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PLANT FACILITATION OF A BELOWGROUND PREDATOR

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Abstract. Interest in facilitative predator–plant interactions has focused upon aboveground systems. Underground physical conditions are distinctive, however, and we provide evidence that bush lupine, *Lupinus arboreus*, facilitates the survival of the predatory nematode *Heterorhabditis marelatus*. Because *H. marelatus* is prone to desiccation and lupines maintain a zone of moist soil around their taproots even during dry periods, we hypothesized that dry-season nematode survival under lupines might be higher than in the surrounding grasslands. We performed field surveys and measured nematode survival in lupine and grassland rhizospheres under wet- and dry-season conditions. Nematodes survived the crucial summer period better under lupines than in grasslands; however, this advantage disappeared in wet, winter soils. Modeling the probability of nematode population extinction showed that, while even large nematode cohorts were likely to go extinct in grasslands, even small cohorts in lupine rhizospheres were likely to survive until the arrival of the next prey generation. Because this nematode predator has a strong top-down effect on lupine survival via its effect on root-boring larvae of the ghost moth *Hepialus californicus*, this facilitative interaction may enable a belowground trophic cascade. Similar cases of predator facilitation in seasonally stressful environments are probably common in nature.

Key words: facilitation; Hepialus californicus; Heterorhabditis marelatus; Lupinus arboreus; *mutualism; predator–prey interactions; seasonality; trophic cascade.*

Introduction

Interspecific facilitation plays an important role in determining food web structure and function, and has been shown to influence the fitness and population density of plants, fungi, and soil invertebrates (Callaway and Walker 1997, Bertness et al. 1999, Whelan 2001, Wolfe et al. 2005). Species involved in such interactions can benefit other organisms either directly or indirectly, via their effect on a third species. Indirect facilitation is exemplified by trophic cascades, where predators benefit plants by reducing herbivory (Carpenter and Kitchell 1993, Estes et al. 1998, Schmitz et al. 2000). Less clear in such interactions is the extent to which the plant itself influences predator presence and efficiency. Effects of vegetation structure on predator foraging and prey avoidance of predation have been noted in a variety of systems (Whelan 2001), and can influence the effect of natural enemies on herbivory and plant fitness. Such facilitation of natural enemies has been demonstrated only in aboveground systems, however; despite the well-known vulnerability of plants to root-feeding herbivores, similar interactions have not been documented belowground.

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Facilitative interactions play a particularly important role in physically stressful environments (Stachowicz 2001). By buffering the effects of physical disturbance and temperature, some species in harsh environments can act as "nurse plants" that facilitate the survival of more vulnerable species (Tewksbury and Lloyd 2001). An intriguing possibility is that natural enemies of herbivores might also benefit from the refuge provided by such nurse plants. Facilitative predator–plant interactions may produce an indirect mutualism whereby species acting as refuges to predators, enabling them to survive seasonally stressful conditions, benefit from the local reduction in herbivore density.

We provide evidence for facilitation by a plant (the bush lupine, *Lupinus arboreus*) of the survival of a belowground predator (the entomopathogenic nematode *Heterorhabditis marelatus,* nematode hereafter) via the provision of a moisture-rich seasonal refuge. An organism that immediately kills its host yet reproduces for several generations within the preserved cadaver, *H. marelatus* is neither precisely a parasite nor parasitoid. Although its size and population dynamics are akin to those of microparasites, we refer to it here as a predator in recognition of its trophic role in this system. Because the nematode exerts top-down control of belowground herbivores (larvae of the ghost moth *Hepialus californicus*) that would otherwise devastate large stands of bush lupine, this facilitative interaction may in turn help enable a powerful trophic cascade. Previous research has shown that soil moisture affects the persistence of

PLATE 1. A large patch of bush lupine (*Lupinus arboreus*) in the Bodega Marine Reserve, showing >10 000 healthy bush lupines in 2001 (left) that experienced >98% mortality in 2002 due to ghost moth (*Hepialus californicus*) damage (right). Photo credit: D. Strong.

