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Climate Affects Predator Control of an Herbivore Outbreak

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abstract: Herbivore outbreaks and the accompanying devastation of plant biomass can have enormous ecological effects. Climate directly affects such outbreaks through plant stress or alterations in herbivore life-history traits. Large-scale variation in climate can indirectly affect outbreaks through trophic interactions, but the magnitude of such effects is unknown. On the California coast, rainfall in years during and immediately previous to mass lupine mortality was two-thirds that of years without such mortality. However, neither mature lupines nor their root-feeding herbivores are directly affected by annual variation in rainfall. By increasing soil moisture to levels characteristic of summers following El Niño/Southern Oscillation (ENSO) events, we increased persistence of a predator (the entomopathogenic nematode *Heterorhabditis marelatus*). This led to suppression of an outbreak of the herbivorous moth *Hepialus californicus*, indirectly protecting bush lupine (*Lupinus arboreus*). Our results are consistent with the marine-oriented Menge-Sutherland hypothesis (Menge and Sutherland 1987) that abiotic stress has greater effects on higher than on lower trophic levels. The mechanisms producing these results differ from those proposed by Menge-Sutherland, however, highlighting differences between trophic processes in underground and terrestrial/marine food webs. Our evidence suggests that herbivore outbreaks and mass lupine mortality are indirectly affected by ENSO's facilitation of top-down control in this food web.

Keywords: trophic cascade, ENSO, abiotic factors, community regulation.

Herbivore outbreaks are the major form of natural disturbance in North American forests (Logan et al. 2003). The power of such devastating herbivory has focused ecologists' attention on the factors controlling outbreaks. The link between outbreaks and large-scale processes such as climatic variation is especially strong. Climate can mediate herbivore-plant interactions, leading to outbreaks, in several ways. Drought-induced stress can make plants more vulnerable to herbivory (Coley 1998; Hogg et al. 2002), alterations in herbivore life-history traits can increase insect population densities (Logan et al. 2003), and the two factors can act synergistically (Fox et al. 1999; Dale et al. 2001).

Climate can also affect herbivore outbreaks through food web interactions (Spiller and Schoener 1995; Chase 1996; Bertness and Ewanchuck 2002). In a laboratory study of the effect of increased temperature on food web interactions, parasites were more affected than their prey, and parasitism rates increased 300% in the elevated temperature treatment (Bezemer et al. 1998). If ecosystems are controlled by top-down effects of consumers, temperature and moisture can impact ecosystems by modifying consumer-resource interactions. Because of this, climate may mediate herbivore outbreaks (in which predators cannot control herbivore population growth) through its effect on predator control. Significant indirect interactions occur in a variety of systems (Pace et al. 1999); however, the large scale and patchy distribution of herbivore outbreaks in space and time make experimental study of interactions between predator control and climate difficult.

In the Mediterranean climate of the northern coast of California, herbivore outbreaks and associated mass lupine mortality are inversely related to rainfall. Mean annual (fall, winter, and spring) rainfall at the Bodega Marine Reserve (BMR) in the year previous to and during four large-scale (10,000+ mature bushes) lupine die-offs was 35% lower than rainfall over the same period for years without die-offs (fig. 1*A*). While the 1985 and 1990 die-offs came before our study and their causes cannot now be determined, those of 1992 and 2002 were caused by ghost moth (*Hepialus californicus*) herbivory (Strong et al. 1996). The root-feeding larvae of ghost moths excavate large tunnels within the roots and stems and are a major source of lupine mortality at BMR. Many thousands of these mature woody plants die after heavy root herbivory (Strong et al. 1995). Low rainfall could directly influence either herbivores or plants, producing an outbreak. While ghost moth herbivory threatens lupine survival, the larvae

