Bottom-up, top-down, and within-trophic level pressures on a cactus-feeding insect

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Abstract. 1. The relative importance of host-plants and predators in the population dynamics of herbivorous insects, and the frequency and intensity of inter-specific competition among herbivores, have both been intensively studied and debated. The joint effects of bottom-up, top-down, and within-trophic level interactions, however, have rarely been integrated in a single system.

2. I studied the dynamics of the cactus bug (*Narnia pallidicornis*), a specialist feeder on tree cholla cactus (*Opuntia imbricata*), in response to variable host-plant quality, spider predation, and interactions with cactus-feeding beetles (*Moneilema appressum*). Previous work suggests that cactus reproductive effort (the proportion of meristems allocated to reproduction) is an important component of host-plant quality for *Narnia*. I conducted a 2-year field experiment to test the hypotheses that *Narnia* abundance is positively related to host-plant reproductive effort, and that interactions with predators and putative competitors alter the shape of this relationship.

3. I found strong support for the first prediction (positive *Narnia*–plant quality relationship) in both years, but neither predator removal nor beetle exclusion had detectable effects on this relationship in either year. I conclude that the dynamics of this insect herbivore are driven predominantly from the bottom-up, and that available data from this work and from previous studies are too variable to permit broad generalisations for the combined effects of host-plants, predation, and competition on herbivore dynamics.

Key words. Bottom-up factors, competition, *Opuntia*, predator–prey interactions, resource allocation, tritrophic.

Introduction

The relative impacts of multiple trophic levels on herbivore populations and communities have been a subject of intensive study since Hairston *et al.* (1960) offered an explanation for why the world is green. Their conceptual model made two important predictions regarding the factors that limit herbivores. First, the observation that plants are in abundant supply suggested that herbivores are limited by predators and parasites (top-down), rather than resource availability (bottom-up). Second, given that plant resources appear virtually unlimited, Hairston *et al.* (1960) inferred that competition among herbivores should be infrequent and weak. These predictions sparked debates about the relative importance of top-down vs bottom-up limitation of herbivore populations (e.g. Murdoch, 1966; Ehrlich

& Birch, 1967; Oksanen *et al.*, 1981; Hunter & Price, 1992), and about the frequency and intensity of inter-specific competition among herbivores (e.g. Janzen, 1973; Lawton & Hassell, 1981; Damman, 1993; Denno *et al.*, 1995).

Eventually, both predictions of the green world model were significantly modified or outright rejected. It is now widely accepted that herbivore dynamics can be influenced by both bottom-up and top-down forces, and their relative importance can vary spatially and temporally (Hunter & Price, 1992; Walker & Jones, 2001). The current paradigm for terrestrial systems suggests that bottom-up factors generally dominate, but that top-down impacts of predators can become increasingly important on high-quality plants or in high-productivity environments (Oksanen *et al.*, 1981; Hunter & Price, 1992; Stiling & Rossi, 1997; Forkner & Hunter, 2000; Denno *et al.*, 2002). The logic behind this argument is that resource-poor habitats support insufficient numbers of herbivores to sustain predator populations; appreciable impacts of predation occur only when resources are sufficient to drive herbivores to higher densities.

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It is also now widely accepted that, despite the green world, inter-specific competition among herbivores is common (Damman, 1993; Denno *et al.*, 1995). Even when herbivores do not deplete plant resource availability, negative interactions can occur via feeding-induced changes in plant defensive chemistry or nutrient content. These plant-mediated indirect competitive interactions can occur among herbivores feeding on the same tissues at the same time (Karban, 1986, 1989), or among herbivores separated temporally (Denno *et al.*, 2000; Viswanathan *et al.*, 2005; McGuire & Johnson, 2006) or spatially within a host-plant (Moran & Whitham, 1990; Masters *et al.*, 2001; Ferrenberg & Denno, 2003). Indirect competition can also be mediated by the trophic level above. The co-occurrence of multiple herbivore species can support elevated predator densities and lead to greater top-down impacts, compared with predator impacts when each species occurs alone (Holt, 1977; Redman & Scriber, 2000; Gonzales *et al.*, 2002).

Despite their common origin in the Hairston *et al.* (1960) paper, debate about bottom-up/top-down limitation and debate about herbivore–herbivore competition progressed along trajectories that were largely, and surprisingly, independent. Consequently, there are few studies that consider the joint impacts of top-down, bottom-up and within-trophic level interactions on herbivore dynamics (Karban, 1989; Morris, 1992; Moon & Stiling, 2002). Integrating these forces into a holistic view of population dynamics and community structure remains an important challenge in ecology.