nematode populations, determining the strength of top-down control (Preisser and Strong 2004), and that lupines maintain a moist microclimate in the soil surrounding their taproot during the dry summer (Davidson 1975). A mathematical model of nematode–ghost moth interactions also predicts that low rates of nematode mortality are crucial for nematode population persistence (Dugaw et al. 2005). This information led us to suspect that bush lupine, by facilitating the survival of desiccation-prone nematodes during periods of seasonal dryness, increases the probability of nematode population persistence. We used surveys, experiments, and modeling to address this question; our findings provide evidence for a potentially widespread form of plant facilitation of the natural enemies of their herbivores.

MATERIALS AND METHODS

Our work was conducted at the Bodega Marine Reserve (BMR) in Bodega Bay, California, USA (see Plate 1). The reserve's coastal prairies are a matrix of grasslands (native and invasive grasses and forbs) interspersed with bush lupine (*Lupinus arboreus*). A detailed description of the natural history of the system is contained in Appendix A.

Field surveys

We surveyed surface soil (0–10 cm in depth) for *H. marelatus* infective juvenile nematodes using the standard assay technique of baiting soil samples with larvae (waxworms) of the wax moth *Galleria mellonella*. We chose to sample the top 10 cm of soil because research has shown that, perhaps in response to prey availability, a sizeable majority of both Steinernematid and Heterorhabditid entomopathogenic nematodes are found within 8 cm of the soil surface (Lewis 2002). Nematodes in the soil are attracted to and kill the waxworms (Strong et al. 1996, Kaya and Stock 1997). Each sample was ~100 g of surface soil placed in a plastic container, moistened to ~20% (0.2 mL H_2O/g soil) with six waxworms added, and sealed with a snap-top lid. Containers were maintained at field soil temperatures of ~17°C. One week after collection, we classified each waxworm as alive, dead by unknown cause, or killed by *H. marelatus*.

Our choice of a bioassay approach to surveying nematode populations is motivated by the fact that microparasites are commonly studied using host infection rates vs. propagule counts as the most appropriate unit of study (Anderson and May 1981). The rationale for this approach includes the fact that microparasite propagules can be extremely numerous, highly variable in viability and infectivity, dispersed through the medium with unequal access to hosts, and difficult to distinguish from similar organisms in environmental samples. *Heterorhabditis marelatus* is vastly outnumbered in BMR soil by detritivorous and bactivorous nematodes, and makes up <0.1% of the nematode fauna by number (D. Strong, *unpublished data*). In addition, bioassays are a well-known and frequently used tool for studying entomopathogenic nematodes, and their accuracy and relative ease of use make them the preferred method for working with the large number of samples necessary to survey natural populations (Hominick 2002). Finally, because only a fraction of infective juveniles (IJ) emerging from a host cadaver are capable of infecting and killing prey (Campbell et al. 1999), and our interest in *H. marelatus* centers on its role as a potential predator of ghost moth larvae, the use of bioassays provides the most accurate assessment of the "effective" abundance of *H. marelatus* in the environment.

Lupine rhizospheres were surveyed for *H. marelatus* at five BMR sites on four dates: March 2002 and 2004 (winter, wet season), and July 2002 and August 2003 (summer, dry season). At each date and site we sampled 25 mature, 2–3 year old bush lupines (500 total bushes).

We sampled soil from the top 10 cm around the lupine stem, where *H. marelatus* is most often found (Strong et al. 1996). Data are presented as the proportion of 25 bushes within each site that tested positive for *H. marelatus*.

Grassland rhizospheres >5 m away from lupines were sampled in the same five sites on two wet season (March 2002, 2003) and two dry season (September 2001, 2002) sampling dates. Grassland samples were taken on a 4×4 m grid at each site, with one sample (called a subsample) from each of the 16 1-m^2 intersections. Data from grassland rhizospheres are presented as the proportion of 16 subsamples within each site that tested positive for *H. marelatus*.

