Article:

Sullivan, MJP, Thomsen, MA and Suttle, KB (2016) Grassland responses to increased rainfall depend on the timescale of forcing. Global Change Biology, 22 (4). pp. 1655-1665. ISSN 1354-1013

https://doi.org/10.1111/gcb.13206

Grassland responses to increased rainfall depend on the timescale of forcing

Running head: Contrasting responses to weather and climate

Martin J. P. Sullivan[1]*, Meredith Thomsen[2], and K.B. Suttle[3]*

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

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

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

*Corresponding authors: Martin Sullivan, tel +44 (0) 113 34 31039, email: m.j.sullivan@leeds.ac.uk; Blake Suttle, email: ksuttle@ucsc.edu

Key words: Prediction, Time Series, Correlation, Extrapolation, Trophic Level, Context, Climate Change

Type of paper: Primary Research Article

Abstract

Forecasting impacts of future climate change is an important challenge to biologists, both for understanding the consequences of different emissions trajectories and for developing adaptation measures that will minimize biodiversity loss. Existing variation provides a window into the effects 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 uncertainties, simulating directional shifts to examine outcomes of new levels and sustained changes in conditions. Here we explore the translation between short-term responses to climate variability and 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 subjected to natural and experimental variation in precipitation. For some biological responses (plant productivity), responses to long-term extension of the rainy season were consistent with short-term 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. These differences between biological responses mean that sustained directional changes in climate can restructure ecological relationships characterizing a system. Importantly, a positive relationship between plant diversity and productivity turned negative under one scenario of climate change, with a similar change in the relationship between plant productivity and consumer biomass. Inferences from experiments such as this form an important part of wider efforts to understand the complexities of climate change responses.

Introduction

Understanding how species and ecosystems respond to directional environmental changes is critical to 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 ecosystems and the abundance and distribution of different species will respond to future climate change is to ask how they have responded to the changes we have already seen (e.g. Johnston et al., 2013, Kurz et al., 2008, MacNeil et al., 2010). A critical challenge is that the windows we have into these impacts—natural climatic variability and the directional forcings apparent therein, experiments simulating climate forcing, and directional changes in baseline conditions already evident—are typically short in duration or small in magnitude relative to the climatic changes expected from 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 chronic and larger magnitude shifts (Shaver et al., 2000, Smith et al., 2009).

The translation between effects of short-term forcings and effects of sustained forcings is not always 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, 1995), presumably owing to interactions among different species or groups of species. Changes in climate can alter the strength and nature of ecological interactions, leading to indirect effects that alter response trajectories and are often lagged relative to direct physiological responses (Forchhammer et al., 2002, Smith et al., 2009, Suttle et al., 2007, Wiedermann et al., 2007). Thus species interactions have been borne out as important drivers of non-linear responses to changing climate through a large body of research (reviews in Cahill et al., 2012, Ockendon et al., 2014, Shaver et al., 2000, Walther, 2010), even as they have come to be understood as one class of a suite of such drivers. Physiological thresholds and tipping points can likewise cause ecological trajectories to deviate in sudden and 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., 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.

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

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 climate change, and we are making progress toward understanding how and why responses to the more chronic directional forcing may change direction through time. The possibility that we may be 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 prediction (Shaver et al., 2000, Smith et al., 2009) and encourages further study. Researchers have already produced evidence of such sorting by ecosystem type: a recent meta-analysis found herbaceous systems tend to show continuous directional ANPP responses to global change drivers while stepped responses are more common in forests and other systems (Smith et al., 2015). In the 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.

Materials and Methods

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 old-growth 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.

Experimental Design

Since January 2001, thirty-six 70m^2 circular plots have been exposed to one of three water amendment treatments assigned in a randomized block design. Treatments consist of an ambient control, a wintertime addition over ambient precipitation that simulates an intensified rainy season, and a springtime addition over ambient that simulates an extended rainy season. The Intensified rainy season treatment and the Extended rainy season treatment were developed to approximate projections 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 Research and the Canadian Centre for Climate Modeling and Analysis projected substantial increases 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 (CCM1) calling for an extended rainy season into the spring and summer.

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 natural variability in both amount and timing at the study site (details in Suttle et al., 2007). Water is collected from a natural spring on a forested slope immediately to the east of the grassland, with a 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 replenished via gravity-feed from the spring, and water has been tested and found to contain nitrogen 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™ sprinkler (Rainbird, Azusa, CA USA) in the center of each plot. The water delivery protocol is identical for the Intensified and Extended rainy season treatments, except that the applications are staggered by three months, with the Intensified rainy season addition running from January through 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 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 of the watered area, as described under Response Variables below.

