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Ecosystem Evolution and Conservation

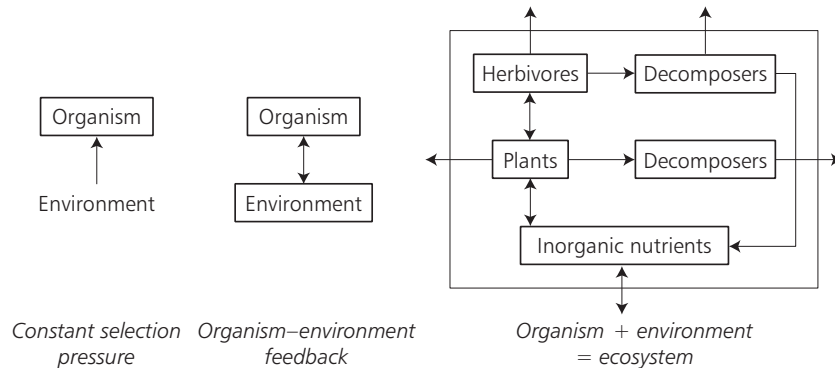
Michel Loreau, Claire de Mazancourt, and Robert D. Holt

17.1 Introduction

A major problem in conservation biology is to decide the target of conservation: should conservation efforts aim to preserve species or ecosystems? The traditional approach has, by necessity, focused on particular species threatened by extinction. With the increasing attention on preserving biodiversity at large, for which the species-by-species approach falls short, a trend is now emerging that centers on ecosystems or habitats as the conservation targets (Schei *et al.* 1999). These two approaches, however, should not be opposed. Species and ecosystems are bound together by mutual ecological constraints and a shared evolutionary history, so that in the long term it may be impossible to conserve one without conserving the other (Loreau *et al.* 1995). Species' traits and their evolution are ultimately constrained by ecosystem processes, just as ecosystem properties are constrained by the ecological and evolutionary history of interacting species (Holt 1995). It is the web of interactions at the heart of an ecosystem that maintains both species and ecosystems as they are, or (more exactly) as they are evolving.

Another way to address this problem is to phrase it in terms of a basic issue in evolutionary biology: what are the constraints within which natural selection operates? Traditionally, evolutionists considered these constraints to arise internally, such as from allocations among competing physiological needs. However, feedbacks via ecosystem processes can also act as constraints, and can channel selection in directions that are different from those expected in the absence of such constraints. Box 17.1 contrasts three views of how natural selection operates: the “classic” view of a constant environment, the “modern” view of an organism–environment feedback, and the “ecosystem” view of a web of interactions among organisms and abiotic factors. Although inherent in the very definition of an ecosystem, rarely has this third view been applied consistently to evolutionary problems so far. Recognizing the ecosystem as the proper context within which natural selection, and hence evolution, operates is a major challenge for ecology today, with important implications in both basic science and applied areas, such as conservation biology and ecosystem management. This challenge emphasizes the need to overcome the barrier that has increasingly separated population ecology and evolutionary ecology, on the one hand, from ecosystem ecology, on the other hand.

In this chapter we show the potential importance of this perspective using plant–herbivore interactions to illustrate:

Box 17.1 Three views of the operation of natural selection

Natural selection is based on the selective multiplication of types in a population through environmental constraints on organisms:

- In the “classic” view, the environment is regarded as external to the organism and constant. Although most evolutionary biologists today would probably agree that this view is an oversimplification of reality, for simplicity’s sake it has been, and still is, widely used in theoretical evolutionary biology as an implicit conceptual framework.
- The “modern” view recognizes that organisms modify and interact with their environment, which generates an organism–environment feedback in the operation of natural selection. This feedback is formalized, for instance, in the theory of adaptive dynamics (see Chapter 11).
- A further step is necessary to understand the full implications of this feedback: an organism’s environment has to be resolved into its real physical, chemical, and biological constituents and their interactions. This is what we call the “ecosystem” view, because an ecosystem is defined as a locally interacting system of abiotic and biotic components.

Since the environment of each organism or component comprises other organisms or components, the ecosystem concept contains both the organisms and their environments. In this sense, it provides a higher-level perspective that transcends the duality between organism and environment (Loreau 2002).

- How incorporating organism–environment feedbacks (moving from the first to the second view of natural selection in Box 17.1) may change the direction of evolution compared with classic predictions for a constant environment;
- How explicit considerations of nutrient cycling as a key whole-ecosystem process (moving from the second to the third view of natural selection in Box 17.1) can further alter our view of the very nature of species’ interactions, from both ecological and evolutionary perspectives;
- Some potential interactions between local evolution and biological invasions and their implications for conservation biology.

17.2 Evolution under Organism–Environment Feedback

If organisms collectively have a significant impact on their environment, to ignore the organism–environment feedback may lead to serious flaws in predictions of the qualitative direction of evolution and expected species' traits in ecological systems. We focus on the evolution of plant defense against herbivores as an example, assuming for the time being that herbivores only consume plants and do not provide them with any indirect benefits (see Section 17.3 for such indirect effects).

Understanding the evolution of plant antiherbivore defense

The classic “resource availability hypothesis” (Coley *et al.* 1985) proposes that low resource availability favors plants with inherently slow growth rates, which in turn favor large investments in antiherbivore defense. This hypothesis has been influential and attractive, because it seemed to explain patterns of plant defense and herbivory in a wide range of ecosystems. It hinged, however, on a very simple theoretical argument with a number of simplifying assumptions, in particular that the quantity of available resources is unaffected by plants. This implicit assumption of a constant environment led Coley *et al.* (1985) and subsequent authors (de Jong 1995; Yamamura and Tsuji 1995) to measure fitness by what they called the plant “realized growth rate”, which in effect is a potential growth rate that ignores the feedback generated by plant resource consumption.