I studied the effects of host-plant quality, predators, and putative competitors on a specialist insect herbivore, the cactus bug [*Narnia pallidicornis* Stål (Hemiptera: Coreidae)], on tree cholla cactus [*Opuntia imbricata* (Haw.) D.C.] in Chihuahuan desert grassland. Previous studies suggest that cactus resource allocation is an important component of host-plant quality for this herbivore. The proportion of available cactus meristems that are allocated to reproduction – which I term reproductive effort – was found to positively influence cactus bug abundance and demographic parameters (Miller *et al.*, 2006; Miller, 2007a). The present study examines the effects of top-down interactions and inter-specific competition on cactus bug dynamics, overlaid on to the bottom-up effects established in the previous work. Predatory arthropods, especially spiders, occur on tree cholla cacti and both juvenile and adult cactus bugs are vulnerable to spider predation (pers. obs.). In addition, cactus bug abundance is negatively correlated across sites and years with the abundance of another cactus-feeding insect, the long-horned cactus beetle *Moneilema appressum* (Coleoptera: Cerambycidae), suggesting the potential for negative within-trophic level interactions (Fig. 1). Because I never observed direct interactions between cactus bugs and cactus beetles, nor spider predation on cactus beetles, I hypothesised that negative bug–beetle interactions were mediated by their shared host-plants.

Here, I report the results of a 2-year field experiment in which I manipulated the densities of arthropod predators and putative competitors, in combination, across host-plants that varied naturally in quality (reproductive effort), and quantified effects on *Narnia*, the focal herbivore. The experiment was designed to test the following three hypotheses (Fig. 2). First, based on the previous work, I hypothesised that *Narnia* abundance would be positively related to the bottom-up factor of host-plant reproductive effort. Second, based on current theory, I hypothesised that the top-down effects of spiders on *Narnia* would increase with increasing plant quality, yielding a steeper slope for the relationship between reproductive effort and *Narnia* abundance in the absence of predators. Third, based on the negatively correlated distributions of the two herbivores (Fig. 1), I hypothesised that inter-specific interactions with *Moneilema* would negatively affect *Narnia* across the range of plant quality, yielding a higher intercept for the *Narnia*–reproductive effort relationship in the absence of beetles.

Methods

Natural history of study system

This research was conducted at the Sevilleta National Wildlife Refuge (NWR), a long-term ecological research (LTER) site in central New Mexico, U.S.A. See Miller *et al.* (2006) for detailed site description.

Host-plants. Opuntia imbricata (tree cholla) is a perennial arborescent cactus that grows in cylindrical stem segments. This plant is common throughout desert grassland and scrub habitats of the Southwest U.S.A. (Kinraide, 1978; Benson, 1982). Early in the growing season (late April–early May in central New Mexico), meristems appear in clusters at the terminal ends of stem segments produced during the previous year, and these
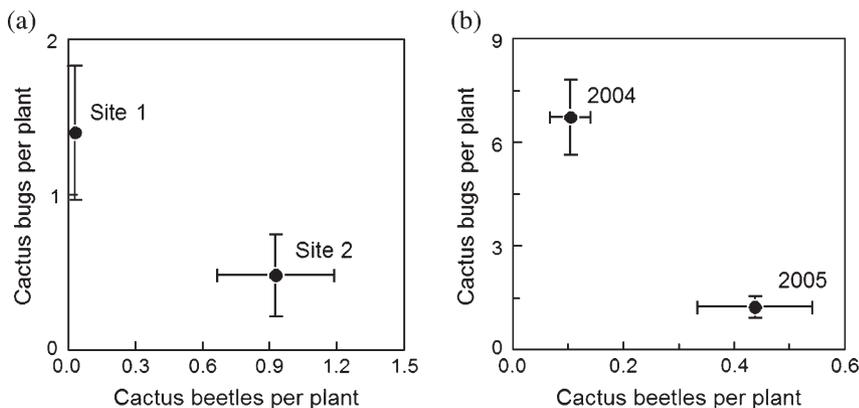
Fig. 1. Abundance of cactus bugs (*Narnia pallidicornis*) and cactus beetles (*Moneilema appressum*) on tree cholla cacti across (a) two sites (separated by 3 km) and (b) 2 years at the Sevilleta National Wildlife Refuge, New Mexico, U.S.A. Data in (a) represent 20 plants at site 1 and 27 plants at site 2 visited in July 2003. Data in (b) represent 88 plants visited in July 2004 and revisited in July 2005.
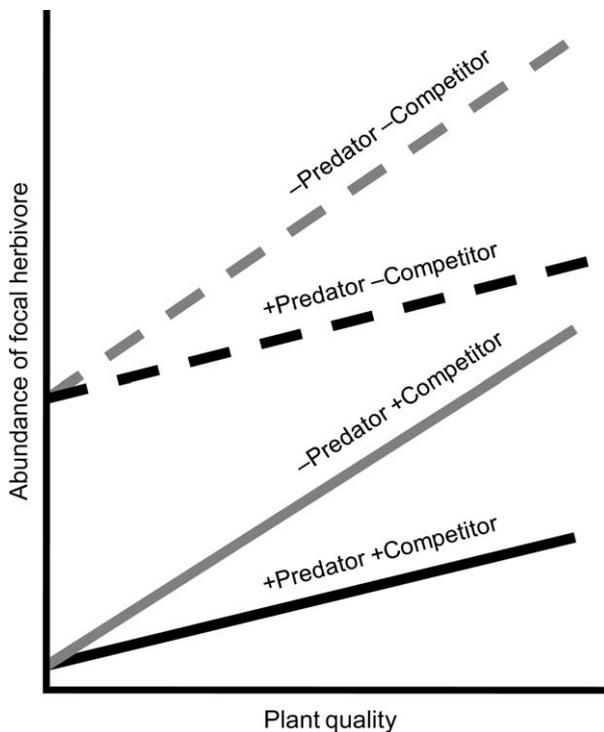
Fig. 2. Hypotheses for the effects of plant quality, predation, and competition on the abundance of a focal herbivore. Note: this graphical model assumes host-plant-mediated competition; predictions would differ for predator-mediated (apparent) competition.

