Species Response to Environmental Change: Impacts of Food Web Interactions and Evolution

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Supporting Online Material

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Species Response to Environmental Change: Impacts of Food Web Interactions and Evolution

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How environmental change affects species abundances depends on both the food web within which species interact and their potential to evolve. Using field experiments, we investigated both ecological and evolutionary responses of pea aphids (*Acyrthosiphon pisum*), a common agricultural pest, to increased frequency of episodic heat shocks. One predator species ameliorated the decrease in aphid population growth with increasing heat shocks, whereas a second predator did not, with this contrast caused by behavioral differences between predators. We also compared aphid strains with stably inherited differences in heat tolerance caused by bacterial endosymbionts and showed the potential for rapid evolution for heat-shock tolerance. Our results illustrate how ecological and evolutionary complexities should be incorporated into predictions of the consequences of environmental change for species' populations.

Species throughout the world face many anthropogenic environmental disturbances (*1*). Some disturbances, such as land-use change, occur progressively and predictably. Others take place as increases in the frequency or magnitude of environmental shocks, such as the anticipated increase in tropical storm severity (*2*). Regardless of the mode of disturbance, changes in species abundance will depend on the multigenerational response of their survival and reproduction within ecosystems. Although the response of species' populations depends on the direct effects of environmental disturbances on species physiology, behavior, and life history (*3*, *4*), three additional complexities may play major roles in the long-term change in species' populations (*5*).

First, the change in a species' population growth rate in response to an environmental disturbance depends on how the species interacts ecologically with other species in the ecosystem (*6*). For example, if a competitively dominant species is sensitive to a disturbance, then a competitively subordinate species may benefit indirectly from the disturbance through competitive release (*7*). Although the role of food web interactions is well-known in theoretical work (*8*) and a growing number of empirical studies document these effects (*9*–*11*), most of this work has not considered how the strength of these interactions might change because of density-dependent effects during the environmental change.

A second complexity is the possibility that species may evolve tolerance to the environmental change (*12*). Empirical studies have now documented a growing list of species that have undergone evolutionary responses to environmental changes (*13*, *14*). If genetic variation exists, then environmental disturbances with large impacts on population growth rates may drive rapid evolution of tolerance.

The third complexity is that ecological and evolutionary complexities might interact (*15*). If ecological interactions modify the response of population growth rates to environmental changes, then they might also modify the selective regime for tolerance and, hence, evolution. In turn, evolution may change population growth rates and interactions among species, thereby increasing the complexities of predicting population changes.

Here, we investigate these three complexities for predicting population changes of pea aphids in response to increasing frequency of episodic heat shocks. To show that ecological interactions can modify population responses to environmental disturbances, we subjected field-caged populations of pea aphids and predators to an experimentally increased frequency of heat shocks (*16*). Our goal was to contrast the effects of two similar ladybeetle predators, investigating how species-specific differences in aphid density–dependent attack rates affect the change in aphid population growth rates when subjected to environmental change. To investigate the potential for evolution, we constructed aphid strains that differed in the presence of stably inherited endosymbionts that affect heat-shock tolerance. We

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deployed these strains in field experiments run at the same time scale as the ecological experiments to measure the rate of evolution of heat-shock tolerance. Finally, we derived a model parameterized exclusively from field data that illustrates how these ecological and evolutionary processes may interact. We selected heat shocks as an environmental disturbance because global climate models predict that short exposures to high temperature will occur with increasing frequency and intensity (*17*).

The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), is an ecologically and evolutionarily well-studied organism. Heat shocks affect pea aphid population growth rates by reducing fecundity or even sterilizing females, with less severe effects on survival and development times (*16*). These effects are similar to those documented for many species; even short periods of high temperatures can denature proteins and cause numerous physiological and developmental problems (*18*). Tolerance to heat shocks in pea aphid strains may be conferred by certain secondary (facultative) bacterial symbionts (*19*, *20*) and is also strongly affected by a common mutation affecting heat-shock genes in the obligate bacterial symbiont *Buchnera* (*21*). Because endosymbionts are invariably transmitted during parthenogenetic reproduction, they are analogous to inherited traits in monoclonal aphid lines (*22*). Secondary symbionts conferring heat tolerance have higher prevalence after periods of summer heat (*19*) and are present in 100% of pea aphids in hot desert sites (*16*), consistent with selection for heat-shock tolerance. The secondary endosymbiont we used occurs naturally at low frequency in populations at our study site; in 2008, 2 out of 57 assayed aphids contained the endosymbiont conferring heat-shock tolerance (*16*). The *Buchnera* allele conferring heat sensitivity occurs variably in field populations; it occurred in 21% of individuals in one sample from our study area (*21*) and, in others, ranged from 66% in 1999 to 0% in 2008. The existence of natural strains varying in tolerance (and our knowledge of the bases of this variation) makes pea aphids a good model system for studying the consequences of environmental changes.