This fitness measure may make sense for pioneer species colonizing temporary environments, but is inappropriate for species competing for limited resources in more stable environments. Whenever plants have accumulated enough biomass to affect the amount of resources in their environment, they compete for these resources, and their growth hinges on their ability to tolerate low concentrations of the resource that is limiting. If the environment is homogeneous, fitness is determined by the ability to deplete the limiting resource (Tilman 1982). If the environment is structured spatially, fitness is determined by the basic reproduction ratio (Loreau 1998a). All these fitness measures can be derived as special cases of the more general concept of “invasion fitness” in the theory of adaptive dynamics (Metz *et al.* 1992; Dieckmann 1997; Geritz *et al.* 1998).

To explore the effects of this organism–environment feedback, we constructed a simple model of evolution of plant allocation to antiherbivore defense in a system that incorporates plant–resource dynamics (Loreau and de Mazancourt 1999). Assume that plants allocate a constant fraction x of a limiting resource to defense, and the remainder $1 - x$ to growth. Thus, x measures the level of defense investment. The dynamics of total plant biomass N_p can be described by

$$\frac{dN_p}{dt} = r(N_n, x)N_p, \quad (17.1a)$$

$$r(N_n, x) = r_{\max}\phi(N_n)(1 - x) - \psi(x) - m, \quad (17.1b)$$

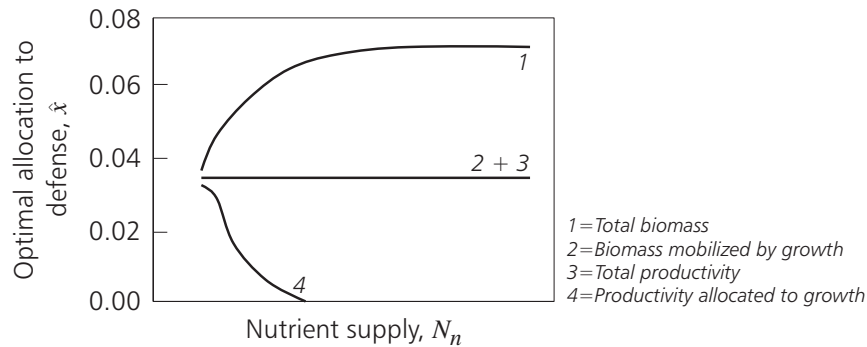


Figure 17.1 Evolutionary optimal plant allocation to defense \hat{x} as a function of nutrient supply in a spatially structured environment in which fitness is determined by any of the following quantities, total biomass, the part of biomass that is mobilized for growth, total productivity, or the part of productivity that is allocated to growth. Plants cannot survive below a threshold nutrient supply; the curves start after this threshold. *Source:* Loreau and de Mazancourt (1999).

where $r(N_n, x)$ is the plant population growth rate per unit biomass, r_{\max} is the maximum rate of resource uptake by plants, $\phi(N_n)$ is the plant functional response to resource concentration N_n [$\phi(N_n)$ increases monotonically with N_n and is scaled so that $0 \leq \phi(N_n) \leq 1$], $\psi(x)$ is the rate of herbivory (which is a monotonic decreasing function of x), and m is the loss rate of biomass. Resource concentration also changes with time in dependence on N_p , but its dynamic equation is irrelevant to the argument that follows, and so is ignored here.

In the long term, plant biomass reaches an ecological equilibrium such that the population growth rate $r(N_n, x)$ in Equation (17.1) is zero. Plants then control resource concentration at a level N_n^* set by Equations (17.1). But this ecological equilibrium itself changes gradually because of the natural selection that acts on x . The evolutionary equilibrium is attained when the population growth rate at the ecological equilibrium can no longer be increased, that is, when

$$\left. \frac{\partial r(N_n, x)}{\partial x} \right|_{N_n=N_n^*} = 0. \quad (17.2a)$$

(It can be shown that r is then indeed maximal.) The solution of Equation (17.2a) provides the evolutionary optimal allocation to defense \hat{x} . Using Equations (17.1), Equation (17.2a) reduces to

$$\psi'(\hat{x})(1 - \hat{x}) + \psi(\hat{x}) + m = 0, \quad (17.2b)$$

where $\psi'(\hat{x})$ is the derivative of ψ with respect to x evaluated at \hat{x} .

It is evident from Equation (17.2b) that the optimal defense investment is affected by features of the plant–herbivore interaction, encapsulated in the function ψ . In general, the higher the intrinsic herbivore voracity, the higher the plant defense investment. This is independent of the maximum rate of resource uptake r_{\max} , which is also a measure of the maximum growth rate and, indeed, of any conceivable measure of resource availability.



Sea otter
Enhydra lutris

Green sea urchin
Strongylocentrotus
droebachiensis

Brown macroalgae
Sargassum sp.

These results are based on the assumptions that the environment is homogeneous and plants have unrestricted global access to the limiting resource. However, usually plants have only local access to resources such as soil nutrients (Huston and DeAngelis 1994; Loreau 1996, 1998b). A homogeneous environment may be viewed as one extreme in the range of possibilities, the other extreme being a perfectly structured environment in which each plant occupies an isolated site (Loreau 1998a). A model for the latter case, in which competition obeys a “competitive lottery” for vacant sites, shows that the outcome is strongly dependent on the factor that determines a plant’s ability to produce successful propagules that establish in vacant sites, which itself determines fitness. The optimal defense investment may then either increase, stay constant, or decrease with nutrient supply (Figure 17.1). The effects of maximum growth rate, as measured by r_{\max} , are identical to those of nutrient supply on the optimal defense investment in the various scenarios.