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 sensor faults led to missing data, precipitation estimates were interpolated from nearby weather stations in Laytonville (39.7023, -123.4849; $R^2 = 0.727$), or, when data from Laytonville were not available, from Eel River (39.8253, -123.0825; $R^2 = 0.398$) based on regression equations from 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 directly from weather stations at the Angelo Reserve, with the remaining 10% interpolated.

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 two separate pre-designated 0.09 m^2 subplots. Samples were taken on or around 20 May, 1 July, and 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 annual grass, summer annual grass, perennial grass, spring annual forb, summer annual forb, late-summer annual forb, perennial forb, and nitrogen-fixing forb) and dried at 72ºC for 48 hours prior to weighing. Each species was included once in ANPP estimates for each year. Each subplot was harvested in this manner only once and then eliminated from the future sampling scheme. A five-year allotment of subplots (i.e. 30 total, with six subplots sampled per plot each year) was laid out at regular intervals along two parallel transects running in a randomly drawn cardinal direction through 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 biomass of each different functional-phenological group at its annual peak biomass. Litter was not included in ANPP estimates.

Plant diversity was measured as the mean species richness of two central 0.25 m^2 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 clips). Sample containers were immediately capped after the last sweep and then frozen until sorting. 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 sunk vertically into the soil in opposite quadrants in each plot, using a sledge hammer to anchor each 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 onto which the cap secured. To initiate a pitfall sample, caps were removed and the open containers suspended in each pipe just below ground surface were filled to 2cm depth with a dilute solution of water and unscented dish soap. This minimized soil and vegetation disturbance immediately prior to collection and any biases that could result. Upon collection, invertebrates were transferred into vials of 70% ethanol for storage until sorting, and the pitfall traps were recapped in place in the plots. Invertebrates were identified to family, with morphotypes sorted within families. Replicate 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.

Hypothesis Tests and Statistical Analyses

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

Analyses focused on testing how well responses to short-term forcings predicted responses to the 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 the water addition treatments (between 326 mm and 380 mm above long-term means for each season); 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 dividing short- and long-term responses as it allows both initial responses and lagged effects of precipitation in the previous year to be observed, but did not include evident indirect effects that became pronounced in the third year and thereafter (Suttle et al., 2007). Longer-term forcings were then defined as the subsequent years in the Intensified (Int) and Extended (Ext) rainy season treatments (Years 3-10). Using control plots for baseline levels, and the forcings provided by natural rainfall anomalies and the experimental manipulations, we were able to conduct a four-way comparison for each scenario of rainy season change (Table 1). Each response variable was modelled as a function of forcing type (i.e. control, short-term natural variation, short-term experimental manipulation and long-term experimental manipulation), with separate models for each rainy season change scenario. Post-hoc tests implemented in the R package multcomp (Hothorn et al., 2008) were used to test for significant differences between each forcing type. Full details of these models are 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.

Results

Intensification of the winter rainy season had only minor effects on plant production (Figs. 1a, 2a), 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 not change with the duration of forcing. Higher plant production in the later years of the Int treatment ($Int_{1,2}$ vs $Int_{3\text{-}10}$: $z = 3.81$, $P < 0.001$, Fig. 2a) likely reflects a weak but significant increase in primary production across treatments during the experiment (Year effect: $t = 2.23$, $P = 0.03$, Fig. 1a). Plant 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 significantly increased plant production (Ext effect: $t = 4.72$, $P < 0.0001$). The effect of rainy season extension did not change with the duration of forcing (Fig. 2b), with no significant differences in short-term and long-term responses ($Ext_{1,2}$ vs $Ext_{3\text{-}10}$: $z = 0.35$, $P = 0.984$) nor significant interaction between Ext and Year ($t = 0.31$, $P = 0.757$). Plant production responded positively but non-significantly to naturally extended rainy seasons (C vs C_{ext}: $z = 1.18$, $P = 0.622$).

Plant species richness was significantly depressed in years with naturally intense winter rainy seasons (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 ($Int_{1,2}$ vs $Int_{3\text{-}10}$: $z = 0.39$, $P = 0.979$; 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 significantly different ($Ext_{1,2}$ vs $Ext_{3\text{-}10}$: $z = 8.70$, $P <0.0001$; Ext – Year interaction: $t = 6.49$, $P <$

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), with no significant differences evident from the control treatment in years of more typical winter rainfall (comparisons of C_{int}, $Int_{1,2}$ and $Int_{3\text{-}10}$ with C: $z \leq 1.35$, $P \geq 0.508$). These herbivores showed 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}, $z = 6.42$, $P < 0.0001$) and in Ext treatment plots in the initial years of the study (C vs $Ext_{1,2}$: $z = 7.99$, $P < 0.0001$). Responses to rainy season extension changed with the duration of forcing ($Ext_{1,2}$ vs $Ext_{3\text{-}10}$: $z = 5.66$, $P < 0.0001$; Ext –Year interaction: $z = 5.00$, $P < 0.0001$), with herbivore abundances in $Ext_{3\text{-}10}$ plots similar to those in control plots (Figs. 1b, 3b).