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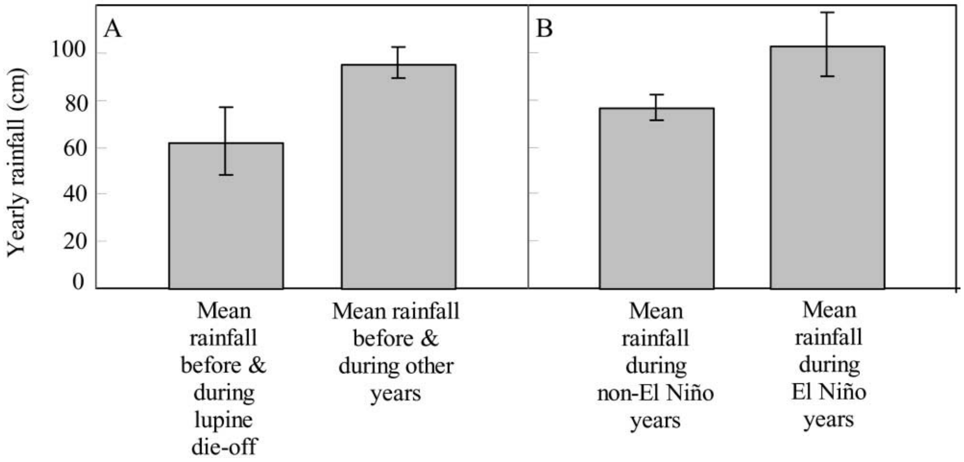

Figure 1: *A*, Mean 1980–2002 July–June rainfall in Bodega Bay, California, preceding and during years ($n = 4$) in which there was large-scale (10,000+ mature bushes) lupine damage versus years in which no large-scale mortality occurred ($n = 19$; mean ± SE; means differ at $P < .050$; $F = 4.33$, df $= 1, 21$). Lupine data for 1985, 1990, and 1992 from Strong et al. (1995). *B*, Mean 1969–2002 July–June rainfall at Bodega Marine Reserve during consensus non-ENSO (including La Niña events; $n = 23$) and ENSO ($n = 11$) climatic events. Means differ at $P < .040$ ($F = 4.61$, df $= 1, 32$). Consensus data on ENSO events gathered from list maintained at http://ggweather.com/enso/years.htm. This consensus list is based on records maintained by the Western Region Climate Center, Climate Diagnostics Center, Climate Prediction Center, and the Multivariate ENSO Index from the Climate Diagnostics Center. A consensus event occurs when three or more of the four records agree as to the classification of a year as ENSO or non-ENSO.

themselves are prey for the entomopathogenic nematode *Heterorhabditis marelatus*. While both correlational (Strong et al. 1996) and experimental (Strong et al. 1999; Preisser 2003) evidence suggests that *H. marelatus* can regulate ghost moth populations, the nematode's dependence on soil moisture to facilitate movement and prevent desiccation (Grant and Villani 2003) may make it sensitive to climatic fluctuations. If unusually dry conditions lessen the nematode's control over ghost moth populations, leading to an outbreak, then heavy winter and spring rains may be more suitable for predator persistence and herbivore control.

In 2002, fortuitous circumstance provided us a means of experimentally discriminating between direct and indirect climatic control of ghost moth outbreaks. On the northern coast of California, heavy winter and spring rains are associated with El Niño/Southern Oscillation (ENSO) events, and intervening years are much dryer (fig. 1*B*). As is typical with large-scale climatic events, the correlation between ENSO and increased rainfall may vary locally. The 1992 outbreak, for example, occurred during an ENSO year with below-average rainfall at BMR (1992: 66.7 cm; 1969–2002 mean ± SE: 85.4 ± 5.9 cm). On average, however, large-scale herbivore outbreaks at BMR occur during successive years of below-average rainfall (fig. 1*A*), and ENSO years at BMR are characterized by above-average rainfall (fig. 1*B*). In 2001, a dry, non-ENSO year, we experimentally elevated summer soil moisture and measured the effect of predator presence and soil moisture on the nematode/ghost moth/lupine cascade (Strong 1997; Strong et al. 1999; Preisser 2003). The predator treatment tested the nematode's capacity to indirectly affect lupines via their effect on ghost moth density. The summer watering treatment (hereafter referred to as ENSO) tested whether higher rainfall affected each of the species in the food web. The interaction of the two treatments tested whether the predator's impact was affected by variation in soil moisture. If either lupines or their ghost moth herbivores are directly affected by soil moisture, their response to watering should be independent of predator presence. If their response is the indirect result of soil moisture effects on the nematode predator, however, then only organisms in the predator treatment should respond to increased soil moisture.

