

## Biogeographical Perspectives on Arms Races

Michael E. Hochberg and Robert D. Holt

### 14.1 Introduction

Natural enemies include parasites, pathogens, parasitoids, and predators (in the order of how we generally perceive their increasing impact on the survival of their individual victims). It has been increasingly recognized since the 1970s that the ecological dynamics of natural enemies and their victims can be diverse (Begon *et al.* 1996), and that understanding such dynamics has important implications for applied disciplines such as pest control (Chapter 32) and conservation biology (Dobson and McCallum 1997; Clarke *et al.* 1998; Hochberg 2000).

It is undeniably the case that natural enemies can be geographically widespread, yet most individuals spend their lives within the limited range of environments suitable for their species. Environmental differences over the geographical range of a natural enemy could, in turn, lead to spatial variation in population and adaptive dynamics. Large-scale environmental variation manifests itself in at least three ways.

First, all species have geographical boundaries, either abiotic barriers such as mountains or lakes, or biotic variables such as the abundance and quality of food, and the presence of competitors or predators (Brown *et al.* 1996; Holt *et al.* 1997). For many (but by no means all) species, geographical boundaries approximate those experienced by their resources. However, a more functional view of geographical boundaries of a species would include all of those habitats in which natural selection operates (Holt 1996). Such habitats could include vectors (for some parasites and pathogens), breeding grounds (for migrating predators), and nectar sources (for some species of parasitoid wasp).

Second, all species exhibit variations in community structure (Cornell and Lawton 1992). This notion combines:

- Spatial variation in the degree to which an enemy exploits each of its potential victim species;
- Spatial changes in community composition;
- Spatial variation in the types and strengths of indirect interactions between the natural enemy and other community members.

Such variation in community structure can lead to spatial variation in the population dynamic role of a specialized natural enemy on itself and other interacting species within the communities (Hochberg 1996).

Third, natural enemies and the interacting members of their communities exhibit spatial variation in the genetic structure of their populations. Such structure integrates gene flow, mutation, recombination, selection, and drift. Adaptation of natural enemies to their victims and vice versa may be rapid, especially if population sizes are large and generation times short. Given pronounced geographical differentiation in environmental factors, two-species interactions may vary considerably (and, as argued below, predictably) over geographical ranges. Despite an increasing appreciation of the spatial dynamics of natural enemies (e.g., Hassell *et al.* 1991; 1994), their importance in determining ecological and evolutionary patterns over geographical spatial scales has, thus far, received little attention (Hochberg and Van Baalen 1998).

In this chapter, we focus on a nearly neglected facet of natural enemy population biology: biogeography. As with single-species perspectives, examining multiple-species interactions should lend itself to biogeographical interpretations. MacArthur and Wilson's (1967) theory of island biogeography dealt with geographical patterns in species diversity fueled by chance historical events (colonization and extinction) and local adaptation. Much of their theory was inspired by terrestrial animals, especially birds and insects. Their basic ideas surely apply to the world of natural enemies, albeit with modifications because of the (often astonishing) array of local habitats available for persistence and evolution. Just how natural selection in local habitats interacts with migration over larger spatio-environmental scales should be, in our view, a major focus of research in the future (Thompson 1994).

Our aim is to elucidate how the impact of natural enemies on their victims could vary over geographical ranges. Causes for such variation may include:

- Ecology [i.e., no evolution occurs, but because of ecological factors (see Section 14.2) the impact varies among localities];
- Adaptive reasons independent of the species interaction (i.e., parameters that affect impact may evolve as a correlated response to other selected factors);
- Adaptive reasons arising from the interaction, but not reciprocally (i.e., selection is not tightly coupled between natural enemy and victim);
- Reasons of reciprocal evolution or coevolution [i.e., the interaction is sufficiently coupled such that selection and counter-responses to selection dominate evolution in both species (Thompson 1994)].

This chapter is divided into three sections. First, we briefly discuss why a biogeographical perspective may be necessary to understand natural enemy impacts. Second, a simple model of a predator-prey interaction is presented and its behavior discussed. Finally, we speculate on how our model framework may be of use in understanding applied issues such as biological control and population conservation.

