

Species Interactions Reverse Grassland Responses to Changing Climate

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Predictions of ecological response to climate change are based largely on direct climatic effects on species. We show that, in a California grassland, species interactions strongly influence responses to changing climate, overturning direct climatic effects within 5 years. We manipulated the seasonality and intensity of rainfall over large, replicate plots in accordance with projections of leading climate models and examined responses across several trophic levels. Changes in seasonal water availability had pronounced effects on individual species, but as precipitation regimes were sustained across years, feedbacks and species interactions overrode autecological responses to water and reversed community trajectories. Conditions that sharply increased production and diversity through 2 years caused simplification of the food web and deep reductions in consumer abundance after 5 years. Changes in these natural grassland communities suggest a prominent role for species interactions in ecosystem response to climate change.

Impacts of recent climate change on plants and animals are already evident, as geographic distributions shift poleward (1, 2) and toward higher elevations (3, 4), phenological events advance in time (5–7), and some species disappear altogether (8). With further climate change still expected, prediction of future impacts has become critical to conservation planning and management. To forecast ecological change under continued climate warming, how-

ever, we need a better understanding of the relative importance of direct responses by individual species to climate versus responses mediated by changing interactions with resources, competitors, pathogens, or consumers (9–14). We imposed projected future precipitation regimes over grassland in northern California to evaluate the importance to ecosystem response of direct effects on grassland species versus indirect effects arising from species interactions.

Much of the California coastal region experiences a Mediterranean climate, characterized by wet winters and long summer droughts. Ecological responses to climate change in regions with Mediterranean climate regimes may be strongly driven by the redistribution of water in time and space (15). Changes in seasonal water

availability that affect plant phenology, for example, could lead to temporal mismatch between resource availability and consumer demand (16), which can have important effects on resource flow and ecosystem function (17). General circulation models developed at the Hadley Centre for Climate Prediction and Research (HadCM2) and the Canadian Centre for Climate Modeling and Analysis (CCM1) (18) predict substantial increases in precipitation over most of California but differ in the projected seasonality of these increases. The Hadley model calls for all additional rain to fall during the current winter rainy season, whereas the Canadian model projects increased rainfall extending into the current summer drought. The discrepancy between the two scenarios may be critical to the fate of grassland ecosystems in California, where summer drought severely constrains plant growth and the timing of rainfall is more important to annual production and species composition than the amount (19–22).

In 2001, we began a large-scale rainfall manipulation in a northern California grassland to examine the consequences of these two projected regimes for production and diversity of grassland plants and invertebrates. In a grassland at the Angelo Coast Range Reserve in Mendocino County, California (39° 44' 17.7" N, 123° 37' 48.4" W), 18 circular 70-m² plots were subjected to one of three watering treatments: a winter addition of water (January through March), a spring addition of water (April through June), and an unmanipulated ambient control (Fig. 1). Each watered plot received about 44 cm of supplementary water over ambient rainfall per year, roughly a 20% increase over mean annual precipitation but within natural variability in both amount and timing at the study site (fig. S1). We

