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Wet years have more caterpillars: interacting roles of plant litter and predation by ants

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Abstract. Climate is widely recognized as an important factor that affects temporal and spatial patterns of occurrence and abundance of herbivorous insects, although the ecological mechanisms responsible are poorly understood. We found that precipitation and standing water were positively correlated with locations and years of high abundance of caterpillars of the ranchman's tiger moth, *Platyprepia virginalis*. We analyzed 30 years of survey data and found that the number of large rainfall events was a better predictor of caterpillar abundance than total annual accumulation. We considered three ecological mechanisms that could drive this relationship and conducted observations and manipulative experiments to evaluate these mechanisms. (1) Rainfall facilitates more plant growth, although we found no evidence that increased food quality or quantity was causing the positive association between precipitation and caterpillar abundance. (2) Large rainfall events cause predatory ground-nesting ants to be less abundant and we found that the number of ants that recruited to local sites was negatively associated with survival and abundance of caterpillars. (3) We found that litter from wet sites provided a refuge from ant predation; litter from wet sites was not beneficial to caterpillars in the absence of ants. Both abiotic factors (precipitation) and biotic factors (predatory ants) affected the temporal and spatial abundance of caterpillars directly and interactively. Climate models predict that rainfall will become more variable, suggesting that populations of this caterpillar may also become more variable in the future.

Key words: climate change; herbivore; population; precipitation; refuge; variability.

INTRODUCTION

Scientists from many disciplines are in broad agreement that the Earth's climate is rapidly changing (IPCC 2014). In addition to the general warming pattern, regional patterns of precipitation are predicted to become more variable with increased frequency and severity of droughts and floods. We can expect more extreme maximum and minimum conditions, and future climates are likely to include longer-lasting sequences of high or low precipitation (Tuljapurkar and Haridas 2006, Zhang et al. 2007, Allan et al. 2010, Coumou and Rahmstorf 2012). For example, one region that is projected to be affected by climate change is California's central coast where warmer temperatures and more variable precipitation are expected (Berg and Hall 2015, Swain et al. 2016).

Entomologists have recognized that insect populations are sensitive to climate; in a 231-page paper published in 1931, Boris Uvarov reviewed over 1,300 studies on effects of climate on insects. John Lawton (1994) noted that despite this early literature, we still had little understanding of the effects of climate on any single species and furthermore that studies focusing solely on direct effects were likely to be misleading. The recent renaissance of

interest in effects of global climate change has emphasized shifts in species' ranges and phenologies, but rarely population dynamics or interactions (Parmesan 2006).

The field currently lacks an understanding of the mechanisms by which climatic drivers influence population dynamics and species interactions over multi-annual time frames and across space (Stenseth et al. 2002, Walther et al. 2002, Tylianakis et al. 2008, Post 2013, Mooney et al. 2016). Studies have attempted to investigate climatic drivers on long-term temporal dynamics through correlations between climate (or indices such as ENSO) and abundance, but not through manipulative experiments (Stenseth et al. 2002, Berteaux et al. 2006, Pardikes et al. 2015). On the other hand, mechanisms of climatic effects on species interactions have been explored, but only through short-term manipulative experiments that may or may not explain larger scale patterns (e.g., Suttle et al. 2007, Tylianakis et al. 2008, Schott et al. 2010, Mooney et al. 2016). Studies that combine long-term dynamics and manipulations are rare. Similarly, studies of climate have generally not considered the complexity of real communities including species interactions (Gilman et al. 2010, Kiers et al. 2010, but see Wilmers and Post 2006, Barton and Ives 2014*a, b*, Mooney et al. 2016).

