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1	Grassland res	ponses to	increased	rainfall	depend	on the	timescale	of for	cing
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- 2 Running head: Contrasting responses to weather and climate
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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 timeframes of forcing expected under directional climatic change. Experiments help us to fill in these 18 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, we compare effects of short-term and long-term forcings across three trophic levels in grassland plots 22 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 predators) there was pronounced divergence of long-term trajectories from short-term responses. 26 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.

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 period of global climate change. A useful starting point for investigating how the functioning of 37 ecosystems and the abundance and distribution of different species will respond to future climate 38 change is to ask how they have responded to the changes we have already seen (e.g. Johnston et al., 39 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 simulating climate forcing, and directional changes in baseline conditions already evident-are 42 typically short in duration or small in magnitude relative to the climatic changes expected from 43 44 current emissions trajectories and resulting earth-surface energy imbalances. Ecologists must therefore grapple with how responses to pulsed or small-magnitude changes relate to responses to 45 chronic and larger magnitude shifts (Shaver et al., 2000, Smith et al., 2009). 46

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 responses changed direction relative to controls through time (Chapin et al., 1995, Harte & Shaw, 49 1995), presumably owing to interactions among different species or groups of species. Changes in 50 climate can alter the strength and nature of ecological interactions, leading to indirect effects that alter 51 response trajectories and are often lagged relative to direct physiological responses (Forchhammer et 52 al., 2002, Smith et al., 2009, Suttle et al., 2007, Wiedermann et al., 2007). Thus species interactions 53 have been borne out as important drivers of non-linear responses to changing climate through a large 54 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 smaller forcing (Grottoli et al., 2014, Kirby & Beaugrand, 2009, Kortsch et al., 2012, Nelson et al., 59 60 2013). Species may acclimate to changing climate, so that initially pronounced effects taper off with

repeated exposure (Donelson *et al.*, 2011, Grottoli *et al.*, 2014, McLaughlin *et al.*, 2014). Populations
may also adapt to selective pressures of changing climate (Colautti & Barrett, 2013, van Asch *et al.*,
2013). Each of these factors can cause long-term trajectories under sustained climate forcing to
deviate from short-term effects of initial or itinerant forcing. Understanding the causes of these
deviations, the urgent question becomes whether being able to identify these complexities and
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 et al., 2009). Smith and colleagues outline a temporal hierarchy of mechanisms governing ecosystem 80 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 nonlinearity in responses and how we might generalize these according to starting conditions, response 86 type, and ecosystem type. 87

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

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

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

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

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

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

126 Experimental Design

127 Since January 2001, thirty-six 70m² 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 Assessment Synthesis Team, 2000). Models from both the Hadley Centre for Climate Prediction and 133 134 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) calling for the entirety of the increase during the existing winter rainy season and the Canadian model 136 137 (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 year, representing roughly a 20% increase over mean annual precipitation but within the range of 139 natural variability in both amount and timing at the study site (details in Suttle *et al.*, 2007). Water is 140 collected from a natural spring on a forested slope immediately to the east of the grassland, with a 141 142 portion of its flow filtered to 40 microns and diverted via irrigation piping to a 4500-liter irrigation tank placed approximately 40 vertical meters upslope of the meadow. The tank is continually 143 144 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).

Water is delivered evenly over the surface of each plot from a single RainBird® RainCurtain[™] 146 147 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 additions begin approximately two hours after dawn every third day. Valves leading to the sprinklers 151 152 are actuated by battery-operated timers set to "rain" 14 to 16 mm of water onto the plots over one hour. The watering radius is 5m, and all samples are collected at least 0.5m in from the outside edge 153 of the watered area, as described under Response Variables below. 154

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

163 *Response Variables*

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

Plant production was measured from biomass samples collected three times each growing season from 168 two separate pre-designated 0.09 m² subplots. Samples were taken on or around 20 May, 1 July, and 169 170 30 August, dates that collectively target the peak biomass of each different species in the system. All vegetation was clipped at the soil surface, sorted into eight functional/phenological groups (spring 171 annual grass, summer annual grass, perennial grass, spring annual forb, summer annual forb, late-172 summer annual forb, perennial forb, and nitrogen-fixing forb) and dried at 72°C for 48 hours prior to 173 174 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 perpendicular to this first set (see Figure S1). Plant production was estimated by summing the 179 180 biomass of each different functional-phenological group at its annual peak biomass. Litter was not 181 included in ANPP estimates.

