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INVITED CONTRIBUTION

Linking community, evolutionary and ecosystem ecology: another perspective on plant-herbivore interactions

Michel Loreau

Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure,
46 rue d'Ulm, F-75230 Paris Cedex 05, France

ABSTRACT. Community ecology, evolutionary ecology and ecosystem ecology provide different perspectives on ecological systems, and have followed increasingly divergent pathways for decades. Integration of these perspectives is now critical to progress in our understanding of species interactions and ecological systems. A vivid example of the complexity generated by ecosystem processes on the very nature of species interactions is provided by the effect of material cycling on the ecology and evolution of plant-herbivore interactions. Even though they have a direct negative effect on plants through biomass consumption, herbivores can have a positive indirect effect on plant productivity through nutrient recycling. Theory shows that this indirect effect can be so strong as to prevail over the direct effect 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, an exploitative interaction can turn into an ecological, and even an evolutionary, mutualism through ecosystem-level constraints. Species traits and 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. Therefore, merging the evolutionary and ecosystem perspectives, which have been increasingly separated in modern ecology, is fundamental to predicting the responses of ecological systems to environmental changes.

KEY WORDS: Plant-herbivore interactions, ecosystems, evolution, nutrient cycling, grazing optimisation, indirect mutualism.

INTRODUCTION

The vigorous growth of ecology from its origins as a distinct scientific discipline in the early years of this century has been accompanied by the creation of numerous subdisciplines. Although specialisation may be inevitable, it also creates problems. The conceptual frameworks in each area tend to become increasingly divergent over time, hampering communication across the discipline as a whole. This divergence is nowhere more apparent than between two of the major subdisciplines of ecology: population and community ecology on the one hand, and ecosystem ecology on the other hand. These two subdisciplines have grown largely independently, each having its own concepts, theories and methodologies. Ecosystem ecology is mainly concerned with the functioning of the overall system composed of biological organisms and their abiotic environment; its object is the flow of matter or energy among functional compartments; it emphasises physical and chemical constraints, and regularity and predictability at the system level. Population and community ecology is mainly concerned with the dynamics of the biological components of ecosystems; its object is biological diversity, the populations of organisms and their interactions with other populations; it emphasises biological constraints, and change and variability within systems. A third subdiscipline, evolutionary ecology, focuses on changes at long, evolutionary time-scales. It has traditionally had strong links with population and community ecology, but there has been virtually no cross-fertilisation with ecosystem ecology.

This separation of subdisciplines is understandable insofar as they partly address issues at different hierarchical levels and different spatial and temporal scales. But it is harmful insofar as it is an obstacle to their unity and mutual enrichment. In the real world, populations and communities

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Corresponding author: M. Loreau, e-mail: loreau@ens.fr do not exist in isolation; they are parts of ecosystems, and, as such, they are subjected to constraints arising from ecosystem functioning, in particular energy dissipation and nutrient cycling. These constraints can deeply alter the nature of species interactions and community properties such as food-web stability. On the other hand, ecosystems do not exist without their biological components; the latter impose their own constraints on ecosystem processes, as the disruptions generated by some biological invasions attest. In the face of the growing threat of a massive loss of biological diversity, an increasing interest is being taken in the role of biodiversity in ecosystem processes. Therefore there is today an urgent need for integration of the different perspectives (JONES & LAWTON, 1995; LOREAU, 2000). This need is felt particularly acutely at the theoretical level, where new approaches must be devised to lay conceptual bridges across subdisciplines. Theoretical studies of that kind have been few so far, but they are developing fast, and are stimulating the emergence of a new area at the interface of community, ecosystem and evolutionary ecology.

NATURAL SELECTION WITHIN ECOSYSTEMS

It is useful to start with one of the fundamental concepts of evolutionary biology, namely, natural selection. Predicting and understanding evolutionary changes and their implications require identifying the proper context of constraints within which natural selection operates.

