

progress at the Parkes, Green Bank, and Arecibo observatories, and it is expected that even more relativistic binary pulsars will be found. With the advent of the Square Kilometer Array, a huge sample of relativistic binaries will be available (13). At the same time, VLBI techniques are rapidly evolving, which will provide an accurate location of these clocks within the Galaxy. A rich array of perfectly clocked shrinking binary systems, exactly located in different zones of the Galaxy, will be available, constituting a powerful gravity probe. As the present uncertainties in the gravitational potential of the

Galaxy would be averaged by such an array, orbital decays and other non-Newtonian effects would be estimated with better accuracy, thus providing an unprecedented test of relativistic gravity. It would then pose challenging questions to those alternative theories of gravity.

References

1. A. T. Deller, M. Bailes, S. J. Tingay, *Science* **323**, 1327 (2009); published online 5 February 2009 (10.1126/science.1167969).
2. LIGO Scientific Collaboration: B. Abbott *et al.*, <http://arxiv.org/abs/0711.3041v1> (2007).
3. A. Giazotto, S. Braccini, in *Proceedings of the 14th SIGRAV Conference on General Relativity and*

Gravitational Physics, Genova, Italy, September 2000, (Springer, Berlin, 2002), pp. 111–119.

4. D. R. Lorimer, *Living Rev. Relativity* **11**, 8 (2008).
5. R. A. Hulse, J. H. Taylor, *Astrophys. J.* **195**, L51 (1975).
6. I. Ciufolini, J. A. Wheeler, *Gravitation and Inertia* (Princeton Univ. Press, Princeton, NJ, 1996).
7. S. Dodelson, M. Liguori, *Phys. Rev. Lett.* **97**, 231301 (2006).
8. T. Damour, G. Esposito-Farese, *Phys. Rev. D* **54**, 1474 (1996).
9. N. Yunes, D. N. Spergel, <http://arxiv.org/abs/0810.5541v1> (2008).
10. M. Burgay *et al.*, *Nature* **426**, 531 (2003).
11. A. G. Lyne *et al.*, *Science* **303**, 1153 (2004).
12. R. P. Breton *et al.*, *Science* **321**, 104 (2008).
13. R. Smits *et al.*, *Astron. Astrophys.* **493**, 1161 (2009).

10.1126/science.1170936

ECOLOGY

Warming Up Food Webs

Jason M. Tylianakis

Human changes to the global environment have long been known to affect organisms, for example by altering their physiology, range, or longevity (1, 2). However, responses vary widely across species, making it difficult to predict how entire ecosystems will respond in the future (3). A key problem is that species do not respond to extrinsic drivers (such as climate) in isolation. Rather, species responses may be determined to a greater or lesser extent by other species with which they interact. On page 1347 of this issue, Harmon *et al.* elucidate one such interaction in a study of pea aphids and two of their ladybird predator species (4).

Early population models showed that interactions among species could weaken or strengthen within-species responses to environmental change (5). More recently, empirical evidence has demonstrated that species interactions can reverse the response of individual grassland species to climate change and subsequently alter their community trajectory (6). At the same time, numerous studies have identified rapid evolutionary responses to climate change (2). For example, evolutionary studies indicate that under strong climate-induced selection pressure, life history traits (such as phenology, longevity, and reproductive rates) may evolve within just a few generations (7).

The question thus arises whether ecological interactions among species can alter their respective evolutionary responses to external

drivers such as climate change. Harmon *et al.* have now met the enormous challenge of addressing this question with an elegant study in which they tested the ecological and evolutionary responses of an insect herbivore to the combined effects of climate change and food web interactions.