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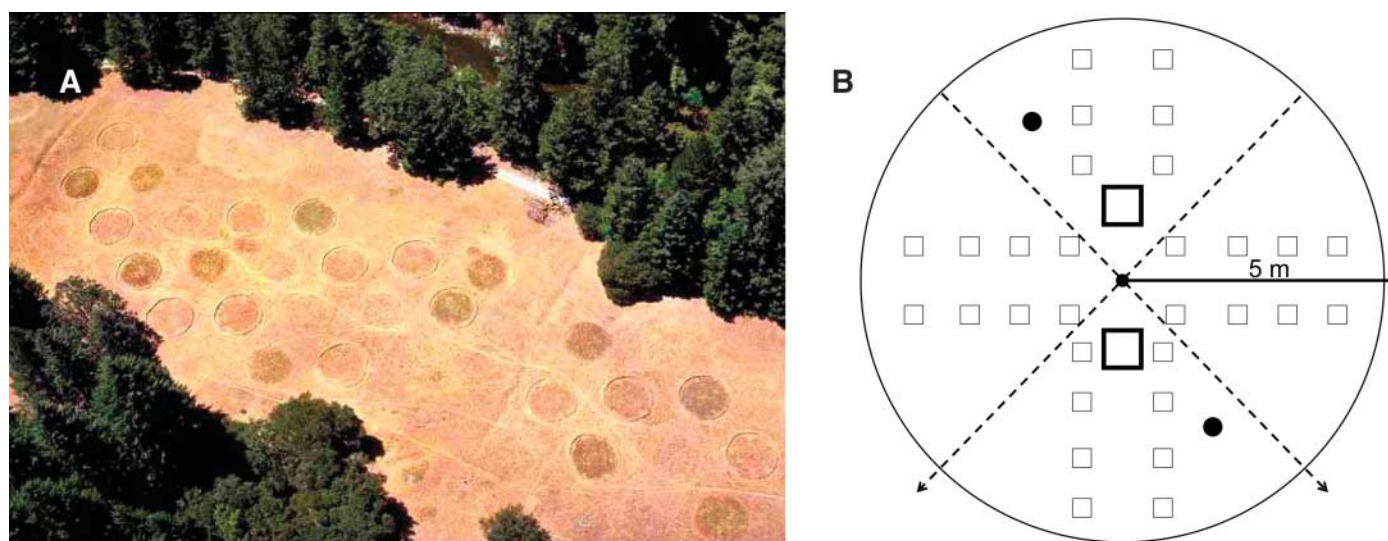


Fig. 1. (A) Bird's-eye view of experimental communities in July 2002. A nearby road is visible as a gray strip, top right. Research described here is from 18 open-grassland plots (18 additional plots were used in separate research). (B) Schematic representation of an experimental plot, shown as partitioned for measurement of plant biomass (30 900-cm²

subplots, small squares), plant species richness (two 2500-cm² subplots, large squares), foliar and flying invertebrates (two perpendicular sweep-net transects, dashed arrows), and ground-dwelling invertebrates (two pitfall traps, circles) (not to scale). Detailed methods are available online (23).

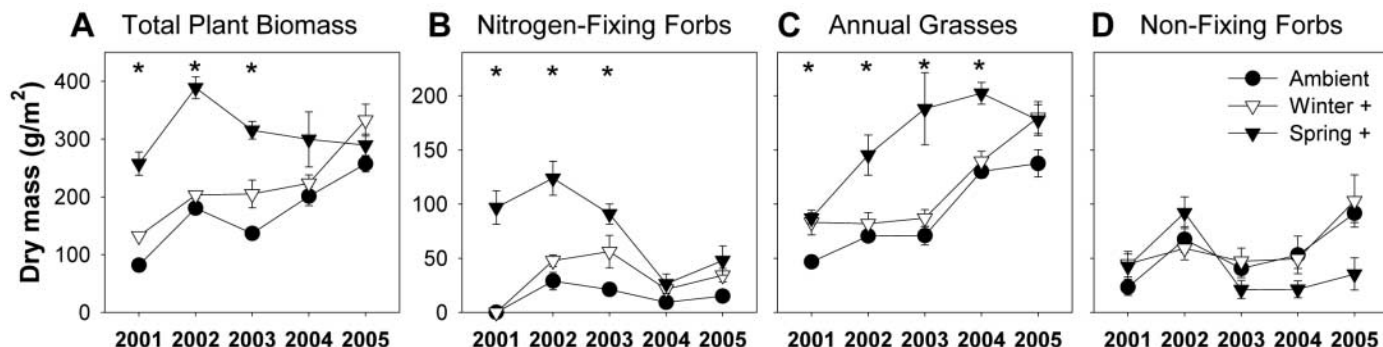


Fig. 2. Watering treatment effects on (A) total plant biomass and (B to D) biomass of individual plant groups (note difference in scales). Data represent treatment means \pm 1 SE. An asterisk denotes a statistically significant treatment difference after Bonferroni correction for multiple comparisons. See table S1 for factor significance.