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 $Int_{3\text{-}10}$ with C: $z \leq 1.60$, $P \geq 0.358$, 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 $Ext_{3\text{-}10}$, $z = 4.18$, $P = 0.0002$; 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}: $z = 1.63$, $P = 0.353$).

Neither intensification nor extension of the rainy season significantly altered parasitoid abundance ($z \leq 2.28$, $P \geq 0.091$), 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).

Plant species richness and plant production were positively related in both control and Int plots ($\beta = 5.034 \pm 1.904$ SE, $t = 2.64$, $P = 0.0097$, Fig 4a). Initial positive responses in plant species richness and 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 extended annual rainy seasons turned from positive to sharply negative (Fig. 2d), so over time did the 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 positive relationship between diversity and production in the grassland system negative (significant 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 plots ($\beta = 0.004 \pm 0.001$ SE, $t = 3.52$, $P = 0.006$). However, a significant interaction with Ext ($t = 2.43$, $P = 0.0166$) meant that this relationship was not evident under extension of the rainy season (Fig. 4b). This interaction effect was not lagged (Fig. S1b).

Discussion

We find that responses to short-term forcings are reliable predictors of trajectories under longer-term 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 directional climatic changes in certain variables, but would mislead us as to expected changes in other 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 rainy season treatment shifted. Response variables of plant species richness and invertebrate abundances, however, showed greater complexity, with the notable consequence of reshaping relationships between plant production and diversity and between primary and secondary production 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 factors can be context specific, depending on environmental conditions and the specific variable under 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 incidence of these discrepancies varied between the two scenarios of climate change tested. Short-term responses of plant species richness, herbivore abundance and predator abundance to extension of the rainy season differed from responses to sustained directional forcing. In contrast, we did not detect any stark misalignments between short-term and long-term effects of intensified winter rainy 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 plant production, herbivore abundance and predator abundance to extension of the rainy season), responses to natural rainy season variation were always in the same direction as responses to experimental water addition, but were weaker and only statistically significant for herbivore 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 experimental rainy season intensification (Fig. 3c). Differences in responses to natural and experimental short-term forcing demonstrate the importance of the context and manner in which forcings are applied. Our basis in comparing natural rainy season anomalies with systematic experimental additions was equivalency of total amount, not accounting for differences in frequency and duration of rainfall events, or for other factors such as total insolation or average temperature, which could also have some ecological effect. It is further possible that legacy effects, interannual 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 effects of these variables, however increases in plant production, herbivore abundance and predator abundance following a naturally extended rainy season in 2005 but not following similar conditions in 2003 (Fig. 1) illustrate their importance.

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 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 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 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 trophic levels (Suttle et al., 2007). Results reported here demonstrate that these indirect effects do not represent short-term dynamics, but leave a strong legacy on system dynamics, with plant species richness remaining suppressed in extended rainy season plots throughout the course of the experiment and herbivores and predators remaining at significantly lower abundances than their initial responses.

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 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 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 effects of a particularly intense or particularly extended rainy season relative to more typical rainy season (along with any effects of the myriad other environmental conditions that vary among years). These demographic effects can be seen in the positive responses of herbivores (and potentially in the 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 extended rainy seasons increased the dominance of annual grasses and reduced plant species richness. 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 treatments, the abundance of herbivores and predators was lower in extended rainy season plots than 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 invertebrate consumers, possibly due a reduction in the structural complexity of vegetation (Dennis et 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 studies may not match the levels or timeframes of forcings that will accompany directional climatic change, it is important to understand the translation of short-term effects into long-term trajectories. The prevalence of thresholds, biotic interactions, acclimation, and adaptation in ecological responses to climate change means that this translation may not be straightforward. Hence experimental results 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, Harte & Shaw, 1995, Hollister et al., 2005, Wiedermann et al., 2007), populations that show a strong response to initial exposure to certain conditions may show little or no response over longer terms (Donelson et al., 2011, Grottoli et al., 2014, McLaughlin et al., 2014, Shaver et al., 2000, Smith et al., 2015), and populations that show little response to initial or itinerant exposure may show pronounced responses to repeated or sustained exposure (Grottoli et al., 2014, Kirby & Beaugrand, 2009, Kortsch et al., 2012) .