develop into either reproductive or vegetative structures. Meristems allocated to reproduction develop into flower buds in late spring; the fruits ripen and fall off of plants in early autumn. Meristems allocated to new stem segments grow from May through August and produce new meristems the following spring. Reproductive effort by an individual plant in a given year is defined as the proportion of total available meristems allocated to reproductive structures. This metric is bounded by zero and one, where a plant with a reproductive effort value of zero or one allocates all meristems to growth or reproduction, respectively.

Herbivores. The cactus bug, *Narnia pallidicornis* (Hemiptera: Coreidae), specialises on *Opuntia* spp. and is commonly found on *O. imbricata* throughout its range (Mann, 1969). There are two generations within a year, and nymphs and adults co-occur throughout the growing season. Adults over-winter among debris near the base of the plant and deposit eggs on cactus spines from March to May; the first cohort of nymphs reaches maturity in May, and the second, larger cohort in August. Juveniles are flightless and complete their development on a single host-plant, while adults are flight-capable and can move among host-plants. These insects feed on all cactus parts but prefer reproductive structures (Mann, 1969). Results of previous studies indicate that host-plant reproductive effort positively influences *Narnia* fecundity (Miller *et al.*, 2006) and mediates the strength of density dependence in *Narnia* population dynamics (Miller, 2007a). Furthermore, *Narnia* abundance is not related to traits more

commonly associated with host-plant quality, including tissue % nitrogen ($r = -0.048$, $P = 0.66$, $n = 85$) and tissue % water ($r = -0.023$, $P = 0.83$, $n = 86$). Based on these data, here I use plant quality and reproductive effort synonymously.

The long-horned cactus beetle *Moneilema appressum* (Coleoptera: Cerambycidae) is another common herbivore of *O. imbricata*. Adults are active throughout summer, and their feeding on stem segments leaves distinctive damage marks. In late summer, adults lay eggs within bite marks, larvae burrow into the plant, over-winter internally, and emerge as adults in early summer. *Moneilema* are flightless and considerably larger than *Narnia*, which facilitated selective exclusion. Unlike *Narnia*, *Moneilema* does not respond to variation in reproductive effort (unpubl. data); plant quality traits important for beetle host choice and abundance are presently unknown. Cactus beetles generally occur at low densities (often only one or two beetles per plant), but individuals can inflict large amounts of damage (pers. obs.).

Natural enemies. Spiders in the families Salticidae, Theridiidae, and Thomisidae are the most common predators on *O. imbricata*. Mantids and predatory hemipterans also occur but are relatively rare (pers. obs.) All of these predators feed on *Narnia* juveniles and adults but I have never observed predation on *Moneilema*, likely due, in part, to the beetle's large size and tough exoskeleton. For this reason, I did not expect any predator-mediated indirect interactions between beetles and cactus bugs. Tree cholla cacti secrete extra-floral nectar and participate in mutualism with nectar-feeding ants. The ant species that occurred at the site of the present study (*Crematogaster opuntiae*), however, is known to provide very weak protection against herbivores (Miller, 2007b), and so I do not consider ants as a component of the natural enemy guild.