Pea aphids sometimes attain very high population densities and destroy crops of their legume hosts (*23*). However, in south-central Wisconsin, USA, pea aphids in alfalfa rarely reach densities high enough to cause economic crop damage due to a suite of natural enemies, especially two predatory ladybird beetles: *Coccinella septempunctata* L. and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (*24*). Although both predators occur in alfalfa, they have distinctly different behavioral responses to pea aphid abundance (*16*). As a consequence, *C. septempunctata* occurs when few pea aphids are in alfalfa fields and is only slightly more abundant when more aphids are present. In contrast, *H. axyridis* is absent from fields with low aphid abundance but becomes more common quickly as aphid abundance increases (Fig. 1). These differences in predator responses to aphid densities lead to contrasting predictions about how predation will modify pea aphid population growth rates when subjected to heat shocks. Because *C. septempunctata* populations do not rapidly decline with decreasing pea aphid abundance, *C. septempunctata* should continue to exert predation pressure in the presence of the heat shocks that can directly reduce aphid abundance. Conversely, predation pressure from *H. axyridis* rapidly decreases with declining aphid densities, and therefore, its effect on aphid population growth should diminish when aphids face heat-shock disturbances. This would indirectly ameliorate the impact of heat shocks on pea aphids, because the shocked aphid population would suffer less predation.

To test these predictions, we conducted a field experiment using 2- × 2- × 2-m mesh cages and a pea aphid strain sensitive to heat shocks, having a heat-sensitive genotype in the primary symbiont and lacking secondary endosymbionts that provide protection (*16*). We used a 2 × 2 factorial design: with or without supplemented heat shocks and with or without predators. Heat shocks were experimentally imposed by covering cages with clear plastic sheeting for 4 hours at midday three times per week. This increased temperatures by ~5°C, exceeding the threshold at which pea aphid fecundity is affected but remaining within the temperature range naturally observed at the study site. Hence, these manipulations represent increasing frequency of heat shocks rather than increasing magnitude of temperature beyond natural variation.

We performed the experiment twice, once with *C. septempunctata* and once with *H. axyridis* as the predator. In both experiments, heat shocks

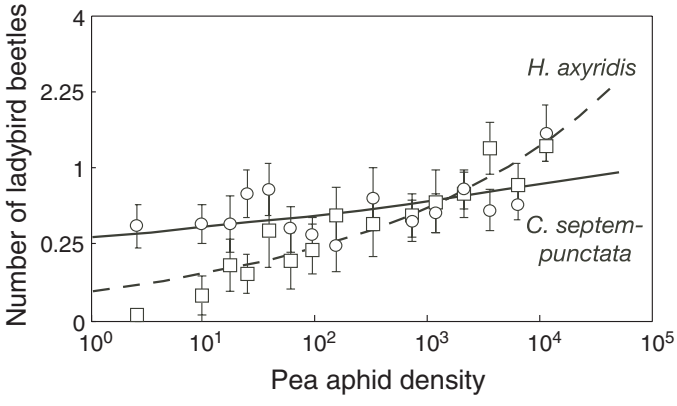

Fig. 1. Relation between pea aphid density in alfalfa fields and the relative densities of adult *C. septempunctata* (circles, solid line) and *H. axyridis* (squares, dashed line) for 2003–2007. For display, we grouped data into 15 aphid density bins having equal numbers of samples. *C. septempunctata* and *H. axyridis* differed strongly in their responses to changing pea aphid density for data from the first and second cycles ($t_{647} = 6.01$, $P < 10^{-6}$) (*16*). Error bars indicate ± 1 SE.