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 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 short-term responses for some variables than for others, an important consequence was to alter basic relationships between ecological variables. Rainy season extension had a persistent positive effect on plant production, but its effect on plant diversity changed from (non-significantly) positive to strongly negative over time, leading to a reversal in the relationship between plant production and diversity through time as well. The form of this relationship is of considerable interest to conservation planning, with focus on whether management actions that promote ecosystem services also benefit diversity and vice versa (e.g. Hulme et al., 2013). In this study we found that a measure of diversity (plant species richness) was positively correlated with plant production (a provisioning ecosystem service) under ambient conditions and one scenario of directional climate change, and initially under the other scenario of directional climate change, but the correlation turned negative over time. A similar but less drastic change was evident for the relationship between plant production and consumer biomass. That fundamentally different relationships can emerge between key ecological variables under sustained forcing from those that prevail under ambient conditions further underscores the need to consider evidence from multiple approaches and sources in planning for and managing climate change impacts.

Acknowledgements

The experiment was established with funds from the US Environmental Protection Agency and the Canon National Parks Sciences Scholarship Program. Support for the research was provided by US National Science Foundation grant DEB-0816834, the US National Science Foundation's National Center for Earth Surface Dynamics, the California Energy Commission's Public Interest Energy Research program, the University of California at Berkeley, the University of Wisconsin at La Crosse, and Imperial College London. MS is currently funded by the European Research Council grant "Tropical Forests in the Changing Earth System".   We wish to thank Peter Steel and the University of California Natural Reserve System for stewardship and protection of the study site.

References

Bates D, Maechler M, Bolker BM, Walker S (2014) Lme4: Linear mixed-effects models using eigen and s4. pp Page.

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC *et al.* (2012) How does climate change cause extinction? *Proceedings of the Royal Society of London B: Biological Sciences,* **280**.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology,* **76**, 694-711.

Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science,* **342**, 364-366.

Coulson T, Macnulty DR, Stahler DR, Vonholdt B, Wayne RK, Smith DW (2011) Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science,* **334**, 1275-1278.

Dennis P, Young MR, Gordon IJ (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology,* **23**, 253-264.

Donelson JM, Munday PL, Mccormick MI, Nilsson GE (2011) Acclimation to predicted ocean warming through developmental plasticity in a tropical reef fish. *Global Change Biology,* **17**, 1712-1719.

Forchhammer MC, Post E, Stenseth NC, Boertmann DM (2002) Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Population Ecology,* **44**, 113-120.

Fordham DA, Akcakaya HR, Brook BW *et al.* (2013) Adapted conservation measures are required to save the iberian lynx in a changing climate. *Nature Clim. Change,* **3**, 899-903.

Grottoli AG, Warner ME, Levas SJ *et al.* (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Global Change Biology,* **20**, 3823-3833.

Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community: Results of a climate-warming experiment. *Science,* **267**, 876-880.

Heikkinen RK, Luoto M, Virkkala R, Pearson RG, Körber J-H (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography,* **16**, 754-763.

Hobbs RJ, Yates S, Mooney HA (2007) Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs,* **77**, 545-568.

Hollister RD, Webber PJ, Bay C (2005) Plant response to temperature in northern alaska: Implications for predicting vegetation change. *Ecology,* **86**, 1562-1570.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal,* **50**, 346-363.

Hulme MF, Vickery JA, Green RE *et al.* (2013) Conserving the birds of uganda’s banana-coffee arc: Land sparing and land sharing compared. *PLoS ONE,* **8**, e54597.

Johnston A, Ausden M, Dodd AM *et al.* (2013) Observed and predicted effects of climate change on species abundance in protected areas. *Nature Clim. Change,* **3**, 1055-1061.

Kirby RR, Beaugrand G (2009) Trophic amplification of climate warming. *Proceedings of the Royal Society B: Biological Sciences*.

Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lønne OJ, Gulliksen B (2012) Climate-driven regime shifts in arctic marine benthos. *Proceedings of the National Academy of Sciences,* **109**, 14052-14057.

Kurz WA, Dymond CC, Stinson G *et al.* (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature,* **452**, 987-990.

Luoto M, Virkkala R, Heikkinen RK (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography,* **16**, 34-42.

Macneil MA, Graham NaJ, Cinner JE *et al.* (2010) Transitional states in marine fisheries: Adapting to predicted global change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* **365**, 3753-3763.

Mclaughlin BC, Xu C-Y, Rastetter EB, Griffin KL (2014) Predicting ecosystem carbon balance in a warming arctic: The importance of long-term thermal acclimation potential and inhibitory effects of light on respiration. *Global Change Biology,* **20**, 1901-1912.

National Assessment Synthesis Team (2000) Climate change impacts on the united states: The potential consequences of climate variability and change. pp Page, Washington, D>C., US Global Change Research Program.

Nelson WA, Bjørnstad ON, Yamanaka T (2013) Recurrent insect outbreaks caused by temperature-driven changes in system stability. *Science,* **341**, 796-799.

Ockendon N, Baker DJ, Carr JA *et al.* (2014) Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology,* **20**, 2221-2229.