Spatial patterns are even less studied than temporal dynamics. Climatic conditions have been linked to local extinctions and changes in herbivore–plant interactions (e.g., Boughton 1999, Johnson 2005, Peters et al. 2006,

Kurz et al. 2008). Changing conditions have also been found to cause regional extinctions in synchronized, extinction-prone populations (e.g., Harrison and Quinn 1989, Heino et al. 1997, Leibhold et al. 2004). Climatic drivers can vary over space (Tylianakis et al. 2008), which may dramatically affect population dynamics, but mechanistic studies of this variation are uncommon (e.g., Boughton 1999, Johnson 2005, Parn et al. 2012, Mooney et al. 2016). Past studies of spatial dynamics have not generally considered multiple species or multiple effects of climate (e.g., Brook et al. 2009).

We have been studying populations of the ranchman's tiger moth (*Platyprepia virginalis*, Lepidoptera: Erebidae) at the Bodega Marine Reserve in northern California, USA. During their univoltine life cycle, caterpillars move from wet marshy habitats, where eggs and caterpillars survive, to dry upland habitats, where they pupate and mate (Grof-Tisza et al. 2015). Early-instar caterpillars live in the leaf litter, consuming detritus and living and dead vegetation. As a result, more caterpillars were found at sites with deep litter and experimentally adding litter beneath bushes increased caterpillar numbers locally (Karban et al. 2012*a*).

Caterpillars are parasitized by a locally specialized tachinid parasitoid (*Thelaira americana*). Rates of parasitism may be as high as 70% of all individuals (English-Loeb et al. 1993), although we have found no evidence that parasitoids affect the temporal dynamics of this caterpillar (Karban and de Valpine 2010). Predation of young caterpillars by ants (particularly *Formica lasioides*) and predation of pupae by mice and ants were found to be unexpectedly important sources of mortality (Grof-Tisza et al. 2015). Experimental protection from ants increased caterpillar survival in the field (Karban et al. 2013). Deeper litter increased caterpillar survival in short-term assays only when ants were present. Ants did not recruit to caterpillars as readily in deep litter in field assays (Karban et al. 2013) and wet litter reduced ant recruitment and increased caterpillar survival in lab experiments (Karban et al. 2015).

Population surveys have been conducted in two wet habitats at our field site since 1985, described elsewhere (Karban and de Valpine 2010). During the last week in March of each year, the number of caterpillars encountered along five transects (10 × 4 m) were recorded. Estimates of annual densities varied by at least two orders of magnitude (Fig. 1). Preliminary analyses of temporal dynamics indicated that caterpillars were more common following wet years although precipitation explained relatively little variation (<5%) in caterpillar abundance (Karban and de Valpine 2010). Population dynamics also varied spatially; wet sites had more caterpillars and tended to have positive population growth in most years while dry sites acted as population sinks in most years and were prone to local extinction (Karban et al. 2012*b*).

The ecological mechanisms linking precipitation to caterpillar abundance over space and time are not clear. In this current study, our goal was to elucidate those
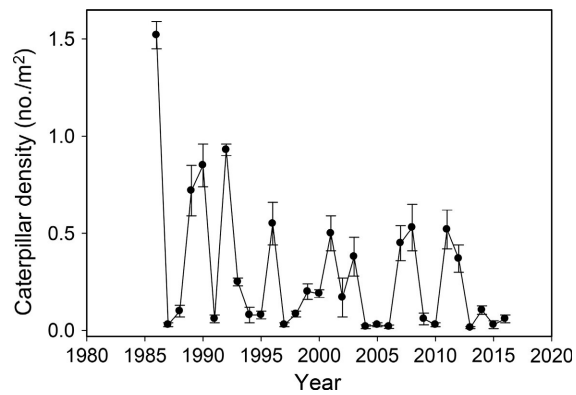

FIG. 1. Density of caterpillars observed along transects in wet habitat dominated by *Conium maculatum* during annual surveys at the end of March of each year. Values are mean ± SE.

causal mechanisms. Observations during and following large rain events indicated that sites that we characterized as wet had standing water when rainfall exceeded 4–5 cm over a 24-h period. These observations suggested that the number of large rainfall events might be a better predictor of population dynamics than total annual precipitation (Easterling et al. 2000, Jentsch et al. 2007). Here, we collected additional weather data and conducted statistical analyses to examine the quantitative relationships between changes in annual caterpillar population sizes and large rainfall events.