Material and Methods

The experiment reported in this article is the same as the one described by Preisser (2003) but presents new data from the second year of the experiment (in which an unexpected herbivore outbreak occurred) while analyzing the experiment for the effects of supplemental watering. We simulated the soil moisture conditions of summers following heavy winter/spring rains produced by ENSO climatic events with watering. Our experiment began in winter 2001 in the coastal grasslands of BMR as a two-factor crossed design: predator (the nematode *Heterorhabditis* *marelatus* added) or no predator versus ENSO (supplemental water added twice weekly) or ambient (no water added). While this treatment simulates aspects of an ENSO year, it is not an exact simulation since we did not provide higher winter rainfall. We applied four experimental treatments (predator/ENSO, predator/ambient, no predator/ENSO, no predator/ambient) to eight plots divided into two 20 × 13-m contiguous blocks of mixed lupine grassland.

There were two replicate plots in each of the four treatments, with each plot representing the mean response of 10 lupine bushes. Preliminary surveys of lupine in the area revealed very low ghost moth (*Hepialus californicus*) densities (mean of one larvae/bush) and a low incidence of *H. marelatus* (one out of 140 bushes surveyed). We selected 10 mature lupines/plot with comparable stem diameters (mean ± SE: 3.79 ± 0.068 cm), no detectable *H. marelatus*, and no visible ghost moth damage. To mitigate effects of intraspecific competition, lupines in contact with experimental bushes were removed. In spring 2001, we added *H. marelatus* using four nematode-infected waxworm (*Galleria mellonella*) cadavers/bush in a mesh cage through which nematodes escaped (to prevent animals from removing them) and burying the cage at the base of each lupine in the predator treatment. To control for any effects of disturbance, we used the same procedure to add cold-killed waxworms to each lupine in the no predator treatment. *Heterorhabditis marelatus* is polyphagous (Cottrell et al. 2001) and can prey on ground-dwelling herbivorous and detritivorous insect larvae. Aluminum flashing (4 cm aboveground and 10 cm belowground) fenced off each plot to prevent *H. marelatus* movement.

One week after nematode addition, we added 24 second to third instar ghost moth larvae to the soil at the base of each experimental lupine. We chose these instars to maximize the chance that some caterpillars would survive the transition onto the lupine root. This number of larvae is within the range of natural densities previously recorded at BMR (Strong et al. 1995). We did not prevent natural ghost moth oviposition, since doing so might have interfered with pollinators, predators, and/or the underground food web. The larvae were raised from eggs collected by capturing mated ghost moth pairs at BMR in winter 2001. Previous to their release, they were fed sliced carrots, a standard culture technique for ghost moth larvae (Wagner 1985) that produces caterpillars of approximately the same size as those fed lupine roots. We repeated the addition of 24 second to third instar *H. californicus* larvae in spring 2002.

ENSO Treatment

We calibrated a drip irrigation system to produce conditions of increased summer soil moisture in our ENSO treatment. Water was added to lupines in the ENSO treatment during the dry season (April–November) using the drip irrigation system operating 2 h/d twice a week.

Testing the Accuracy of the ENSO Treatment

To evaluate whether our ENSO treatment satisfactorily reproduced the levels of summer soil moisture expected following ENSO events, we tested for a relationship between summer (July–August) soil moisture and winter/spring (September–June) rainfall by collating data on mean summer soil moistures under lupines in coastal prairies. We gathered data for summer 1973 (BMR; Davidson 1975), 1985, and 1986 (Año Nuevo State Reserve, Calif.; Alpert and Mooney 1996) and collected data from 2001 and 2002 (BMR). For each soil moisture mean, we determined winter/spring rainfall using the nearest rainfall gauge.

