*, 2009) and encourages further study. Researchers have  
95 already produced evidence of such sorting by ecosystem type: a recent meta-analysis found  
96 herbaceous systems tend to show continuous directional ANPP responses to global change drivers  
97 while stepped responses are more common in forests and other systems (Smith *et al.*, 2015). In the  
98 present paper, we consider how predictability varies with the type of response variable under focus.

99 We used watering amendments in a northern California grassland to push the annual rainy season to  
100 the tails of existing variability in either intensity or duration, in order to test how well effects of  
101 background variation predict effects of sustained forcing. From ten years of data on plant production  
102 and richness and on herbivore, predator, and parasitoid abundances, we examine the translation  
103 between short-term responses of each variable to both background variation and initial years of rainy  
104 season modification and to long-term trajectories under sustained changes in the rainy season.

105

## 106 **Materials and Methods**

### 107 *Natural History of the Study System*

108 Research was undertaken in a 2.7-hectare grassland at the Angelo Coast Range Reserve in Mendocino  
109 County, California (39° 44' 17.7" N, 123° 37' 48.4" W) (Suttle *et al.*, 2007). Part of a network of 39  
110 natural areas protected across the state for research and teaching by the University of California's  
111 Natural Reserve System, the Angelo Reserve consists predominantly of mixed-oak woodland and old-  
112 growth conifer forest surrounding headwater streams of the South Fork Eel River. Grassy meadows

113 are interspersed within the forest on abandoned river terraces, with vegetation consisting of a well-  
114 mixed assemblage of grasses and forbs of both native and exotic origins.

115 The region experiences a Mediterranean-type climate, with hot dry summers and cool wet winters.  
116 Annual rainfall averages 2160 mm and falls predominantly between October and April. Seasonal  
117 precipitation levels have a well-established role in structuring annual patterns of plant production and  
118 composition in California grasslands. Successional dynamics are generally not apparent in these  
119 systems, and production and composition instead vary non-directionally from year to year according  
120 to annual climatic variation – and particularly the timing and amount of precipitation that falls each  
121 year (Hobbs *et al.*, 2007, Pitt & Heady, 1978, Stromberg & Griffin, 1996).

122 Between 20 and 40 vascular plant species are present in the grassland in a given year. Annual grasses  
123 of Mediterranean origin typically make up the major share of ground cover, with populations of three  
124 native perennial bunchgrass species and numerous native and exotic forbs co-existing with the exotic  
125 grasses.

### 126 *Experimental Design*

127 Since January 2001, thirty-six 70m<sup>2</sup> circular plots have been exposed to one of three water  
128 amendment treatments assigned in a randomized block design. Treatments consist of an ambient  
129 control, a wintertime addition over ambient precipitation that simulates an intensified rainy season,  
130 and a springtime addition over ambient that simulates an extended rainy season. The Intensified rainy  
131 season treatment and the Extended rainy season treatment were developed to approximate projections  
132 for the region from leading climate models at the time the experiment was initiated (National  
133 Assessment Synthesis Team, 2000). Models from both the Hadley Centre for Climate Prediction and  
134 Research and the Canadian Centre for Climate Modeling and Analysis projected substantial increases  
135 in annual rainfall for coastal northern California by mid-century, with the Hadley model (HadCM2)  
136 calling for the entirety of the increase during the existing winter rainy season and the Canadian model  
137 (CCM1) calling for an extended rainy season into the spring and summer.

138 Each watered plot received approximately 440 mm of supplementary water over ambient rainfall each  
139 year, representing roughly a 20% increase over mean annual precipitation but within the range of  
140 natural variability in both amount and timing at the study site (details in Suttle *et al.*, 2007). Water is  
141 collected from a natural spring on a forested slope immediately to the east of the grassland, with a  
142 portion of its flow filtered to 40 microns and diverted via irrigation piping to a 4500-liter irrigation  
143 tank placed approximately 40 vertical meters upslope of the meadow. The tank is continually  
144 replenished via gravity-feed from the spring, and water has been tested and found to contain nitrogen  
145 concentrations within the range present naturally in rainwater at the study site (Suttle *et al.*, 2007).

146 Water is delivered evenly over the surface of each plot from a single RainBird® RainCurtain™  
147 sprinkler (Rainbird, Azusa, CA USA) in the center of each plot. The water delivery protocol is  
148 identical for the Intensified and Extended rainy season treatments, except that the applications are  
149 staggered by three months, with the Intensified rainy season addition running from January through  
150 March and the Extended rainy season addition running from April through June. Experimental rain  
151 additions begin approximately two hours after dawn every third day. Valves leading to the sprinklers  
152 are actuated by battery-operated timers set to “rain” 14 to 16 mm of water onto the plots over one  
153 hour. The watering radius is 5m, and all samples are collected at least 0.5m in from the outside edge  
154 of the watered area, as described under *Response Variables* below.

155 Ambient precipitation throughout the study was measured with automated Campbell sensors located  
156 at two different meteorological monitoring stations in grasslands on the reserve. Where occasional  
157 sensor faults led to missing data, precipitation estimates were interpolated from nearby weather  
158 stations in Laytonville (39.7023, -123.4849;  $R^2 = 0.727$ ), or, when data from Laytonville were not  
159 available, from Eel River (39.8253, -123.0825;  $R^2 = 0.398$ ) based on regression equations from  
160 surrounding days when sensor data were available for both the Angelo Reserve and these stations  
161 Approximately 90% of daily precipitation totals for the ten-year record from 2001 through 2010 come  
162 directly from weather stations at the Angelo Reserve, with the remaining 10% interpolated.

163 *Response Variables*



164 In 2000, prior to initiation of the watering amendments, eighteen plots were partitioned for concurrent  
165 long-term measurements of plant production, plant diversity, and invertebrate abundances (Fig. S1).  
166 The remaining eighteen plots were set aside for other work not part of this study, so that all data  
167 reported here are from six replicates of each of the three watering treatments.