Precipitation can plausibly affect caterpillars by at least three mechanisms that we examined in this study (Fig. 2). (1) More rainfall allows more plant growth and deeper litter, benefitting caterpillars directly by providing food and habitat. We tested this hypothesized mechanism by measuring litter fall at wet and dry sites and measuring caterpillar growth and survival when provided with litter at those quantities. (2) More rainfall reduces the number of ground-nesting ants and this numerical reduction in predators indirectly benefits caterpillars. We tested this hypothesized mechanism by measuring ant numbers at wet and dry field sites. We also measured caterpillar survival at wet and dry sites with different numbers of recruiting ants. (3) More rainfall produces deeper, denser litter, providing caterpillars with a refuge from ants, making ants less effective predators. We evaluated this hypothesis by measuring caterpillar survival in containers that ants could access when they were housed with litter from wet and dry sites. These experiments were conducted in wet and dry sites in the field and ant recruitment to each site was included as a covariate.

METHODS

Relationships between large precipitation events and caterpillar dynamics

We quantified the number of rainfall events at our site by examining rainfall records recorded at the Bodega
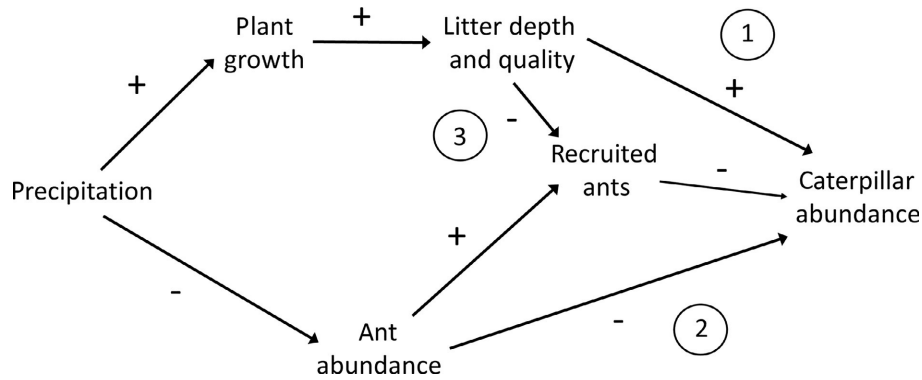
Fig. 2. Three possible mechanisms linking large precipitation events (>4 cm/24 h) to increased caterpillar abundance. Mechanism 1 involves improved litter quality as a source of food and habitat for caterpillars. Mechanism 2 involves reduced abundances of ant predators. Mechanism 3 involves the interaction between habitat quality and ants, wherein litter provides a refuge that prevents ant predation.

Marine Lab between 1983 and 2016. Caterpillar abundance during the last week in March from 1985 to 2016 was estimated by counting the number of caterpillars observed along five transects, each 10 × 4 m. These transects were placed in wet habitat dominated by *Conium maculatum* interspersed with bushes of *Lupinus arboreus* and *Juncus* spp. in the understory. Because these host plants are relatively short lived, the precise position of the transects changed slightly from year to year. Previous analyses indicated that caterpillar numbers were affected by numbers in the previous year (Karban and de Valpine 2010). As such, we analyzed the annual change in abundance by comparing the natural log of caterpillar numbers in successive years. We analyzed the relationship between the number of rainfall events over 5 cm between year t and $t − 1$ and the change in the log caterpillar numbers between year t and $t − 1$ using a generalized linear model (gls in the nlme package in R; Pinheiro et al. 2016). In preliminary analyses, we used a simple general linear model (lm in R) and tested for autocorrelated residuals using a Durbin-Watson test. Because autocorrelation was highly significant, we conducted the analyses using a generalized linear model that included first-order autocorrelation in the error structure. We report the results assuming a single autocorrelation vector for sites and years combined. We also explored using the correlation matrix from site × year but found very similar results to the single combined correlation vector.