Their study system involved the pea aphid, an important pest species, which has populations that differ in their susceptibility to short periods of high temperature (heat shocks), in part because of differences in internal microorganisms that are passed on from parents to offspring and confer heat tolerance. Harmon *et al.* introduced these symbiotic microorganisms to different aphid populations to simulate a mutation event conferring heat tolerance to the aphid line. Aphids are attacked by many natural enemies, including two species of ladybirds that differ in their foraging behavior (see the figure). Harmon *et al.* used field experiments to test the ecological and evolutionary responses of aphids to increased frequency of heat shocks, and to contrast the effects of the two predators on population growth rates after these shocks.

The authors found that behavioral differences between the predator species affected the prey population response: One predator reduced its attack rates at low prey densities after heat shocks, such that it did not compound the negative effect of heat on aphid pop-

How do predator-prey interactions influence ecosystem responses to climate change?



Interactive effects. Harmon *et al.* show that predation rates of aphids by ladybirds depend on the response of the predator species to altered aphid density following heat shocks.

ulation growth. In contrast, the other predator kept attacking aphids at the same rate, increasing aphid mortality beyond the rates caused by the heat shocks. Aphids did evolve tolerance to heat shocks (that is, tolerant strains increased in frequency), but in a model based on field data, predator-prey interactions, despite their effects on aphid population growth, did not affect the evolution of heat shock tolerance.

Future research is needed across species to determine whether rapid evolutionary responses to food web interactions and external drivers are generally additive in this way, such that the selection effects of predation operate independently of climate change and vice versa. If in other cases these forces have interactive effects—for example, if traits conferring resistance to one threat (such as climate change) are negatively correlated

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with traits providing protection from another (such as predation)—then an evolutionary stalemate could prevent adaptation at the rate necessary for species to cope with predicted climatic changes.

In the study by Harmon *et al.*, predator density dependence plays a key role in determining the effects of climate change on the growth of the prey population. This raises a complex issue for ecologists, because environmental disturbances strongly affect prey density. Quantitative food webs depict links between species as having a certain strength (the frequency of the interaction is often used as a surrogate), yet the interaction strength may be a nonlinear function of prey density. Altered interaction frequencies in food webs after environmental perturbations (8) could be driven by relative shifts in the abundance of different species and/or by nonlinear responses of different predators to altered prey densities. Environmental

changes could even alter the response of predators to prey density—for example, if habitat simplification alters search efficiency (9). Metrics of food web structure that are advocated for their insensitivity to differing relative abundances of prey species (10) may not detect these ecologically important changes.

When Earth undergoes climatic change, species either adapt or go extinct (11). However, during each period of change, the spatial rearrangement of extant species and the emergence of new lineages will provide a novel context within which evolution takes place. Thus, even if the genetic variation necessary for selection exists in a population, food web interactions may impose constraints on the rate or direction of evolutionary change. The work of Harmon *et al.* suggests that the difficulties inherent in studying the combined complexities of ecological and evolutionary forces can be overcome. This will be neces-

sary if we are to predict the survival of species in an uncertain future.

References and Notes

1. G. R. Walther *et al.*, *Nature* **416**, 389 (2002).
2. C. Parmesan, *Annu. Rev. Ecol. Evol. Syst.* **37**, 637 (2006).
3. J. M. Tylianakis, R. K. Didham, J. Bascompte, D. A. Wardle, *Ecol. Lett.* **11**, 1351 (2008).
4. J. P. Harmon, N. A. Moran, A. R. Ives, *Science* **323**, 1347 (2009).
5. A. R. Ives, *Ecology* **76**, 926 (1995).
6. K. B. Suttle, M. A. Thomsen, M. E. Power, *Science* **315**, 640 (2007).
7. S. J. Franks, S. Sim, A. E. Weis, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 1278 (2007).
8. J. M. Tylianakis, T. Tscharntke, O. T. Lewis, *Nature* **445**, 202 (2007).
9. R. K. Didham, J. M. Tylianakis, N. J. Gemmill, T. A. Rand, R. M. Ewers, *Trends Ecol. Evol.* **22**, 489 (2007).
10. N. Blüthgen, J. Fründ, D. P. Vazquez, F. Menzel, *Ecology* **89**, 3387 (2008).
11. R. Jansson, M. Dynesius, *Annu. Rev. Ecol. Syst.* **33**, 741 (2002).
12. Supported by Marsden Fund of New Zealand grant UOC-0705. This manuscript benefited from comments by R. K. Didham, T. A. Rand, and T. E. Steeves.