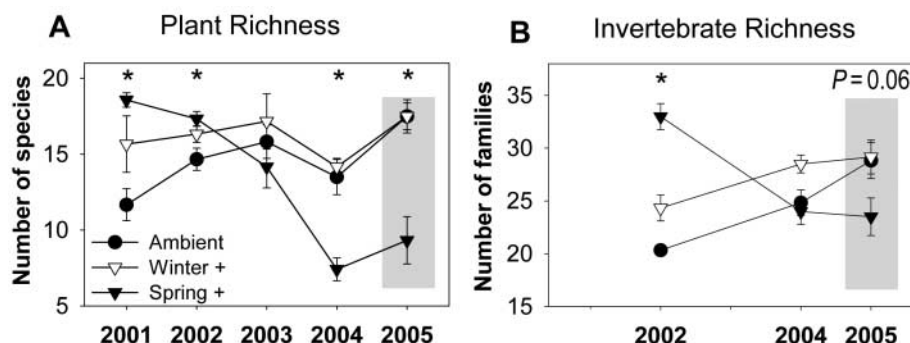


Fig. 3. Watering treatment effects on (A) plant species richness and (B) invertebrate family richness. Data represent treatment means \pm 1 SE. Gray shading highlights the year that late natural rainfall mirrored the spring-addition watering treatment. See tables S2 and S3 for taxonomic listings of plant species and invertebrate families, respectively.

examined treatment effects on plant production and species composition over 5 consecutive years and quantified responses of invertebrate herbivores and their natural enemies over 3 years (23).

Effects of increased rainfall depended critically on the seasonality of the increase. Supplemental water addition during the wet winter period produced moderate increases in plant production in some years of the study (Fig. 2), but effects did not extend to higher trophic levels (Figs. 3 and 4). In general, communities in winter-addition and ambient rainfall plots responded similarly across years to annual variation in rainfall.

Extending the rainy season via spring water addition produced much more dramatic changes in the grassland community. Plant production more than tripled in the first year and more than doubled in the second compared with the control (Fig. 2A). The strongest initial response was by nitrogen-fixing forbs, whose production increased by nearly two orders of magnitude with extended spring rainfall (Fig. 2B). Exotic annual grasses showed a weaker response to the first year of spring water addition, but after the proliferation of nitrogen-fixing forbs that year, annual grass production rose dramatically (Fig. 2C). These grasses, so-called winter annuals because they are the first plants to germinate

each year and are among the earliest to complete their life cycle and senesce, generally do not respond to extensions of the rainy season beyond April (22, 24). Early phenology thus limited the direct response of annual grasses to extended rainfall but allowed these plants to benefit in the subsequent growing season from a fertilization effect after decomposition of abundant N-fixer litter (25–27). As this process was repeated year after year, the accumulation of annual grass litter suppressed germination and regrowth of leafy forbs (Fig. 2D), as has often been seen in California annual grasslands (26, 28–30), and drove steep declines in plant species richness (Fig. 3A).

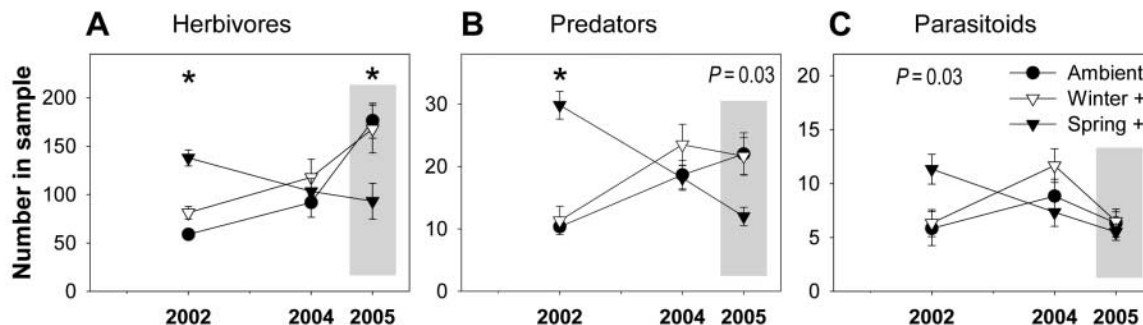
Shifts in plant composition in spring-addition plots had important consequences for biodiversity and food web structure. Initially, extended rainfall promoted increased plant species richness (Fig. 3A), and this increase, coupled with greater primary production and water availability, supported greater diversity and abundance of invertebrate herbivores, predators, and parasitoids (Figs. 3B and 4). As forbs were eliminated from spring-addition plots by annual grasses, however, plant species richness collapsed to nearly half that in control plots. With early-senescing annual grasses increasingly dominating the resource base, food availability and habitat quality for higher trophic levels dimin-

ished. This was especially true during summer, when late-blooming forbs provide a critical food resource for invertebrate herbivores (fig. S2). In contrast, annual grass litter has low nutritional value, and monocultures of these plants offer less structural complexity than mixed grass-forb assemblages.