## 14.2 Importance of Species and Space in Population Dynamics

Little is known about the extent to which spatiotemporal dynamics are dominated by the dynamic entities themselves and/or by underlying variation in the abiotic

environmental template over which they play out their dynamics. Most models consider the dynamic entities in isolation, and are often referred to as “self-structuring” models (e.g., de Roos *et al.* 1991; Hassell *et al.* 1991, 1994; Rand *et al.* 1995). The presence of spatial time lags in population densities (or allelic frequencies) is a key aspect in the structure of these systems. In many respects, these models dominate the way we view the role of space in ecological systems (Tilman and Kareiva 1997).

Relatively few models include both species interactions and spatial variation in the environment extraneous to the interaction. These are “landscape-dynamic” models, and they have been increasingly applied in problems of population ecology (e.g., Oksanen *et al.* 1981; Holt 1984, 1985; McLaughlin and Roughgarden 1992; Leibold 1996; Clarke *et al.* 1997) and adaptive evolution (e.g., García-Ramos and Kirkpatrick 1997; Hochberg and Van Baalen 1998). Given that the self-structuring approach is a potential component of the landscape-dynamic approach, it will be an important challenge in the future to learn the conditions under which environmental templates are necessary to explain spatial variation in nature, or whether we can often rely on self-assembly rules. Our approach below includes both species interactions and landscape effects.

### 14.3 (Co)Evolution of Impact by Natural Enemies

A simple way to interpret how species demography may drive geographical variation in natural enemy impact is to make ecological parameters functions of spatial position  $x$ . Given that selection acts differently in different parts of a species' range, individual movement among sites can influence the realized spatial pattern of adaptation: even if dispersing individuals are maladapted to novel environments, once present, they may reproduce (producing more or less adapted offspring) and compete with residents (reducing the fitness of resident genotypes). Understanding how gene flow and selection combine to influence geographical patterns of variation is a major issue in the study of microevolution. Much of the relevant literature has concentrated on genetic dynamics alone (e.g., for host-parasite systems, see May and Anderson 1983a; Seger 1992). However, it is increasingly apparent that to analyze adaptive dynamics and population dynamics simultaneously can be useful, because different population dynamic scenarios can entail different conclusions about the importance of gene flow as a constraint on local adaptation (Holt and Gomulkiewicz 1997).

Several indices are relevant to how a natural enemy affects its victim; these include population density of the victim, both with and without the natural enemy (Beddington *et al.* 1975), selective impact of the enemy on the victim (e.g., Abrams and Matsuda 1997), and attack rate (e.g., Hochberg 1991). We focus on what we call “impact,” which in the model given below is the per capita attack rate of enemies on their victims. Since we consider only nonpolymorphic, coevolutionarily stable strategies, impact translates readily into the notion of risk of attack (i.e., fraction of victims killed over a particular span of time).

## Model assumptions and structure

The model is based on a recent study of predator–prey dynamics (for details, see Hochberg and Van Baalen 1998). It can apply to predators as well as to pathogens and parasitoids that kill their host rapidly after infection/attack.

A number of simplifying assumptions are made at the outset. With respect to genetics, we assume clonal variation. With respect to basic ecology, we assume that the victim exhibits continuous generations. Further, we assume random encounters between the two species. The two species interact over a network of patches. Species flows among patches (and mutation) are assumed to be sufficient to maintain all genetic variants in all patches, but insufficient to have density effects on dynamics (but see Discussion). Therefore, we do not consider in detail colonization–extinction dynamics or “swamping” effects of migration.

Let  $N$  and  $P$  be the densities of prey and predators, respectively. Within any given patch, the interaction is described by

$$\frac{dN_j}{dt} = (b_N - d_{N_j})N_j - \kappa N_j \sum_j N_j - N_j \sum_k \beta_{j,k} P_k. \quad (14.1a)$$

$$\frac{dP_k}{dt} = \phi P_k \sum_j \beta_{j,k} N_j - d_{P_k} P_k, \quad (14.1b)$$

where the indices  $j$  and  $k$  refer to genetically different clones. Any of the parameters  $b_N$ ,  $d_N$ ,  $\phi$ ,  $\beta$ ,  $\kappa$ , or  $d_P$  could be patch-specific. The prey is limited by two forms of density dependence: logistic-type limitation (the  $\kappa N$  term), resulting in a standing crop of  $(b_N - d_N)/\kappa$  prey; and predator-driven limitation at a per capita rate of  $\beta P$ , with the production of  $\phi$  predator offspring per prey consumed. We call  $\beta P$  the impact  $\lambda$  of the predator. In studies on host–parasite associations this is often called the “force of infection.”