Data Collection

We assessed predator (*H. marelatus*) persistence in lupine (*Lupinus arboreus*) rhizospheres by collecting soil in a plastic container from underneath each lupine on October 25, 2002, and wetting it with distilled water to approximately 30 mg H_2O/g dry soil. Six *G. mellonella* larvae were added to each soil container as bait for the nematode. After 1 wk, predation by *H. marelatus* was assessed visually using the distinctive orange color of nematode-killed cadavers. Using these data, the soil sample from each lupine was scored either positive (one or more nematode-killed cadavers) or negative (no nematode-killed cadavers) for the presence of *H. marelatus*.

We measured ghost moth larval abundance on August 15, 2002, using counts of frass extrusions from their larval galleries (Mo and Tanton 1995). There is an approximately 1 : 1 correlation between the number of frass extrusions/root and larvae/root (J. Havstad, E. L. Preisser, and D. R. Strong, unpublished data).

We measured lupine trunk diameter at ground level on September 19, 2001 (the end of the first year of the experiment), and September 15, 2002 (end of the second year of the experiment). Diameter data were used to calculate basal area, log transformed, and lupine trunk diameter growth expressed as $\ln(\text{basal area})_{\text{end of second year}} - \ln(\text{basal area})_{\text{end of first year}}$.

Seedset/lupine was determined on July 29, 2002, by counting all seedpods on experimental lupines and then multiplying by the average seeds/pod (the mean of 20 haphazardly gathered seed pods/bush) to determine total seedset/bush. On July 16, 2001, and August 13, 2002, we sampled soil moisture by collecting soil under all experimental lupines and determining its percent H_2O/g dry soil. This was done by collecting 100 g of soil from 0–5 cm deep at the trunk-soil interface of each experimental lupine, immediately weighing it, then reweighing it after drying it at 60°C for 2 d.

Statistical Analysis

Experimental data were analyzed using a two-way ANOVA (predator × ENSO). When necessary, data were square root transformed before analysis to meet the assumption of normality. The analyses tested for the main effects predator, ENSO, and the predator × ENSO interaction. Each ANOVA also included block to test for site-specific differences; if not significant ($P < .05$), the term was removed and the analyses rerun. If the predator × ENSO interaction was significant in an analysis, we compared treatment means using Student's *t*-test. Planned contrasts between the no predator/ENSO and no predator/ambient treatments were used to examine the direct effect of the ENSO treatment.

Rainfall data were analyzed using one-way ANOVA. In the analysis of rainfall during and immediately preceding lupine mass mortality, the one-way ANOVA used die-off; in the analysis of rainfall during ENSO events, the ANOVA used ENSO.

Linear regression was used in the analysis of winter/spring (September–June) rainfall versus the following summer's (July–August) mean soil moisture/lupine (measured in mL H_2O/g dry soil). All data were analyzed using JMP version 4.03 (SAS Institute 2001).

Results

ENSO Treatment

Mean summer soil moisture in lupine rhizospheres was strongly related to winter/spring rainfall ($F = 24.30$, $\mathrm{df} = 1, 3$, $P < .016$; $r^2 = 0.89$; soil moisture [mL H_2O/g dry soil] = 0.103 × rainfall [cm] − 2.64). We calculated with this regression formula the range of summer soil moistures expected at BMR during ENSO events on the basis of rainfall records from 1969 to 2002 and a list of consensus ENSO years maintained by http://ggweather.com/enso/years.htm. Soil moisture in lupine rhizospheres in the ENSO treatment (sampled in summer 2001) was higher than that found in summer 2001 and 2002 at BMR and within the range predicted under lupine bushes in summers following an ENSO event at BMR (treatment 4 h postwatering [mean response of four plots ± SE]: 0.137 ± 0.002 mL H_2O/g dry soil; treatment 2 d postwatering: 0.086 ± 0.004; predicted range of summer soil moisture following an ENSO event: 0.066–0.093).