168 Plant production was measured from biomass samples collected three times each growing season from  
169 two separate pre-designated 0.09 m<sup>2</sup> subplots. Samples were taken on or around 20 May, 1 July, and  
170 30 August, dates that collectively target the peak biomass of each different species in the system. All  
171 vegetation was clipped at the soil surface, sorted into eight functional/phenological groups (spring  
172 annual grass, summer annual grass, perennial grass, spring annual forb, summer annual forb, late-  
173 summer annual forb, perennial forb, and nitrogen-fixing forb) and dried at 72°C for 48 hours prior to  
174 weighing. Each species was included once in ANPP estimates for each year. Each subplot was  
175 harvested in this manner only once and then eliminated from the future sampling scheme. A five-year  
176 allotment of subplots (i.e. 30 total, with six subplots sampled per plot each year) was laid out at  
177 regular intervals along two parallel transects running in a randomly drawn cardinal direction through  
178 the centre of each plot, and an additional five years allotment was arrayed along two transects  
179 perpendicular to this first set (see Figure S1). Plant production was estimated by summing the  
180 biomass of each different functional-phenological group at its annual peak biomass. Litter was not  
181 included in ANPP estimates.

182 Plant diversity was measured as the mean species richness of two central 0.25 m<sup>2</sup> subplots in each  
183 plot. Diversity subplots were surveyed regularly over the growing season to account for phenological  
184 differences in the seasonal growth patterns of different species.

185 Invertebrate abundances were sampled on or around 1 August every year. Foliar and flying  
186 invertebrates were sampled via a 30.5 cm diameter sweep net modified to connect securely to a  
187 holding container open at the base of the net. Samples were collected by a quick succession of ten  
188 sweeps along a transect running through the centre of the plot and then a second set of ten sweeps  
189 running back through the plot along a perpendicular transect (at 45° offsets from transects for biomass

190 clips). Sample containers were immediately capped after the last sweep and then frozen until sorting.  
191 Ground-dwelling invertebrates were sampled over 48 hours in 5cm diameter pitfall traps. Prior to  
192 initiation of the experiment in 2001, two 15cm sections of hollow rubber pipe (diameter 5.2cm) were  
193 sunk vertically into the soil in opposite quadrants in each plot, using a sledge hammer to anchor each  
194 approximately 1cm below the soil surface. Into each section of pipe was placed a capped plastic  
195 container of 5cm diameter, suspended from the top of the pipe by a lip at the top of each container  
196 onto which the cap secured. To initiate a pitfall sample, caps were removed and the open containers  
197 suspended in each pipe just below ground surface were filled to 2cm depth with a dilute solution of  
198 water and unscented dish soap. This minimized soil and vegetation disturbance immediately prior to  
199 collection and any biases that could result. Upon collection, invertebrates were transferred into vials  
200 of 70% ethanol for storage until sorting, and the pitfall traps were recapped in place in the plots.  
201 Invertebrates were identified to family, with morphotypes sorted within families. Replicate  
202 specimens of each morphotype were weighed for plot-wise biomass estimations. Invertebrate families  
203 were assigned to herbivore, predator, and parasitoid feeding groups based on natural history records.

#### 204 *Hypothesis Tests and Statistical Analyses*

205 All statistical analyses were carried out within a mixed effects model framework, implemented in R  
206 (R Core Team, 2014) using the package lme4 (Bates *et al.*, 2014). Invertebrate abundances were  
207 modelled using a Poisson error structure and log link. All responses were modelled using plot identity  
208 as a random effect to account for the repeated measurements from each plot, where factors such as  
209 soil texture and seed bank could lead to correlation among measurements. For invertebrates, within-  
210 year correlations between observations could arise from site-wide responses to weather, so  
211 invertebrate responses were modelled with year as a random effect to account for this. Both year and  
212 plot identity random effects were specified as random intercepts, where year and plot identity are  
213 crossed grouping factors. In total there were 180 observations of each response variable, collected in  
214 18 plots over ten years.

215 Analyses focused on testing how well responses to short-term forcings predicted responses to the  
216 same forcings applied over longer terms. We consider two different kinds of short-term forcing: (1)  
217 natural anomalies in rainfall that entailed seasonal precipitation levels within the range experienced by  
218 the water addition treatments (between 326 mm and 380 mm above long-term means for each season);  
219 and (2) experimental amendments that delivered seasonal precipitation levels 440 mm greater than  
220 long-term means in the first two years of the experiment. Two years was chosen as a threshold for  
221 dividing short- and long-term responses as it allows both initial responses and lagged effects of  
222 precipitation in the previous year to be observed, but did not include evident indirect effects that  
223 became pronounced in the third year and thereafter (Suttle *et al.*, 2007). Longer-term forcings were  
224 then defined as the subsequent years in the Intensified (Int) and Extended (Ext) rainy season  
225 treatments (Years 3-10). Using control plots for baseline levels, and the forcings provided by natural  
226 rainfall anomalies and the experimental manipulations, we were able to conduct a four-way  
227 comparison for each scenario of rainy season change (Table 1). Each response variable was modelled  
228 as a function of forcing type (i.e. control, short-term natural variation, short-term experimental  
229 manipulation and long-term experimental manipulation), with separate models for each rainy season  
230 change scenario. Post-hoc tests implemented in the R package multcomp (Hothorn *et al.*, 2008) were  
231 used to test for significant differences between each forcing type. Full details of these models are  
232 given in Table S1, with full results of post-hoc tests given in Table S2.

233 To ensure our results are not affected by the choice of timescale for dividing short-term and long-term  
234 responses we also analysed the dataset treating time as a continuous variable. In this analysis, each  
235 response variable was modelled as a function of experimental treatment (Int, Ext or Control), year  
236 since the start of the experiment and the interaction between treatment and year. A significant  
237 treatment-year interaction in the opposite direction to the effect of treatment would indicate differing  
238 short-term and long-term responses to that treatment. Full details of these models are presented in  
239 Table S3.