We assume that the capacities of predator attack and prey defense each incur costs according to a quantitative genetic model for the respective species [see Hochberg and Van Baalen (1998) for details], such that the predation constant between strains  $k$  of the parasite and  $j$  of the victim is

$$\beta_{j,k} = \beta_0 + \beta_1(k - j). \quad (14.2)$$

Impact  $\lambda$  on victim strain  $j$  is therefore

$$\lambda = [\beta_0 + \beta_1(k - j)]P_k, \quad (14.3)$$

where  $\beta_0$  and  $\beta_1$  are constants. Thus, impact has components influenced by a combination of environment ( $\beta_0$ ,  $\beta_1$ ), evolution ( $k$ ,  $j$ ), and ecology ( $P$ ).

The costs of the interaction are deducted from the natural survival rates of each species. Such costs could include reductions in life span because of increased mortality by generalist natural enemies, or reductions in reproductive rate through a shifting of resource allocation from reproduction to the interspecific interaction modeled here.

The natural mortality rate of a predator expressing level  $k$  attack is

$$d_{Pj} = d_{P0} + d_{P1}k^{c_P}, \quad (14.4a)$$

whereas the mortality rate of a prey expressing level  $j$  defense is

$$d_{Nj} = d_{N0} + d_{N1}j^{c_N}. \quad (14.4b)$$

The quantities  $d_{P0}$ ,  $d_{P1}$ ,  $d_{N0}$ , and  $d_{N1}$  are constants; the mortality rate for the most efficient predator strain is  $d_{P0} + d_{P1}$ , and for the most defensive prey strain it is  $d_{N0} + d_{N1}$ . The constants  $c_P$  and  $c_N$  reflect nonlinearities in trade-offs involving impact (Frank 1994a). If  $c > 1$  ( $c < 1$ ), then costs increase at a greater than (less than) linear rate with marginal increases in character state  $j$  or  $k$ .

### Geographically labile parameters

Numerous biological characters of a species are likely to vary over geographical ranges for many reasons peripheral to the predator-prey interaction. Environmental suitability for the prey is the propensity of the prey population to grow, and is measured by parameters such as  $b_N$ ,  $d_N$ , and  $\kappa$ . Suitability may also influence impact-related parameters (i.e.,  $\beta_0$  and  $\beta_1$ ).

Below, we briefly discuss how, in predator-prey systems, local environments influence the dynamic impact of enemies on their victims. Three classes of factors are likely to vary over the prey's geographical range: the prey's net rate of reproduction  $r = b_N - d_N$ , the intensity of density-dependence acting on the prey  $\kappa$ , and predator attack  $\beta$ :

- Spatial variation in the net rate of increase,  $r$ , is fundamental to defining range limits (Holt and Kiett 2000) and spatial variation in abundance (Holt *et al.* 1997). Low values of  $b_N$  could result from unfavorable abiotic conditions or low quantity and quality of the prey's own resources (e.g., for a herbivore, its preferred plants may be rarer or of low nutritional quality). Higher values of  $d_N$  may also reflect scarce, low-quality resources, or the greater impact of other (e.g., generalist) natural enemies near the edges of the prey's distribution.
- Variation in the intensity of prey density-dependence  $\kappa$  could result from variation in the impact of, for example, (1) other natural enemies, (2) intraspecific interference, and/or (3) levels of resources in the system. Areas with low prey densities could arise from higher impacts of natural enemies, competitors, or lower resource levels. Were  $\kappa$  to be decomposed into a different component for each of these factors, then certain components might increase from the center to the periphery of the prey's distribution (e.g., effects of lack of resources), whereas others decrease (e.g., effects of generalist natural enemies). We equate high  $\kappa$  with habitat marginality for the prey.
- With regard to the negative effects that the predator has on its prey,  $\beta$ , it is reasonable to expect that as the prey's environment becomes less favorable, successful attacks are more frequent (i.e., higher  $\beta$ ), although it could equally be argued that the conditions for predator attack decrease even more rapidly than those for prey defense (meaning lower  $\beta$ ).

