

Evolutionary Processes in Ecosystems

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Volume 2, **The Earth system: biological and ecological dimensions of global environmental change**, pp 292–297

Edited by

Professor Harold A Mooney and Dr Josep G Canadell

in

Encyclopedia of Global Environmental Change
(ISBN 0-471-97796-9)

Editor-in-Chief

Ted Munn

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Evolutionary Processes in Ecosystems

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Environmental changes are major drivers of evolutionary changes. Although evolution is typically a slow process, there is increasing evidence that the time-scale of evolution can be shorter than previously believed under strong selective pressures.

The prediction and understanding of these evolutionary changes and their implications, however, require identification of the proper context of constraints within which natural selection operates. The ecosystem provides such a context, because an organism's environment is made up of interacting biotic and abiotic components which constitute a local ecosystem. Ecosystem processes can channel selection in different directions from those expected in the absence of these constraints. In particular, nutrient cycling is a key process which transmits predictable indirect effects in ecosystems. These indirect effects can be so strong that they 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 between traits associated with the direct and indirect effects.

Thus, the merging of evolutionary and ecosystem perspectives, which have been increasingly separated in modern ecology, is fundamental to predict the responses of ecological systems to environmental changes.

ENVIRONMENTAL CHANGES AND EVOLUTIONARY PROCESSES

All organisms experience environmental changes continuously. Many of these changes, however, are regular or frequent enough so that organisms can adapt to them. Diurnal or seasonal cycles, for instance, are so regular and predictable for most organisms that they are perceived as an integral part of a constant environment. Other changes are catastrophic or directional, and impose new environmental conditions on organisms, either suddenly or gradually. Most environmental changes generated by human activities – habitat destruction, biological invasions, changing atmospheric composition, global warming, and pollution – are of that kind. What distinguishes them from similar changes in the past is their rhythm and scale, which are, in many respects, unprecedented.

Faced with such changes, organisms have three basic alternatives: to migrate, adapt, or die. Catastrophic changes, such as habitat destruction, often result in

massive mortality, population extinctions, and eventually, species extinctions. This is the unfortunate fate of an increasing number of species today. More gradual changes, such as climatic changes, often result in progressive migrations and shifts in species distributions, as testified by palaeoecological records. A less obvious but widespread outcome is the adaptation to changed conditions through the evolution of species traits.

Evolution is ultimately the result of three basic processes: mutation, which generates genetic variability within populations; genetic drift, which increases genetic variability among populations; and selection, which reduces genetic variability selectively within populations. There is increasing evidence that environmental stress can directly affect mutation frequencies or the expression of accumulated *silent* mutations in organisms as different as bacteria or fruit flies (Pennisi, 1998; Rutherford and Lindquist, 1998), thereby increasing the genetic variability allowing rapid evolution. It is also known that habitat fragmentation and population subdivision favor genetic drift, and ultimately, speciation; this is the basis of the widely accepted model of allopatric speciation, in which new species are formed in geographically distinct areas. Finally, environmental changes modify the adaptive landscape of species and the selective pressures that are exerted on them; they determine the direction in which natural selection drives evolution. Thus, environmental changes are major drivers of evolutionary changes, and ultimately, of the generation of species diversity. This shows that they are not intrinsically detrimental to biodiversity. The current (and unfortunately, mostly future) biodiversity crisis is fundamentally a problem of the rhythm and scale of environmental changes. Massive numbers of species are currently driven to extinction without being replaced by new species because evolution simply cannot keep pace with the current environmental changes for most organisms.

Evolution is typically a slow process because it is based on changes in gene frequencies between generations. However, there is increasing evidence that the time-scale of evolution can be shorter than previously believed under strong selective pressures i.e., in the order of a few generations (Thompson, 1998). This is still long in *human* time-scales for long-living organisms such as trees, but it may be very fast for short-lived organisms such as bacteria. Even in vertebrates, significant evolutionary changes have been documented in the field over a period of a few years, using long-term experiments or observations of populations under changing conditions (Grant and Grant, 1995; Reznick *et al.*, 1997; Losos *et al.*, 1997). Small organisms with short generation times and high population abundances can even adapt to genuine environmental catastrophes. The most dramatic examples of such rapid evolutions include the resistance of bacteria to antibiotics and the resistance of pests to insecticides. These examples point to the limits

of our ability to control nature, even when we orchestrate large-scale chemical or biochemical catastrophes to destroy the organisms in question. Thus, the potential for, and implications of, evolutionary changes resulting from environmental changes cannot be ignored.