Experimental Results

In the first year of the experiment (2001), we discovered powerful top-down control in this system, with predators decreasing herbivore density and increasing lupine growth and seedset (Preisser 2003). We restocked ghost moth larvae but not nematodes the second year. Our decision not to restock nematodes during 2002 ensured that the only nematode predators present in the second year of the experiment were those populations that had either persisted or immigrated into the experimental rhizospheres.

The ENSO summer watering treatment did not directly affect herbivore density, lupine growth, or lupine seedset in 2001 or 2002. Planned contrasts between the no predator/ENSO and no predator/ambient treatments revealed no direct effect of increased soil moisture on either herbivores or mature lupines ($F = 0.740$ for herbivores, $F = 1.073$ for lupines, $\mathrm{df} = 1, 3$, all $P > .05$). Since *Hepialus californicus* larvae enter lupine roots in the second to third instars and leave as adults (Wagner 1985), their direct exposure to soil is minimal. The lupine's lack of response is understandable in light of their physiology. While lupine seedlings are sensitive to water stress, mature lupines have deep taproots several meters in length that reach into the water table (Davidson 1975). The growth of mature lupines is thus largely buffered against seasonal moisture variation in the upper soil horizons.

A ghost moth outbreak occurred in the spring/summer of 2002 during a second consecutive year of unusually low rainfall. Caterpillar densities at BMR increased 16-fold to (mean ± SE) 9.84 ± 1.12 larvae/root in 2002 from 0.6 ± 0.6 larvae/root in 2001. In our plots, caterpillar density doubled between 2001 and 2002 (larvae/root across all treatments, 2001: 3.18 ± 0.43; 2002: 6.58 ± 0.73). This provided the opportunity to test whether climate-induced variation in abiotic stress could indirectly control a naturally occurring herbivore outbreak.

The higher soil moisture in the ENSO treatment increased nematode persistence approximately ninefold in lupine rhizospheres into the second year relative to the ambient treatment (fig. 2*A*). Nematodes were detected during 2002 in 19 out of 20 ENSO predator rhizospheres versus only two out of 20 ambient predator rhizospheres (predator × ENSO interaction: $F = 29.02$, $\mathrm{df} = 1, 3$, $P < .013$). Nematodes decreased herbivore density by 42% in predator/ENSO plots over the average of the other treatments (fig. 2*B*; predator × ENSO interaction: $F = 11.42$, $\mathrm{df} = 1, 3$, $P < .043$).

The indirect effect of nematode predation on lupine performance during the outbreak was substantial. Lupine trunk diameter growth in the second year of the experiment increased 84% in the predator/ENSO treatment versus the average of the other three treatments, a marginally