## Population ecological results

In the case where neither species evolves (i.e.,  $j = k$  fixed at 1) it can be shown that the equilibrium impact

$$\lambda^* = r - \kappa d_P / \phi \beta, \quad (14.5)$$

which means that independent of evolution, impact varies over geographical ranges purely through population–environment interactions. Since habitat suitability is positively correlated with  $r$  and negatively correlated with  $\kappa$  and  $\beta$ , impact should decrease with decreases in habitat suitability, but only if components of suitability extrinsic to the interaction (i.e.,  $r$  and  $\kappa$ ) change more over the geographical range of the victim than does vulnerability to the natural enemy  $\beta$ .

## Coevolutionary results

Now we consider what happens when both species evolve. Hochberg and Van Baalen (1998) presented a technique for finding the coevolutionarily stable strategy (CoESS) solution to this system for cases in which the parameters that control nonlinearities in trade-offs [see Equations (14.4)] are both greater than one (Box 14.1). Employing the CoESS approach, the system evolves toward a single observed equilibrium point for  $c > 1$ . When  $c < 1$ , numerical techniques are needed to find the polymorphic solutions. We present here only the CoESS solutions (for additional results, see Hochberg and Van Baalen 1998).

Figure 14.1 shows how impact and its components are expected to vary with four habitat suitability parameters. In all cases, declining habitat suitability is associated with lower natural enemy impact. Higher natural enemy impact  $\lambda$  is always associated with less evolved victim defense,  $j^* - k^*$ ; or, in other words, the victim defends itself less in productive environments than in nonproductive ones! Note from these figures that components of  $\lambda$  may (Figures 14.1a, 14.1c, and 14.1d) or may not (Figure 14.1b) vary in the same fashion, meaning that focusing on single correlates of impact may belie other components of the index  $\lambda$ .

How does migration affect these results? By employing numerical simulations of Equations (14.1a) and (14.1b), Hochberg and Van Baalen (1998) showed that migration tended to expunge spatial patterns in local adaptation (e.g., patterns in impact explored in this chapter); this was especially true when there was no spatial pattern in habitat suitability (see their figures 3–5). Migration tends to differentially favor the global representation of adaptations to productive environments, leading to the expectation of overall heightened natural enemy impact in dispersive systems through a species' range.

Thus, increasing habitat suitability for the victim should be associated with higher impact by the natural enemy. However, this central result overlooks an important consideration: interactions between habitat and gene, which are encapsulated in parameters  $\beta_1$ ,  $d_{N1}$ , and  $d_{P1}$ . Such interactions mean that marginal changes in genotypes (i.e., the ability of the natural enemy to attack, or the ability of the victim to defend itself) have different weightings in different habitat types.

**Box 14.1** Determining coevolutionarily stable strategies

The strategy set for a natural enemy and victim that resists invasion from all possible mutants is called a coevolutionarily stable strategy (CoESS). The victim's strategy is denoted by  $x$ , and  $y$  is the enemy's strategy. Assume there is one resident strain of each species,  $x_{\text{res}}$  for the victim and  $y_{\text{res}}$  for its enemy. If  $x^*$  and  $y^*$  are a CoESS, then  $x_{\text{mut}} = x^*$  and  $y_{\text{mut}} = y^*$  should both be local fitness optima for mutants  $x_{\text{mut}}$  or  $y_{\text{mut}}$  in the environment created by the pair  $(x_{\text{res}}, y_{\text{res}}) = (x^*, y^*)$  (Vincent and Brown 1989; Van Baalen and Sabelis 1993).

The fitness of a rare mutant victim strain with strategy  $x_{\text{mut}}$  is

$$f_{\text{victim}}(x_{\text{mut}}; x_{\text{res}}, y_{\text{res}}) = \left. \frac{dN_{\text{mut}}}{N_{\text{mut}} dt} \right|_{\text{res}}^*$$