Plant diversity was measured as the mean species richness of two central 0.25 m² subplots in each
plot. Diversity subplots were surveyed regularly over the growing season to account for phenological
differences in the seasonal growth patterns of different species.

Invertebrate abundances were sampled on or around 1 August every year. Foliar and flying
invertebrates were sampled via a 30.5 cm diameter sweep net modified to connect securely to a
holding container open at the base of the net. Samples were collected by a quick succession of ten
sweeps along a transect running through the centre of the plot and then a second set of ten sweeps
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 initiation of the experiment in 2001, two 15cm sections of hollow rubber pipe (diameter 5.2cm) were 192 sunk vertically into the soil in opposite quadrants in each plot, using a sledge hammer to anchor each 193 194 approximately 1cm below the soil surface. Into each section of pipe was placed a capped plastic container of 5cm diameter, suspended from the top of the pipe by a lip at the top of each container 195 onto which the cap secured. To initiate a pitfall sample, caps were removed and the open containers 196 suspended in each pipe just below ground surface were filled to 2cm depth with a dilute solution of 197 water and unscented dish soap. This minimized soil and vegetation disturbance immediately prior to 198 199 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 were assigned to herbivore, predator, and parasitoid feeding groups based on natural history records. 203

204 Hypothesis Tests and Statistical Analyses

All statistical analyses were carried out within a mixed effects model framework, implemented in R 205 206 (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 as a random effect to account for the repeated measurements from each plot, where factors such as 208 soil texture and seed bank could lead to correlation among measurements. For invertebrates, within-209 210 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) natural anomalies in rainfall that entailed seasonal precipitation levels within the range experienced by 217 the water addition treatments (between 326 mm and 380 mm above long-term means for each season); 218 219 and (2) experimental amendments that delivered seasonal precipitation levels 440 mm greater than long-term means in the first two years of the experiment. Two years was chosen as a threshold for 220 221 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.

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

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

most likely to be the response variable in each relationship (plant productivity and consumer biomass
respectively) as a function of the corresponding explanatory variable (plant species richness and plant
productivity respectively), precipitation addition treatment and their interaction. A significant
interaction with treatment would indicate that the slope of these relationships changed under certain
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 was not significant (t = 0.53, P = 0.598), indicating that the effect of rainy season intensification did 251 252 not change with the duration of forcing. Higher plant production in the later years of the Int treatment (Int_{1,2} vs Int₃₋₁₀: z = 3.81, P < 0.001, Fig. 2a) likely reflects a weak but significant increase in primary 253 254 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 precipitation (C vs C_{int} : z = 1.34, P = 0.526). In contrast, experimental extension of the rainy season 256 257 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_{1.2} vs Ext_{3.10}: z = 0.35, P = 0.984) nor significant interaction between Ext and Year (t = 0.31, P = 0.757). Plant production responded positively but non-260 261 significantly to naturally extended rainy seasons (C vs C_{ext} : 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_{int}: z = 3.54, P = 0.002, Fig. 2c), but showed no response to experimental intensification of the

rainy season (Int effect: t = 1.42, P = 0.163). The effect of Int did not change with duration of forcing

265 (Int_{1,2} vs Int₃₋₁₀: z = 0.39, P = 0.979; Int – Year interaction: t = 1.21, P = 0.233). In contrast, the short-

- term and long-term response of plant species richness to extension of the rainy season was

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

Invertebrate herbivores showed little abundance response to intensified winter rainy seasons (Fig. 3a), 271 with no significant differences evident from the control treatment in years of more typical winter 272 rainfall (comparisons of C_{int}, Int_{1,2} and Int₃₋₁₀ with C: $z \le 1.35$, $P \ge 0.508$). These herbivores showed 273 274 pronounced responses to an extended rainy season (Fig. 3b), however, with large increases in abundance in years of naturally high April, May, and June precipitation (C vs C_{ext}, z = 6.42, P 275 <0.0001) and in Ext treatment plots in the initial years of the study (C vs Ext_{1.2}: z = 7.99, P < 0.0001). 276 Responses to rainy season extension changed with the duration of forcing (Ext_{1.2} vs Ext₃₋₁₀: z = 5.66, P 277 278 < 0.0001; Ext –Year interaction: z = 5.00, P < 0.0001), with herbivore abundances in Ext₃₋₁₀ plots similar to those in control plots (Figs. 1b, 3b). 279