THE ECOSYSTEM AS THE PROPER CONTEXT OF NATURAL SELECTION

Predicting and understanding these evolutionary changes and their implications, however, requires identification of the proper context of the constraints within which natural selection operates. Traditionally, evolutionists have considered constraints to be internal to the organisms, such as from allocations among competing needs. In the classical view, the environment is regarded as external to the organism and constant (Figure 1A). Although most evolutionary biologists today would probably agree that this view is an oversimplification of reality, it has been, and still is, widely used in theoretical evolutionary biology as an implicit conceptual framework because of its simplicity. The modern view of natural selection recognizes that organisms modify and interact with their environment, which generates an organism–environment feedback in the operation of natural selection (Figure 1B; Lewontin, 1983). However, in order to understand the full implications of this feedback, it is further necessary to resolve an organism’s environment into its real physical, chemical and biological constituents and their interactions. This is what I call the ecosystem

view of natural selection, for an ecosystem is precisely a local system of interacting biotic and abiotic components (Figure 1C). Since each organism’s environment is constituted by other organisms or components, the ecosystem concept contains both the organisms and their environments, and thus, transcends the duality between organism and environment. 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 and evolutionary ecology on one hand, and ecosystem ecology on the other hand.

Feedbacks via ecosystem processes can channel selection in different directions to those expected in the absence of these constraints. As an example of a simple organism–environment feedback that has this property, consider the effect of changing soil nutrient supply on the evolution of plant antiherbivore defense. The classical resource availability hypothesis (Coley *et al.*, 1985) predicts that low resource availability favors plants with inherently slow growth rates, which in turn favors large investments in antiherbivore defense. This hypothesis has been influential and attractive because it seemed to explain the patterns of plant defense and herbivory in a wide range of ecosystems. It hinges, however, on a simple theoretical argument with a number of simplifying assumptions, in particular, the assumption that the amount of available resources is unaffected by plants. This implicit assumption of a constant environment led Coley *et al.* (1985) and subsequent authors to measure plant fitness by what they called the plant *realized growth rate*, which, in effect, is a potential growth rate which 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 spatially structured, fitness is determined by the basic reproductive rate (Loreau, 1998).

Taking into account this plant–resource feedback explicitly changes the theoretical predictions altogether (Loreau and de Mazancourt, 1999). If the environment is homogeneous, with all plants having equal access to the limiting nutrient, and the plant–nutrient system is allowed to reach an ecological equilibrium, the evolutionary optimal defense investment is determined by features of the plant–herbivore

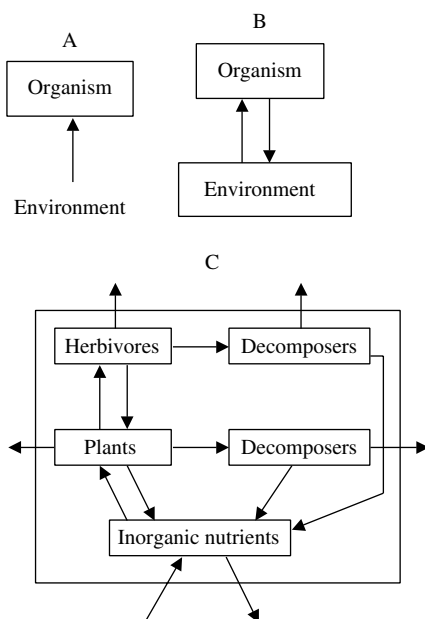


Figure 1 Three views on how natural selection operates: (A), the ‘classical’ view; (B), the ‘modern’ view; and (C), the ‘ecosystem’ view