where  $N$  is the population density of the victim (the density of the enemy will be denoted by  $P$ ), and  $\left. \right|_{\text{res}}^*$  denotes "evaluated at the resident equilibrium ( $N_{\text{res}}^*, P_{\text{res}}^*$ )."  
If  $f_{\text{victim}}(x_{\text{mut}}; x_{\text{res}}, y_{\text{res}})$  is positive, then the mutant strain with strategy  $x_{\text{mut}}$  invades. To find the evolutionarily stable strategy (ESS)  $x^*$ , for a given fixed value of  $y$ , one must first find the optimum strategy  $x_{\text{mut}}^0$  for rare mutants arising in a population dominated by a resident population  $x_{\text{res}}$ , the so-called best reply, and then identify that resident strategy  $x^*$  that is its own best reply. To find the CoESS pair, this procedure has to be followed for the pair  $(x, y)$  simultaneously, that is, determine the optimal  $(x_{\text{mut}}^0, y_{\text{mut}}^0)$  for each possible  $(x_{\text{res}}, y_{\text{res}})$  and then determine the  $(x_{\text{res}}, y_{\text{res}}) = (x^*, y^*)$  such that  $(x^*, y^*)$  and the corresponding  $(x_{\text{mut}}^0, y_{\text{mut}}^0)$  coincide.

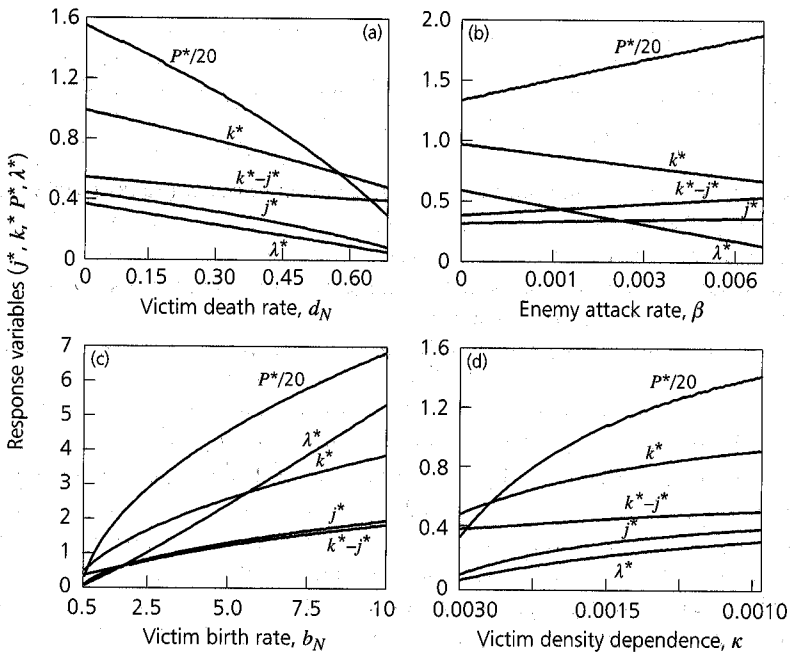
Setting the partial derivatives  $\partial f_{\text{victim}}(x_{\text{mut}}; x_{\text{res}}, y_{\text{res}})/\partial x_{\text{mut}}$  and  $\partial f_{\text{enemy}}(y_{\text{mut}}; x_{\text{res}}, y_{\text{res}})/\partial y_{\text{mut}}$  equal to zero to obtain the mutant optimum and at the same time setting mutant and resident equal to  $x^*$  for the victim and  $y^*$  for the enemy, gives two equations in two unknowns

$$\left. \frac{\partial f_{\text{victim}}(x_{\text{mut}}; x_{\text{res}}, y_{\text{res}})}{\partial x_{\text{mut}}} \right|_{x_{\text{mut}}=x_{\text{res}}=x^*, y_{\text{res}}=y^*} = 0,$$

$$\left. \frac{\partial f_{\text{enemy}}(y_{\text{mut}}; x_{\text{res}}, y_{\text{res}})}{\partial y_{\text{mut}}} \right|_{x_{\text{mut}}=x^*, y_{\text{mut}}=y_{\text{res}}=y^*} = 0.$$

from which CoESS can be determined.

For example, the marginal cost to the prey of evolving from a given strategy  $j$  to  $j + 1$  would be expected to be higher in marginal environments than in productive ones (in which case  $d_{N1}$  would decrease with productivity). Although not discussed in detail here, larger  $d_{N1}$  and  $\beta_1$  (predicted to be associated with poorer habitats for the prey) actually lead to higher impact. Therefore, strong habitat and gene interactions can produce the opposite trends predicted for variation in habitat alone, and their relative weighting as compared to habitat-based effects should be more relevant to the overall effect on natural enemy impact on its victim.