Traditionally, evolutionary biologists considered constraints to be internal to the organisms, such as from allocations among competing needs. On this classical view, the environment is regarded as external to the organism and constant. The modern view of natural selection recognises that organisms modify and interact with their environment, which generates an organism-environment feedback in the operation of natural selection (LEWONTIN, 1983). The simplest way to obtain such a feedback is through frequency-dependent selection within a population. But there are many other ways – whether physical, chemical or biological – by which organisms modify their environment. In order to understand the full implications of the organism-environment feedback, it is further necessary to break up 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 (LOREAU, 2001). Since each organism's environment is constituted by other organisms or components, the ecosystem concept contains both the organisms and their environments. In that sense, it provides a higher-level perspective that transcends the duality between organism and environment. Recognising 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 more applied areas, such as conservation biology and ecosystem management.

A multitude of indirect interactions is likely to occur among organisms because of the complexity of ecosystems (PUCCIA & 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 (LOREAU, 1998). How do these constraints affect the interactions and evolution of species? Plant-herbivore interactions provide a controversial but illuminating case of this question. In what follows I focus on these interactions as one example illustrating the importance of integration of community, evolutionary and ecosystem ecology, and the fundamental enrichment that it makes possible.

GRAZING OPTIMISATION: HOW PLANTS BENEFIT FROM HERBIVORES

> *"Coupled transformers are presented to us in profuse abundance, wherever one species feeds on another, so that the energy sink of the one is the energy source of the other.*
>
> *A compound transformer of this kind which is of very special interest is that composed of a plant species and an animal species feeding upon the former. The special virtue of this combination is as follows. The animal (catabiotic) species alone could not exist at all, since animals cannot anabolise inorganic food. The plant species alone, on the other hand, would have a very slow working cycle, because the decomposition of dead plant matter, and its reconstitution into CO_2, completing the cycle of its transformations, is very slow in the absence of animals, or at any rate very much slower than when the plant is consumed by animals and oxidized in their bodies. Thus the compound transformer (plant and animal) is very much more effective than the plant alone."* (LOTKA, 1925, p. 330)

The idea that animals are detrimental to their food resources is deeply engraved on our civilisation, both culturally and economically. The need for a smooth functioning of the economy imposes a constant fight against other animal species feeding on our plant food resources, which are therefore viewed as undesirable pests from which we must protect ourselves. Ecology as a science has had to establish a more balanced view of nature. The above quote from LOTKA (1925) shows the grand view that early ecologists attempted to develop. Since then, however, even in ecology, plant-herbivore interactions have been regarded as essentially antagonistic because herbivores have a negative direct effect on plants through biomass consumption.

This traditional view has been challenged again recently by the "grazing optimisation hypothesis", which states that primary productivity, or even plant fitness, is maximised at an intermediate rate of herbivory (OWEN & WIEGERT, 1976, 1981; MCNAUGHTON, 1979; HILBERT et al., 1981). This hypothesis is supported by some empirical data, notably from the Serengeti grassland ecosystem (MacNaughton, 1979). One mechanism capable of producing grazing optimisation is nutrient cycling, which mediates a positive indirect effect of herbivores on plants. 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 at the heart of a recent controversy (e.g., Silvertown, 1982; Belsky, 1986; McNaughton, 1986; Belsky et al., 1993; Lennartsson et al., 1997).

Given the ambiguity in interpretations of empirical data, we have attempted to answer these questions theoretically, using mathematical models. We have first identified the ecological conditions under which herbivores increase primary production and lead to grazing optimisation through nutrient cycling in nutrient-limited ecosystems at equilibrium (Figs 1 and 2). These conditions are two: (1) nutrient inputs (as determined by inward arrows in Fig. 1) into the ecosystem must exceed a threshold value, which is determined by the sensitivity of plant uptake rate to soil mineral nutrient, and (2) the proportion of nutrient lost along the herbivore recycling pathway must be sufficiently smaller than the proportion of nutrient lost along the plant recycling pathway (Loreau, 1995; de Mazancourt et al., 1998). Contrary to what has been assumed traditionally, nutrient turnover rates have no impacts on 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. They are also potentially relevant to natural ecosystems: grazing optimisation 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 & Loreau, 2000b).