Statistical analysis.—We analyzed the field survey data using as our response variable the percentage of samples/site that tested positive for nematode presence per sampling date. The data on percentage nematode occurrence/site were arcsine transformed. Because the field surveys of the different rhizosphere types occurred on different dates, we chose to analyze the survey data from each rhizosphere type separately. We performed a repeated-measures ANOVA using JMP-IN (Version 5.1, SAS Institute 2004) to test for the main effects of season (summer, winter) and site.

Survival experiment: how does rhizosphere type and seasonal moisture affect the survival of H. marelatus?

In this experiment we evaluated nematode survival in the field without hosts (and thus without reproduction) as a function of lupine vs. grassland rhizospheres and seasonal moisture. We assessed survival in soil inside 50-mL Falcon plastic centrifuge tubes buried in the field. To allow soil moisture levels to equilibrate with surrounding conditions, we cut off the tapered 5-mm end of each tube and covered the hole with plastic mesh (0.56-mm^2 mesh size) secured with a rubber O-ring. The mesh allowed movement of gases and moisture between the tube interior and the surrounding soil while excluding potential nematode host insects. We then added 30 g of moist (0.2 mL H_2O/g soil) soil gathered from areas where *H. marelatus* has never been detected despite extensive sampling (D. R. Strong and E. L. Preisser, *unpublished data*) We coarsely sieved (4-mm^2 mesh size) the soil to remove roots, stones, or potential nematode prey, but did not otherwise treat the soil. We then added 0.5 mL of a water suspension containing 1100 *H. marelatus* cultured from the field site (Kaya and Stock 1997) to each tube, then replaced the screw top lid. We did not include a zero-nematode control treatment because a previous experiment showed that *H. marelatus* did not move from the soil into these tubes in the field (Preisser et al. 2005).

Our experiment was a full-factorial design, with treatment factor rhizosphere type (lupine, L; grassland, G) crossed with soil moisture (watered in summer, W; ambient, dry conditions, A) for a total of four treatment combinations: LW, LA, GW, and GA. Soils in the W treatment received supplemental watering (applied with ultra-low-pressure sprinklers) in summer in order to produce soil moisture levels characteristic of wet, winter soil. Plots in the A treatment received no supplemental watering and dried out during the dry mediterranean summer. Each treatment combination was replicated in four plots for a total of 16 plots. Plots were spaced at least 5 m apart to avoid clumping. We buried the tubes 5–10 cm underground next to the trunks of mature, 2–3 year old *L. arboreus* (rhizosphere type L) or beneath grassland sod (rhizosphere type G). Each of the 16 plots had 50 tubes in five groups of 10 sampling tubes. There were a total of 800 tubes in the experiment (16 plots $\times$ 50 tubes/plot).

We began the experiment on 29 May 2002. On 27 June 2002, we haphazardly selected one of the five 10-tube groups in each of the 16 plots for removal. We repeated this procedure four more times on 13 August and 11 October 2002, and 6 February and 26 November 2003. Winter rains began after October 2002, so the first three sampling dates occurred during the dry season. Although we sampled over five dates, only data from the first three dry season sampling dates are discussed in this paper. BMR recorded a total of 7.31 cm of precipitation during May–October 2002; this is well within the range of May–October precipitation reported from 1985 to 2001 (9.82 $\pm$ 5.31 cm, mean $\pm$ SD; data courtesy BMR archives).

We determined soil moisture in 2–3 g of soil per tube by weighing the soil, oven drying it at 60°C for two days, then reweighing it. We tested whether within-tube soil moistures were similar to the surrounding soil by testing three samples from the soil immediately surrounding each of the 10-tube groups during the first through third sampling dates.

We measured nematode survival by moistening the remaining soil in each tube to ~20% (0.2 mL H_2O/g soil), adding four waxworms, and recapping each tube. After one week we unsealed the tubes and assessed each waxworm. All waxworms were then removed and we performed a second four-waxworm assay. Previous research has shown that two rounds of bioassays, each consisting of two waxworms (vs. the four waxworms per assay used here), are sufficient to extract >93% of the surviving nematodes from the soil (Preisser et al. 2005). Waxworms infected by *H. marelatus* were chilled to 2–4°C to stop nematode development, then dissected, digested in a pepsin solution, and heated at 40°C for 2 h (Kaya and Stock 1997) to facilitate counting the nematodes.