**Figure 14.1** Numerical results of CoESSs as a function of habitat suitability for the victim: (a) victim death rate  $d_N$ , (b) enemy attack rate  $\beta$ , (c) victim birth  $b_N$ , and (d) victim density dependence  $\kappa$ . Vertical axis shows response variables  $j^*$  (investment by victim),  $k^*$  (investment by exploiter),  $k^* - j^*$  (difference in investments by exploiter and victim),  $P^*$  (equilibrium density of exploiter), and  $\lambda^* = \beta_{j,k} P^*$  (impact). Note that by assuming an effectively infinite number of strains in enemy and victim populations, the variables  $j$  and  $k$  can be expressed as continuous variables. Other parameter values:  $c_N = c_P = 2$ ,  $d_{P1} = 5$ ,  $d_{N1} = 0.7$ ,  $d_{P0} = 1$ ,  $d_{N0} = 0.1$ ,  $\beta_0 = 0.001$ ,  $\beta_1 = 0.02$ ,  $b_N = 1$ ,  $\phi = 1$ , and  $\kappa = 0.001$ .

## 14.4 Discussion

According to our analysis, increasing habitat suitability for a victim should be associated with higher natural enemy impact as long as there are no interactions between habitat and gene. Below, we discuss how other factors may impinge on these findings, some empirical support of the model predictions, and ways in which the results can be applied to real-world problems.

### Main factors

We begin our discussion by identifying several major factors at work in determining patterns of natural enemy impact over geographical ranges:

- **Landscape.** Aspects of species biologies that evolve independently of the interaction set the template for the evolution of impact. It remains to be seen in real systems whether spatial pattern formation in impact reflects the underlying



variation in habitat suitability for the victim, but preliminary empirical studies indicate this (see subsection on empirical support below). We expect the most detectable patterns to occur for a victim that experiences a wide range of habitat suitabilities over its geographical range.

- *Reciprocal selection.* Natural enemy monophagy (see Holt and Lawton 1993 for discussion) is not a prerequisite for selection to occur (Takasu 1998). Conversely, little or no evolution may occur in some tightly coupled systems (Hochberg and Holt 1995; Holt *et al.* 1998). We suggest that systems in which the natural enemy has the latitude to have a major impact on its victim are the most likely to yield spatial patterns.
- *Genetic systems and genetic structure.* The genetic mechanisms that control reconnaissance (e.g., distinguishing self from nonself) and response (e.g., defending self, or mounting an immune response) in natural enemy–victim interactions (Frank 1993a; 1996c), and the genetic diversity of these interactions (Frank 1993a; Hochberg 1997), can be pivotal determinants of evolutionary trajectories. For instance, if indeed the selection pressure exerted by natural enemies varies predictably across geographical gradients, then this leads to the predictions that (1) the diversity and amplitude of defenses should increase from habitats of low to high suitability (Hochberg 1997), and (2) defenses and countermeasures to these defenses should be less specific in high-quality as opposed to low-quality habitats (Hochberg and Van Baalen 1998). How genetic systems of reconnaissance and response impinge on geographical patterns of impact and its components requires further research, but preliminary analyses suggest that the relative constraints (e.g., trade-offs, allelic diversity, single or multilocus genetic systems, or metabolic costs) associated with each of these two broad categories have a major impact on their relative contributions to geographical patterning (Hochberg 1998; Hochberg and Strand, unpublished simulations).
- *Patch size.* Patch size influences the local extinction of genotypes and even entire populations. In an island biogeographical setting for our models, we expect that local adaptation and the maintenance of genetic diversity on small islands should be hampered compared with that on large islands because of demographic stochasticity and other factors (Frankham 1997; Holt 1997). Thus, the spatial patterns in impact we predict will be more obscure in systems of small patches.
- *Interpatch flows.* Dispersal may either promote or destroy local adaptation. It promotes local adaptation by introducing novel genotypes to areas where they may proliferate (e.g., Holt 1996); but if flows are too intense, it destroys local adaptation and overall diversity by shunting maladapted genotypes that compete with locally adapted genotypes (García-Ramos and Kirkpatrick 1997; Hochberg and Van Baalen 1998).
- *Landscape ruggedness.* Which-patch-is-next-to-which can have very important implications for geographical patterns in impact, whereby continuous variation in environments from patch to patch tends to conserve more genotypes of

each species globally, and make geographical differentiation of impact more identifiable than a more rugged variation (Hochberg and Van Baalen 1998). In other words, when patch suitability varies irregularly through space, swamping effects from productive to neighboring unproductive patches are much more commonplace than in systems in which neighboring patches tend to have similar productivities.