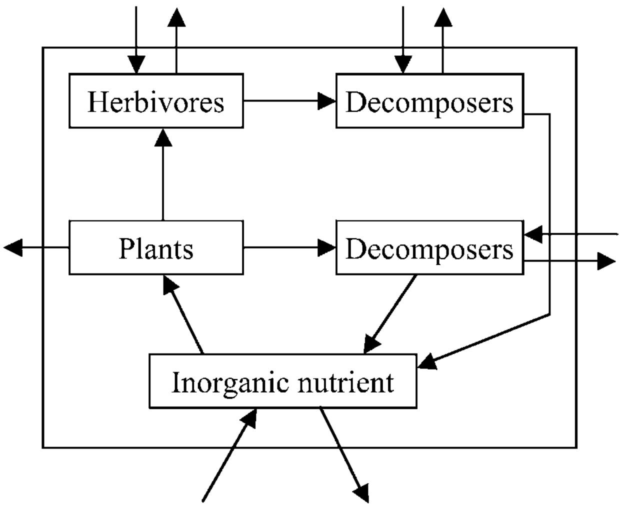

Fig. 1. – Flow diagram of the theoretical ecosystem model used to investigate the ecological conditions for grazing optimisation through recycling of a limiting nutrient. After Loreau (1995) and de Mazancourt et al. (1998).

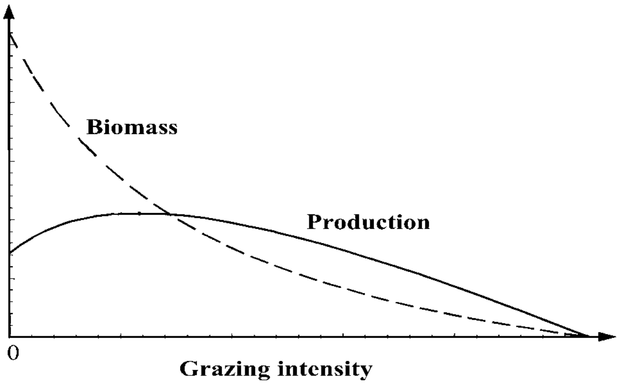

Fig. 2. – Typical grazing optimisation curve obtained for primary production at equilibrium using the model described in Fig. 1. Plant biomass, however, always decreases as grazing intensity increases. After de Mazancourt et al. (1998).

THE EVOLUTIONARY PUZZLE

Does this imply that ecosystem-level constraints make the plant-herbivore interaction actually mutualistic, not antagonistic? The evolutionary consequences of grazing optimisation, 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. It is still unclear which plant traits determine fitness. If the seed production or other measures of fitness of a plant are mainly determined by its biomass, then no mutualistic interaction with herbivores is possible, because plant consumption by herbivory always decreases plant biomass (Fig. 2). On the other hand, if a plant's fitness is mainly determined by its productivity, 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, 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 (Fig. 3). As a result, tolerance should

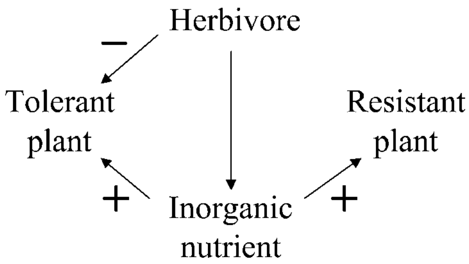

Fig. 3. – The evolutionary puzzle: if two plant types are mixed, one of them being tolerant and the other resistant to herbivory, the resistant type is expected to outcompete the tolerant type because it benefits from the positive indirect effect of increased nutrient cycling but does not suffer the negative direct effect of herbivore consumption.