240 We examined whether precipitation addition changed relationships between plant diversity and plant  
241 productivity and between plant productivity and consumer biomass by modelling the variable thought

242 most likely to be the response variable in each relationship (plant productivity and consumer biomass  
243 respectively) as a function of the corresponding explanatory variable (plant species richness and plant  
244 productivity respectively), precipitation addition treatment and their interaction. A significant  
245 interaction with treatment would indicate that the slope of these relationships changed under certain  
246 precipitation addition treatments.

247

## 248 **Results**

249 Intensification of the winter rainy season had only minor effects on plant production (Figs. 1a, 2a),  
250 with no overall effect of the Int treatment ( $t = 1.64$ ,  $P = 0.108$ ). The interaction between Int and Year  
251 was not significant ( $t = 0.53$ ,  $P = 0.598$ ), indicating that the effect of rainy season intensification did  
252 not change with the duration of forcing. Higher plant production in the later years of the Int treatment  
253 (Int<sub>1,2</sub> vs Int<sub>3-10</sub>:  $z = 3.81$ ,  $P < 0.001$ , Fig. 2a) likely reflects a weak but significant increase in primary  
254 production across treatments during the experiment (Year effect:  $t = 2.23$ ,  $P = 0.03$ , Fig. 1a). Plant  
255 production in control plots did not significantly change in years with naturally elevated winter  
256 precipitation (C vs C<sub>int</sub>:  $z = 1.34$ ,  $P = 0.526$ ). In contrast, experimental extension of the rainy season  
257 significantly increased plant production (Ext effect:  $t = 4.72$ ,  $P < 0.0001$ ). The effect of rainy season  
258 extension did not change with the duration of forcing (Fig. 2b), with no significant differences in  
259 short-term and long-term responses (Ext<sub>1,2</sub> vs Ext<sub>3-10</sub>:  $z = 0.35$ ,  $P = 0.984$ ) nor significant interaction  
260 between Ext and Year ( $t = 0.31$ ,  $P = 0.757$ ). Plant production responded positively but non-  
261 significantly to naturally extended rainy seasons (C vs C<sub>ext</sub>:  $z = 1.18$ ,  $P = 0.622$ ).

262 Plant species richness was significantly depressed in years with naturally intense winter rainy seasons  
263 (C vs C<sub>int</sub>:  $z = 3.54$ ,  $P = 0.002$ , Fig. 2c), but showed no response to experimental intensification of the  
264 rainy season (Int effect:  $t = 1.42$ ,  $P = 0.163$ ). The effect of Int did not change with duration of forcing  
265 (Int<sub>1,2</sub> vs Int<sub>3-10</sub>:  $z = 0.39$ ,  $P = 0.979$ ; Int – Year interaction:  $t = 1.21$ ,  $P = 0.233$ ). In contrast, the short-  
266 term and long-term response of plant species richness to extension of the rainy season was  
267 significantly different (Ext<sub>1,2</sub> vs Ext<sub>3-10</sub>:  $z = 8.70$ ,  $P < 0.0001$ ; Ext – Year interaction:  $t = 6.49$ ,  $P <$

268 0.0001), with a non-significant but positive effect of natural and experimental short-term extensions  
269 of the rainy season contrasting with a significant negative effect of repeated extensions of the rainy  
270 season (Figs. 1a, 2d).

271 Invertebrate herbivores showed little abundance response to intensified winter rainy seasons (Fig. 3a),  
272 with no significant differences evident from the control treatment in years of more typical winter  
273 rainfall (comparisons of  $C_{\text{int}}$ ,  $\text{Int}_{1,2}$  and  $\text{Int}_{3-10}$  with C:  $z \leq 1.35$ ,  $P \geq 0.508$ ). These herbivores showed  
274 pronounced responses to an extended rainy season (Fig. 3b), however, with large increases in  
275 abundance in years of naturally high April, May, and June precipitation (C vs  $C_{\text{ext}}$ ,  $z = 6.42$ ,  $P$   
276  $< 0.0001$ ) and in Ext treatment plots in the initial years of the study (C vs  $\text{Ext}_{1,2}$ :  $z = 7.99$ ,  $P < 0.0001$ ).  
277 Responses to rainy season extension changed with the duration of forcing ( $\text{Ext}_{1,2}$  vs  $\text{Ext}_{3-10}$ :  $z = 5.66$ ,  $P$   
278  $< 0.0001$ ; Ext – Year interaction:  $z = 5.00$ ,  $P < 0.0001$ ), with herbivore abundances in  $\text{Ext}_{3-10}$  plots  
279 similar to those in control plots (Figs. 1b, 3b).

280 Predators followed the same pattern as herbivores (Figs. 1b, 3c, 3d), with no evident responses to  
281 intensified winter rainy seasons (comparisons of  $C_{\text{int}}$ ,  $\text{Int}_{1,2}$  and  $\text{Int}_{3-10}$  with C:  $z \leq 1.60$ ,  $P \geq 0.358$  , and  
282 strong positive responses to the extended rainy season treatment (C vs  $\text{Ext}_{1,2}$ :  $z = 5.97$ ,  $P < 0.0001$ )  
283 that diminished when this regime was sustained across years ( $\text{Ext}_{1,2}$  vs  $\text{Ext}_{3-10}$ ,  $z = 4.18$ ,  $P = 0.0002$ ;  
284 Ext – Year interaction:  $z = 2.16$ ,  $P = 0.031$ ). Natural extensions of the rainy season had a non-  
285 significant positive effect on predator abundance (C vs  $C_{\text{ext}}$ :  $z = 1.63$ ,  $P = 0.353$ ).

286 Neither intensification nor extension of the rainy season significantly altered parasitoid abundance ( $z$   
287  $\leq 2.28$ ,  $P \geq 0.091$ ), although the weakening of the positive response to Ext with sustained forcing  
288 echoed the responses of herbivores and predators. Parasitoid abundance declined during the  
289 experiment across all treatments (Year effect:  $z = 3.81$ ,  $P = 0.0001$ , Fig. 1b).