- *Temporal dynamics.* Holt *et al.* (1998) showed that unstable temporal population dynamics can hamper the evolution of resistance of a victim species to its exploiter. An important issue to examine in future studies is the influence of geographical-scale variation in population instability on the spatial patterning of impact.

## Empirical support

Three studies go some way to explain how natural enemies and their victim may evolve in areas of different habitat suitability for the victim.

Work by Lenski and colleagues vividly illustrates how habitat productivity for a host influences the persistence of susceptible and resistant forms to a phage pathogen. Their basic approach was to vary the level of glucose input into chemostats and monitor the population dynamics of susceptible and resistant forms of *Escherichia coli* and various bacteriophages. Bohannan and Lenski (1997) demonstrated that both predation pressure increases and the rate of replacement of phage-sensitive clones by resistant clones increases with nutrient enrichment. As the phage did not evolve in this experimental set-up, invasion of the resistant bacteria resulted in the system being transformed from parasite-limitation to resource-limitation.

Another system that yields results consistent with our predictions about transmissibility is wild oats (*Avena*) and their rust parasite *Puccinia coronata* in New South Wales, Australia. Burdon *et al.* (1983) showed that northern populations of oats in more favorable (mesic) conditions were more resistant to the rust than populations in southern, arid environments. Oates *et al.* (1983) considered the flip-side of the interaction and showed a trend for increasing parasite virulence from arid to mesic sites. These studies suggest that both antagonists show spatially varying adaptations in their association, and that both are increasingly engaged in the interaction as habitat quality increases.

A third example involves fruit fly hosts (*Drosophila melanogaster*) and their insect parasitoids (*Asobara tabida* and *Leptopilina boulardi*). Mollema (1988) and later Kraaijeveld and van Alphen (1994, 1995) showed that the highest levels of virulence of *A. tabida* to a single reference strain of *D. melanogaster* tends to occur in the southernmost latitudes of Western Europe, and that the highest encapsulation abilities of the host to a single reference strain of *A. tabida* occur in the central latitudes of Western Europe. Why *D. melanogaster* does not exhibit a geographical pattern in encapsulation to another parasitoid (*L. boulardi*) is unknown.

## Managing natural enemies

Our approach and the results we present here have applications in the reintroduction of endangered or locally extinct species and in the introduction of exotic natural enemies to biologically control pest species. However, one should be cautious in interpreting the discussion below, as it is designed to elucidate some potential ways to apply a biogeographical approach. More studies are necessary to evaluate our findings, and only specific models applied to particular systems of interest should ever be employed in real policy making.

*Reintroduction of endangered natural enemies.* The conservation of natural enemies has received relatively little attention in the applied literature, and theoretical models (which could be useful to understanding the important factors of their conservation) are rarely applied to this type of problem (Hochberg *et al.* 1998; Hochberg 2000). Natural enemies are generally candidates for conservation as long as they are perceived to have some kind of "value"; detailed discussion for the case of insect parasitoids can be found in Hochberg (2000). What is relevant to the present scenario is the conservation of a natural enemy that is part of a protected community. That is, it is important in conserving the natural enemy that neither its victim nor other interacting species are endangered by the conservation efforts directed at the enemy.

Assume that the novel victim (which receives the introduced enemy species) is distributed over its geographical range as in the model presented above, and the enemy we desire to introduce is found on a different (but related) exotic victim species that has no overlap in its distribution with the focal victim. The question is, where along an exotic victim's distribution should one procure the enemy?