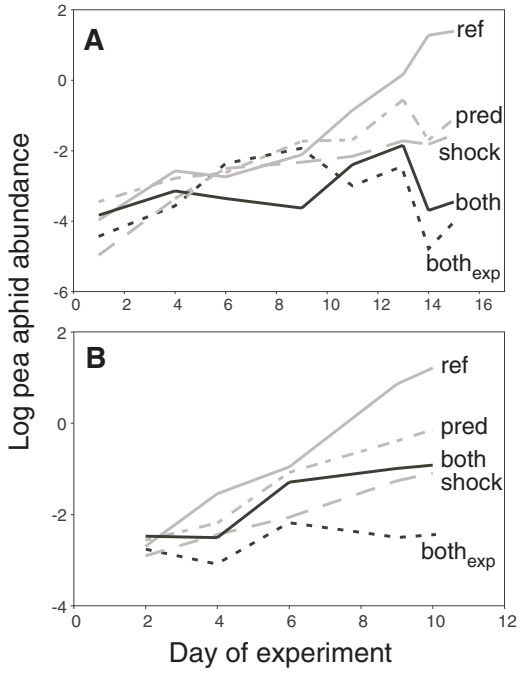

Fig. 2. Interactive effects of heat shocks and predation by (**A**) *C. septempunctata* and (**B**) *H. axyridis* on pea aphid populations in 20 field cages, as revealed by coefficients estimated in a generalized linear mixed model (GLMM) (*16*). The different lines indicate no heat shocks and no predators (solid gray lines, labeled "ref"); heat shocks and no predators (gray lines with long dashes, "shock"); no heat shocks and predators (gray lines with short dashes, "pred"); and heat shocks and predators (solid black lines, "both"). The black dashed line ("$both_{exp}$") gives the expected pea aphid densities if there were no interactions between heat shock and predators. The graphs present the expected values for each treatment day, calculated from the GLMM (*16*). Although for *C. septempunctata* the interaction of heat shock*predators*day was significant ($\chi^2_8 = 76.8$, $P < 10^{-6}$), it was significant only because of the negative interactions on days 6 and 9; confining the statistical analysis to the last 4 days gave no interaction ($\chi^2_4 = 2.4$, $P > 0.5$). For *H. axyridis*, there was a statistically significant positive interaction ($\chi^2_5 = 41.8$, $P < 10^{-6}$).

caused statistically significant reductions in pea aphid abundances, as did the presence of predators. When *C. septempunctata* was the predator, heat shocks caused the same proportional reduction in aphid population growth rates when the predator was absent (Fig. 2A, "ref" versus "shock") or present ("pred" versus "both"); by the end of the experiment, the pea aphid densities that were expected if the effects of heat shock and predation were additive matched the observed densities ("$both_{exp}$" versus "both"). In contrast, when *H. axyridis* was the predator, the effect of heat shock was ameliorated in the presence of predation (Fig. 2B,"$both_{exp}$" versus "both"); at low aphid densities, predation by *H. axyridis* diminished. If the data set for *C. septempunctata* is shortened to the same length as that of the *H. axyridis* data, this contrast is even stronger with a statistically significant interaction for *C. septempunctata* in the opposite direction from *H. axyridis* (*16*). This pattern of predation by *H. axyridis* is consistent with the field observations (Fig. 1); both patterns are probably driven by a suite of correlated behaviors that encourages *H. axyridis* to focus foraging at high aphid densities (*16*). These results show that the impact of heat-shock disturbance on pea aphids depends not just on the presence of predators, but also on the identity of the predator that is present.

To investigate the potential for evolution for heat-shock tolerance, we used four clones that differed in endosymbionts to maximize differences in heat sensitivity. Pea aphids have two genetically based color morphs, green and red, and we took advantage of this color polymorphism to measure the population growth rate of two different clones within the same field cages. We used two different pairs of green and red clones such that in pair A, the green clone was heat-shock tolerant (contained heat-resistant primary endosymbiont plus a protective secondary endosymbiont) and the red clone was susceptible to heat shocks; in pair B, the red clone was tolerant and the green clone was susceptible. These two pairs allowed us to control for potential ecological differences that have been attributed to pea aphid color morph (*25*). We conducted an experiment subjecting either pair A or B to either ambient or increased heat-shock conditions (*16*). For both pairs, the heat-shock sensitive clone had slightly higher population growth rates than did the heat-shock tolerant clone in the absence of experimental heat shocks, but both heat-shock sensitive clones also had greatly reduced population growth rates in the presence of heat shocks. These population growth rates translate into strong selection against heat-sensitive clones in the presence of heat shocks (Table 1).