Litter as food and habitat

We estimated litter fall at wet and dry sites during the time when early instars were vulnerable to predation. Wet sites were characterized by *Juncus* as the predominant understory plant and were within 30 m of standing water during wet seasons. First, we measured litter depth at four randomly selected locations at each of our 12 sites (Fig. 3). We compared litter depth at wet sites and dry sites using a linear mixed model with sites as a random

effect and wet vs. dry as a fixed effect (lme4 package in R; Bates et al. 2015). Next we collected new litter that accumulated in cups (237 mL; Sweetheart Cup, Mason, Michigan, USA) beneath three lupine bushes at each of the 12 sites. Cups were anchored at each site on 16 July 2015 and litter falling into the cups was collected, dried, and weighed on 2 August and 17 August. New litter accumulation during this time was compared using a linear mixed model with sites as a random effect and wet vs. dry as a fixed effect (lme4 package in R; Bates et al. 2015).

We evaluated litter as a source of food and habitat by caging second-instar caterpillars in containers in the lab with litter from each site at a depth that matched the depth that naturally occurred at that site. We weighed 10 caterpillars and placed each in separate containers on 17 July 2015. We reweighed them on 18 August. We included 10 caterpillars that experienced four more treatments in addition to litter from each of the 12 sites: control with no litter, lupine leaves as the only litter constituent, lupine petals as the only litter constituent, and frass from tussock moths (*Orygia vetusta*) as the only litter constituent.

Over this same time period, we evaluated the survival and growth of second-instar caterpillars at each of the 12 sites in the field. We did not know a priori how much growth occurred over the summer. Caterpillars were caged in plastic deli containers (11 cm diameter) that either had window screen bottoms that allowed access by all ant species or spun polyester bottoms that prevented access by ants. Caterpillars were caged with litter from each site at a depth that matched the depth found at that site. Since we expected survival of the caterpillars at wet sites to exceed survival at dry sites, we compared estimates of survival at wet vs. dry sites using Fisher's one-tailed exact test of independence.

Ant recruitment

We estimated ant recruitment at each of the four locations at our 12 sites where we measured litter depth. We

FIG. 3. An aerial photograph of our study showing the 12 sampling sites (red and blue circles) and the extent of wet (dashed blue polygons) habitats. The remaining habitat is dry, upland grassland and dune. [Color figure can be viewed at wileyonlinelibrary.com]

placed two bait stations at each of these locations on 15 July 2015, during mid-day when ants were active and during the part of the season when early-instar caterpillars were vulnerable to ant predation. Previous studies indicated that most predation of caterpillars and baits occurs during the first few hours: ants either discover and exploit the new food source, or they don't (Karban et al. 2013). The bait stations at each location consisted of a cotton ball soaked in a sugar solution (one part sugar to three parts water) and 1 cm^3 of hot dog on separate petri dishes placed on the litter. We recorded the number of ants of each species that were on each dish after 2 h and summed the ants from the eight dishes at each site. Ant numbers were not normally distributed but were modelled more accurately by a negative binomial distribution with sites as a random effect and wet vs. dry as a fixed effect (glmmADMB package in R; Fournier et al. 2012). We compared the number of *F. lasioides* workers and the total number of ants of all species that recruited to baits at wet and dry sites.

Relative roles of litter quality and ant recruitment

We estimated the relative contributions of litter quality, ant recruitment, and the interaction between these two in a field experiment that monitored survival of second-instar caterpillars. Caterpillars were placed at each of our 12 sites and survival was assessed after 48 h. Caterpillars were kept in deli containers with window screen bottoms that allowed access by ants but prevented the caterpillars from escaping. Caterpillars that were not recovered after 48 h were considered to have been killed and removed by ants since we observed no other sources of mortality or mechanisms responsible for missing caterpillars. Two cases were excluded because the cause of the disappearance was ambiguous due to