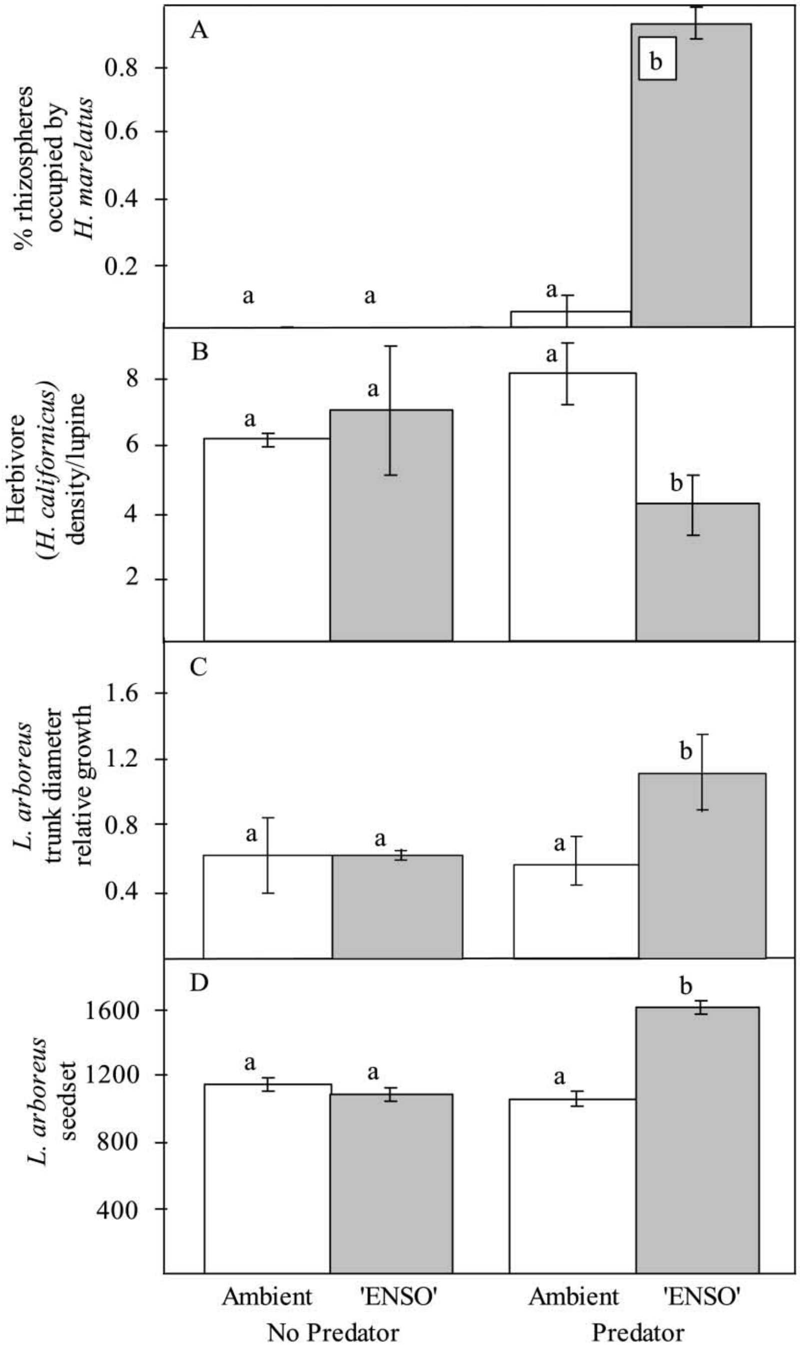

Figure 2: Effect of experimental treatments in 2002 on (*A*) nematode persistence, (*B*) ghost moth presence, (*C*) lupine trunk diameter growth, and (*D*) lupine seedset. Bars represent the mean of two plots/treatment taken from 10 lupine bushes/plot, and error bars are ±SE of the plot means. Lowercase letters indicate statistically different means, $P < .05$ (Student's *t*-test).

significant difference (predator × ENSO interaction: $F = 8.50$, $\mathrm{df} = 1, 3$, $P < .062$). Pairwise treatment comparisons of mean lupine growth revealed that the predator/ENSO treatment differed significantly from the other three treatments (fig. 2*C*). Similarly, lupine seedset increased 44% over the average of the other three treatments, showing that nematode presence increased plant fitness in the presence of ENSO levels of summer soil moisture (predator × ENSO interaction: $F = 89.3$, $\mathrm{df} = 1, 2$, $P < .01$; fig 2*D*).

Discussion

Soil moisture indirectly increased lupine (*Lupinus arboreus*) growth and seedset by fostering the predatory nematode *Heterorhabditis marelatus*, which suppressed the herbivorous ghost moth *Hepialus californicus* in the predator/ENSO treatment. The effect of ENSO-induced variation in soil moisture on this trophic cascade is striking. The predator is greatly affected by soil moisture, relying on the film of moisture surrounding soil particles for movement and to resist desiccation (Grant and Villani 2003). In the first year, nematodes suppressed herbivores in both the ENSO and ambient treatments (Preisser 2003). Rainfall in both 2001 and 2002 was unusually low, however, and by 2002, the nematode populations in the predator/ambient treatment were largely extirpated (fig. 2*A*). In contrast, nematodes persisted in 19 out of 20 watered lupine rhizospheres. This produced a trophic cascade in the predator/ENSO treatment during the 2002 herbivore outbreak, where nematodes suppressed ghost moths and indirectly benefited lupine bushes.