Clearly, the resource availability hypothesis fails to describe evolution in a system in which plants and their limiting resources reach an ecological equilibrium. Resource supply and maximum growth rate may increase, decrease, or (in most cases) have no effect on the optimal investment in defense. A common argument used to justify this hypothesis is that herbivory is more costly in resource-poor environments because lost biomass is more costly to replace. However, this argument ignores that investment in defense is also costly. It is the balance between the two costs that determines the optimal investment, and in most cases this does not change in the way assumed in the resource-availability hypothesis. Indeed, the dynamics of coevolution between plants and herbivores, which we have not considered here, may contribute an increase to the intensity of their antagonistic interaction, and hence to plant investment in antiherbivore defense when resource availability increases (see Section 17.4).

Conservation implications

Current species’ traits result from the evolution of a dynamic interaction between organisms and their environment. A neat empirical example that shows the

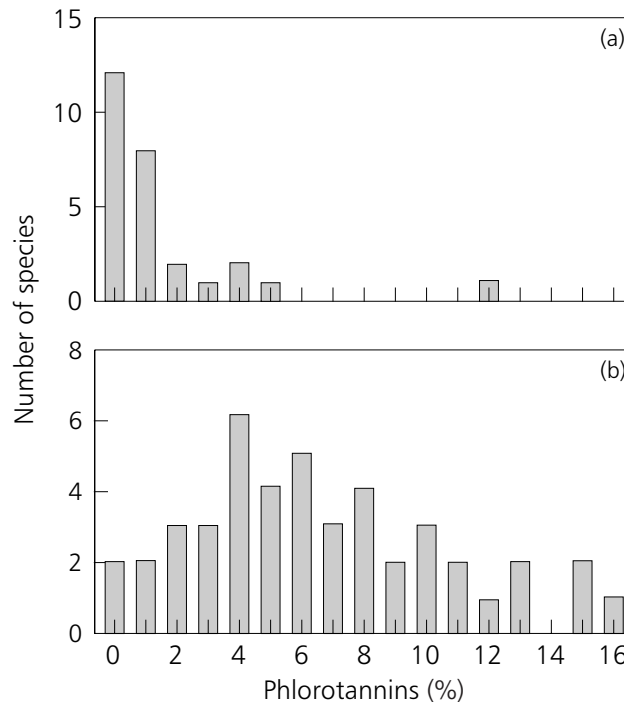


Figure 17.2 Frequency distribution of mean levels of phlorotannins, the principal secondary metabolites, in brown macroalgae. (a) From the North Pacific Ocean, where the predation of sea otters on invertebrate herbivores is important. (b) From Australasia, where sea otters are absent. The figure shows that Australasian seaweeds have been under strong selection to evolve chemical defenses. Data are average percentage dry weight phlorotannins. *Source:* Steinberg *et al.* (1995).

importance of evolutionary dynamics in plant defenses is provided by the work of Steinberg *et al.* (1995). In the North Pacific, sea otters keep invertebrate herbivores like sea urchins at low levels of abundance, which allows the establishment of luxurious algal beds. By contrast, in comparable environments in Australasia, sea otters are absent and herbivore pressure is high. Corresponding to this, macroalgae have much higher levels of secondary defensive compounds in Australasia (Figure 17.2).

One potential implication of this model for conservation is an initial asymmetry between the indirect effect of predator removal and exotic predator introductions. If a predator has had a strong impact on herbivore abundance over evolutionary time scales, plants in these systems should have a low investment in defense against herbivory. This makes them vulnerable to increased herbivore numbers following predator removal. The introduction of exotic predators can be devastating for herbivores, but plants may show a more muted initial response to this reduction in herbivory, for they have already experienced low herbivory because of a high investment in defense. Following predator removal or addition, over a longer time scale further changes in the plant communities are expected because of a shift in the optimal allocation to defense.

17.3 Evolution in an Ecosystem Context

The organism–environment feedback examined above is simple and direct. In reality, ecosystems are complex dynamic systems potentially capable of generating a multitude of indirect interactions among their components (Puccia and Levins 1985; Wootton 1994; Menge 1995) and hence of indirect feedbacks between an organism and the rest of the ecosystem. Some of these indirect effects are weak or unpredictable (Yodzis 1988), but some can be strong and predictable. In particular, material cycling is a key ecosystem process that drives a circular causal chain in ecosystems and transmits predictable indirect effects to their components (Loreau 1998a). Therefore, it is likely to affect the evolution of component species.

Indirect ecological effects of material cycling

Traditionally, in ecology plant–herbivore interactions have been considered as antagonistic because herbivores have a negative direct effect on plants through biomass consumption. This assumption has been challenged by the so-called grazing optimization hypothesis, which states that primary productivity increases with grazing and reaches a maximum at a moderate rate of herbivory (Owen and Wiegert 1976, 1981; McNaughton 1979, 1983; Hilbert *et al.* 1981; Dyer *et al.* 1986). This hypothesis is supported by some empirical data, notably from the Serengeti grassland ecosystem (Figure 17.3). One mechanism that could produce such a beneficial effect is nutrient cycling, which mediates positive indirect effects among ecosystem components. Should the traditional view of antagonistic plants and herbivores be changed, can these even be mutualistic, and under what conditions? These questions, which have important consequences for both ecosystem functioning and the evolution of plant–herbivore interactions, have been much debated over the past 20 years (Silvertown 1982; Belsky 1986; Paige and Whitham 1987; Bergelson and Crawley 1992; Paige 1992; Belsky *et al.* 1993; Mathews 1994; Bergelson *et al.* 1996; Gronemeyer *et al.* 1997; Lennartsson *et al.* 1997, 1998).