holes in the seal securing the screen. The deli containers were placed under lupine bushes and each bush had one container with each of two litter treatments: litter from wet sites (mostly *Juncus* stems and thatch plus lupine leaves), and litter from dry sites (mostly lupine leaves). The containers were completely filled with litter from either the wet or dry sites so that the quantity of litter was similar in all containers. The vegetation and litter beneath each container was cleared so that all containers were placed on mineral soil. This experimental design allowed us to separate effects due to characteristics of the litter (dominated by *Juncus* at wet sites and lupine at dry sites) vs. effects due to moisture or other traits of the surrounding environment (wet vs. dry). This experiment was conducted four times during July 2016 using two bushes at each site and each of these four runs was considered as a random variable (block) in our analyses. We also recorded ant recruitment to baits beneath each bush over a 4-h period immediately prior to the start of each run. The baits at each location consisted of a cotton ball soaked in a sugar solution (one part sugar to three parts water) and 1 cm^3 of hot dog on petri dishes placed on the soil surface. The number of ants that recruited to our baits was included as a covariate. We modeled the survival of caterpillars in each container using a binomial distribution with sites as a random effect and litter type (*Juncus* from wet sites or lupine from dry sites) as a fixed effect (glmmADMB package in R).

RESULTS

Relationships between large precipitation events and caterpillar dynamics

Caterpillar numbers increased on average when the preceding winters had more large rainfall events and
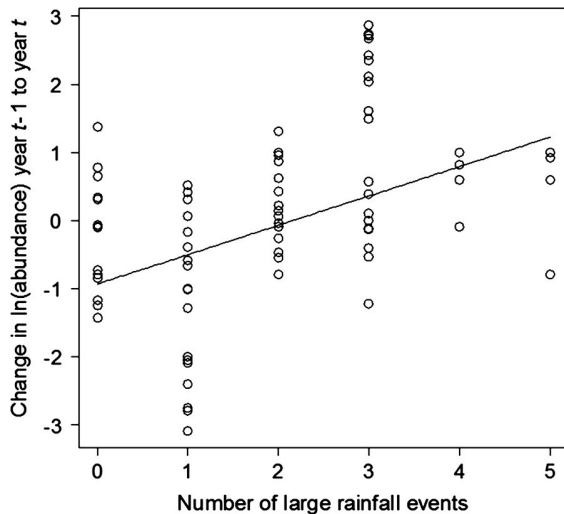
FIG. 4. Change in caterpillar abundance and the number of large precipitation events (>5 cm) over the same time period.

tended to decrease when the preceding winters had only one or no large rainfall events (Fig. 4). The best fit model was change in caterpillar abundance = 0.596 × number of rain events − 1.20 (R^2 = 0.21). The standard error of the slope was 0.129 (Student's t = 4.53, df = 93, P < 0.0001). This model contained autocorrelated residuals and running a generalized linear model that included autocorrelation confirmed that the pattern was significant.

Litter as food and habitat

Lupine bushes growing in wet sites accumulated more litter beneath their canopies than those growing in dry sites. Bushes at wet sites had almost four times the litter depth as those at dry sites in mid July (Fig. 5a, t = 3.27, df = 10, P = 0.008). This difference increased as 80% more new litter fell beneath lupine bushes at wet sites between mid July and mid August (Fig. 5b, t = 2.18, df = 10, P = 0.05).

Caged caterpillars in all the litter treatments lost mass over the summer month of our experiment. All of these treatments provided fresh material only once over the 30 d period. This indicates that uncaged caterpillars in the field normally eat newly fallen litter, eat fresh leaves attached to plants, or lose mass during this dry stressful time.