The differences between the 2 yr of the experiment are evident in the data on lupine growth. In 2001, there was no significant ENSO effect, and the relative growth of bushes in the predator treatment was 67% higher than no predator bushes (Preisser 2003). Between 2001 and 2002, however, the basal trunk area growth of bushes in the predator/ENSO treatment was twice that of the bushes in the predator/ambient treatment and 84% higher than the average of all three other treatments. The fact that the predator/ambient treatment was indistinguishable from the no predator treatments in the second year, 2001–2002, indicates that any benefit of nematode presence under ambient soil moisture conditions did not carry over into the second year. Data from the first year of this experiment showed an overall effect of predator presence on lupine growth within 2 mo (Preisser 2003). The fact that lupine growth during the second year (September 2001 to September 2002) showed no similar overall effect suggests that the impact of predator addition in the predator/ambient treatment was rapid but short-lived, dissipating by the end of the first year.

Climate cycles such as ENSO can strongly influence food web dynamics (Stenseth et al. 2002). An ENSO shift in ocean currents affects climate on a continent-wide basis; in northern California, ENSO produces heavy winter and spring rains (fig. 1*B*). Summer soil moistures under lupines are correlated with winter/spring rainfall; our ENSO treatment falls within the predicted soil moisture range following ENSO events (see "Material and Methods"). The cascade thus varies with climate, providing winter and spring protection for lupines most years interspersed with year-round protection following years with high winter/spring rainfall. Conversely, several unusually dry years (in our case, two successive years of below-average rainfall) can greatly reduce or extirpate nematode populations in lupine rhizospheres. This releases the root-feeding herbivores from top-down control. Mean rainfall in the 3 yr before an herbivore outbreak (with the herbivore outbreak occurring in the third year) was marginally ($P < .06$) below average, suggesting an accumulating effect of abiotic stress over periods of several years. It should be noted that the correlation between ENSO and high yearly rainfall exists over a large spatial scale and may be subject to local variation. An example of this was the 1992 outbreak, which occurred during an ENSO year in which the rainfall at BMR was below average (1992: 66.7 cm; 1969–2002 mean ± SE: 85.4 ± 5.9 cm). Thus, not all outbreaks occur during non-ENSO years; similarly, not all non-ENSO winters were followed by outbreaks. On average, however, large-scale herbivore outbreaks at BMR occur during successive years of below-average rainfall (fig. 1*A*), and ENSO years at BMR are characterized by above-average rainfall (fig. 1*B*). Wetter years generally prevent outbreaks, making ENSO conditions a good (but not perfect) predictor of nonoutbreak years. In other systems, ENSO has been linked to fluctuations in herbivore populations (Todd et al. 2002); at BMR, top-down effects on lupines are influenced by ENSO events affecting the nematode predator. Our research supports the hypothesis that climate indirectly affects herbivore outbreaks and plant performance through tritrophic interactions.

Weather, especially in the form of rainfall, can affect terrestrial biotic interactions (Stenseth et al. 2002). Direct (interference) and indirect competition between lizards for resources occurred only during dry years (Dunham 1980), and the effect of predatory lizards on spiders was positively related to rainfall (Spiller and Schoener 1995). Less is known about the impact of abiotic stress on indirect terrestrial food web interactions. The ecosystem exploitation hypothesis (Fretwell 1977; Oksanen et al. 1981) addresses how these interactions might change across a productivity gradient but does not explicitly link productivity to abiotic factors. Several empirical studies have shown that temperature affects grassland trophic cascades through its effect on herbivore feeding rates (Chase 1996; Ritchie 2000); other studies have found that seasonality (Dawes-Gromadzki 2002; Norrdahl et al. 2002) and elevation (Preszler and Boecklen 1996) affect indirect food web interactions.