Given the ambiguity in interpretations of empirical data, we attempted to answer these questions theoretically using mathematical models. We first identified the ecological conditions under which herbivores increase primary production and achieve grazing optimization through recycling of a limiting nutrient (Loreau 1995; de Mazancourt *et al.* 1998). These conditions are:

- The proportion of nutrient lost while flowing along the herbivore recycling pathway must be sufficiently less than the proportion of nutrient lost while flowing in the rest of the ecosystem;
- Nutrient inputs into the system must exceed a threshold value, which depends on the sensitivity of plant uptake rate to an increase in soil mineral nutrient.

Contrary to traditional assumptions, nutrient turnover rates have no impacts on the long-term equilibrium primary production. These results are very general: they do not depend on the structure of the ecosystem or on the functional form of herbivore consumption (de Mazancourt *et al.* 1998). They are also potentially relevant to

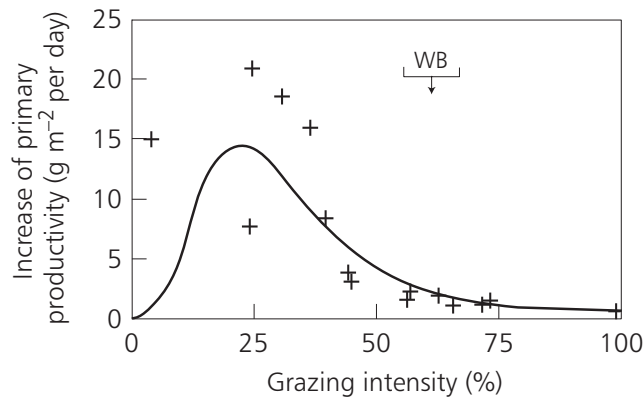


Figure 17.3 Relationship between the stimulation of above-ground grassland productivity and grazing intensity in the Serengeti National Park, Tanzania. Above-ground net productivity was calculated from positive biomass increments in temporary exclosures. Grazing intensity was calculated as $1 - N_{p,g}/N_{p,ng}$, where $N_{p,g}$ is the plant biomass in grazed areas unprotected by fencing and $N_{p,ng}$ is the plant biomass in the permanent exclosure. The effect of soil moisture was not incorporated into the curve (incorporating this extra factor reduced the unexplained variance by 9%). WB indicates the mean and 95% confidence interval of wildebeest grazing intensity in these grasslands during the wet season. *Source:* McNoughton (1979).

natural ecosystems: grazing optimization was found to be likely for an African humid savanna (de Mazancourt *et al.* 1999) and it can occur even if herbivory results in the replacement of a productive plant species by a less productive one (de Mazancourt and Loreau 2000b).

Evolutionary consequences of grazing optimization

The existence of a positive indirect effect of herbivory on primary production does not automatically lead to an indirect mutualism between plants and herbivores, for two reasons. First, increased plant productivity does not necessarily translate into increased plant fitness. It is still unclear which plant traits determine fitness. If a plant's fitness is mainly determined by its biomass, because a greater biomass means a greater nutrient stock available for seed production at the end of the season, then no mutualistic interaction with herbivores is possible, because plant consumption by herbivory always decreases plant biomass. Alternatively, if a plant's fitness is mainly determined by its productivity, because a higher productivity means a larger nutrient flow that is constantly allocated to seed production or vegetative propagation [as assumed in physiological models of plant resource allocation; see Mole (1994)], then herbivory can increase plant fitness through increased productivity. Reality probably lies between these two extremes, and thus we may expect herbivory to increase plant fitness in some cases. Second, it is not absolute fitness, but relative fitness that is important. If two plant types (species or genotypes) are mixed, one of them being tolerant ("mutualistic") and the other resistant ("antagonistic") to herbivory, the resistant type is expected to outcompete the tolerant type because it benefits from the positive indirect effect of increased

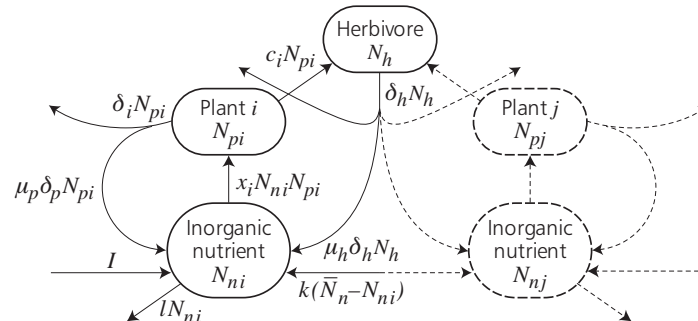
nutrient cycling, but does not suffer the negative direct effect of herbivore consumption. As a result, tolerance should not evolve, even though it is indirectly beneficial. This might seem to put to an end the idea of any plant–herbivore indirect mutualism, indeed of any evolved indirect interaction, as some authors have suggested (Belsky *et al.* 1993).

This conclusion is premature, however, as two factors counteract this advantage of antiherbivore defense. First, the spatial structure of the plant–herbivore system can generate spatially heterogeneous nutrient cycling. If herbivores recycle nutrient in the vicinity of the grazed plants, or plants from the same type are aggregated, herbivores tend to recycle proportionally more nutrient onto the plants that are grazed more heavily, and thus augment the indirect benefit of grazing for the grazed plants. In such conditions, evolution is governed by the balance between two conflicting levels of selection, just as in the evolution of altruism (Wilson 1980); individual selection within patches, which favors the resistant type over the tolerant one because it has a higher relative fitness, and group selection between patches, which favors patches with a higher proportion of the tolerant type because they have a higher average absolute fitness. The outcome of evolution then depends on the strength of spatial aggregation and patch size; tolerance to grazing evolves provided that spatial aggregation is strong enough or patch size is small enough (de Mazancourt and Loreau 2000a).