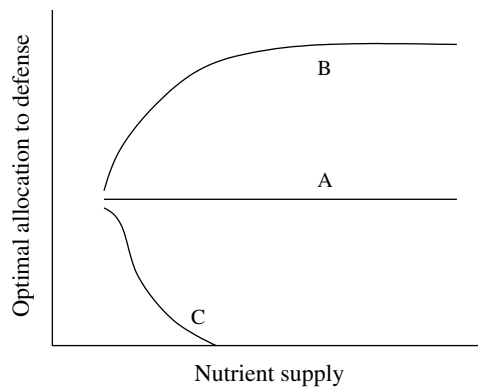


Figure 2 Evolutionary optimal plant allocation to defense as a function of nutrient supply. Optimal defense investment is: (A) independent of nutrient supply in most cases i.e., when either the environment is homogeneous, or the environment is spatially structured and plant fitness is proportional to the part of biomass that is mobilized for growth or to total productivity; (B), increases with nutrient supply when plant fitness is proportional to total biomass; and (C), decreases with increasing nutrient supply when plant fitness is proportional to the part of productivity that is allocated to growth. (Loreau and de Mazancourt, 1999)

interaction, but is independent of both plant maximum growth rate and nutrient availability. If the environment is spatially structured and competition obeys a competitive lottery for vacant sites, the outcome is strongly dependent on the factor that determines a plant's ability to produce successful propagule establishment in vacant sites, which, in itself, determines fitness. The optimal defense investment may then either increase, stay constant or decrease with nutrient supply (Figure 2). Thus, the classical view that lower resource availability favors evolution towards larger investment in antiherbivore defense has little theoretical support once the interaction between plants and their limiting resources is taken into account.

EVOLUTION OF INDIRECT INTERACTIONS IN ECOSYSTEMS

Many indirect interactions, and hence, of indirect organism–environment feedbacks, are likely to occur among organisms because of the complexity of ecosystems (Puccia and Levins, 1985; Wootton, 1994). These indirect effects can be 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, thus transmitting predictable indirect ecological effects and evolutionary constraints to their component species. Thus, plants (*autotrophs*) and decomposers (*heterotrophs*) are involved in an indirect mutualistic interaction through the cycling of limiting nutrients, such as nitrogen or phosphorus. The ecological and evolutionary

dynamics of this indirect interaction can explain broad-scale successional and evolutionary trends in the functional properties of ecosystems, in particular those towards increased productivity and biomass, a decreased productivity/biomass ratio, and tighter nutrient cycles (Loreau, 1998).

A more controversial, but illuminating case of the mutual dependency between autotrophs and heterotrophs generated by material cycling is provided by plant–herbivore interactions. These interactions have been traditionally regarded as antagonistic because herbivores have a negative direct effect on plants through biomass consumption. This view, however, has been challenged by the *grazing optimization hypothesis*, which states that primary productivity, or even plant fitness, is maximized at an intermediate rate of herbivory (Owen and Wiegert, 1976; McNaughton, 1979; Hilbert *et al.*, 1981). One mechanism capable of producing grazing optimization is nutrient cycling, which mediates a positive indirect effect of herbivores on plants. Although this hypothesis has been hotly debated (e.g., Silvertown, 1982; Belsky, 1986; Paige and Whitham, 1987; Bergelson and Crawley, 1992; Belsky *et al.*, 1993; Lennartsson *et al.*, 1997), recent theoretical work has been able to identify general rules that govern grazing optimization in the form of increased primary production through cycling of a limiting nutrient (Loreau, 1995; de Mazancourt *et al.*, 1998). Qualitatively, this requires that: (1), the proportion of nutrient lost while flowing along the herbivore recycling pathway is sufficiently smaller than the proportion of nutrient lost while flowing in the rest of the ecosystem; and (2), nutrient inputs into the system exceed a threshold value, which depends on the sensitivity of the plant uptake rate to soil mineral nutrient. These results are very general; they do not depend on the structure of the ecosystem or on the functional form of herbivore consumption. They are also potentially relevant to natural ecosystems (de Mazancourt *et al.*, 1999).

Does this imply that ecosystem-level constraints make the plant–herbivore interaction actually mutualistic, not antagonistic? The evolutionary consequences of grazing optimization, and of ecological indirect interactions in general, are complex, for two main reasons. First, increased plant productivity does not necessarily translate into increased plant fitness. Second, when it does, it is not absolute, but relative fitness that counts. 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.