Statistical analysis.—We analyzed nematode survival using as our response variable the total number of nematodes recovered from 10 sampling tubes in each of the plots per treatment combination per sampling date. Because the observed distribution of nematode abundances was highly aggregated, we used a negative binomial model for our analyses. The negative binomial distribution is appropriate for biological count data

because of its ability to accommodate over-dispersed data (White and Bennetts 1996). The negative binomial distribution is described by

$$P(Y=y)=\binom{r+y-1}{y}\left(\frac{r}{m+r}\right)^{r}\left(\frac{m}{m+r}\right)^{y}$$

$$m,\ r>0 \qquad y=1,2,3,\ldots \tag{1}$$

where y is the number of surviving nematodes, m is the mean of the distribution, and r is the dispersion parameter. The variance is given by $m(1 + m/r)$. We used the SAS statistical software GENMOD (Version 8.2, SAS Institute 2001) procedure to fit a negative binomial distribution to the data. The mean of the distribution decreased with time due to nematode death $m(t) = Ce^{-kt}$, where C represents the initial nematode density and k is the daily mortality rate (a function of the factors rhizosphere type and soil moisture) We assessed the goodness of fit using Pearson's χ^2 statistic; if the value of the χ^2 divided by the degrees of freedom is near one, the model is considered a good fit (McCullagh and Nelder 1989). We used residual plots to check for outliers and residual trends. Because only a fraction of nematodes have the potential to infect hosts (Campbell et al. 1999), we also used maximum likelihood to fit the y-intercept, providing an estimate of the number of effective nematodes at the beginning of the experiment. This alternate fit to the model is thus derived without assumptions regarding the initial effective nematode density.

We estimated the daily nematode mortality rate, k, for the four treatment combinations using the negative binomial equation. We made these estimates during the first six months of the experiment, May until October 2002. The W treatment created winter soil moisture levels that estimated winter mortality, compared with the A treatment of dry summer soil that estimated summer mortality. Because the tubes were buried, any differences in soil temperature between the wet and dry treatments were unlikely to affect nematode mortality (Jaffee et al. 1996).

Statistical analysis of soil moisture.—We analyzed soil moisture levels using as our response variable the mean within- and outside-tube soil moisture in each of the plots per treatment combination per sampling date. We performed a repeated-measures ANOVA using JMP-IN (Version 5.1, SAS Institute 2004) on data from the first through third sampling dates testing for the effect of date, rhizosphere type, seasonal moisture regime, and location (within- vs. outside-tube) on soil moisture. Soil moisture levels ranged from 0.78 to 23.02 mL H_2O/g soil; this range was consistent with data reported from BMR (Barbour et al. 1973, Davidson 1975).

Modeling nematode cohort survival

We modeled the extinction of a nematode cohort over one year under lupines and grasses using the negative binomial model and parameters from our experiments. We obtained the probability of cohort extinction over the year as a function of initial nematode cohort size for each rhizosphere type using $y = 0$ and the appropriate estimates of k in Eq. 1. Because ghost moth eggs are laid in February–April, most of the nematodes' host larvae will be between the third and fourth instar entering the dry season (Wagner 1985); accordingly, we modeled the survival of nematode cohorts emerging from third- and fourth-instar hosts. Cohort size was determined experimentally in the laboratory (see Appendix B). For the first six months (dry season) of the model, we used the values of k estimated in the A treatment and the extinction probability follows directly from Eq. 1. Probability of extinction in the last six months (wet season) is calculated using k from the W treatment.