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PLANT SCIENCE

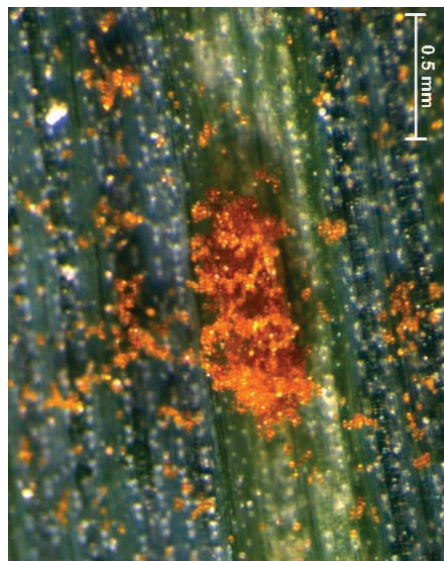
Anti-Rust Antitrust

Daniel J. Kliebenstein and Heather C. Rowe

Human civilization rests upon the products of agriculture, but numerous fungi, bacteria, and viruses compete with us for the crops that we cultivate. Given the growing human population and demand for increased food production from less land, minimizing crop loss from pathogen infection is critical. Two reports in this issue, by Fu *et al.* on page 1357 (1) and by Krattinger *et al.* on page 1360 (2), identify molecular mechanisms that control durable, broad-spectrum, disease resistance in wheat, the second-most-produced cereal crop in the world.

Understanding the molecular basis of specific plant resistances has enabled the development of crop varieties that resist common diseases. These resistance mechanisms follow a “gene-for-gene” model, whereby specific plant recognition of a pathogen gene product yields near-absolute resistance to pathogens containing the recognized gene. However, this form of resistance is vulnerable to rapid counter-evolution by the pathogen (3). This generates a continuous and resource-intensive cycle of plant resistance gene discovery, crop breeding, and eventual resistance gene

“defeat” by the pathogen, which has driven interest in identifying durable forms of resistance to pathogens. In most plant-pathogen systems, durable resistance has been identified through quantitative trait locus (QTL) mapping. Although identified QTL provide quantitative resistance to a range of pathogen



Wheat rust. Close-up of a wheat leaf rust pustule releasing orange urediospores (orange spots) on a leaf of the susceptible spring wheat cultivar Thatcher.

The identification of genes that confer durable, multipathogen resistance may help breeders overcome devastating wheat fungal diseases.

species and genotypes therein, the molecular bases of these broad quantitative resistances have remained largely unknown (4).

Krattinger, Fu, and their colleagues begin to show that mechanisms underlying quantitative resistance are not simply weak alleles of genes involved in specific gene-for-gene resistance, as has been proposed. Rather, each plant species may contain multiple, possibly independent, mechanisms of quantitative resistance. The latter may reveal similar processes in other plants or may be taxonomically limited.

Krattinger *et al.* describe the cloning of the wheat *Lr34* QTL that has been used to confer resistance to multiple rusts (see the figure) and a mildew in the field for nearly 50 years (5). The locus harbors the gene *Lr34*, which encodes an ATP-binding cassette (ABC) transporter (4). ABC transporters, or pleiotropic drug resistance transporters, move diverse chemical compounds, including plant natural products, across membranes. The *Lr34* transporter is weakly homologous to *PEN3*, an ABC transporter from the plant *Arabidopsis thaliana*, which facilitates resistance to the same mildew via the targeted export of plant metabolites (6, 7). The mechanistic similarity between *Lr34* and *PEN3* reinvigorates hypotheses that specific and