Pitt MD, Heady HF (1978) Responses of annual vegetation to temperature and rainfall patterns in northern california. *Ecology,* **59**, 336-350.

R Core Team (2014) R: A language and environment for statistical computing. pp Page, Vienna, Austria, R Foundation for Statistical Computing.

Rosenheim JA, Meade T, Powch IG, Schoenig SE (1989) Aggregation by foraging insect parasitoids in response to local variations in host density: Determining the dimensions of a host patch. *Journal of Animal Ecology,* **58**, 101-117.

Sala OE, Gherardi LA, Reichmann L, Jobbagy E, Peters D (2012) Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **367**, 3135-3144.

Sandel B, Goldstein LJ, Kraft NJB *et al.* (2010) Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist,* **188**, 565-575.

Shaver GR, Canadell J, Chapin FS *et al.* (2000) Global warming and terrestrial ecosystems: A conceptual framework for analysis. *BioScience,* **50**, 871-882.

Smith M, La Pierre K, Collins S *et al.* (2015) Global environmental change and the nature of aboveground net primary productivity responses: Insights from long-term experiments. *Oecologia,* **177**, 935-947.

Smith MD, Knapp AK, Collins SL (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology,* **90**, 3279-3289.

Stromberg MR, Griffin JR (1996) Long-term patterns in coastal california grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications,* **6**, 1189-1211.

Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science,* **315**, 640-642.

Trainor AM, Schmitz OJ (2014) Infusing considerations of trophic dependencies into species distribution modelling. *Ecology Letters,* **17**, 1507-1517.

Trainor AM, Schmitz OJ, Ivan JS, Shenk TM (2014) Enhancing species distribution modeling by characterizing predator-prey interactions. *Ecological Applications,* **24**, 204-216.

Van Asch M, Salis L, Holleman LJM, Van Lith B, Visser ME (2013) Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Clim. Change,* **3**, 244-248.

Walther G-R (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365**, 2019-2024.

Wiedermann MM, Nordin A, Gunnarsson U, Nilsson MB, Ericson L (2007) Global change shifts vegetation and plant–parasite interactions in a boreal mire. *Ecology,* **88**, 454-464.

Supporting information

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

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

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

Figure S1. Experimental manipulation and sampling.

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

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

Table 1. Rainy season scenarios investigated in this study.

Timescale	Manipulation	Intensification of winter rainy season	Extension of winter rainy season	N[1]
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 to Int treatment (C_{int}). [2]	Control plots, data from years with spring rainfall within range experienced by Ext treatment (C_{ext}). [3]	2
	Experimental manipulation	Rainy season intensification treatment plots (Int), years 1 and 2 ($Int_{1,2}$)	Rainy season extension treatment plots (Ext), years 1 and 2 ($Ext_{1,2}$)	2
Long-term change	Experimental manipulation	Int treatment plots, years 3 through 10 (Int_{3-10})	Ext treatment plots, years 3 through 10 (Ext_{3-10})	8