Results

Field survey

Native incidence of *Heterorhabditis marelatus* was 5.5 times greater in lupine rhizospheres (nematodes were found in 17.2% of samples/site) than in grassland rhizospheres (3.1%). Nematode incidence was higher in the wet season than during the dry season for both lupine and grassland rhizospheres (lupine, $F_{1,5} = 17.5$, $P = 0.009$; grassland, $F_{1,5} = 15.4$, $P = 0.011$). Nematode incidence in grasslands was ninefold higher in winter vs. summer surveys (winter, 5.63% of samples/site; summer, 0.63% of samples/site), but only twofold higher in winter vs. summer surveys under lupines (winter, 22.8%; summer, 11.6%). There was also a site effect in both the lupine and grassland surveys (lupine, $F_{4,5} = 10.7$, $P = 0.011$; grassland, $F_{4,5} = 7.4$, $P = 0.025$).

Survival experiment

Fitting the negative binomial model with a fixed intercept of 1100 initial nematodes/tube produced a trend in the deviance residuals (Pearson's χ^2 value/df = 0.45). When we allowed the model to estimate the intercept, there was no such trend (Pearson's χ^2 value/df = 1.04). As with all microparasites, mortality of entomopathogenic nematodes is high, and not all nematodes can successfully infect hosts (Campbell et al. 1999). Because of this, the "viable" number per tube is better determined from an estimated-intercept model than from the absolute number of nematodes added at the beginning of the experiment; we thus used the estimated-intercept model for our analyses. The initial number of nematodes (C) in the model was 144 ± 0.39 nematodes and the dispersion parameter (r) was 1.0 ± 0.24. This low value of r indicates that survival is highly aggregated (McCullagh and Nelder 1989).

Twice as many nematodes survived in lupine rhizospheres than in grassland rhizospheres over the duration of the experiment (Fig. 1). Although nematode survival rates were higher in lupines vs. grasslands in the A treatment, there was no significant habitat difference in the W treatment (Appendix C). This was because

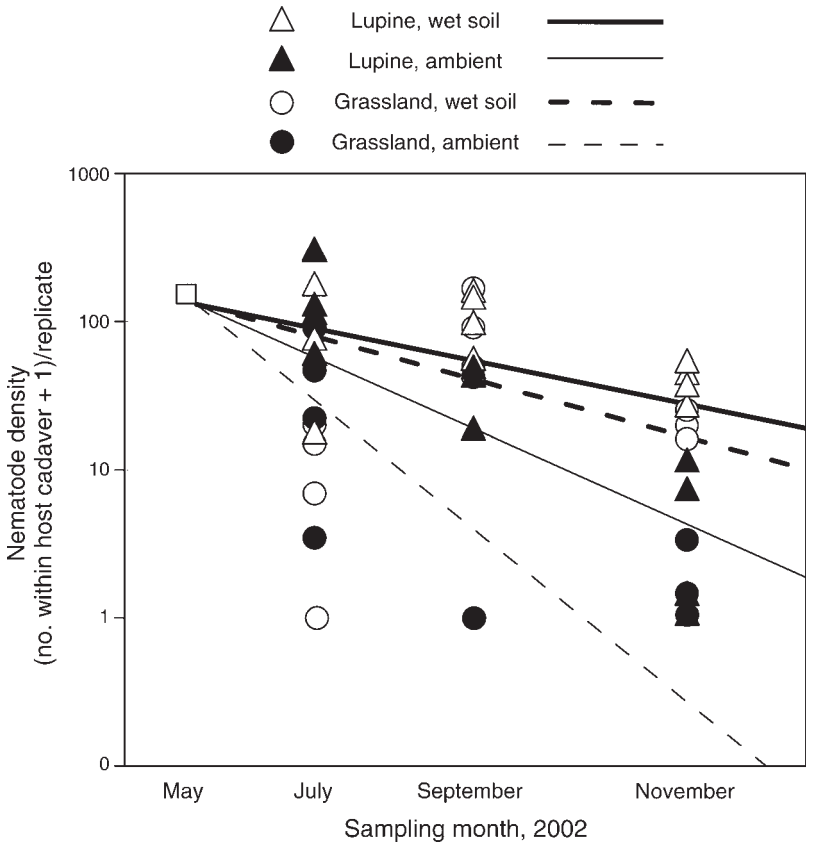

FIG. 1. Density of nematodes in the survival experiment (May–October 2002); note the log scale. Treatments are indicated by different symbols and line types; fitted lines are the mean of the distribution for each treatment, $m(t)$. There were 144 nematodes initially present per replicate; this was determined by using the data gathered on survivorship to estimate the initial number of nematodes.