Table 1. Per capita population growth rates and selection coefficients for heat-sensitive and heat-tolerant pea aphid clones in a field experiment in which the presence of heat shocks was manipulated (*16*). Selection coefficients are placed under the aphid clone selected against for a given pair of aphid clones in a given treatment.

Parameter	Sensitive	Tolerant
	Pair A	
Population growth rate, r (no shock)	0.243 ± 0.009	0.214 ± 0.007
Selection coefficient*	–	0.25
Population growth rate, r (shock)	0.155† ± 0.027	0.234† ± 0.023
Selection coefficient	0.55	–
	Pair B	
Population growth rate, r (no shock)	0.269 ± 0.008	0.247 ± 0.010
Selection coefficient	–	0.20
Population growth rate, r (shock)	0.129† ± 0.033	0.208† ± 0.031
Selection coefficient	0.55	–

*Selection coefficients are calculated as $1 - \exp(-|r_s - r_t|T)$, where r_s and r_t are the population growth rates of heat-sensitive and heat-tolerant clones, and assuming a generation time of $T = 10$ days. †For both pair A and pair B (different combinations of color morphs), the decrease in r of the heat-sensitive clone due to heat shocking was greater than the decrease in r of the heat-tolerant clone; likelihood ratio test, pair A: $\chi^2_1 = 12.1$, $P < 0.001$; pair B, $\chi^2_1 = 6.96$, $P < 0.01$.

To illustrate the possible combined effects of predation and evolution on the long-term response of pea aphid populations to increased exposure to heat shocks, we produced a simplified mathematical model that uses only information derived from our studies. Although not designed to make quantitative predictions, our model nonetheless addresses qualitative expectations about interactions between ecological and evolutionary processes. In the model, there are sensitive and tolerant aphid clones, but initially the pea aphid population is almost entirely composed of heat-sensitive clones. Sensitive and tolerant clones have different population growth rates under ambient and shocked regimes corresponding to the average growth rates of sensitive and tolerant clones under each environmental regime in the evolution experiment (Table 1). We included predation in the model by assuming that predation pressure follows the same function of aphid density as we observed in field surveys of ladybeetle abundance, with *C. septempunctata* showing a smaller reduction in abundance than *H. axyridis* when pea aphid densities are low (Fig. 1). We then assumed that the environmental regime changes from our experimental conditions without heat shocks to those with heat shocks. This led to a direct change in the pea aphid population growth rates and an indirect change in predation pressure.

In the model parameterized for *C. septempunctata* (Fig. 3A), a rapid decrease in the population abundance of pea aphids is followed by a substantial recovery that coincides with the evolutionary increase in tolerance (Fig. 3B). In the absence of evolution, however, the pea aphid population would have declined to extinction because of the combined deleterious effects of the heat shock and *C. septempunctata* (Fig. 3A). In contrast, in the model parameterized for *H. axyridis*, the initial decrease in pea aphid density is more modest, and evolution leads to a recovery of the population to near the level before the change in environmental regimes. The rate of evolution was identical, regardless of the predator modeled (Fig. 3B) because, in the model, the rate of evolution depends on the relative fitness of tolerant versus sensitive phenotypes, not on their absolute fitness. The only way that predation could change the rate of evolution is if predators selectively attacked heat-tolerant or -sensitive

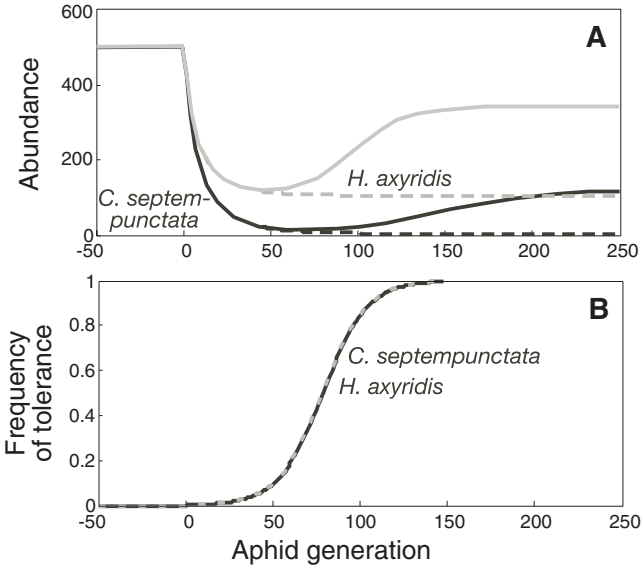

Fig. 3. Model incorporating results from field studies (Fig. 1 and Table 1) on pea aphid responses to heat shock environmental regimes in the presence of different ladybeetle species. (**A**) Pea aphid abundance with *H. axyridis* (gray lines) and *C. septempunctata* (black lines), with (solid lines) and without (dashed lines) evolution. (**B**) The frequency of tolerant phenotype in the population (results for both predators coincide). At generation 0, the environmental regime was changed to include heat shocks, and the tolerant phenotype was introduced at a frequency of 0.002.

