

# The ecological play of predator–prey dynamics in an evolutionary theatre

Marc T.J. Johnson and Anurag A. Agrawal

Department of Botany, 25 Willcocks St, University of Toronto, Toronto, ON, Canada M5S 3B2

**Although over 40 years of theory have addressed how evolutionary processes can affect the ecology of predator–prey interactions, few empirical data have addressed the same issue. Shertzer *et al.* and Yoshida *et al.* have recently combined manipulative experiments with mathematical models to demonstrate that evolutionary change in an algal prey strongly affects community dynamics with their rotifer predator. These studies contribute to recent developments in community genetics and the diversity–stability debate.**

Population fluctuations in space and time are common in nature and are important throughout the field of biology, from human health to conservation. In studying population dynamics, much research has addressed how predator–prey interactions affect population stability. Ecologists typically treat predator and prey populations as homogeneous sets of individuals, rather than genetically diverse populations that are capable of evolution. Predator and prey do frequently coevolve, however, because they respond to reciprocal biotic selection [1]. Some 70 years ago, E.B. Ford was perhaps the first to document that evolutionary change and population fluctuations can occur concurrently and interdependently [2]. The first models to depict how evolution in the predator and/or prey could affect predator–prey population dynamics followed 30 years later [3,4] and, in the past decade, there has been an explosion of interest and development of this theory [5], including the prediction that evolution in prey populations could drive out-of-phase predator–prey cycles [6]. Shertzer *et al.* [7] and Yoshida *et al.* [8] have now combined mathematical theory with experimental results to provide the strongest support yet that evolution within a predator–prey community can shape population dynamics.

This story began with the observation that an alga (*Chlorella*) and a rotifer (*Brachionus*), which eats the alga, exhibit predator–prey cycles [9,10]. Fussmann *et al.* [11] modeled the predator–prey dynamics of *C. vulgaris* and its predator *B. calyciflorus* in a chemostat, and predicted one of several outcomes: (i) predator–prey equilibrium; (ii) stable limit cycles; or (iii) extinction of the predator or both the predator and the prey. The outcome depended on the input concentration of the algal-limiting nutrient (nitrogen), and the rate at which the medium was delivered and removed (the dilution rate). Experiments corroborated the patterns and mechanisms predicted from the model, but the model poorly described quantitative aspects of the predator–prey cycles. The predator–prey cycles were longer than the predictions of the model and exactly out of phase (i.e. prey

maxima coincided with predator minima, and vice versa) as opposed to predator maxima being one-quarter of a cycle behind the prey minima, as suggested by the model.

To explore the mechanistic basis of the predator–prey cycles, Shertzer *et al.* [7] compared mathematical models, which represented different ecological and evolutionary hypotheses, with experimental data. These hypotheses examined the effect of predator and prey quality and quantity on cycles, whereas the previous model by Fussmann *et al.* [11] only considered prey quantity. The new models from Shertzer *et al.* showed that the cycle period and phase relationships between *Chlorella* and *Brachionus* could be explained by rapid evolution of prey resistance to the predator.

Most recently, Yoshida *et al.* demonstrated heritable variation for antipredator resistance in *Chlorella* using selection lines (*Chlorella* were grown in the presence or absence of *Brachionus*), and validated the model assumption of a tradeoff between resistance to *Brachionus* and competitive ability in the absence of the predator. Previous models [7,11] were refined by explicitly defining genetic structure as different clones, which continuously varied in food quality and competitive ability. Simulations with diverse algal populations (i.e. two or more clones) typically exhibited long predator–prey cycles that were perfectly out of phase, as previously observed [7,11]. Simulated populations with a single clone exhibited short cycles with predators being one-quarter out of phase with prey populations. Yoshida and colleagues tested these refined model predictions by manipulating chemostat communities to have either a single clone in the prey population or a mixture of clones. Experimental results were strikingly congruent with predictions of both cycle period and phase for simple and diverse communities.