watering increased survival more in grassland than lupine rhizospheres (type III analysis of k: log-ratio χ^2 with df = 1, $P = 0.029$). Overall nematode survival rates were three times higher in the W than the A treatment (type III analysis of k: log-ratio χ^2 with df = 1, $P < 0.001$). Both habitat types were similarly affected: watering increased survival by 2.8- and 3.4-fold in lupine and grassland rhizospheres, respectively.

Soil moisture manipulation.—Soil moisture inside the tubes did not differ from that of the soil surrounding the tubes ($F_{1,25} = 0.261$, $P > 0.5$), suggesting rapid equilibration of experimental and ambient moisture. Lupine rhizospheres were much wetter than grassland rhizospheres in ambient summer conditions ($F_{1,25} = 26.87$, $P < 0.001$). In August 2002, soil moisture levels in A lupine rhizospheres were 4.13 ± 0.81 vs. 1.19 ± 0.08 mL H_2O/g soil (mean ± SE) for A grassland rhizospheres. In August and October, average soil moisture in the W treatment was six times higher than in the A treatment (13.68 ± 0.88 and 2.26 ± 0.94 mL H_2O/g soil, respectively). Davidson (1975) reported wet-season soil moisture levels (after the winter rains had started in November) of ~17% and 18% in lupine vs. grassland rhizospheres, respectively. Our W treatment produced soil moisture on the low end of reported winter soil moisture levels and is likely a conservative estimate of the effect of such conditions.

Nematode cohort survival

Heterorhabditis marelatus produced at the end of the wet season must persist for approximately one year in the soil until the next generation of host larvae arrives in the subsequent spring. The probability of cohort extinction increased rapidly during the dry season in both rhizosphere types, then less rapidly in the subsequent wet, winter months before the next host generation becomes available.

Extinction probabilities rose faster and to higher levels in the drier grassland rhizospheres than in the moister lupine rhizospheres (Fig. 2). Third-instar ghost moth larvae (with a mean mass of 27.5 mg and producing ~200 nematodes) had a 13% chance of cohort survival through the year in a lupine and a 0.1% chance of survival in a grassland rhizosphere. Nematode cohorts produced by fourth-instar larvae (7338 individuals) had an 85% chance of surviving for one year under lupines, but only a 3.3% chance of survival in grasslands over the same time period. The