Evolution toward plant–herbivore mutualism

Another factor that counteracts the advantage of antiherbivore defense is its cost. Although the empirical evidence for costs of defense is still equivocal (Simms and Rausher 1987; Mole 1994; Bergelson and Purrington 1996; Strauss and Agrawal 1999), some cost seems inevitable in many cases because the production of defense diverts resources from other functions, such as growth and reproduction. This factor is investigated in the previous section, and its consequences are explored further here in an ecosystem context. To this end, we constructed a simple model of a material cycle in a spatially structured ecosystem (Box 17.2). In this model, different plant strategies have different abilities to take up nutrient and to resist herbivory, and there is a trade-off between these two traits. Evolution of the plant traits is analyzed using the theory of adaptive dynamics.

Two major conclusions emerge from this analysis (de Mazancourt *et al.* 2001). First, for most ecologically plausible trade-offs between nutrient uptake and antiherbivore defense, evolution in plants leads to a single continuously stable strategy (CSS), that is to a strategy toward which evolution converges and that cannot be invaded by any other strategy (Eshel and Motro 1981; Eshel 1983). By ecologically plausible trade-off, we mean a trade-off such that plants cannot build defenses that are completely efficient, even when they allocate all their resources to defense, and such that they cannot increase their nutrient uptake rate beyond a maximum value, even when they allocate all their resources to nutrient uptake. The possibility of a single CSS has interesting implications for plant coexistence. Previous studies proposed that the presence of herbivores allows the coexistence of several

Box 17.2 Modeling the evolution of plant defense in an ecosystem context

As an example of a model of evolution in an ecosystem context, consider the problem of the evolution of a costly plant antiherbivore defense when herbivory contributes to recycling a limiting nutrient in the ecosystem.

First, the ecological model setting the scene for evolutionary changes must be constructed. We assume a spatially structured ecosystem in which each plant occupies a site during its lifetime and absorbs mineral nutrient in a local resource-depletion zone around its roots at this site (Huston and DeAngelis 1994; Loreau 1996, 1998b). Mineral nutrient migrates laterally in the soil among the resource-depletion zones through diffusion, transport, or other processes. The flow of mineral nutrient into a local depletion zone is proportional to a migration coefficient k and the difference between the mean concentration in the soil and the local concentration. Each resource-depletion zone is replenished with a constant nutrient inflow I , and loses nutrient to the external world at a rate l . The total number of occupied sites is assumed to be constant, of which plants with strategy i occupy a fraction p_i . Herbivory is assumed to be donor controlled – it is determined by the plant's strategy, and does not depend on herbivore density. Plant strategies differ in the rates at which they absorb mineral nutrient and are consumed by herbivores. There is a trade-off between the ability of plant strategy i to take up nutrient and grow, as measured by its nutrient uptake rate r_i , and its ability to resist herbivory, as measured by its herbivore consumption rate c_i . Plants are assumed to be equivalent in all other respects. The nutrient stock N_{pi} in plant strategy i is recycled through two different recycling pathways, those of the plant and the herbivore. Part of the nutrient is not consumed by herbivores and follows the plant pathway; plant detritus is produced at a rate δ_p , of which a fraction μ_p is mineralized and recycled to the local nutrient pool (with nutrient stock N_{ni}) around the plant. The rest of the plant nutrient stock is consumed by

continued

plant species for some trade-offs (e.g., Holt *et al.* 1994). However, coexistence on an ecological time scale does not imply that coexistence can be maintained in the course of evolution. Although there are differences between the two types of models [in particular, coexistence in Holt *et al.*'s (1994) ecological model requires herbivore numerical response, which is not considered in de Mazancourt *et al.*'s

Box 17.2 *continued*

herbivores (with nutrient stock N_h per plant) and follows the herbivore pathway; herbivore detritus is produced at a rate δ_h , of which a fraction μ_h is recycled and distributed uniformly among sites.

The model is thus given by the equations

$$\frac{dN_{ni}}{dt} = I - lN_{ni} + k(\bar{N}_n - N_{ni}) - x_i N_{ni} N_{pi} + \mu_p \delta_p N_{pi} + \mu_h \delta_h N_h, \quad (a)$$

$$\frac{dN_{pi}}{dt} = x_i N_{ni} N_{pi} - \delta_p N_{pi} - c_i N_{pi}, \quad (b)$$

$$\frac{dN_h}{dt} = \sum_i p_i c_i N_{pi} - \delta_h N_h. \quad (c)$$

The productivity of plant strategy i is here measured by its nutrient inflow, $r N_{ni} N_{pi}$.

This model is intended to describe ecological interactions on a relatively short time scale – say, within a year – such that the spatial distribution of plants can be regarded as constant. On a longer time scale, however, this spatial distribution changes; the plant strategy with the highest reproductive ability increases its occupation of space at the expense of other strategies. The dynamics of the fraction of sites occupied by plant strategy i from year t to $t + 1$ obeys a “competitive lottery” for vacant sites,

$$p_i(t + 1) = (1 - \alpha)p_i(t) + \alpha \frac{p_i(t)R_i(t)}{\sum_j p_j(t)R_j(t)}, \quad (d)$$

where α is the fraction of sites made vacant by mortality each year, and R_i is the reproductive ability of strategy i . We consider two plausible scenarios for the determination of R_i :

- It is proportional to biomass, hence to the plant nutrient stock;
- It is proportional to plant productivity, as measured by the plant nutrient inflow.

We assume that within each year nutrient concentrations attain equilibrium.