290 Plant species richness and plant production were positively related in both control and Int plots ( $\beta =$   
291  $5.034 \pm 1.904$  SE,  $t = 2.64$ ,  $P = 0.0097$ , Fig 4a). Initial positive responses in plant species richness and  
292 plant production to experimental extension of the rainy season (Fig. 2b) did not alter the direction of  
293 this relationship (Fig. S1a: years 1 and 2). However, as the long-term response of plant richness to

294 extended annual rainy seasons turned from positive to sharply negative (Fig. 2d), so over time did the  
295 direction of the relationship between plant species richness and plant production in these plots (Fig  
296 S1a, years 3 to 10). Thus extension of the rainy season, when sustained across years, turned the  
297 positive relationship between diversity and production in the grassland system negative (significant  
298 interaction between effect of plant species richness and Ext,  $t = 2.83$ ,  $P = 0.0057$ , Fig. 4a). Plant  
299 production and consumer biomass (natural log transformed) were positively related in control and Int  
300 plots ( $\beta = 0.004 \pm 0.001$  SE,  $t = 3.52$ ,  $P = 0.006$ ). However, a significant interaction with Ext ( $t =$   
301  $2.43$ ,  $P = 0.0166$ ) meant that this relationship was not evident under extension of the rainy season  
302 (Fig. 4b). This interaction effect was not lagged (Fig. S1b).

303

#### 304 **Discussion**

305 We find that responses to short-term forcings are reliable predictors of trajectories under longer-term  
306 forcing in some variables but not others. Thus measurements taken under background variability at  
307 the study site or from a short-term experiment would reliably predict effects of more sustained  
308 directional climatic changes in certain variables, but would mislead us as to expected changes in other  
309 variables. In keeping with the pattern documented in a recent cross-ecosystem synthesis (Smith *et al.*,  
310 2015), we find a consistent directional response in ANPP even as species composition in the extended  
311 rainy season treatment shifted. Response variables of plant species richness and invertebrate  
312 abundances, however, showed greater complexity, with the notable consequence of reshaping  
313 relationships between plant production and diversity and between primary and secondary production  
314 in the system.

315 There are many factors that can cause long-term trajectories under directional climate forcing to  
316 deviate from responses to shorter-term forcings: physiological thresholds, species interactions,  
317 acclimation, and adaptation can all introduce non-linearities into ecological responses (Grotoli *et al.*,  
318 2014, Ockendon *et al.*, 2014) as can differences in the time these processes take to manifest  
319 themselves (Smith *et al.*, 2009). The challenge for ecological prediction is that the influence of these

320 factors can be context specific, depending on environmental conditions and the specific variable under  
321 consideration (e.g. Voigt *et al.* 2003). Thus in our study, not only were long-term effects in line with  
322 the direction of short-term effects in some variables while in opposite directions in others, but the  
323 incidence of these discrepancies varied between the two scenarios of climate change tested. Short-  
324 term responses of plant species richness, herbivore abundance and predator abundance to extension of  
325 the rainy season differed from responses to sustained directional forcing. In contrast, we did not  
326 detect any stark misalignments between short-term and long-term effects of intensified winter rainy  
327 seasons, where effects were generally much weaker overall than effects of extended rainy seasons.

328 Where short-term experimental water addition had a statistically significant effect (i.e. responses of  
329 plant production, herbivore abundance and predator abundance to extension of the rainy season),  
330 responses to natural rainy season variation were always in the same direction as responses to  
331 experimental water addition, but were weaker and only statistically significant for herbivore  
332 abundance (Fig. 3b). In contrast, we measured significant declines in plant richness in years with  
333 particularly intense winter rainfall, but did not detect any such effect in plots subjected to  
334 experimental rainy season intensification (Fig. 3c). Differences in responses to natural and  
335 experimental short-term forcing demonstrate the importance of the context and manner in which  
336 forcings are applied. Our basis in comparing natural rainy season anomalies with systematic  
337 experimental additions was equivalency of total amount, not accounting for differences in frequency  
338 and duration of rainfall events, or for other factors such as total insolation or average temperature,  
339 which could also have some ecological effect. It is further possible that legacy effects, interannual  
340 variation in precipitation outside of our focal seasons and variation in climatic conditions besides  
341 precipitation affected response variables. With 10 years of data it is not possible to disentangle the  
342 effects of these variables, however increases in plant production, herbivore abundance and predator  
343 abundance following a naturally extended rainy season in 2005 but not following similar conditions in  
344 2003 (Fig. 1) illustrate their importance.

345 Differences in short-term and long-term responses to extended rainy seasons emphasize the  
346 importance of species interactions in long-term ecological responses to climate change. The reversal

347 from initially (but non-significantly) positive to strongly negative responses in plant richness and the  
348 changes from strongly positive to null responses in invertebrate consumers reflect the influence of  
349 indirect effects from altered competitive and consumer-resource interactions. Research into the first  
350 five years of data from this experiment showed that positive direct effects of extended rainy seasons  
351 on nitrogen-fixing forbs favored improved performance by annual grasses, which then competitively  
352 suppressed broad-leaved forbs and due to their early senescence limited upward energy flow to higher  
353 trophic levels (Suttle *et al.*, 2007). Results reported here demonstrate that these indirect effects do not  
354 represent short-term dynamics, but leave a strong legacy on system dynamics, with plant species  
355 richness remaining suppressed in extended rainy season plots throughout the course of the experiment  
356 and herbivores and predators remaining at significantly lower abundances than their initial responses.

357 Results at consumer trophic levels require more nuanced interpretation than responses by plants;  
358 because plots were open to the surrounding grassland, measurements taken in experimental plots can  
359 reflect patterns of aggregation and dispersion within the overall invertebrate populations existing in  
360 the broader system. Thus abundances in water-addition plots better reflect aggregation or avoidance  
361 based on treatment effects on the environment of those plots, while comparisons of year to year  
362 changes in abundance in control plots (i.e.  $C_{int}$  Vs  $C$  and  $C_{ext}$  vs  $C$ ) mostly reflect net demographic  
363 effects of a particularly intense or particularly extended rainy season relative to more typical rainy  
364 season (along with any effects of the myriad other environmental conditions that vary among years).  
365 These demographic effects can be seen in the positive responses of herbivores (and potentially in the  
366 non-significant positive responses of predators) to naturally extended rainy seasons.