[1] Number of years experiencing rainy season scenario

[2] 2004 and 2006

[3] 2003 and 2005

Figures

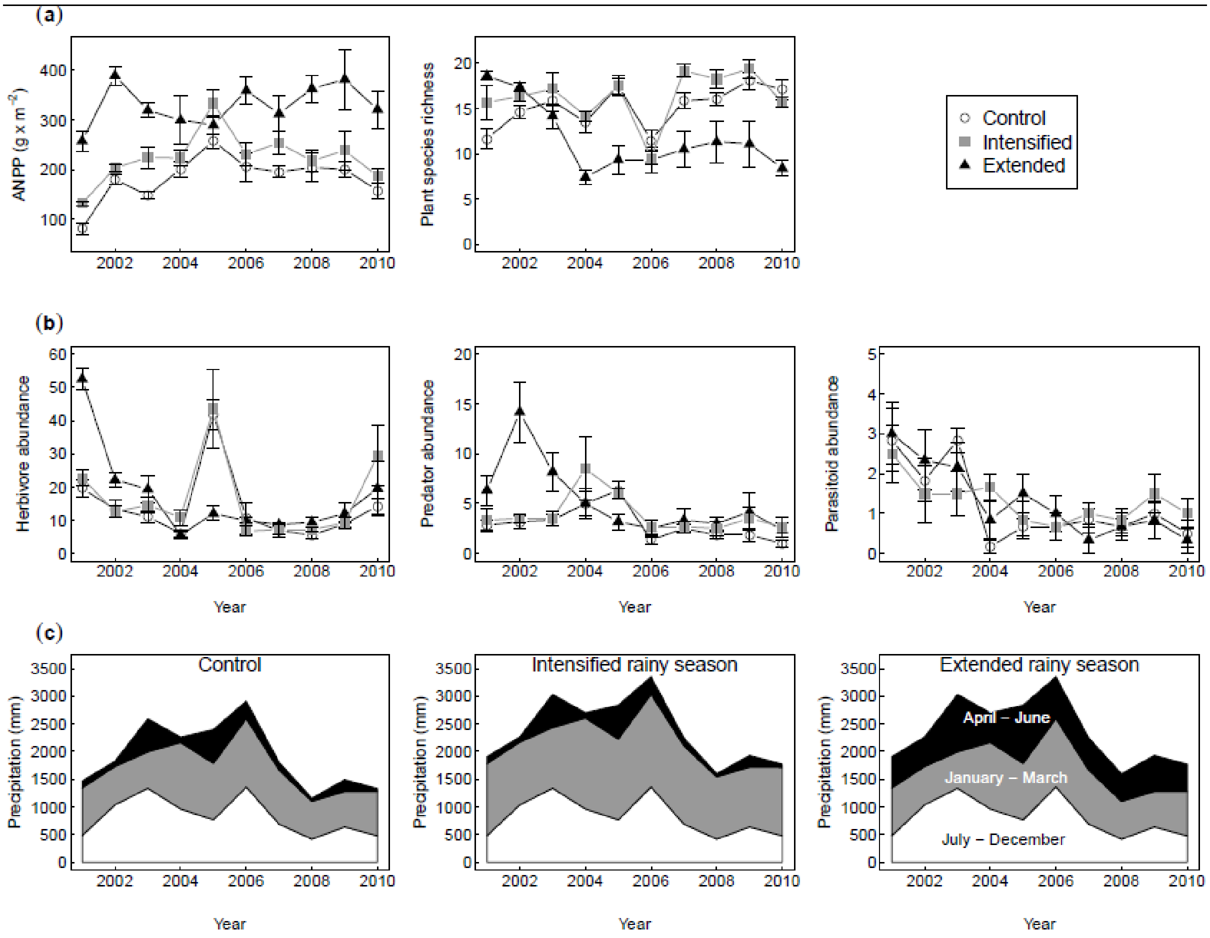

Figure 1. Change in (a) plant productivity and species richness, (b) consumer abundance and (c) precipitation over the study period. For biotic response variables, mean values ± SE are shown for each treatment in each year, with data from control plots shown by open circles, the Int treatment shown by 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.