An important question remains: how is genetic variation maintained in prey populations? Strong and rapid selection can erode genetic diversity, but model simulations by Yoshida *et al.* typically resulted in the maintenance of two–three algal genotypes [8]. Predation and the competition–resistance tradeoff are probably responsible for the maintenance of this variation. Predator density increases when there is an abundance of predator-susceptible algae; as rotifer density increases, they drive the abundance of susceptible algae down, favouring the proliferation of resistant algae. Eventually, predators decrease in abundance because of a lack of high-quality food, enabling the cycle to repeat itself once susceptible algae multiply and outcompete the resistant algae.

Corresponding author: Marc T.J. Johnson (johnson@botany.utoronto.ca).

### Experimental support for past theory

A previous synthesis of theory about how evolution can affect population cycles has led to several general predictions [5], which are supported by the *Brachionus–Chlorella* system. First, evolution of either the predator or prey is most likely to affect predator–prey dynamics when natural selection results in rapid evolution. This condition is clearly met in *Brachionus–Chlorella* chemostat communities, and adds to an increasing list of examples of rapid evolution [12]. Second, predator–prey dynamics are more likely to be affected by rapid evolution of the prey, as opposed to evolution of the predator population. Yoshida *et al.* [8] provide support for the ecological effects of prey evolution, although the effect of predator evolution on the ecology of this community is still unclear (but see [13]). We know of no studies testing the ecological effects of rapid evolution in predator populations, although rapid evolution in herbivores, seed predators and parasites have been documented [12]. Third, the presence of out-of-phase stable-limit cycles between *Brachionus* and *Chlorella* support earlier theoretical predictions about the influence of the evolution of prey resistance on predator–prey dynamics [6]. Finally, Abrams [5] reported that evolution in either the predator or prey could stabilize or destabilize the ecological interaction, depending on the type of model and the assumptions made about the biology of the predator and prey. As we discuss below, the mathematical models and chemostat communities presented by Yoshida *et al.* [8] suggest that evolution in the algal population does increase stability in predator–prey dynamics under some conditions.

### Community genetics and the diversity–stability relationship

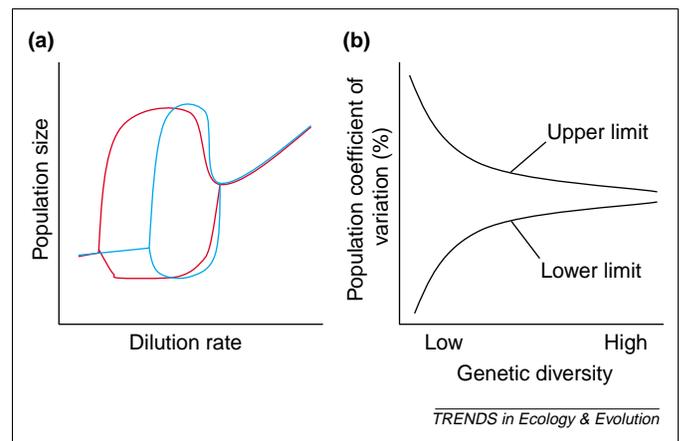
The results of Shertzer *et al.* and Yoshida *et al.* emphasize the importance of studying species interactions within a community genetics framework. Community genetics is the study of intraspecific genetic variation and its ecological and evolutionary consequences within communities [14]. An increasing number of studies have taken such an approach to understand species interactions. For example, Whitham and colleagues studied the macroecological significance of evolutionary processes [15]. In particular, they showed that genetic variation in plants can affect diverse communities of insect herbivores, nesting birds and fungi [16,17]. A community genetics framework has also been applied to studying the evolutionary consequences of ecological processes in simple communities. These studies found that population dynamics and trophic interactions can affect the rate of resistance evolution in pests to genetically engineered crops [18]. The *Chlorella–Brachionus* studies add to our understanding of community genetics by demonstrating that rapid evolution can have predictable ecological consequences.