To investigate the evolution of plant traits in this model ecosystem, we use the theoretical framework of adaptive dynamics based on the invasion success of a rare mutant strategy invading a resident strategy (Dieckmann 1997; Geritz *et al.* 1998; Chapter 11). Here, the condition for the mutant strategy to invade the resident is $p_{mut}(t + 1) > p_{mut}(t)$, which, according to Equation (d), is equivalent to $R_{mut} > R_{res}$, this condition being evaluated for $p_{mut} \rightarrow 0$ and $p_{res} \rightarrow 1$. This invasion condition requires simply that in an environment determined by the resident strategy, the mutant has a higher reproductive ability than the resident (de Mazancourt *et al.* 2001).

(2001) evolutionary model], this analysis suggests that herbivore-mediated plant coexistence may not be an evolutionarily robust phenomenon.

A second major conclusion concerns the nature of the plant–herbivore interaction. Our model can be used to explore different ecological and evolutionary scenarios of herbivore addition or removal, which leads immediately to a problem of

definition: what is called “mutualism”? The classic approach to identify mutualistic interactions in ecology is based on removal experiments or press perturbations (Schoener 1983; Bender *et al.* 1984; Krebs 1985): if each of two populations is affected negatively (in density, biomass, or production) after the other has been depressed or removed, the interaction between them is considered to be mutualistic. Despite its interest, however, this approach has a number of limitations, in particular that the effects of a removal or a perturbation may be different on ecological and evolutionary time scales. It is therefore useful to distinguish two types of mutualism: an ecological mutualism, in which each species gains a benefit from the presence of its partner in the absence of any evolutionary change (as revealed, e.g., by an ecological press perturbation), and an evolutionary mutualism, in which the mutual benefit persists even after evolution has occurred. The conditions for evolutionary mutualism are generally more stringent than those for ecological mutualism, because interacting species may have evolved a mutual dependence, so that the removal of one species may have a negative impact on the other in the short term, but this negative impact may disappear after each species has had the opportunity to evolve and adapt to the new conditions created by the absence of its partner (Douglas and Smith 1989; Law and Dieckmann 1998).

This happens in our model. Not surprisingly, when a plant’s reproductive ability is determined by its biomass, herbivory cannot have a positive effect on plant performance. In contrast, herbivore removal can have a negative effect on plant productivity, on both ecological and evolutionary time scales, provided that herbivore recycling efficiency (as measured by the fraction μ_h of nutrient flowing along the herbivore pathway that is recycled within the ecosystem) be sufficiently greater than plant recycling efficiency (as measured by the fraction μ_p of nutrient flowing along the plant pathway that is recycled within the ecosystem). Thus, when a plant’s reproductive ability is determined by its productivity, herbivory can have a positive effect on plant performance and thus generate a mutualistic interaction. The requirements on herbivore recycling efficiency, however, are more stringent for an evolutionary mutualism than for an ecological mutualism. A surprising result in this case is that, as herbivore recycling efficiency is increased, the plant–herbivore interaction becomes increasingly mutualistic (first ecologically, then evolutionarily), but at the same time plants evolve to increase their level of antiherbivore defense because they gain a higher benefit from not being consumed relative to plants defended less well (Figure 17.4). Thus, mutualism can go hand-in-hand with increased conflict between partners. Although paradoxical at first sight, such evolutionary conflicts are also known to occur in other mutualistic interactions (Anstett *et al.* 1997b; Law and Dieckmann 1998).

Conservation implications

The preceding considerations show that an ecosystem process such as nutrient cycling can alter the very nature of species’ interactions, both in an ecological and in an evolutionary sense. We are not aware of direct empirical evidence for the new

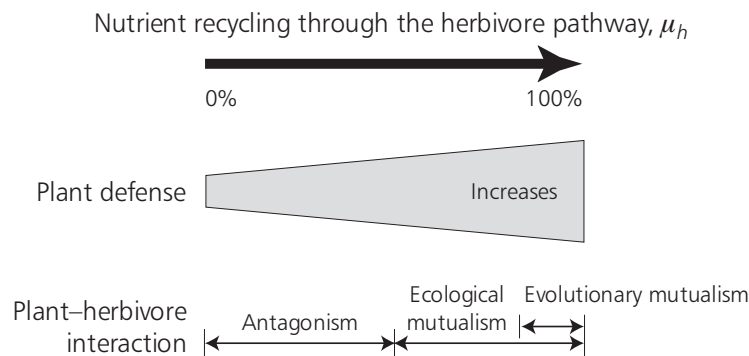


Figure 17.4 Changes in plant–herbivore interaction along a gradient of increasingly efficient herbivore nutrient recycling (μ_h), with the assumption that the plant reproductive ability is proportional to plant productivity. Plant defense increases as herbivores are more efficient at recycling the nutrient, but at the same time the interaction becomes more and more mutualistic. *Source:* de Mazancourt *et al.* (2001).

theoretical insights presented above, but their potential implications for conservation biology are profound. Extinction or introduction of herbivores, for instance, can have different effects on plants in different ecosystems and on different time scales. If herbivores recycle nutrients within the local ecosystem less efficiently than the plants do, their effect should be simple and consistent: their extinction should stimulate plant biomass and productivity. However, if they are more efficient at recycling nutrients within the local ecosystem, their extinction may lead to a cascade of different effects. Plant productivity may increase as a result of a physiological response shortly after herbivore extinction, then decrease because of an ecological response in the medium term, and finally either increase or decrease through species replacement or evolutionary adjustments in the long term. In the process, some plant species will become extinct and others will evolve different traits, so that ultimately the community may be very different in ways that cannot be anticipated from a simple consideration of the immediate, direct plant–herbivore interaction.