280 Predators followed the same pattern as herbivores (Figs. 1b, 3c, 3d), with no evident responses to

intensified winter rainy seasons (comparisons of C_{int}, Int_{1,2} and Int₃₋₁₀ with C: $z \le 1.60$, $P \ge 0.358$, and

strong positive responses to the extended rainy season treatment (C vs Ext_{1,2}: z = 5.97, P < 0.0001)

that diminished when this regime was sustained across years (Ext_{1,2} vs Ext₃₋₁₀, z = 4.18, P = 0.0002;

Ext – Year interaction: z = 2.16, P = 0.031). Natural extensions of the rainy season had a non-

significant positive effect on predator abundance (C vs C_{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

echoed the responses of herbivores and predators. Parasitoid abundance declined during the

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 ($\beta =$

 5.034 ± 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
- 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 S1a, years 3 to 10). Thus extension of the rainy season, when sustained across years, turned the 296 positive relationship between diversity and production in the grassland system negative (significant 297 298 interaction between effect of plant species richness and Ext, t = 2.83, P = 0.0057, Fig. 4a). Plant production and consumer biomass (natural log transformed) were positively related in control and Int 299 plots ($\beta = 0.004 \pm 0.001$ SE, t = 3.52, P = 0.006). However, a significant interaction with Ext (t =300 301 2.43, P = 0.0166) meant that this relationship was not evident under extension of the rainy season (Fig. 4b). This interaction effect was not lagged (Fig. S1b). 302

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 the study site or from a short-term experiment would reliably predict effects of more sustained 307 directional climatic changes in certain variables, but would mislead us as to expected changes in other 308 309 variables. In keeping with the pattern documented in a recent cross-ecosystem synthesis (Smith et al., 2015), we find a consistent directional response in ANPP even as species composition in the extended 310 rainy season treatment shifted. Response variables of plant species richness and invertebrate 311 312 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.

There are many factors that can cause long-term trajectories under directional climate forcing to
deviate from responses to shorter-term forcings: physiological thresholds, species interactions,
acclimation, and adaptation can all introduce non-linearities into ecological responses (Grottoli *et al.*,
2014, Ockendon *et al.*, 2014) as can differences in the time these processes take to manifest
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 the direction of short-term effects in some variables while in opposite directions in others, but the 322 incidence of these discrepancies varied between the two scenarios of climate change tested. Short-323 324 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. Where short-term experimental water addition had a statistically significant effect (i.e. responses of 328

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 particularly intense winter rainfall, but did not detect any such effect in plots subjected to 333 334 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 precipitation affected response variables. With 10 years of data it is not possible to disentangle the 341 342 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 2003 (Fig. 1) illustrate their importance. 344

Differences in short-term and long-term responses to extended rainy seasons emphasize the
 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 changes from strongly positive to null responses in invertebrate consumers reflect the influence of 348 349 indirect effects from altered competitive and consumer-resource interactions. Research into the first five years of data from this experiment showed that positive direct effects of extended rainy seasons 350 351 on nitrogen-fixing forbs favored improved performance by annual grasses, which then competitively supressed broad-leaved forbs and due to their early senescence limited upward energy flow to higher 352 353 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; because plots were open to the surrounding grassland, measurements taken in experimental plots can 358 359 reflect patterns of aggregation and dispersion within the overall invertebrate populations existing in the broader system. Thus abundances in water-addition plots better reflect aggregation or avoidance 360 361 based on treatment effects on the environment of those plots, while comparisons of year to year changes in abundance in control plots (i.e. C_{int} Vs C and C_{ext} vs C) mostly reflect net demographic 362 effects of a particularly intense or particularly extended rainy season relative to more typical rainy 363 364 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.