The genetic structure of a community might not only affect population and evolutionary processes, but also fundamental relationships in community ecology. For example, the results presented by Yoshida *et al.* could have implications for the diversity–stability concept, which has focused on the ecological- and ecosystem-level consequences of interspecific diversity [19,20]. We see a link between Yoshida *et al.*'s results and the traditional diversity concept,

in that increased intraspecific diversity can increase community stability. Two lines of evidence support our proposed intraspecific diversity–stability hypothesis. First, communities with diverse prey populations exhibit equilibria over a greater range of conditions than do communities with a single prey clone. Also, when predator–prey cycles occur, populations are more likely to exhibit extreme values in communities where prey populations have low diversity.

Yoshida *et al.* report that predators and prey exhibit stable equilibria at low and high dilution rates [8], but, as seen in their supplementary figure, the range at which communities with a single prey clone exist at equilibrium is narrower than that of diverse communities. These findings suggest that genetically diverse prey that are capable of rapid evolution will exhibit stable equilibria with their predators over a greater range of conditions than communities with less diverse prey populations. We illustrate this idea by modifying the original bifurcation diagram from Fussmann *et al.* [10] with the data from Yoshida *et al.* [8] (Figure 1a) to show that diverse populations were at equilibrium over a greater range of dilution rates than were genetically uniform populations. Thus, we predict that predators and their prey will exhibit stable equilibria over a greater range of conditions when the prey population is genetically diverse.

When predator and prey do cycle, they are more likely to exhibit large amplitude cycles when the genetic diversity of the prey is low. Using both models and experiments, Yoshida *et al.* [8] consistently found that predators and prey exhibited moderate amplitude cycles when prey populations were genetically diverse. Conversely, genetically uniform prey populations exhibited greater variation in population dynamics. Model simulations showed that, by varying the resistance phenotype of the prey, stable



**Figure 1.** Genetic diversity and community stability (a) and population variation (b). (a) Bifurcation diagrams for prey populations with high (blue line) and low (red line) genetic diversity in a one-prey one-predator community. Stable equilibrium occurs in the high or low diversity populations where there is only a single line for a given dilution rate, whereas predator and prey cycle in the region where lines are separated. Where lines are separated, the maximum and minimum abundance of a population during cycles are indicated by the upper and lower lines, respectively. Predator bifurcation diagrams are excluded for simplicity. (b) Genetic diversity and population variation. The predicted effect of intraspecific genetic diversity in the prey on the variation in either the population of the prey or predator. The lines show the upper and lower limits for the coefficient of variation as would be measured from replicate communities. Large variation would be observed at low genetic diversity where differences in algal resistance would have a strong effect on the amplitude of populations cycles (L.E. Jones and S. Ellner, pers. commun.), leading to greater variation between replicate communities.

equilibrium, small amplitude cycles, or large amplitude cycles that closely approach zero were all possible outcomes for a predator–prey community in a chemostat (L.E. Jones *et al.*, unpublished). Using this result, we predict that the variance of a population in simple communities will itself become smaller as genetic diversity in the prey increases (i.e. the variance of the coefficient of variation will decrease) (Figure 1b). For this reason, communities with low prey genetic diversity will exhibit extreme cycles more frequently than will communities with high prey genetic diversity.

### Future directions

Recent theoretical and empirical research on the biology of predator–prey interactions shows the clear benefit of combining ecology and evolution under the single umbrella of community genetics [14,21]. Within this emerging field, the time is ripe to test questions extending on the work of Yoshida and colleagues. Does coevolution occur on the same time scale as predator–prey cycles, where cycles and evolution in the prey are accompanied by rapid evolution in the offensive traits of the predator [22]? Can the addition of species in the simple two-species community lead to diffuse coevolution [23]? Does increased intraspecific diversity beget ecological stability in ways that are similar to interspecific diversity? Such questions can be challenging to test in natural communities, although their importance is clear. Shertzer *et al.* [7] and Yoshida *et al.* [8] have taken a leap forward in our understanding of the ecological consequences of evolutionary processes.