All of the caged caterpillars in the field that were protected from ants survived. This indicates that abiotic differences in litter depth or quality at dry and wet sites were not causing large differences in mortality. When ants had access to caterpillars, mortality due to predation was higher at dry sites (40%) than at wet sites (23%) (Fisher's exact test; P = 0.05; mortality data for each site are presented in Appendix S1: Table S1). This greater mortality at dry sites could be caused by differences in ant numbers
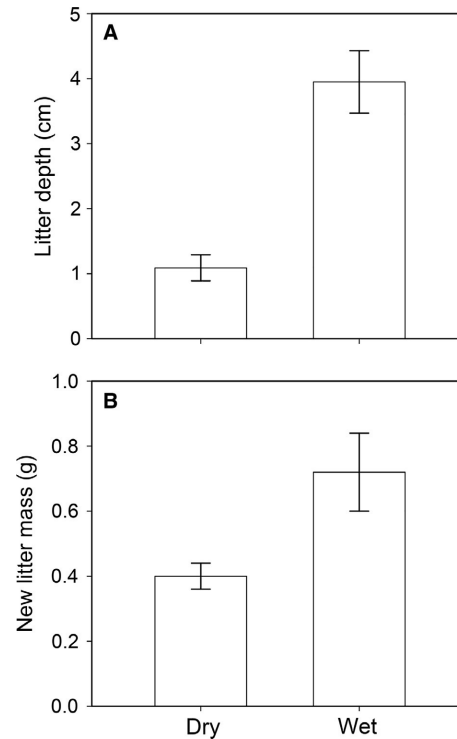

FIG. 5. Litter depth and accumulation beneath lupine bushes at dry and wet sites. (A) Litter depth (mean ± SE) from the upper surface of the litter to the mineral soil in mid-July. (B) Depth of new litter that accumulated (mean ± SE) between mid-July and mid-August.

and/or by differences in the effectiveness of predators at finding and consuming caterpillars.

Ant recruitment

Recruitment of workers of *F. lasioides* occurred almost exclusively to baits in dry habitats rather than wet sites (Fig. 6a, z = 2.98, n = 12, P = 0.003). Recruitment of all ant species also tended to be greater in dry sites (Fig. 6b, z = 1.80, P = 0.07).

Relative roles of litter quality and ant recruitment

Many caterpillars (67/190 = 35%) were consumed by ants during the first 48 h that they were placed out in the field. Caterpillars were 26% more likely to escape predation if they were in a container with litter from a wet site compared to litter from a dry site (Fig. 7a, z = 2.89, P = 0.004). We found no evidence that this effect of litter type depended on the actual field site (wet vs. dry) where the container was placed (z = 0.04, P = 0.97). The number of ants that recruited to baits at each site was also a significant predictor of predation risk (Fig. 7b, z = 1.97, P = 0.05). The interaction between litter type and number of ants that recruited was not significant (z = 0.67, P = 0.50), indicating that
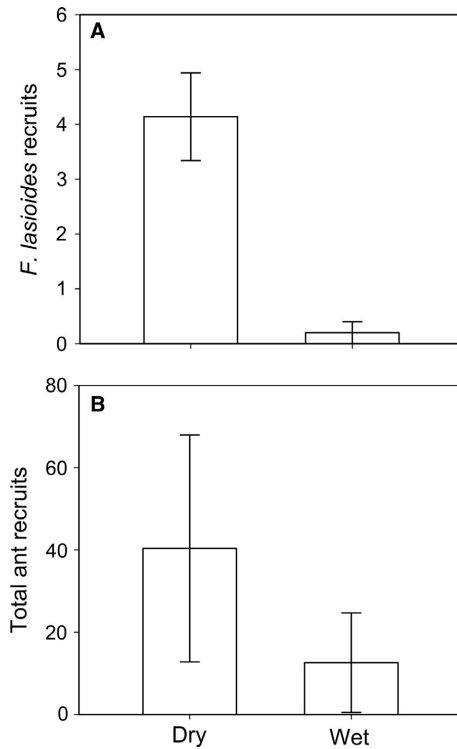
FIG. 6. Workers of (A) *Formica lasioides* and (B) all ant species that recruited to baits at dry and wet sites. Values are mean ± SE.
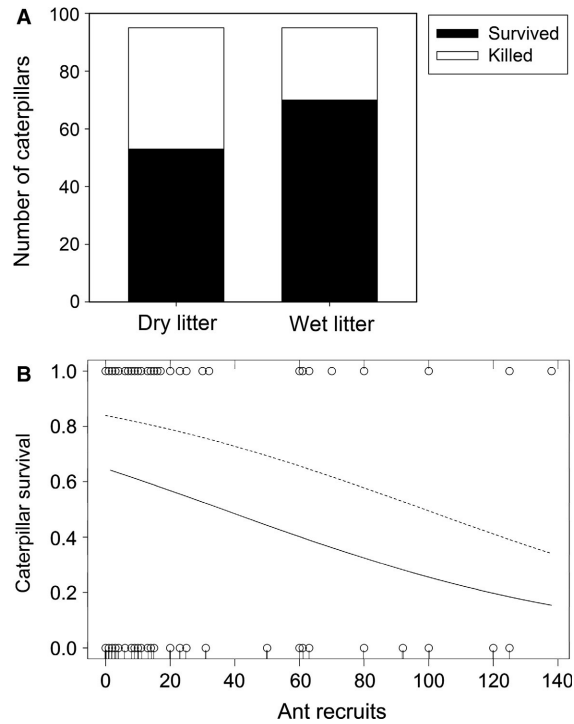