aphids when they are mixed within a population; under laboratory conditions, they show no such selectivity (*16*).

Our results highlight three lessons about the consequences of ecological and evolutionary complexities for how environmental change affects species abundances. First, changes in population abundances depend not only on the interactions with other species in a food web, but also on the strengths of these interactions and how the strengths change during environmental disturbances. *C. septempunctata* and *H. axyridis* had different effects on pea aphid abundances because their attack rates showed different relations to aphid abundance. This complexity is a challenge for studies on the effects of environmental change, because the role of species interactions might depend on the species-specific ecologies that affect these interactions (*26*). Whereas studies have considered direct effects of climate change on species interactions—for example, by increasing transmission or attack rates from pathogens and predators (*27*, *28*) or by causing phenological mismatches between plants and pollinators (*5*, *29*)—in our study, the interaction strengths are affected indirectly through changes in species densities.

Second, ecological and evolutionary processes operate on the same time scales. Our field experiments on ecological species interactions and evolution of heat-shock tolerance were conducted at the same time scales (2 to 3 aphid generations), and they showed strong ecological or evolutionary effects. Our experiments add to the growing number of studies documenting rapid evolution and the artificial distinction between ecological and evolutionary time scales (*30*).

Third, ecological and evolutionary processes that modify how species abundances respond to environmental change may not interact (Fig. 3). For pea aphids, the identity of the predator species affects the absolute aphid population growth rate in response to increasing frequency of heat shocks, but it is unlikely to affect the relative growth rate of sensitive and tolerant aphid strains. Thus, even though species interactions themselves may have evolutionary consequences for traits that affect the interactions (*31*), they may have few consequences for traits that affect species tolerances to a different selective pressure. This separation of ecological and evolutionary complexities may simplify predictions of the impacts of environmental changes.

Our study illustrates the ecological and evolutionary complexities of predicting the responses of species to environmental changes. Changes in species' abundances may depend on the specific characteristics of the species with which they interact, and evolution can occur so rapidly that it cannot be ignored, even in the short term. Nonetheless, it is possible to address both ecological and evolutionary complexities simultaneously, and it is necessary to understand both to predict how environmental changes will affect species.

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Sensing Chromosome Bi-Orientation by Spatial Separation of Aurora B Kinase from Kinetochore Substrates

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Successful cell division requires that chromosomes attach to opposite poles of the mitotic spindle (bi-orientation). Aurora B kinase regulates chromosome-spindle attachments by phosphorylating kinetochore substrates that bind microtubules. Centromere tension stabilizes bi-oriented attachments, but how physical forces are translated into signaling at individual centromeres is unknown. Using fluorescence resonance energy transfer–based biosensors to measure localized phosphorylation dynamics in living cells, we found that phosphorylation of an Aurora B substrate at the kinetochore depended on its distance from the kinase at the inner centromere. Furthermore, repositioning Aurora B closer to the kinetochore prevented stabilization of bi-oriented attachments and activated the spindle checkpoint. Thus, centromere tension can be sensed by increased spatial separation of Aurora B from kinetochore substrates, which reduces phosphorylation and stabilizes kinetochore microtubules.

Accurate chromosome segregation during cell division is essential to maintain genome integrity. Before segregation, kinetochores of sister chromatids attach to microtubules from opposite spindle poles (bi-orientation). This configuration is achieved through a trial-and-error process in which correct attachments exert tension across the centromere, which stabilizes kinetochore-microtubule interactions. Incorrect attachments, for example, if both sister chromatids attach to a single spindle pole, exert less tension and are destabilized, providing a new opportunity to bi-orient (*1*, *2*). How tension is coupled to kinetochore-microtubule stability is not known.

The mitotic kinase Aurora B (Ipl1 in budding yeast) localizes to the inner centromere, between sister kinetochores, and destabilizes