Positive responses of herbivores and predators (and a non-significant positive response of parasitoids) to the initial experimental extension of the rainy season are likely to reflect aggregation to favourable islands of habitat within the broader grassland. In the first year of the experiment, extended rainy season plots were more productive and had higher species richness than control plots (Fig. 1), with forbs, which previous work at the study site has shown to sustain a greater density of invertebrate herbivores than annual grasses (Suttle et al. 2007), accounting for a greater proportion of primary 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 (Fig. 3). Notably, in the one year (2005) when plant production was comparable across all three 376 treatments, the abundance of herbivores and predators was lower in extended rainy season plots than 377 378 in other treatments (Fig. 1). This suggests that once differences in plant production were accounted for, the lower plant species richness of extended rainy season plots had a negative effect on 379 380 invertebrate consumers, possibly due a reduction in the structural complexity of vegetation (Dennis et 381 al., 1998).

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

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

We turn to ecological time series encompassing climatic variability and to experiments simulating
climate change to gain insights into how forcings in different directions affect variables of interest.
Because the forcings manifest in background climate variability and extremes, in cyclical variation
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 responses to experimental manipulations may poorly predict longer-term effects (Chapin et al., 1995, 405 406 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, Grottoli 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 (Grottoli 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 but both transient (invertebrate consumers) and continuous positive responses (plant production, cf 413 414 Smith et al. 2015) to rainy season extension, as well as responses that reverse in direction relative to controls (plant species richness). Because long-term effects extended more straightforwardly from 415 416 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.						
545 546	Figure S2. Year by year change in relationships between plant species richness and annual net 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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	Timescale Manipulation		Intensification of winter rainy	Extension of winter rainy season			
			season				
	Baseline Natural		Control plots, data from years	Control plots, data from years			
		variability	with winter (January – March)	with spring (April – June)			
			rainfall less than range	rainfall less than range			
			experienced by Int treatment.	experienced by Ext treatment.			
	Short-	Natural	Control plots, data from years	Control plots, data from years	2		
	term	variability	with winter rainfall within range	with spring rainfall within range			
	change		experienced by to Int treatment	experienced by Ext treatment			
			(C_{int}). ²	$(C_{ext}).^{3}$			
		Experimental	Rainy season intensification	Rainy season extension treatment	2		
		manipulation	treatment plots (Int), years 1	plots (Ext), years 1 and 2 ($Ext_{1,2}$)			
			and 2 ($Int_{1,2}$)				
	Long-	Experimental	Int treatment plots, years 3	Ext treatment plots, years 3	8		
	term	manipulation	through 10 (Int ₃₋₁₀)	through 10 (Ext ₃₋₁₀)			
	change						
570	¹ Number of years experiencing rainy season scenario						
571	² 2004 and 2006						
572	³ 2003 and 2005						
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Table 1. Rainy season scenarios investigated in this study.





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 ± 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.



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594 Figure 2. Plant responses to intensification and extension of the annual rainy season.

595 Data represent mean + 1 s.e. for above ground net primary production (a, b) and species richness (c, d) under naturally and experimentally intensified (a, c) and extended (b, d) rainy seasons. In each panel, 596 the black line and grey shading show baseline conditions for that variable, as mean values + 1 s.e. 597 598 measured in control plots over the eight years of the study with typical seasonal rainfall levels. $C_{(int)}$ and C_(ext) denote measurements from control plots in years when seasonal rainfall levels were elevated 599 600 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 extension of the rainy season via springtime water addition in years 1 and 2 and years 3 through 10, 604 605 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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Figure 3. Invertebrate responses to intensification and extension of the annual rainy season.
Data represent mean abundance ± 1 s.e. for herbivores (a, b), predators (c, d), and parasitoids (e,f)
under naturally and experimentally intensified (a, c, e) and extended (b, d, f) rainy seasons. See
legend from Fig. 2 for explanation of symbols and terms.



624 Figure 4. Ecological relationships under ambient, intensified, and extended annual rainy seasons.

625 (a) Plant production versus plant species richness across years. (b) Consumer biomass versus plant

626 production across years. Control plots are represented by open circles, intensified rainy season (Int)

627 plots by grey squares, and extended rainy season (Ext) plots by black triangles.

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