FIG. 7. Caterpillar survival was affected by litter quality and ant recruitment when ants were present. (A) Caterpillars were more likely to survive when they were in litter from wet sites than when they were in litter from dry sites. (B) Caterpillars were less likely to survive as the number of ants recruiting to the site increased. The solid line represents the best fit model for caterpillars in litter from dry sites and the dashed line caterpillars in litter from wet sites.

although both of these main effects were found to play a role, their effects were additive and not multiplicative.

DISCUSSION

Caterpillars were more abundant following wet winters (Karban and de Valpine 2010) and at wet sites (Karban et al. 2012*b*). The relationship between precipitation and caterpillar numbers was improved when we considered the number of large rainfall events rather than the total seasonal accumulation (Fig. 4). An experimental approach is required to understand this relationship and to predict effects of changing precipitation patterns in the future.

The link between rainfall events and caterpillar abundance could have been caused by three possible mechanisms (Fig. 2).

1). Rainfall could cause enhanced growth of *L. arboreus* and other plants that caterpillars feed on, either as litter or as fresh food. However, this is unlikely since caterpillars that were fed litter from all of the sites lost mass over a 30-d period and litter treatments were not significantly different. This result suggests that wet years and sites do not produce more, or better, food for caterpillars.

2). Heavy rainfall events could reduce the number of ants since *F. lasioides* and other common species at the sites nest in the ground. Fewer ants could allow increased caterpillar survival and abundances. The data were consistent with this mechanism. All caterpillars survived in experiments that excluded ants completely. Ants recruited in greater numbers at dry sites (Fig. 6). The number of recruiting ants predicted the likelihood of predation (Fig. 7b).

3). When ants were present, wet litter could act as a refuge, reducing the probability of predation. The data were also consistent with this mechanism. When ants were excluded, caterpillars survived equally well in all litter treatments; but when ants were present, litter from wet sites resulted in lower rates of predation than litter from dry sites (Fig. 7a). This result suggests that litter varies in the quality of refuge that it provides. Litter from wet sites afforded greater protection from predation when it was experimentally placed in either wet or dry sites.

Host plant characteristics are well known to affect the success of many herbivores (Ehrlich and Raven 1964, Scriber and Feeny 1979), including this system (Karban et al. 2010). Yet, food does not appear to drive the temporal and spatial patterns of abundance of *P. virginalis*

(Karban et al. 2012b). Wet sites produce more leaves and more litter than dry ones (Fig. 5), yet caterpillars at all sites lost mass over the summer. Young caterpillars gain mass early in the season (≈ June) when lupine and other species produce leaves and litter that have high concentrations of water and other nutrients. Older caterpillars gain mass once winter rains commence and nutritious foliage and litter become available (about February–May).