Field experiment. In May 2004, I located and tagged 88 similarly sized tree cholla cacti (≈ 1 m height) distributed across 11 spatial blocks at the Sevilleta NWR (eight plants per block), with blocks separated from each other by at least 0.25 km. Within each block, I randomly assigned each plant to one of four factorial treatment combinations of predators present/removed and beetles present/removed. There were two replicates of each predator × beetle combination in each block ($n = 22$).

For plants assigned to the predator removal treatment, I removed by hand (forceps and aspirator) all spiders every 3–4 days from early May to late August of 2004 and 2005. I also removed any other predatory arthropods encountered, but spiders were by far the most common (>95% relative abundance). For plants assigned to the beetle exclusion treatment, I constructed fences out of 1/4″ hardware cloth and installed them in early May 2004. Beetle fences were 10–15 cm tall, fully encircled plants, and were staked flush with the ground. The top inch of the fences were folded away from the plant, covered with duct tape, and coated with Tanglefoot (a sticky resin) so that beetles could not climb over the fences. The mesh size was small enough to exclude *Moneilema* but large enough to allow spiders access to fenced plants (Results). Each plant retained its treatment assignment for both years of the experiment. As the fences were maintained for two consecutive growing seasons, fenced plants experienced reductions in external

(adult) beetle damage in both years and internal (larval) beetle damage in the second year.

Narnia colonised and persisted on experimental plants naturally. I censused total *Narnia* abundance (juvenile + adult) on five dates in 2004 (14 May, 2 June, 2 July, 22 July, 16 August) and four dates in 2005 (11 May, 15 June, 15 July, 15 August). I also recorded predator and beetle abundances on these dates. I estimated beetle damage on each plant as the proportion of newly produced stem segments with any sign of beetle feeding (new segments are distinguishable from older plant growth by colour and the presence of true leaves). These data were collected at the end of beetle activity (August), and represent cumulative damage over the growing season. Each May, following cactus meristem differentiation, I counted numbers of reproductive and vegetative structures on each plant and calculated reproductive effort as above. Late-season *Narnia* abundance on an individual plant is not correlated with early-season abundance on that plant in the following year (data from 2003–2004: $r = 0.11$, $P = 0.47$, $n = 47$), and so dynamics in 2005 were likely independent from any treatment effects in 2004.

Statistical analysis

To examine the efficacy of my treatment applications, I compared spider abundances on predator-control and predator-removal plants throughout each growing season using a repeated-measures Analysis of Variance (rmANOVA). The model included predator treatment and time as fixed effects, and block as a random effect. I used the same statistical model (rmANOVA) to compare beetle abundances on fenced and control plants. I also used a *t*-test to compare the proportion of new stem segments with signs of beetle damage between fenced and un-fenced plants in each year.

I used rmANOVA to test for effects of plant quality, predator treatment, beetle treatment, and their interactions on *Narnia* abundance across each growing season. This analysis included the fixed effects of predator treatment, beetle treatment, and time, the random effect of block, and reproductive effort as a continuous variable. My *a priori* hypotheses (Fig. 2) translate, statistically, to significant effects of reproductive effort, beetle exclusion, and predator removal × reproductive effort interaction. In addition, I analysed cumulative *Narnia* abundance using a similar model (without a time effect). To compare results with predictions (Fig. 2), I plotted, for each year, cumulative per-plant abundance vs host-plant reproductive effort and fitted slopes and intercepts for each predator × competitor treatment combination. All count data were square-root transformed, which satisfied model assumptions. I analysed the data from each year separately. All analyses were performed in SAS v.8.0.

Results

I found a wide range of natural variation in reproductive effort by experimental host-plants in both years [2004 mean (min, max): 0.33 (0, 0.86); 2005: 0.42 (0, 0.88)]. Spiders occurred on tree cholla at similar abundances in both years but these were low (on average less than two spiders per plant at peak abundance, Fig. 3A). Removal by hand reduced spider abundance on experimental plants, though this effect varied seasonally in both years as indicated by predator treatment × time interactions (2004 interaction: $F_{4,339} = 2.11$, $P = 0.07$; 2005 interaction: $F_{3,254} = 3.92$, $P = 0.009$). The fencing treatment effectively reduced beetle abundance in both years (Fig. 3B). There was significant seasonal variation in this effect in 2005 (fence × time interaction: $F_{3,235} = 3.1$, $P = 0.027$) but not in 2004 (fence effect: $F_{1,90} = 6.7$, $P = 0.011$; fence × time interaction: $F_{4,333} = 1.66$, $P = 0.16$). External signs of *Moneilema* damage on new stem segments increased from 2004 to 2005 (Fig. 3C), reflecting the increase in beetle abundance between years (Fig. 3B). Fenced plants had less damage than un-fenced plants in both years (2004: $t_{85} = 2.04$, $P = 0.04$; 2005: $t_{84} = 4.15$, $P < 0.001$). Fenced and un-fenced plants had similar spider abundances in both years (tests of cumulative spider abundance in 2004: $t_{85} = 0.93$, $P = 0.35$; 2005: $t_{85} = -0.57$, $P = 0.57$).