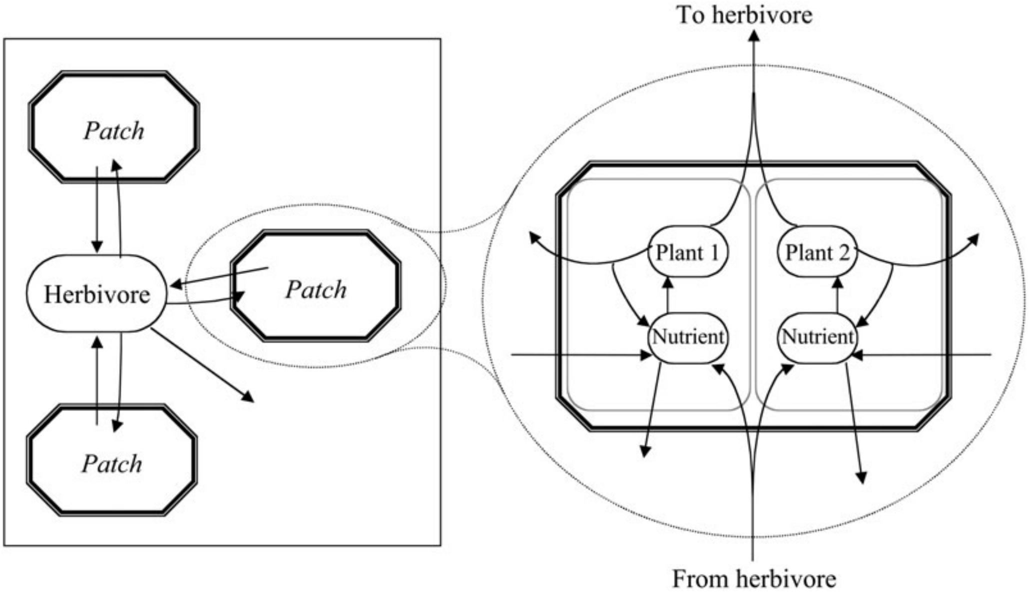

Fig. 4. – Flow diagram of the ecological model used to investigate evolution of plant palatability in a spatially heterogeneous environment. After DE MAZANCOURT & LOREAU (2000a).

not evolve even though it is indirectly beneficial. This might seem to spell the final end for the idea of any plant-herbivore indirect mutualism, indeed of any evolved indirect interaction, as some have suggested (BELSKY et al., 1993).

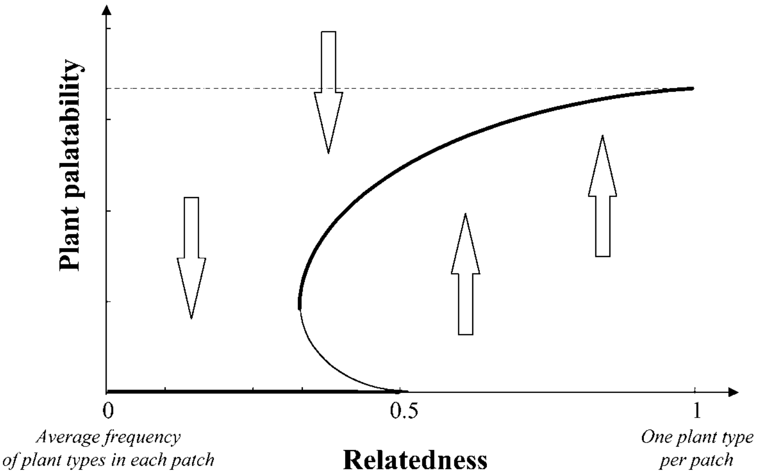

Fig. 5. – Evolutionary continuously stable strategy (CSS) of plant palatability (in bold) as a function of within-patch relatedness between plants in the model described in Fig. 4. Arrows show the direction of selection. The unpalatable plant type is always selected when within-patch relatedness is low (weak spatial heterogeneity or large patch size), but a palatable plant type can be selected when within-patch relatedness is high (strong spatial heterogeneity or small patch size). Horizontal dashed line: plant palatability that maximises primary production. After DE MAZANCOURT & LOREAU (2000a).

This conclusion is premature, however. Two factors counteract this advantage of antiherbivore defence. First, the spatial structure of the plant-herbivore system can generate spatially heterogeneous nutrient cycling (Fig. 4). 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 on the plants that are grazed more heavily, thus augmenting the indirect benefit of grazing for the grazed plants. Evolution is then governed by the balance between two conflicting levels of selection, just as in the evolution of altruism (WILSON, 1980): individual selection within patches, which favours the resistant type over the tolerant one because it has a higher relative fitness, and group selection between patches, which favours 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 evolves provided that spatial aggregation is strong enough or patch size is small enough (Fig. 5; DE MAZANCOURT & LOREAU, 2000a).