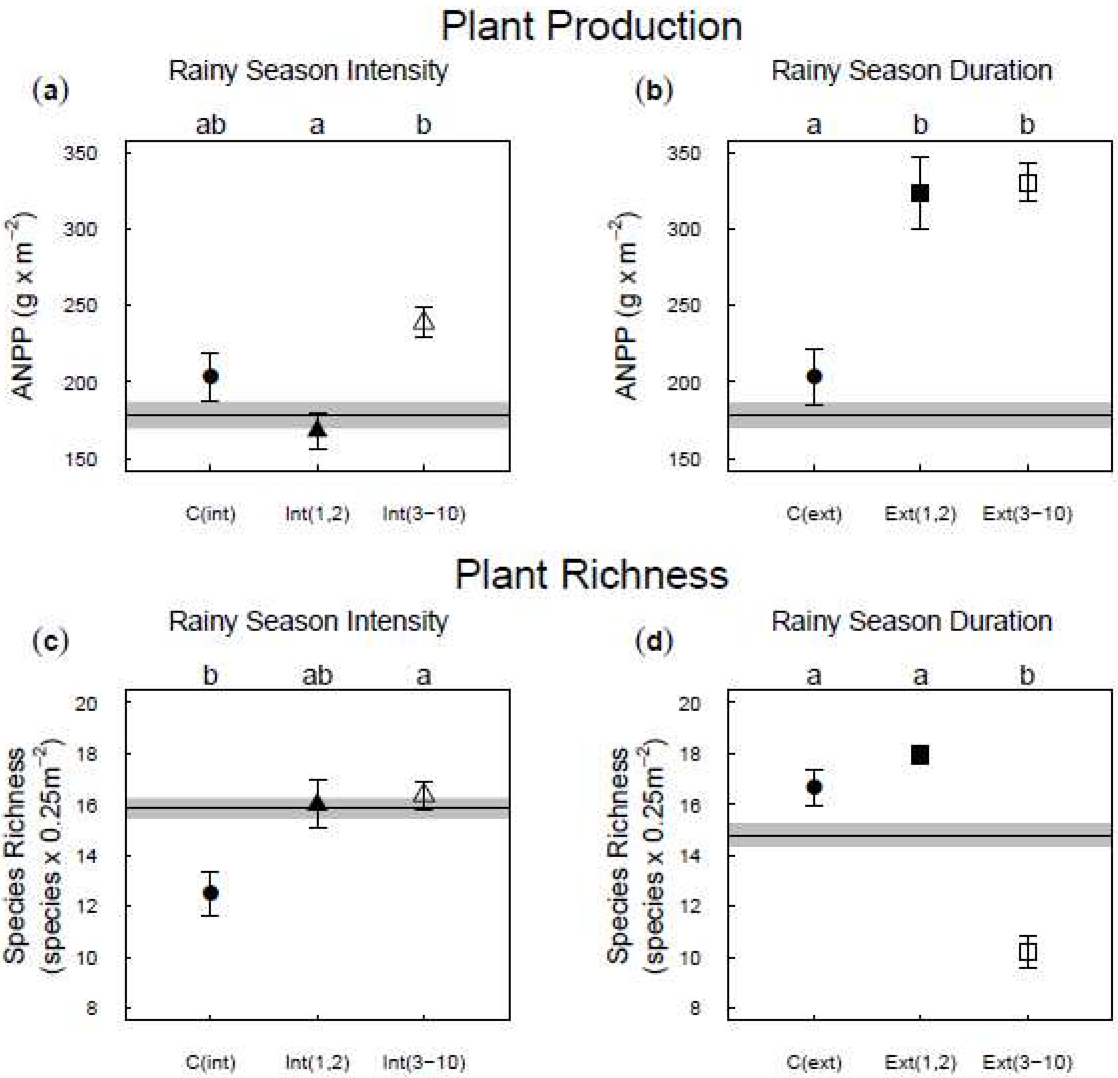

Figure 2. Plant responses to intensification and extension of the annual rainy season.

Data represent mean ± 1 s.e. for aboveground 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, the black line and grey shading show baseline conditions for that variable, as mean values ± 1 s.e. 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 above long-term averages so that they were comparable with levels experienced in precipitation addition treatments. $Int_{(1,2)}$ and $Int_{(3\text{-}10)}$ denote measurements from plots subjected to experimental intensification of the rainy season via wintertime water addition in years 1 and 2 and years 3 through 10, respectively. $Ext_{(1,2)}$ and $Ext_{(3\text{-}10)}$ 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, respectively. Different letters denote statistically significant differences ($P < 0.05$) between treatments; treatments with the letter “a” are not significantly different from control plots in years with typical seasonal rainfall levels.