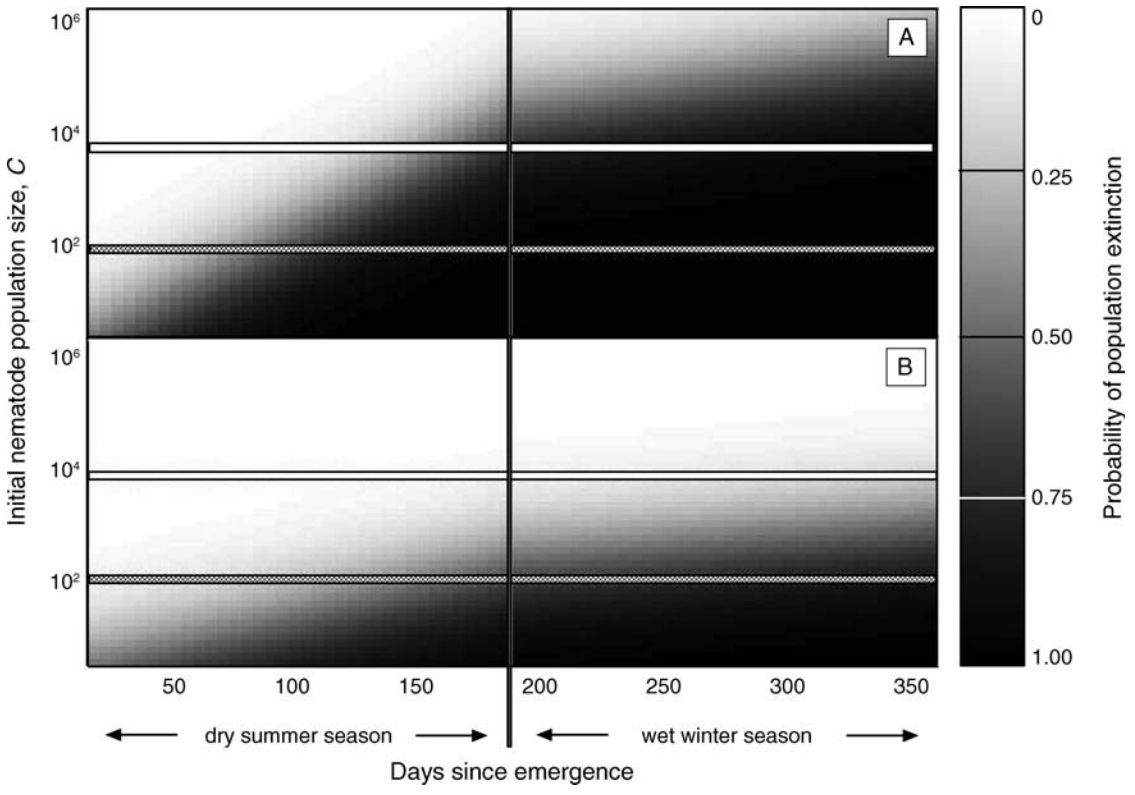

FIG. 2. Cohort extinction probability of *Heterorhabditis marelatus* in the year following their emergence into the soil at the end of the wet season. For each habitat–season combination, the cohort extinction probability was determined using the daily nematode mortality rate, k, estimated for the course of the experiment using a negative binomial model. (A) Extinction probability for nematodes under grassland (for dry season, $k = 0.044 \pm 0.011$ [mean $\pm$ SE]; for wet season, $k = 0.013 \pm 0.0066$); (B) extinction probability under lupines (for dry season, $k = 0.021 \pm 0.0068$; for wet season, $k = 0.0075 \pm 0.0047$). The white line indicates the mean initial cohort size, C, from fourth-instar host larvae (7338 individuals), and the checked line indicates the mean initial cohort size, C, from third-instar host larvae (206 individuals).The vertical line marks the change from dry to wet season. Black regions represent high cohort extinction probability, while white regions represent low extinction probability.

relatively moist lupine rhizosphere thus provides sufficient protection to allow a fraction of nematodes produced at the end of the wet season to survive until conditions are again suitable for finding and killing their prey. This is not the case for grassland rhizospheres, however; identically sized cohorts in these areas have a nearly 100% chance of extinction over the same period.

DISCUSSION

Facilitation plays a critical role in many ecological communities (Bruno et al. 2003). Such interactions can occur indirectly if one species facilitates another by buffering harsh environmental conditions such as salt stress (Bertness et al. 1999) or desiccation (Tewksbury and Lloyd 2001). We provide an example of such facilitation for soil food webs in which the predatory nematode *H. marelatus* survived the dry summer season better under bush lupines than in the surrounding grasslands (Figs. 1 and 2). This dry-season benefit largely disappeared in the moister soils typical of wet mediterranean winters. This transitory advantage is important, however, because heterorhabditids are very susceptible to desiccation (Liu and Glazer 2000) and have to survive dry seasons characterized by high nematode mortality and low prey availability; the lupine's importance stems from its presence during this period.