### Acknowledgements

We are grateful for comments and suggestions from P. Abrams, C. Brassil, S. Ellner, W. Godsoe, N. Hairston Jr, L. Jones, K. Shertzer, A. Sih, D. Viswanathan, T. Whitham and T. Yoshida. Our research (<http://www.herbivory.com>) is funded by grants from the Natural Sciences and Engineering Research Council of Canada to M.T.J.J. and A.A.A., and a Sigma Xi GIAR to M.T.J.J.

### References

- Ehrlich, P.R. and Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution* 18, 586–608
- Ford, E.B. (1949) *Mendelism and Evolution*, Methuen and Co
- Pimentel, D. (1961) Animal population regulation by the genetic feedback mechanism. *Am. Nat.* 95, 65–79
- Rosenzweig, M.L. and MacArthur, R.H. (1963) Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.* 97, 209–223
- Abrams, P.A. (2000) The evolution of predator–prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* 31, 79–105
- Abrams, P.A. and Matsuda, H. (1997) Prey adaptation as a cause of predator–prey cycles. *Evolution* 51, 1742–1750
- Shertzer, K.W. *et al.* (2002) Predator–prey cycles in an aquatic microcosm: testing hypotheses of mechanism. *J. Anim. Ecol.* 71, 802–815
- Yoshida, T. *et al.* (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424, 303–306
- Borass, M.E. (1983) Population dynamics of food-limited rotifers in two-stage chemostat culture. *Limnol. Oceanogr.* 28, 548–563
- Halbach, U. (1970) Influence of temperature on the population dynamics of the rotifer *Brachionus calyciflorus*. *Oecologia* 12, 176–205
- Fussmann, G.F. *et al.* (2000) Crossing the Hopf bifurcation in a live predator–prey system. *Science* 290, 1358–1360
- Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13, 329–332
- Fussmann, G.F. *et al.* (2003) Evolution as a critical component of plankton dynamics. *Proc. R. Soc. Lond. Ser. B* 270, 1015–1022
- Antonovics, J. (1992) Toward community genetics. In *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics* (Fritz, R.S. and Simms, E.L., eds), pp. 426–449, University of Chicago Press
- Whitham, T.G. *et al.* (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84, 559–573
- Whitham, T.G. *et al.* (1999) Plant hybrid zones affect biodiversity: tools for a genetic based understanding of community structure. *Ecology* 80, 416–428
- Dungey, H.S. *et al.* (2000) Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution* 54, 1938–1946
- Neuhauser, C. *et al.* (2003) Community genetics: expanding the synthesis of ecology and genetics. *Ecology* 84, 545–558
- Loreau, M. *et al.* (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804–808
- Elton, C.S. (1958) *The Ecology of Invasions*, Methuen and Co
- Agrawal, A. (2003) Community genetics: new insights into community ecology by integrating population genetics. *Ecology* 84, 543–544
- Karban, R. and Agrawal, A.A. (2002) Herbivore offense. *Annu. Rev. Ecol. Syst.* 33, 641–664
- Janzen, D.H. (1980) When is it coevolution? *Evolution* 34, 611–612

0169-5347/\$ - see front matter © 2003 Elsevier Ltd. All rights reserved.  
doi:10.1016/j.tree.2003.09.001

## Climate–vegetation dynamics in the fast lane

### Eric Post

Department of Biology, The Pennsylvania State University, 208 Mueller Lab, University Park, PA 16802 USA

**Evidence from paleoclimatological research indicates that major climatic changes, such as the rapid increase in temperatures at the end of the Younger Dryas event ~ 11 000 years ago, can occur over the span of a few decades. Vegetation response to climatic variation and change, is, by contrast, often assumed to occur gradually over much longer timescales. Two recent papers confirm earlier, theoretical predictions that changes in species**

**composition of plant communities following climatic shifts can, however, occur with striking rapidity.**

The predominance of large mammalian grazers at high latitudes during the Pleistocene hints at a vegetation composition that is very different from the chemically defended trees and shrubs that are characteristic of the Arctic and sub-Arctic today [1]. Although the demise in the far north of horses, camels, woolly rhinos, steppe bison and woolly mammoths has been ascribed to many factors, including human exploitation, disease, interspecific

Corresponding author: Eric Post (esp10@psu.edu).