Despite the reductions in spider abundance, beetle abundance, and beetle damage, plant quality was the only factor that significantly affected the within-season population dynamics of *Narnia* (Table 1). *Narnia* were consistently more abundant on plants with high (>median) reproductive effort throughout the 2004 and 2005 growing seasons (Fig. 4), and this pattern was support by highly significant effects of reproductive effort and reproductive effort × time in the rmANOVAs (Table 1). Overall *Narnia* abundance was greater in 2004 than in 2005 (Figs 4 and 5). In both years, the relationships between cumulative *Narnia* abundance and cactus reproductive effort were statistically indistinguishable among treatment combinations (Fig. 5). The results of the cumulative abundance analysis were qualitatively identical to the repeated-measures analysis, minus an effect of time (not shown).

Discussion

This study was designed to test the hypotheses that *Narnia* abundance is positively related to host-plant quality, and that predation by spiders and interactions with cactus beetles alter the shape of that relationship (Fig. 2). The data supported only the first of these predictions (*Narnia*–plant quality relationship). *Narnia* dynamics showed no significant response to predator removals or beetle exclusion in 2004 or 2005, suggesting that there are neither plant-mediated competitive effects of *Moneilema* on *Narnia*, nor any detectable demographic impacts of arthropod predators. Rather, the data suggest that within-season *Narnia* dynamics are driven predominantly from the bottom-up.

The conclusion of bottom-up dominance warrants a few caveats. First, the spider removal treatment was not effective until later in each growing season and, even then, spider abundances were reduced but not eliminated (Fig. 3A). Second, I did not consider any sub-lethal effects of predators on *Narnia*, such as reductions in feeding rate. Third, this study was relatively short in duration. Fourth, while I commonly observed spider predation on *Narnia*, I do not know the frequency of
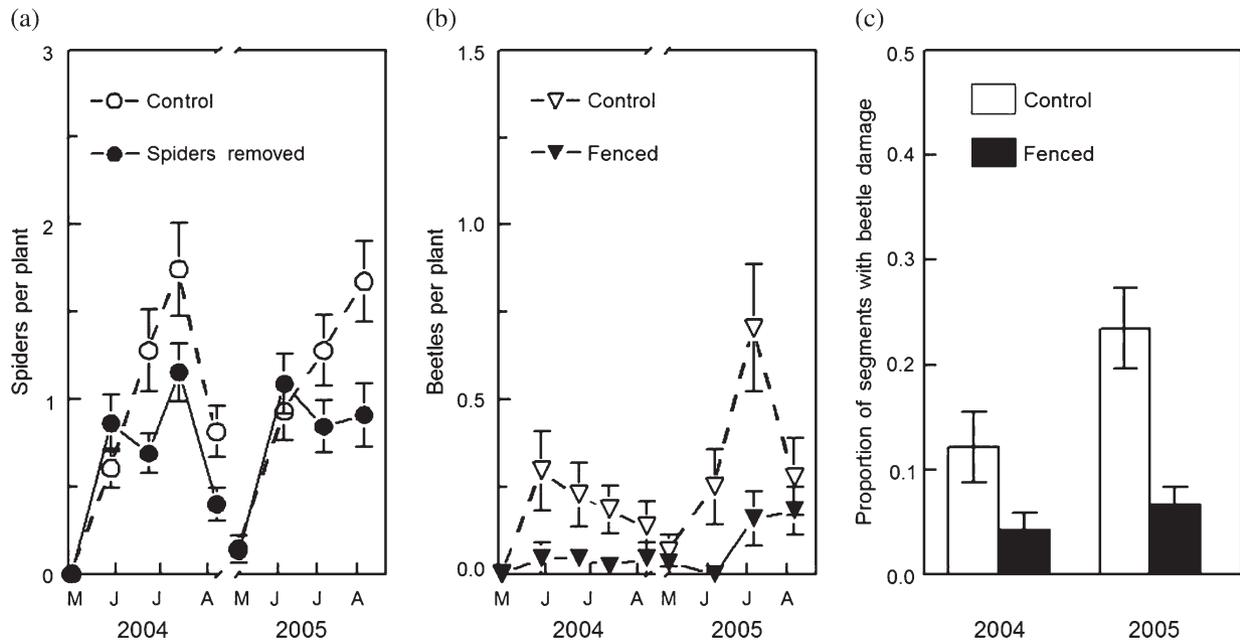
Fig. 3. Efficacy of treatment applications. Abundances of (a) spiders and (b) long-horn cactus beetles (*Moneilema appressum*) on tree cholla cacti over the 2004 and 2005 growing seasons; letters on the *x*-axis correspond to months. Open shapes/dashed lines represent control plants and filled shapes/ solid lines represent plants that received (a) predator removal or (b) fencing treatments. (c) Proportion of new cactus stem segments damaged by cactus beetles in 2004 and 2005 on control (open bars) and fenced (filled bars) plants.