Two factors, however, counteract this advantage of antiherbivore defense. First, the spatial structure of the

plant–herbivore system can generate spatially heterogeneous nutrient cycling (de Mazancourt and Loreau, 2000). If herbivores recycle nutrients in the vicinity of the grazed plants, or plants from the same type are aggregated, herbivores tend to recycle proportionally more nutrient on the plants that are more heavily grazed, thus augmenting the indirect benefit of grazing for the grazed plants. Evolution is then governed by the balance between two conflicting levels of selection (Wilson, 1980): (1), individual selection within patches, which favors the resistant type over the tolerant one because it has a higher relative fitness; and (2), 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 depends on the strength of spatial aggregation and patch size; tolerance to grazing will evolve provided that the spatial aggregation is strong enough or the patch size is small enough (de Mazancourt and Loreau, 2000).

The second factor that counteracts the advantage of antiherbivore defense is its cost in terms of nutrient investment, which generates a trade-off between defense and nutrient uptake in plants. A theoretical study of plant adaptive dynamics (Dieckmann, 1997) in a spatially structured model ecosystem shows that, for most ecologically plausible trade-offs, plant evolution then leads to a single *continuously stable strategy* i.e., a strategy to which evolution converges and which cannot be invaded by any other close strategy (de Mazancourt *et al.*, in preparation). This evolutionary strategy has complex relationships with the strategies that maximize plant production or plant biomass, depending on ecosystem parameters. Due to this complexity, different ecological and evolutionary scenarios of herbivore addition or removal are possible, which highlight the ambiguity of the notion of ‘mutualism’. It is 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 (de Mazancourt *et al.*, in preparation). The conditions for an evolutionary mutualism are more stringent than those for an 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).

When a plant’s reproductive ability is determined by its productivity, herbivory is indeed capable of improving plant performance on both an ecological and an evolutionary time-scale, provided that the herbivore recycling efficiency

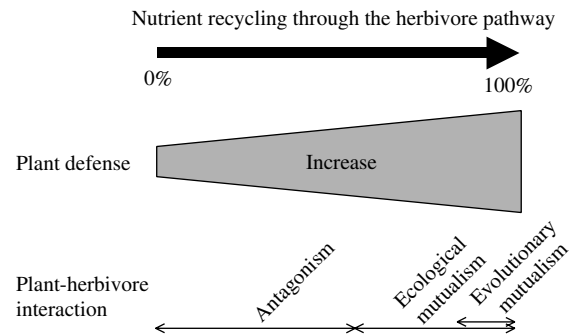


Figure 3 Changes in the plant–herbivore interaction along a gradient of increasing herbivore nutrient recycling efficiency, under the assumption that plant reproductive ability is proportional to plant productivity. Plant defense increases as herbivores are more efficient at recycling the nutrient, but at the same time, the interaction becomes increasingly mutualistic. (de Mazancourt *et al.*, in preparation)

is sufficiently greater than plant recycling efficiency, thus generating a plant–herbivore mutualistic interaction. As expected, the requirements on herbivore recycling efficiency are more stringent for an evolutionary mutualism than for an ecological mutualism. Surprisingly, however, 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 less defended plants (Figure 3). Thus, mutualism can go hand in hand with increased conflict between partners. Although paradoxical at first sight, such evolutionary conflicts are also known in other mutualistic interactions (Anstett *et al.*, 1997; Law and Dieckmann, 1998).

CONCLUSION

Evolutionary processes are capable of leading to a significant transformation in species ecological properties over relatively short time-scales. However, the evolutionary dynamics of species are embedded in the dynamics of ecosystems as complex systems of interactions among species. Species traits and the evolution of species traits are ultimately constrained by ecosystem processes, just as ecosystem properties are constrained by the ecological and evolutionary history of interacting species. Indirect effects mediated by ecosystem processes 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 between traits associated with the direct and indirect effects. They are even able to change the nature of species interactions, both in an ecological and

an evolutionary sense. Thus, merging the evolutionary and ecosystem perspectives, which have been increasingly separated in modern ecology, is fundamental to predict the responses of ecological systems to environmental changes.

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