367 Positive responses of herbivores and predators (and a non-significant positive response of parasitoids)  
368 to the initial experimental extension of the rainy season are likely to reflect aggregation to favourable  
369 islands of habitat within the broader grassland. In the first year of the experiment, extended rainy  
370 season plots were more productive and had higher species richness than control plots (Fig. 1), with  
371 forbs, which previous work at the study site has shown to sustain a greater density of invertebrate  
372 herbivores than annual grasses (Suttle *et al.* 2007), accounting for a greater proportion of primary  
373 productivity (Fig. S3). As rainfall amendments were repeated across years, indirect effects of



374 extended rainy seasons increased the dominance of annual grasses and reduced plant species richness.  
375 This appears to have made these plots no more favourable than the rest of the surrounding grassland  
376 (Fig. 3). Notably, in the one year (2005) when plant production was comparable across all three  
377 treatments, the abundance of herbivores and predators was lower in extended rainy season plots than  
378 in other treatments (Fig. 1). This suggests that once differences in plant production were accounted  
379 for, the lower plant species richness of extended rainy season plots had a negative effect on  
380 invertebrate consumers, possibly due a reduction in the structural complexity of vegetation (Dennis *et*  
381 *al.*, 1998).

382 Although parasitoids showed a qualitatively similar response to rainy season extension as other  
383 invertebrates, these responses were not statistically significant (Fig. 3). In part this could be due to  
384 reduced statistical power to detect trends due to the lower abundance of parasitoids. Parasitoid  
385 abundance did decline across the whole study system over the course of the experiment (Fig. 1). The  
386 reasons for this are unclear, but as parasitoids are wide ranging (Rosenheim *et al.*, 1989) this could  
387 reflect meadow-wide consequences of the reduction in herbivore abundance in extended rainy season  
388 plots.

389 Responses to water addition treatments are likely to be also influenced by factors other than seasonal  
390 precipitation, such as legacy effects from the state of the system in previous years (Sala *et al.*, 2012).  
391 It is therefore possible that short-term responses to water addition would be different if they were  
392 applied in a different year. As long-term responses were influenced by a number of species  
393 interactions following initial water addition, it is also possible that any differences in short term  
394 responses could influence the long-term trajectory of the system, adding further complexity to  
395 predicting climate change impacts.

396 We turn to ecological time series encompassing climatic variability and to experiments simulating  
397 climate change to gain insights into how forcings in different directions affect variables of interest.  
398 Because the forcings manifest in background climate variability and extremes, in cyclical variation  
399 accompanying large-scale oscillations such as El Nino and the NAO, and in short-term experimental

400 studies may not match the levels or timeframes of forcings that will accompany directional climatic  
401 change, it is important to understand the translation of short-term effects into long-term trajectories.  
402 The prevalence of thresholds, biotic interactions, acclimation, and adaptation in ecological responses  
403 to climate change means that this translation may not be straightforward. Hence experimental results  
404 can poorly predict natural patterns that develop over longer timescales (Sandel *et al.*, 2010), initial  
405 responses to experimental manipulations may poorly predict longer-term effects (Chapin *et al.*, 1995,  
406 Harte & Shaw, 1995, Hollister *et al.*, 2005, Wiedermann *et al.*, 2007), populations that show a strong  
407 response to initial exposure to certain conditions may show little or no response over longer terms  
408 (Donelson *et al.*, 2011, Grotoli *et al.*, 2014, McLaughlin *et al.*, 2014, Shaver *et al.*, 2000, Smith *et al.*,  
409 2015), and populations that show little response to initial or itinerant exposure may show pronounced  
410 responses to repeated or sustained exposure (Grotoli *et al.*, 2014, Kirby & Beaugrand, 2009, Kortsch  
411 *et al.*, 2012) .

412 We find similar dynamics at work in our system, with little or no response to intensified rainy seasons  
413 but both transient (invertebrate consumers) and continuous positive responses (plant production, cf  
414 Smith *et al.* 2015) to rainy season extension, as well as responses that reverse in direction relative to  
415 controls (plant species richness). Because long-term effects extended more straightforwardly from  
416 short-term responses for some variables than for others, an important consequence was to alter basic  
417 relationships between ecological variables. Rainy season extension had a persistent positive effect on  
418 plant production, but its effect on plant diversity changed from (non-significantly) positive to strongly  
419 negative over time, leading to a reversal in the relationship between plant production and diversity  
420 through time as well. The form of this relationship is of considerable interest to conservation  
421 planning, with focus on whether management actions that promote ecosystem services also benefit  
422 diversity and vice versa (e.g. Hulme *et al.*, 2013). In this study we found that a measure of diversity  
423 (plant species richness) was positively correlated with plant production (a provisioning ecosystem  
424 service) under ambient conditions and one scenario of directional climate change, and initially under  
425 the other scenario of directional climate change, but the correlation turned negative over time. A  
426 similar but less drastic change was evident for the relationship between plant production and

427 consumer biomass. That fundamentally different relationships can emerge between key ecological  
428 variables under sustained forcing from those that prevail under ambient conditions further underscores  
429 the need to consider evidence from multiple approaches and sources in planning for and managing  
430 climate change impacts.

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540 **Supporting information**

541 Table S1. Statistical models of plant and invertebrate responses to rainy season change.

542 Table S2. Results of post-hoc simultaneous tests of general linear hypotheses.

543 Table S3. Results of analyses treating time as a continuous variable.

544 Figure S1. Experimental manipulation and sampling.

545 Figure S2. Year by year change in relationships between plant species richness and annual net  
546 primary productivity (ANPP) and between ANPP and consumer biomass.

547 Figure S3. Change in the contribution of forbs to ANPP over the course of the experiment.

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569 **Table 1.** Rainy season scenarios investigated in this study.