spider predation relative to other top-down forces (e.g. parasitism) and so the spider removal treatment may have targeted only a subset of the relevant consumers. All of these factors may have limited my ability to detect any effects of predator removal on cactus bug dynamics. In addition, because I did not include sham treatments (e.g. fences with large openings around the beetle-control plants), it is possible that unintended effects of fencing plants and removing spiders influenced my

results. Finally, there was a large amount of unexplained variation in *Narnia* abundance in both years (Fig. 5), indicating that additional factors, not considered here, influenced the dynamics of this herbivore.

Despite these limitations, bottom-up dominance is consistent with previous work in this system, which showed that patterns of cactus meristem allocation, alone, explained widespread variation in *Narnia* abundance across multiple years at the Sevilleta

Table 1. Results of repeated-measures analysis of *Narnia* abundance throughout the 2004 and 2005 growing seasons. Statistically significant effects are in bold. The time series data are shown in Fig. 4.

Effect	2004			2005		
	d.f.	*F*	*P*	d.f.	*F*	*P*
Reproductive effort	**1,78.7**	**44.08**	**<0.0001**	**1,79.2**	**27.48**	**<0.0001**
Beetle	1,79.1	0.31	0.58	1,79.2	0.26	0.61
Reproductive effort × beetle	1,78.7	0.53	0.47	1,79.2	0.67	0.41
Predator	1,79.1	0.14	0.71	1,79.2	0.92	0.34
Reproductive effort × predator	1,78.7	0.25	0.62	1,79.2	0.38	0.54
Beetle × predator	1,79.1	0.04	0.84	1,79.2	0.08	0.78
Reproductive effort × beetle × predator	1,78.7	0.00	0.98	1,79.2	0.09	0.76
Time	**4,310**	**2.38**	**0.05**	3,236	0.46	0.71
Reproductive effort × time	**4,309**	**15.01**	**<0.0001**	**3,236**	**9.68**	**<0.0001**
Beetle × time	4,310	0.91	0.46	3,236	0.32	0.81
Reproductive effort × beetle × time	4,309	1.26	0.29	3,236	0.52	0.67
Predator × time	4,310	0.19	0.95	3,236	0.94	0.42
Reproductive effort × predator × time	4,309	0.7	0.59	3,236	1.7	0.17
Beetle × predator × time	4,310	1.73	0.14	3,236	0.12	0.95
Reproductive effort × beetle × predator × time	4,309	1.95	0.10	3,236	0.97	0.41
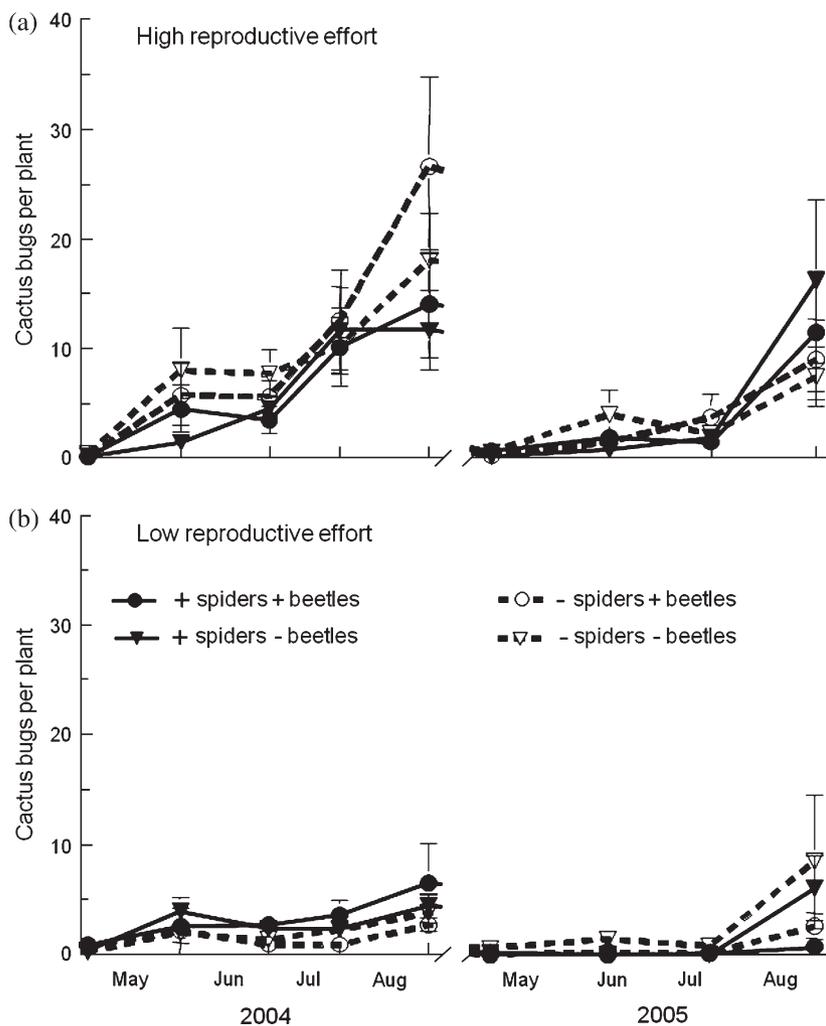
Fig. 4. Time series of cactus bug (*Narnia palidicornis*) abundance on tree cholla cacti over the 2004 and 2005 growing seasons in relation to natural variation in plant quality (reproductive effort) and manipulated densities of predators and cactus beetles. (a) *Narnia* abundance on high-quality host-plants (reproductive effort > median), (b) *Narnia* abundance on low-quality host-plants (reproductive effort < median). See Table 1 for statistical analysis of treatment effects. Treatment codes given in legend.