17.4 Coevolution in Other Exploiter–Victim Interactions

One important limitation of the models discussed so far is that they assume that the rate of herbivory is controlled by plant traits. More realistically, herbivores may be expected to show numerical and evolutionary responses to plants. Adding these extra dimensions can further change the predicted outcome of evolution. Recent years have seen a tremendous growth in theoretical studies of coevolution in exploiter–victim systems, considered more broadly to include host–parasitoid and predator–prey interactions (e.g., Abrams 1986; Brown and Vincent 1992; Seger 1992; Dieckmann *et al.* 1995; Hochberg and Holt 1995; Gandon *et al.* 1996; Abrams and Matsuda 1997). A full analysis of this problem is beyond the scope of this chapter, and as yet little attention has been devoted to the relationship between

coevolution and ecosystem or landscape processes, or to the implications for conservation efforts. Some results in the literature, however, can be reinterpreted in a fashion relevant to conservation.

One general phenomenon in natural exploiter–victim coevolution is that a form of cross-species frequency-dependent selection arises when there are opposing tactics in the two interacting species, such that adaptation in one favors a precise counter-adaptation in the other (as in “gene-for-gene” systems, Frank 1993). Roughly, allele A in species 1 increases, which favors allele B in species 2, the increase of which in turn erodes the selective advantage of allele A, which now declines, and allele B in turn declines with a time lag. The time lag inherent in the cross-species interaction means that models of coevolution often lead to a sustained cycling in allele frequency whenever antagonistic species interact through complementary phenotypes or genotypes (Eshel and Akin 1983).

Often these evolutionary cycles (or more complex patterns of fluctuations) are large in amplitude, which means that in finite populations alleles can be lost when they are rare (Seger 1992). In spatially extended populations with limited dispersal, this is not a problem. Different local populations can be at different evolutionary phases and, with migration, recurrent gene flow will replenish the loss of genetic variation (Gandon *et al.* 1996). However, if habitat destruction and fragmentation are imposed on a system like this, the populations left behind in the habitat remnants tend to lose genetic variation. The exact impact of this loss depends upon a number of details, but we can readily imagine cases of conservation concern. Consider a plant species infected by a fungus. Local populations of the plant are likely to have lower effective population sizes, and the fungus may be more effective at long-distance dispersal. If so, the fungus can maintain its local genetic diversity, even as the plant loses its genetic pool. This means that remnant plant populations face a long-term risk of severe epidemics, and even extinction, because of a stream of novel pathogen genotypes that immigrate and little genetic reservoir from which the plant can mount an adaptive response. More broadly, coevolutionary systems often display geographic mosaics (Thompson 1997). Habitat fragmentation disrupts spatial coupling and so is likely to impact ongoing evolution in many coevolutionary interactions.

Hochberg and van Baalen (1998) examined coevolution of exploiter–victim systems along gradients in victim productivity. For a broad range of models, the interaction evolves toward greater intensity when productivity is high (e.g., as measured by the investment of each species in attack and defensive strategies). The reason is that productivity passes from lower to higher trophic levels, which results in greater impacts of the higher trophic levels when productivity is higher. This translates into a greater selection intensity on the trophic interaction relative to other selective factors. Further, because different genotypes are favored at different productivities, genetic diversity as a whole is maximized when there are viable populations present along all the productivity gradient. This is one rationale for conserving marginal habitats in addition to core productive habitats. It also suggests that anthropogenic impacts upon ecosystem processes could indirectly

influence coevolution of natural exploiter–victim systems in a variety of ways. For instance, with carbon enrichment plants might have higher carbon:nitrogen ratios, and thus be lower in quality for herbivorous insects. All else being equal, this would reduce the productivity of these insects for their own specialist parasitoids and other natural enemies, which then become less important as limiting factors, and evolve toward lower effectiveness.

17.5 Local Evolution versus Biological Invasions

Biological invasions represent, after habitat loss and fragmentation, one of the most important environmental changes and threats to biodiversity. How does local evolution in ecosystems interact with biological invasions? The two processes bear some resemblance, since in both processes a rare local mutant or external immigrant progressively invades a community. However, the two processes do not necessarily obey the same constraints, and thus can have distinctly different consequences. To illustrate this, we discuss some potential implications of our evolutionary analysis of plant–herbivore interactions for situations in which there is a trade-off in plants between growth and resistance to herbivory.

Our analysis shows that plant evolution usually leads to a single CSS, and thus that herbivore-mediated plant coexistence may be ecologically, but not evolutionarily, stable. Since a CSS is a strategy that cannot be invaded by any close mutant strategy, once local evolution has produced this CSS, the community is likely to be resistant to invasion by another plant species that obeys the same trade-off (Figure 17.5). Species that originate from the same regional pool are likely to share a common history of environmental constraints, selective pressures, and phylogenetic relationships, and hence are more likely to obey the same trade-off than exotic species. Thus, local evolution should result in resistance to invasion by species from the same regional pool.

In contrast, if the immigrant is an exotic species that is not subject to the same trade-off as the resident, the community is much less likely to be resistant to invasion. Various scenarios are possible, with either invasion failure, ecological coexistence, or competitive displacement of the resident community (Figure 17.5). In particular, if the exotic species escapes herbivory because local herbivores are not adapted to consume it, it is generally better able to deplete the limiting nutrient, and hence to outcompete resident plants, which require higher nutrient availability to compensate for their additional losses to herbivory. Since extinction of the resident plant also entails extinction of the resident herbivore, a catastrophic outcome with displacement of the resident community by the invader may be likely. Local evolution of the invader after its establishment in the community makes this catastrophic outcome even more likely, because, being free from the selective pressure of herbivory, the invader can evolve toward a pure strategy of allocating all its resources to nutrient uptake, which further increases its competitive ability. Several examples of successful invasion by exotic species may conform to this theoretical scenario (Blossey and Nötzold 1995).