The Menge-Sutherland model of food web interactions predicts that the importance of predation in community interactions decreases as abiotic stress increases (Menge and Sutherland 1976). Moving beyond this model, facilitation and positive interactions between predators and lower trophic levels can lessen this stress and allow predation to remain important even in high-stress communities (Bruno et al. 2003). Facilitation via habitat modification seems to explain how *H. marelatus*, known primarily from freshwater marshy habitats (Stock et al. 1999), survives in the well-drained sandy soils of the California coastal prairie. Bush lupines may have allowed the nematode to expand its range from marshy habitats into these areas by providing a seasonal refuge from desiccation. Our finding that facilitation occurs only during periods of abiotic stress has also been noted in intertidal communities (Bertness et al. 1999).

Similar cases should be common in systems where predators require seasonal protection from abiotic stress. For example, *Spartina patens* in coastal marshes may act as an overwintering refuge for spiders that reduce herbivory in the next growing season (Lewis and Denno 2004). Seasonally varying abiotic stress at the landscape level often plays a critical role in terrestrial food webs (Stenseth et al. 2002). The strong effect of soil moisture on the survival of entomopathogenic nematodes, widespread and common predators of soil-dwelling arthropods, suggests that underground food webs may be equally, if not more, sensitive to facilitation of belowground natural enemies.

The importance of bush lupine to *H. marelatus* in this system is emphasized by the nature of their association. Lupines comprise the vast majority (>90% cover) of woody vegetation in the coastal prairie, and none of the native grass species form the dense hummocks that might provide the nematode equivalent protection from seasonal moisture stress (E. L. Preisser, *personal observation*). Ghost moth larvae are found almost exclusively on lupine roots at BMR (Wagner 1985), and are the largest belowground larvae found in the prairie. Heterorhabditid nematodes are considered generalist predators (Gaugler 2002), and *H. marelatus* is likely capable of killing other arthropods. Laboratory tests of potential alternative hosts reveal that larvae of several species of *Eleodes* beetle, which feed upon detritus and grass roots throughout the area, can serve as hosts for the nematode. While common, however, these larvae are much smaller than ghost moth caterpillars, and therefore are likely to produce many fewer IJs. In addition, we have found no nematode-killed arthropods other than ghost moths in the field in 10 years of research (D. R. Strong, *personal observation*). Thus, ghost moth larvae in lupine roots likely represent the predominant prey for nematodes in this system.

This facilitative interaction may help explain the patchily distributed nature of the nematode–ghost moth–lupine trophic cascade (Strong et al. 1996). The nematode's reported inability to sense long-distance prey cues (Lewis 2002) means that they are unlikely to deliberately colonize isolated lupines. In these areas, ghost moth survival is high and their root-feeding larvae decimate the bushes. Lupines close to preexisting nematode populations are likely to be recolonized, however, preventing the fluctuations in lupine abundance typical of areas with low nematode densities (Strong et al. 1996). Dry summer weather largely extirpates nematodes in the relatively unprotected grasslands, making the population's survival dependent on protected lupine rhizospheres. Once the dry season ends and hosts become available, the surviving nematodes find and kill hosts and their offspring recolonize the landscape. This pattern is reflected in the results of the multiyear field survey. In grasslands, where dry summer conditions extirpate resident populations, the proportion of samples/site with *H. marelatus* increased ninefold in winter vs. summer surveys; under lupines, where nematode survival is higher, there was only a twofold increase in incidence. Bush lupines facilitate nematode survival during the dry season; because they indirectly benefit from the presence of the nematodes during the wet season, this facilitative interaction may ultimately yield an indirect predator–plant mutualism. While our findings do not explicitly link nematode survival under bush lupines to the trophic cascade, top-down control in this system may ultimately be a function of seasonal plant facilitation of predator survival.

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APPENDIX A

Natural history of the system (*Ecological Archives* E087-064-A1).

APPENDIX B

Experimental production of *Heterorhabditis marelatus* nematodes within hosts (*Ecological Archives* E087-064-A2).

APPENDIX C

Daily nematode mortality rates in lupine and grassland rhizospheres, watered and ambient conditions, for March–October 2002, estimated using a negative binomial model (*Ecological Archives* E087-064-A3).