NWR and multiple sites throughout New Mexico (Miller *et al.*, 2006). Reproductive effort is not correlated with plant size for the range of sizes considered in this study ($r = -0.055$, $n = 60$, $P = 0.67$), and so it is unlikely that plant size can account for the positive relationship between reproductive effort and herbivore abundance. Given the importance of reproductive effort, independent of other interactions within the cactus arthropod community, an obvious next step in understanding *Narnia* dynamics is to identify the causes of natural variation in plant meristem allocation. Year-to-year variation in tree cholla reproductive effort in central New Mexico is associated with patterns of winter precipitation (Miller, 2007c). This abiotic factor may therefore be an ultimate driver of temporal patterns of insect abundance via its effect on host-plant quality. Within years, the factors underlying variation in meristem allocation among co-occurring plants are less clear, but likely include effects of genotype, microhabitat, age, plant history (i.e. costs of reproduction in previous years), and their interactions.

Despite apparent inconsistency with predictions, the weak predator effects in this experiment, even on high-quality plants,

could be interpreted as consistent with the hypothesis that the importance of top-down forces is related to resource conditions. The low productivity of the Chihuahuan desert habitat in which this study was conducted may be insufficient to support substantial arthropod predator populations. In fact, spider densities on tree cholla were consistently low in both years (see scale of Fig. 3A), and notably lower than other studies in higher productivity environments where top-down impacts of spiders have been detected (e.g. Spiller & Schoener, 1994; Denno *et al.*, 2002). Thus, resource conditions of the large-scale environmental context may override small-scale, plant-level variation in quality. This seems plausible, especially as much of the early theory for abiotic mediation of top-down forces was intended for the productivity of a habitat or locality, and not for the quality of individual host-plants (Oksanen *et al.*, 1981). At another Chihuahuan desert site, however, Floyd (1996) found impacts of arthropod predators on creosotebush herbivores, even with predator and herbivore densities similar to those I observed. Clearly, top-down impacts are possible in desert environments, although Floyd (1996) did not evaluate the relative importance
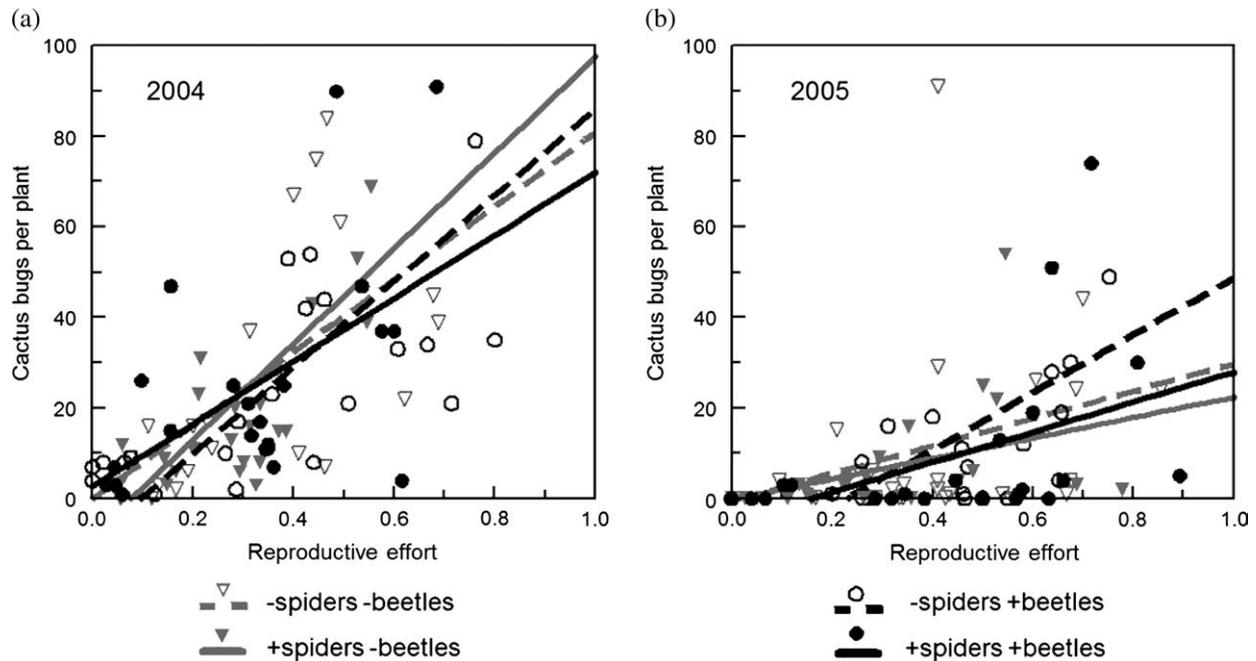