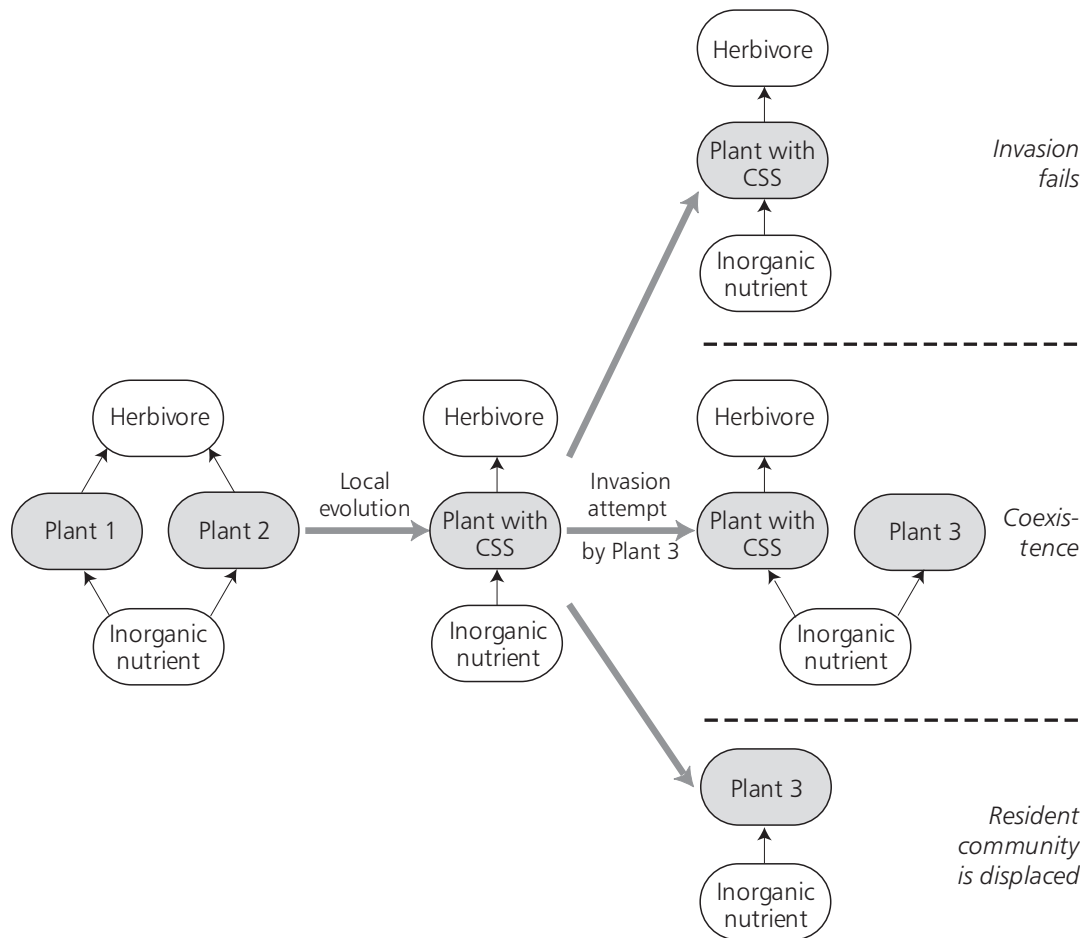


Figure 17.5 Theoretical scenarios for the ecological and evolutionary dynamics of simple nutrient–plant–herbivore communities in which local evolution and biological invasion of plants occur with a trade-off between growth and resistance to herbivory. If the potential invader obeys the same trade-off as the resident species and is consumed by the herbivore, invasion usually fails (top right). If, by contrast, the potential invader escapes herbivory, three cases are possible: invasion fails, the invader coexists with the resident (middle right), or the resident community is displaced by the invader (bottom right).

This suggests that local evolution may increase resistance to invasions by species from the same historical and biogeographic origin, and at the same time be impotent against invasions by exotic species that do not share the same evolutionary history, in particular the same history of herbivory, as the resident species. Local evolution is no guarantee against the disruption of local communities by some invasive exotic species, which are, indeed, a major threat to biodiversity.

17.6 Concluding Comments

Focusing on plant–herbivore interactions as major determinants of ecosystem patterns and processes, we show that the ecosystem is the proper context within which evolution shapes species’ traits. In particular, nutrient cycling is a key ecosystem process that transmits predictable indirect effects in ecosystems. These indirect

ecological effects can be so strong as to prevail over direct effects and exert effective selective pressures on the species involved, provided that there is sufficient spatial heterogeneity in the system or trade-offs exist between traits associated with the direct and indirect effects. Such effects are even able to change the nature of plant–herbivore interactions from antagonistic to mutualistic, both in an ecological and in an evolutionary sense, under some predictable conditions. We also argue that local evolution in ecosystems is likely to increase the resistance to invasions by species from the same historical and biogeographic origin, but at the same time be impotent against invasions by exotic species that do not share the same evolutionary history.

An evolutionary perspective on conservation is useful for two basic reasons. First, an understanding of evolutionary history can provide organizing principles that are useful to identify the sensitivity of species to different components of environmental degradation (Holt 1995). Second, evolutionary dynamics themselves can lead to a dramatic transformation in a species' ecological properties over short time scales (Thompson 1998). Feedback with the environment can also be important over short time scales. A comprehensive evolutionary conservation biology has to merge ecosystem- and population-level perspectives to predict the responses of ecological systems to environmental degradation.

This strongly suggests that conservation efforts should not only aim to preserve species, but also to preserve the rich web of interactions in which species are embedded in natural ecosystems, and which determine their current traits and persistence. Awareness of this need, however, provides no guarantee against species' extinction and ecosystem disruptions that are likely to result from environmental changes such as biological invasions.

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