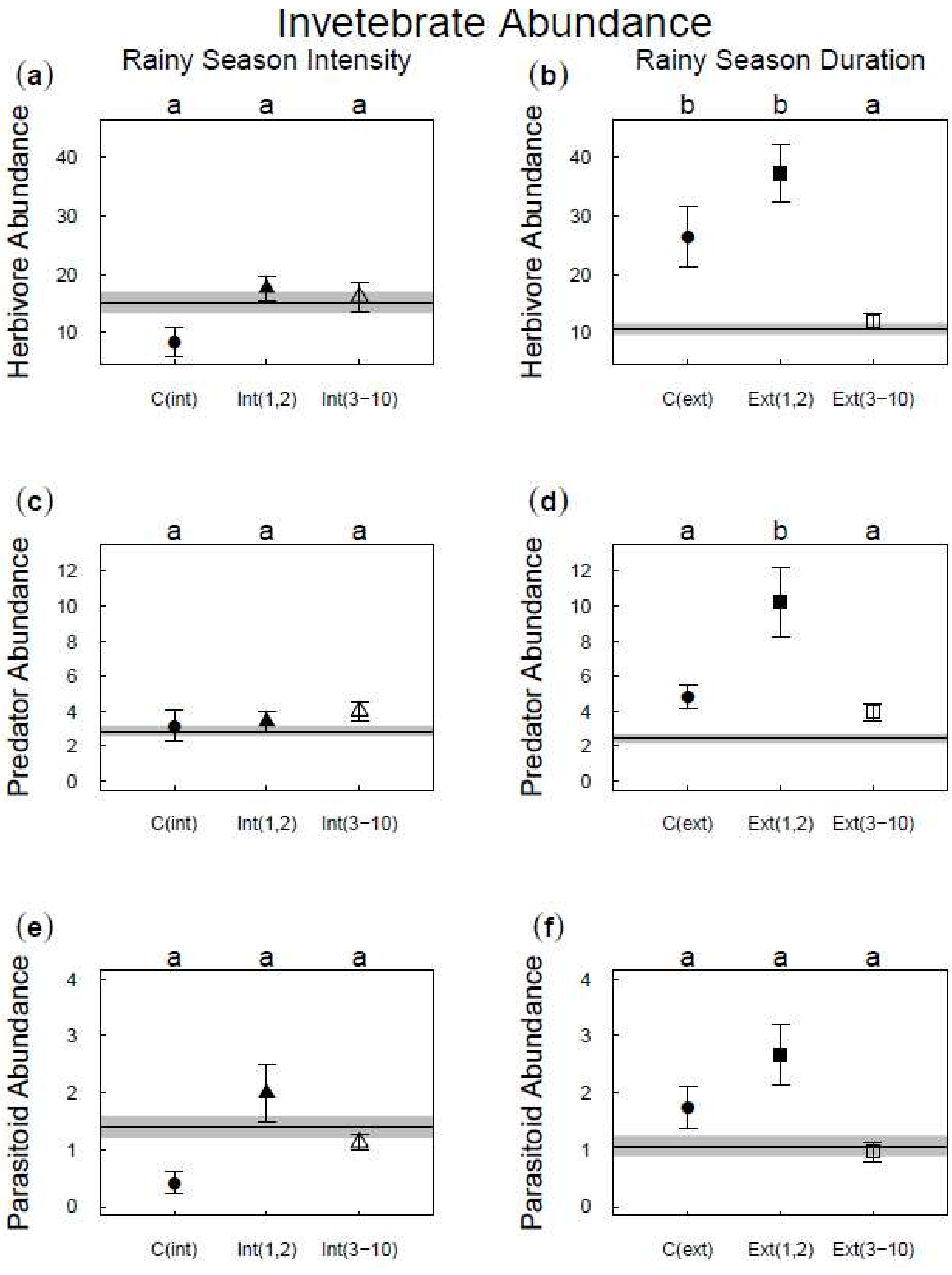

Figure 3. Invertebrate responses to intensification and extension of the annual rainy season. Data represent mean abundance + 1 s.e. for herbivores (a, b), predators (c, d), and parasitoids (e,f) under naturally and experimentally intensified (a, c, e) and extended (b, d, f) rainy seasons. See legend from Fig. 2 for explanation of symbols and terms.

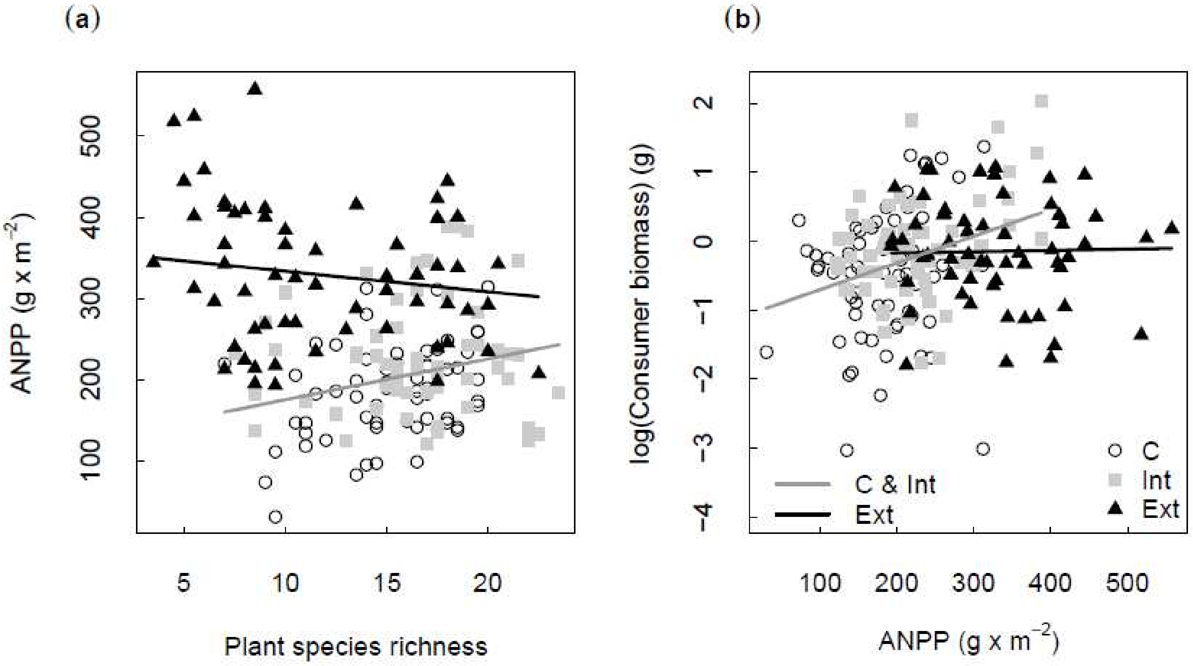

Figure 4. Ecological relationships under ambient, intensified, and extended annual rainy seasons. (a) Plant production versus plant species richness across years. (b) Consumer biomass versus plant production across years. Control plots are represented by open circles, intensified rainy season (Int) plots by grey squares, and extended rainy season (Ext) plots by black triangles.