Fig. 5. Cumulative *Narnia* abundance over the (a) 2004 and (b) 2005 growing seasons in relation to host-plant quality (reproductive effort) for each predator × beetle treatment combination. *Narnia* abundance was significantly, positively related to host–plant reproductive effort, but the shapes of this relationship were statistically identical across all treatment combinations within each year. Treatment codes given in legend.

of predation vs plant quality. More studies of trophic pressures on desert insect herbivores are needed to determine whether the bottom-up dominance I observed is consistent across low productivity environments.

The identity of the dominant predators in this system could also help explain why predator removals had no detectable effects on the focal herbivore. In their review, Halaj and Wise (2001) found that, of all the predator groups they examined, spiders had the weakest effects on herbivore densities. Intra-guild predation, which is pervasive in arachnids (Wise, 1993), may contribute to this pattern. I have commonly observed intra-guild predation among the spiders on tree cholla, and its role in dampening top-down impacts warrants experimental investigation.

Results from the competition treatment are consistent with the findings of Denno *et al.* (1995), who reported, based on their literature review, that negative interactions between sap-feeding and chewing insect herbivores were infrequent. Furthermore, these authors concluded that density dependence can mediate the impact of inter-specific competition, especially for sap-feeders. Density dependence has been detected in *Narnia* population dynamics (Miller, 2007a), suggesting that intra-specific competition might preclude negative interactions with other cactus insects. It remains possible that asymmetric competition occurs in this system, with *Narnia* having negative effects on *Moneilema;* this experiment was not designed to detect such an interaction.

No clear patterns emerge from the few existing studies (Karban, 1989; Morris, 1992; Moon & Stiling, 2002; present study) regarding the joint impacts of top-down, bottom-up, and within-trophic level interactions on herbivore dynamics. Rather, the relative importance of these interactions appears to be highly case-specific, and may be influenced by various factors, including abiotic context, predator identity, intra-guild predation, herbivore feeding modes, or density dependence. I conclude that generalised predictions for multi-trophic interaction outcomes can serve as valuable heuristic tools, but clearly must be modified to suit particular systems.

Acknowledgements

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