Timescale	Manipulation	Intensification of winter rainy season	Extension of winter rainy season	N <sup>1</sup>
Baseline	Natural variability	Control plots, data from years with winter (January – March) rainfall less than range experienced by Int treatment.	Control plots, data from years with spring (April – June) rainfall less than range experienced by Ext treatment.	8
Short-term change	Natural variability	Control plots, data from years with winter rainfall within range experienced by Int treatment (C <sub>int</sub> ). <sup>2</sup>	Control plots, data from years with spring rainfall within range experienced by Ext treatment (C <sub>ext</sub> ). <sup>3</sup>	2
	Experimental manipulation	Rainy season intensification treatment plots (Int), years 1 and 2 (Int <sub>1,2</sub> )	Rainy season extension treatment plots (Ext), years 1 and 2 (Ext <sub>1,2</sub> )	2
Long-term change	Experimental manipulation	Int treatment plots, years 3 through 10 (Int <sub>3-10</sub> )	Ext treatment plots, years 3 through 10 (Ext <sub>3-10</sub> )	8

570 <sup>1</sup> Number of years experiencing rainy season scenario

571 <sup>2</sup> 2004 and 2006

572 <sup>3</sup> 2003 and 2005

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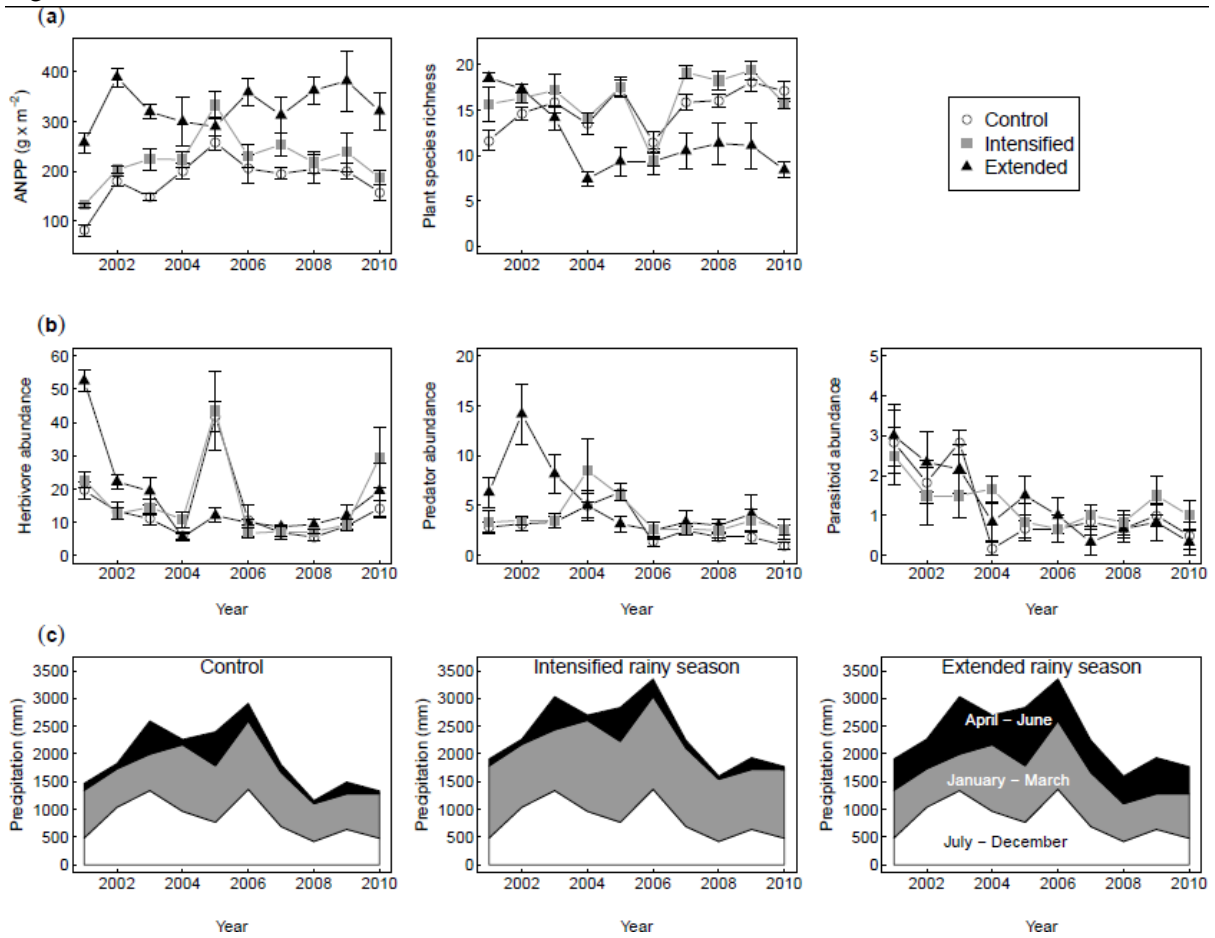
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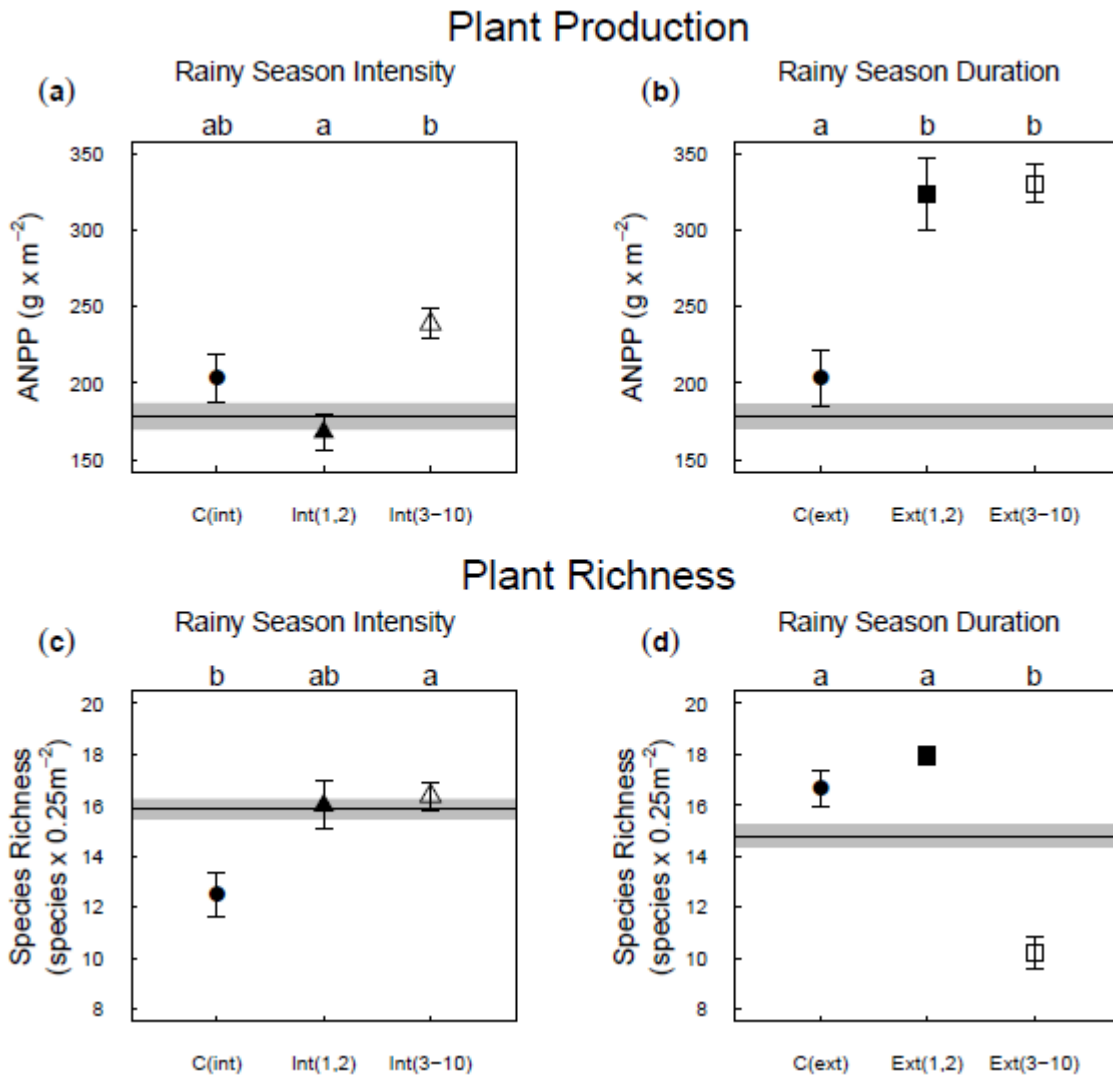
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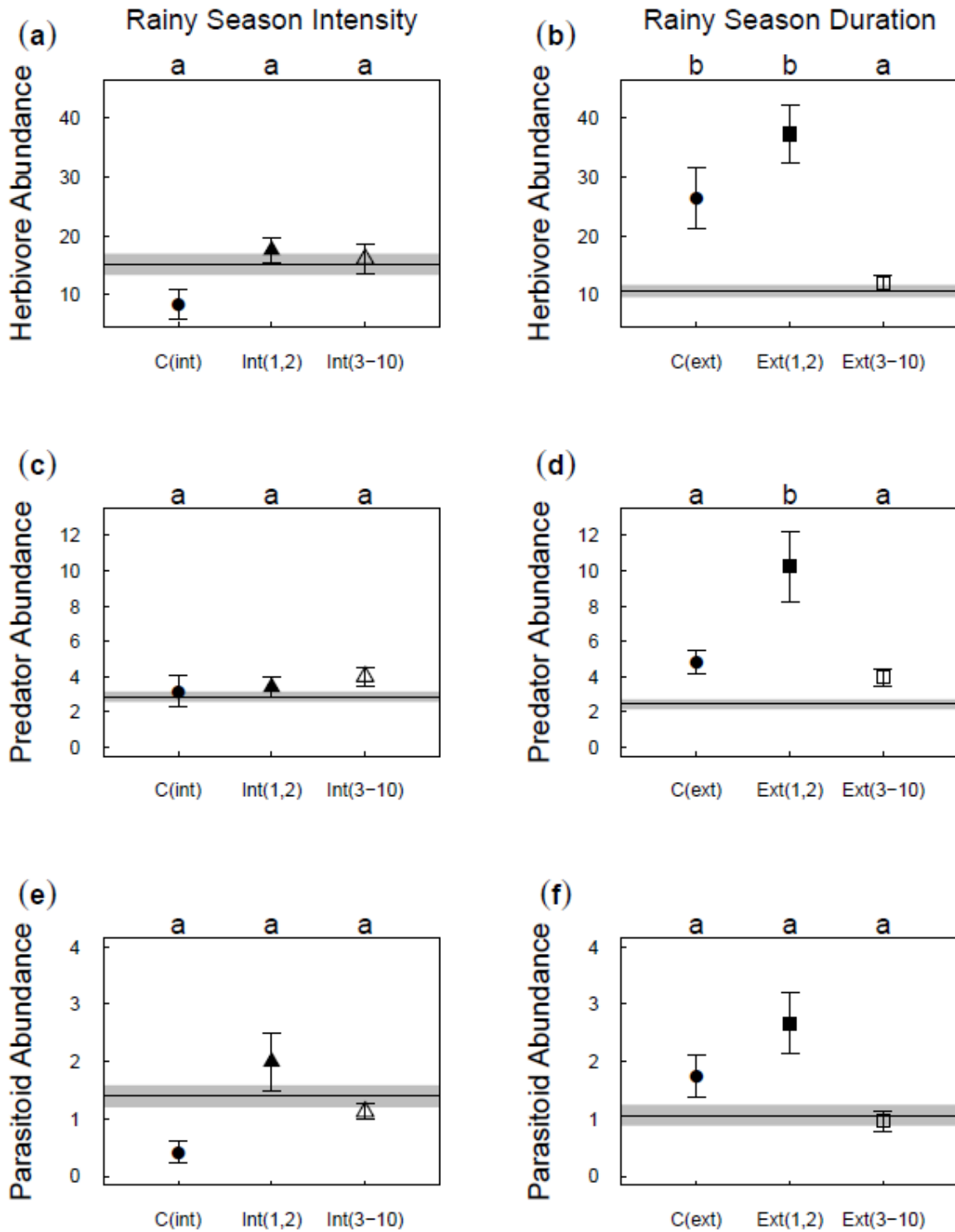
Figure 1. Change in (a) plant productivity and species richness, (b) consumer abundance and (c) precipitation over the study period. For biotic response variables, mean values  $\pm$  SE are shown for each treatment in each year, with data from control plots shown by open circles, the Int treatment shown by grey squares, and the Ext treatment shown by black triangles. Precipitation data are plotted in a stacked graph, with winter (January – March) precipitation shown in black, spring (April to June) precipitation shown in gray, and remaining precipitation in each year (October-December in the year before sampling) shown in white.