If, for example, the enemy is taken from peripheral, nonproductive sites, then a risk is that it will not be preadapted to invade the introduction sites successfully, especially if the productivity of the novel victim is very high through most of its distribution. If, on the other hand, there are large expanses where the novel victim is unproductive, then it is possible for the natural enemy to invade and persist. However, a potential problem may emerge if the introduced enemy has too high an impact on the nonproductive victim, especially in the most marginal sites. In a recent theoretical study on host-parasitoid interactions over geographical gradients in host productivity, it was shown that enemies can readily fragment the geographical distribution of their hosts if the host is relatively poor at defending itself against the parasitoid and the parasitoid is highly vagile (Hochberg and Ives 1999).

Now assume that the enemy is procured from highly productive sites in the exotic victim's geographical range. The problem here is very similar to the latter scenario described above: if the target sites are unproductive relative to the site of origin, then the enemy can disrupt the victim population and species interactions with the victim (e.g., Holt and Lawton 1993). Of course this problem becomes more intense (according to our model) as the discrepancy in productivity grows.

Assuming that the productivities of exotic and introduced sites are comparable and the enemy invades, then what are the evolutionary consequences? With

sufficient (but not too pronounced) migration and mutation, we would expect the natural enemy to gradually spread and adapt over the victim's distribution, occupying that subset of it for which site productivities are sufficient for the enemy to persist. The race between local adaptation and population ecology is relevant here (see Holt and Gomulkiewicz 1997), and unless the migrating enemy is sufficiently preadapted and/or numerous, it will be unable to spread so as to fill its fundamental niche (i.e., that part to which it is potentially able to adapt and persist in the absence of migration). Assuming that geographical adaptation is taking place or has taken place, if the objective is to conserve maximal enemy diversity, then postintroduction measures should aim to conserve the enemy in a range of habitat types to which it is adapting or has adapted (Hochberg and Van Baalen 1998).

*Introduction of natural enemies for control of pests.* Like the application of conservation measures to natural enemies, the problem of pest control over the pest's geographical ranges is little explored. The problem here is that an enemy is most likely to be released in areas where the economic damage inflicted by the pest is most intense. Since our model does not consider the trophic level below the victim, it is difficult to generalize where the pest would be most damaging economically.

If we are searching for an exotic natural enemy to release against the victim (i.e., classic biological control), then where should we take it from: the productive or marginally productive sites of an exotic victim? Let us assume as a first scenario that the pest is most damaging in the nonproductive sites of its range. According to our model, if we take the enemy from productive source sites, then it will have a major impact on the pest, but only temporarily (which may be sufficient to cause local extinction of the pest). As the enemy is not adapted to the marginally productive introduction sites, it must either adapt to a form with less impact  $\lambda$ , or go extinct itself. If, on the other hand, the enemy comes from a nonproductive site, then it may be preadapted to the pest it is about to encounter, and some level of lasting control may be achievable with lower risks of local extinctions following population transients.

Now assume that the pest is of most concern in productive sites. Introduction of a natural enemy from a nonproductive source is unlikely to achieve any control, and unless the enemy can adapt very quickly, it may go extinct. In contrast, introduction from a productive source is likely to give substantial control (i.e., impact  $\lambda$  is predicted to be high). It is interesting that according to the model presented here (see also Hochberg and Ives 1999), although a successfully introduced natural enemy will have the most impact in the most productive sites, pest densities are likely to be lowest in areas where the enemy has least impact! This is simply because density-dependent limitations in this model are such that the enemy always depresses victim density to the same or lower levels as productivity decreases.

Hokkanen and Pimentel (1984) hypothesized that the introduction of natural enemies for pest control often worked so well because the natural enemy was introduced against a pest with which it had never been in evolutionary contact (see also Waage 1990). The idea is that if there had been an evolutionary or coevolutionary interaction, then the impact of the enemy on the pest would have diminished

through time. Indeed, our model suggests that the introduction of an enemy from a productive site to a nonproductive one may well result in an initially impressive control, but then evolve to more moderate results. There appears to be no evidence for evolution in biological control that involves insect parasitoids as natural enemies against arthropod pests. However, scattered evidence for the evolution of resistance does exist for insect pathogens (Holt and Hochberg 1997).

### **Conclusion**

We believe that the framework presented here for exploring enemy–victim interactions over geographical and evolutionary scales is the first step in what will prove to be an interesting and fruitful area of research. Even based upon a variety of oversimplified assumptions, the theory predicts that one must be cautious in introducing natural enemies with the goal of their global conservation or the biological control of other species.