Effects of abiotic stress on multitrophic interactions have long been considered in both aquatic (freshwater; Power 1990; Hill et al. 2001) and marine (Dayton 1971; Connell 1975) systems. In their model of community regulation, Menge and Sutherland (1976, 1987) proposed that abiotic stress affects higher trophic levels more strongly than basal species. In the Menge-Sutherland model, consumers are mobile and can avoid stress, while organisms farther down the food chain are increasingly sessile and less able to shift between environments. Increasing environmental stress causes organisms on upper trophic levels to abandon harsh environments, leaving only a two-level (or, in extreme cases, one-level) food web. While the Menge-Sutherland model addressed both terrestrial and benthic food webs, support for its conclusions has emerged predominantly from marine systems (Menge et al. 2002; but see Polis and Strong 1996).

The results of our experiment provide experimental support for the Menge-Sutherland model in an underground food web. The abiotic stress of low summer soil moisture most affected the nematode predator, with no direct effect on either ghost moth larvae or lupines. Interestingly, this result is produced by a different mechanism than the one hypothesized by Menge-Sutherland. In our case, small and relatively sessile nematodes were unable to avoid abiotic stress, and the unusually low rainfall during 2001 and 2002 prevented immigration and the recolonization of extirpated rhizospheres. In fact, the predator was the only trophic level affected by environmental stress; neither mature lupines nor herbivores were directly affected by soil drying. This result suggests that the cascade's strength should wax during the wet winter months and wane during the dry summer and that this is due to the nematode's ability to deal with abiotic stress. Unusual climatic events like ENSO may affect these broad seasonal patterns, facilitating top-down control throughout the year. Several recent analyses of trophic cascades found no significant effect of experimental duration on the cascade strength (Shurin et al. 2002; Bell et al. 2003); however, it is clear that seasonal changes can profoundly affect terrestrial food web interactions (Gratton and Denno 2003).

The contradiction between the mechanisms driving Menge-Sutherland dynamics and those in our system may be related to differences in food web structure. The Menge-Sutherland model posits that higher trophic level organisms are, on average, large and mobile; in this system, the nematode predator is 100- to 1,000-fold smaller than its ghost moth prey, and adult moths are far more mobile than nematodes. The Menge-Sutherland model correctly predicts that the larger, more mobile organisms in our food web suffer less mortality due to abiotic stress (see also Spiller et al. 1998); in this case, the relationship between size, mobility, and trophic level is reversed. Underground food webs are often characterized by intraguild predation, sometimes supporting five to 10 trophic levels of similarly sized, relatively immobile organisms (Polis 1991; De Ruiter et al. 1995). The lack of predictable differentiation by trophic level makes predictions about the effects of abiotic stress on underground food webs difficult; hypotheses about trophic dynamics developed for use in terrestrial and aquatic/marine food webs may need modification before applying them to underground systems (Wardle 2002).

Seasonal changes in soil moisture and their indirect effect on herbivore outbreaks may produce landscape-level changes in grassland communities. *Lupinus arboreus*, *H. californicus*, and *H. marelatus* range from southern California to Oregon (Davidson 1975; Wagner 1985; Liu and Berry 1996). Hectares of bush lupine can be killed by ghost moth herbivory or protected by populations of *H. marelatus* (Strong et al. 1995). This cascade thus has the potential to occur along the Pacific coast, hidden from casual observation by the cryptic nature of both predator and herbivore. Bush lupine is a prodigious nitrogen fixer whose nitrogen input into coastal soils has been linked to replacement of native grasses by invasive species (Maron and Connors 1996). By affecting the duration and intensity of lupine nitrogen input, nematode protection of the bush lupine may indirectly affect vegetation dynamics across a wide swath of coastal habitat. This protection is, in turn, linked to soil moisture and occurs primarily during summers following intense rainy seasons. Our study illustrates how plant damage from an herbivore outbreak can be indirectly influenced by the interaction between biotic and large-scale abiotic factors.

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