593  
 594 Figure 2. Plant responses to intensification and extension of the annual rainy season.  
 595 Data represent mean  $\pm$  1 s.e. for aboveground net primary production (a, b) and species richness (c, d)  
 596 under naturally and experimentally intensified (a, c) and extended (b, d) rainy seasons. In each panel,  
 597 the black line and grey shading show baseline conditions for that variable, as mean values  $\pm$  1 s.e.  
 598 measured in control plots over the eight years of the study with typical seasonal rainfall levels.  $C_{(int)}$   
 599 and  $C_{(ext)}$  denote measurements from control plots in years when seasonal rainfall levels were elevated  
 600 above long-term averages so that they were comparable with levels experienced in precipitation  
 601 addition treatments.  $Int_{(1,2)}$  and  $Int_{(3-10)}$  denote measurements from plots subjected to experimental  
 602 intensification of the rainy season via wintertime water addition in years 1 and 2 and years 3 through  
 603 10, respectively.  $Ext_{(1,2)}$  and  $Ext_{(3-10)}$  denote measurements from plots subjected to experimental  
 604 extension of the rainy season via springtime water addition in years 1 and 2 and years 3 through 10,  
 605 respectively. Different letters denote statistically significant differences ( $P < 0.05$ ) between  
 606 treatments; treatments with the letter “a” are not significantly different from control plots in years  
 607 with typical seasonal rainfall levels.

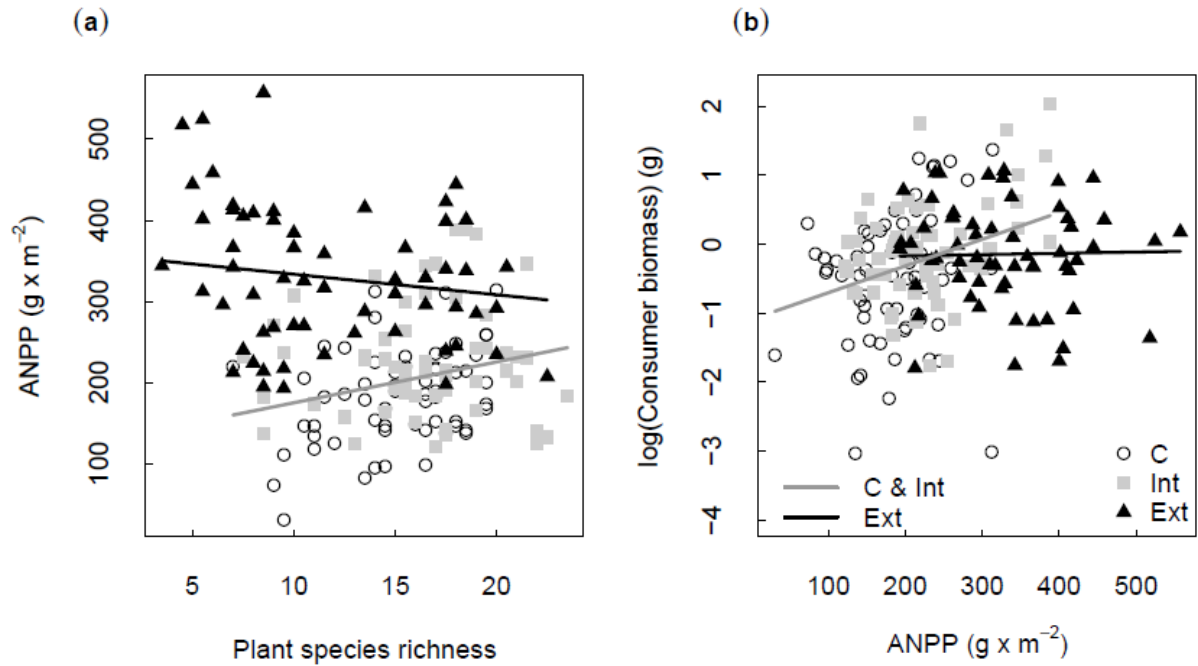
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## Invertebrate Abundance



614 Figure 3. Invertebrate responses to intensification and extension of the annual rainy season.  
 615 Data represent mean abundance  $\pm 1$  s.e. for herbivores (a, b), predators (c, d), and parasitoids (e,f)  
 616 under naturally and experimentally intensified (a, c, e) and extended (b, d, f) rainy seasons. See  
 617 legend from Fig. 2 for explanation of symbols and terms.  
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Figure 4. Ecological relationships under ambient, intensified, and extended annual rainy seasons. (a) Plant production versus plant species richness across years. (b) Consumer biomass versus plant production across years. Control plots are represented by open circles, intensified rainy season (Int) plots by grey squares, and extended rainy season (Ext) plots by black triangles.