Previous work established that ants were important predators of early-instar caterpillars and pupae (Karban et al. 2013, Grof-Tisza et al. 2015). This study confirmed that finding, as ants quickly discovered caterpillars, recruited additional workers, and removed these prey. Ants are important predators of caterpillars and other herbivores in many systems (Styrsky and Eubanks 2007, Rosumek et al. 2009). Spatial patterns of ant abundance matched spatial patterns of caterpillar survival and abundance in our study. Ants were more abundant at dry sites (Fig. 6) and predation was also more likely at dry sites. For each additional ant that recruited to a site, caterpillar survival decreased by 2% (Fig. 7b). Unfortunately, long-term temporal data on ant abundance are unavailable and cannot be included in models of temporal dynamics of caterpillars. Ant population dynamics over time are rare in the literature although existing evidence suggests that annual estimates of abundances of other ant species vary at least twofold (Scherba 1958, Talbot 1961, Chew 1987, Sanders and Gordon 2004, Morris et al. 2005).

The interaction between ant abundance and habitat was a strong determinant of caterpillar survival and abundance. When ants were excluded, habitat was not important for caterpillars. However, when ants were present, caterpillars were more likely to survive in wet sites and in sites with deep litter (Karban et al. 2012a, 2013, 2015). The quality of the litter at wet sites determined whether caterpillars escaped ant predation. Ants in containers with litter from wet sites experienced low predation rates whether these containers were placed in wet sites or dry sites (Fig. 7a). At least two attributes of litter from wet sites may improve the quality of refuges from ant predation. First, caterpillars are able to maintain active movement at lower temperatures than *F. lasioides* workers and wet litter may provide caterpillars with a physiological advantage (Karban et al. 2015). Second, litter from wet sites is made up of *Juncus* sp. stems and other complex structures. Litter from dry sites is thinner and more two-dimensionally layered. It is possible that ants can move more readily and are more effective predators in the less complex dry litter.

There is a long tradition in ecology that recognizes the importance of habitat in determining the extent and consequences of predation. Carl Huffaker's (1958) classic experiments demonstrated that habitat and the relative mobility of predator and prey through the habitat affected the spatial and temporal dynamics of both. George Varley (1959) noted that habitat stability affected the likelihood of effective biological control of herbivores. More recently, habitat

complexity has been found to reduce the hunting success of ants (Gibb and Parr 2010). Prey were discovered by ants more quickly and ants recruited other workers and monopolized resources more effectively in simple habitats. This general result that habitat complexity increases refuge use and decreases predation rates has been found in many different terrestrial and aquatic habitats (Crowder and Cooper 1982, Rosenheim 1990, Diehl 1992, Schriver et al. 1995, Grabowski 2004). Abiotic conditions may affect predator–prey relationships by altering the habitat to favor either predator or prey. For example, vegetation height changes the thermal regime and ants species composition that ultimately determines the outcome of interactions between ants and caterpillars of the threatened butterfly, *Maculinea arion* (Thomas et al. 2009). Similarly, dry conditions affect fire occurrence and intensity, which can reduce the abundance of ants and weaken the interactions that they drive (Paolucci et al. 2016).

CONCLUSIONS

Precipitation along the California coast has been historically variable and almost all models predict that it will become more so. Variability in rainfall, particularly variability in large rainfall events, is likely to affect populations of insects, as exemplified in this study by *P. virginalis*. As rainfall becomes more variable, so will caterpillar population dynamics. Large rainfall events were found to affect temporal and spatial dynamics of caterpillars by at least two mechanisms (the bottom two paths in Fig. 2). First, large rainfall events reduced the abundance of ants, key predators of caterpillars. Second, more rainfall increased the quality and depth of litter, which provides a refuge from ant predation. We found that both abiotic conditions (large precipitation events) and biotic players (predatory ants) were important determinants of the abundance and distribution of a common herbivore. Indeed, abiotic conditions and biotic players interacted to exert strong effects that are likely to become even stronger in response to global change. A detailed understanding of the mechanisms that control insect populations will be required to better predict their temporal and spatial dynamics.

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SUPPORTING INFORMATION