By the fifth year of the study, when heavy rains continued into summer in a naturally extended rainy season throughout northern California, spring-addition plots stood out as islands of low biodiversity and reduced consumer abundances (Fig. 3B and 4). In addition to the nearly 50% reduction in plant species richness in spring-addition relative to control plots, invertebrate richness was 20% lower, and herbivore and predator abundances were each nearly 50% lower than ambient values measured in control plots. This simplification of the grassland community did not result from climatic conditions that were inherently unfavorable to production and diversity. Species at every trophic level benefited strongly from experimental extension of the rainy season in spring-addition plots early in the study, just as they did from a natural extension of the rainy season in winter-addition and control plots late in the study. But as altered environmental conditions persisted across years, individualistic responses by species to climate were overshadowed by the lagged effects of altered community-level interactions. The congruence between initial responses to artificial extension in spring-addition plots and responses in the grassland as a whole to naturally late rainfall in year 5 provides compelling evidence that these mechanisms are real rather than experimental artifacts.

Uncertainty remains in the projections of global climate models; indeed, the next-generation Hadley model (HadCM3) forecasts decreased rainfall over much of California (31). Yet under any scenario of future climate change, prediction of ecological effects will require understanding the web of interactions that mediate species- through ecosystem-level responses (14). To date, forecasts of range shifts and extinction probabilities are based largely on species-climate envelope models (32–34). These models are powerful initial tools

Fig. 4. Watering treatment effects on abundances (mean \pm SE) of (A) invertebrate herbivores, (B) predators, and (C) parasitoids, as measured in sweep net and pitfall trap collections. Gray shading highlights responses in the final year of the study, when late natural rainfall mirrored the spring-addition watering treatment.



with which to explore consequences of alternative climate scenarios, but they cannot forecast lagged impacts of altered higher-order interactions that will govern the trajectories of ecosystems under sustained climatic change. Nonlinearities are expected from the assembly of new combinations of species brought together by climate-induced range shifts, but these can also arise from environmental effects on the strength and direction of interspecific interactions without any change in species composition (35, 36). The nature and scales of these effects are best revealed by long-term experiments in natural field settings that improve understanding of how climate change impacts propagate through ecological communities. Indirect effects of climate on species will commonly lag behind direct effects, but their importance makes system-level interactions crucial to climate change forecasting even at subdecadal time scales.

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Supporting Online Material

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Materials and Methods
Figs. S1 and S2
Tables S1 to S3

17 October 2006; accepted 13 December 2006
10.1126/science.1136401

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An X Chromosome Gene, *WTX*, Is Commonly Inactivated in Wilms Tumor

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Wilms tumor is a pediatric kidney cancer associated with inactivation of the *WT1* tumor-suppressor gene in 5 to 10% of cases. Using a high-resolution screen for DNA copy-number alterations in Wilms tumor, we identified somatic deletions targeting a previously uncharacterized gene on the X chromosome. This gene, which we call *WTX*, is inactivated in approximately one-third of Wilms tumors (15 of 51 tumors). Tumors with mutations in *WTX* lack *WT1* mutations, and both genes share a restricted temporal and spatial expression pattern in normal renal precursors. In contrast to biallelic inactivation of autosomal tumor-suppressor genes, *WTX* is inactivated by a monoallelic "single-hit" event targeting the single X chromosome in tumors from males and the active X chromosome in tumors from females.

Wilms tumor (nephroblastoma) is the most common pediatric kidney cancer and is derived from pluripotent renal precursors that produce undifferentiated blastemal cells, primitive epithelial structures, and stro-

mal components [reviewed in (1)]. In 1972, Knudson and Strong proposed that Wilms tumor, like retinoblastoma, may develop as a consequence of two independent rate-limiting genetic events, subsequently defined as biallelic



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Science **315** (5812), 640-642. [doi: 10.1126/science.1136401]

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