The second factor that counteracts the advantage of antiherbivore defence is its cost in terms of nutrient investment, which generates a trade-off in plants between defence and nutrient uptake. A theoretical study of plant adaptive dynamics (DIECKMANN, 1997) in a spatially structured model ecosystem shows that, for many ecologically plausible trade-offs, plant evolution then leads to a

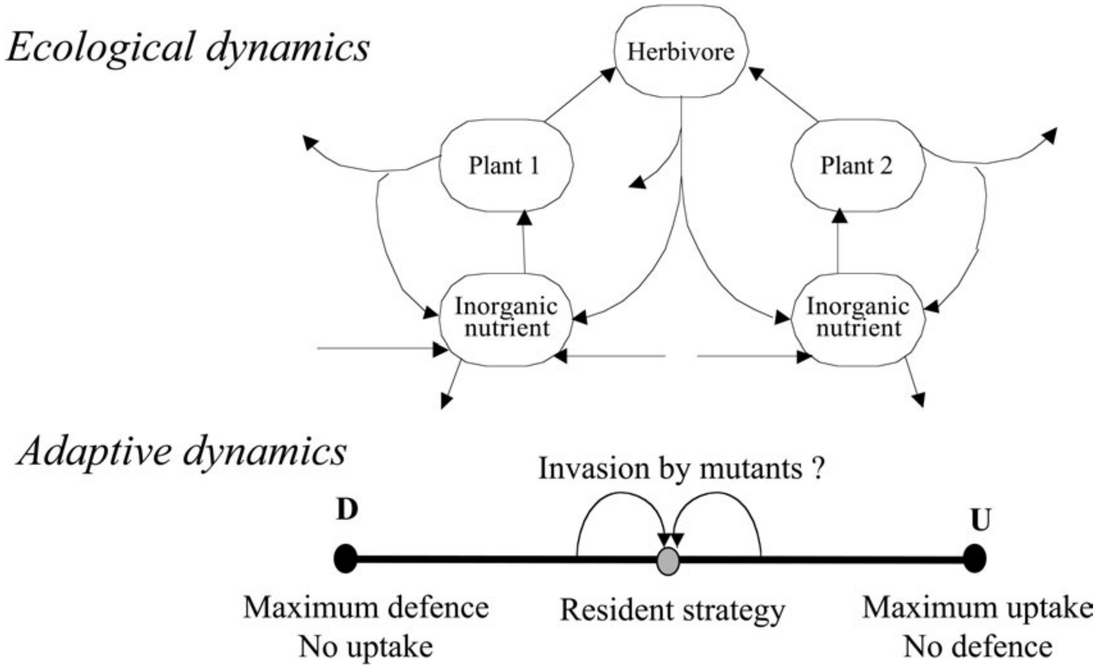

Fig. 6. – Principle of the theoretical model used to investigate evolution of plant defence subject to a trade-off with nutrient uptake (DE MAZANCOURT et al., 2001). Ecological dynamics as described in the flow diagram are assumed to unfold on a fast time-scale until an ecological equilibrium is reached. Adaptive evolutionary dynamics consists of successive invasions of resident strategies at ecological equilibrium by close mutants. Strategies are ordered along a trade-off between the two limiting cases of strategy D, in which plants invest all their resources into anti-herbivore defence, and strategy U, in which they invest all their resources into nutrient uptake.

single "continuously stable strategy" (CSS), i.e., a strategy to which evolution converges and which cannot be invaded by any other close strategy (Fig. 6). This evolutionary CSS has complex relationships with the strategies that maximise plant production or plant biomass, depending on ecosystem parameters. Because of 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 (BENDER et al., 1984; KREBS, 1985), and an evolutionary mutualism, in which the mutual benefit persists even after evolution has occurred (DE MAZANCOURT et al., 2001). 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 & SMITH, 1989; LAW & 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 herbivore recycling efficiency be sufficiently greater than plant recycling efficiency, thus generating a plant-herbivore mutualistic interaction. 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 defence because they gain a higher benefit from not being consumed relative to less defended plants (Fig. 7). Thus, mutualism can go hand in hand with increased conflict between partners. Although paradoxical at first sight, such evolutionary conflicts are known in other mutualistic interactions (ANSTETT et al., 1997; LAW & DIECKMANN, 1998).

CONCLUSION

From this example, we see that species traits may evolve in counter-intuitive ways as a result of the complex indirect effects mediated by functional processes at the level of whole ecosystems. These effects may even change the very nature of species interactions, both in an ecological and in an evolutionary sense, under predictable

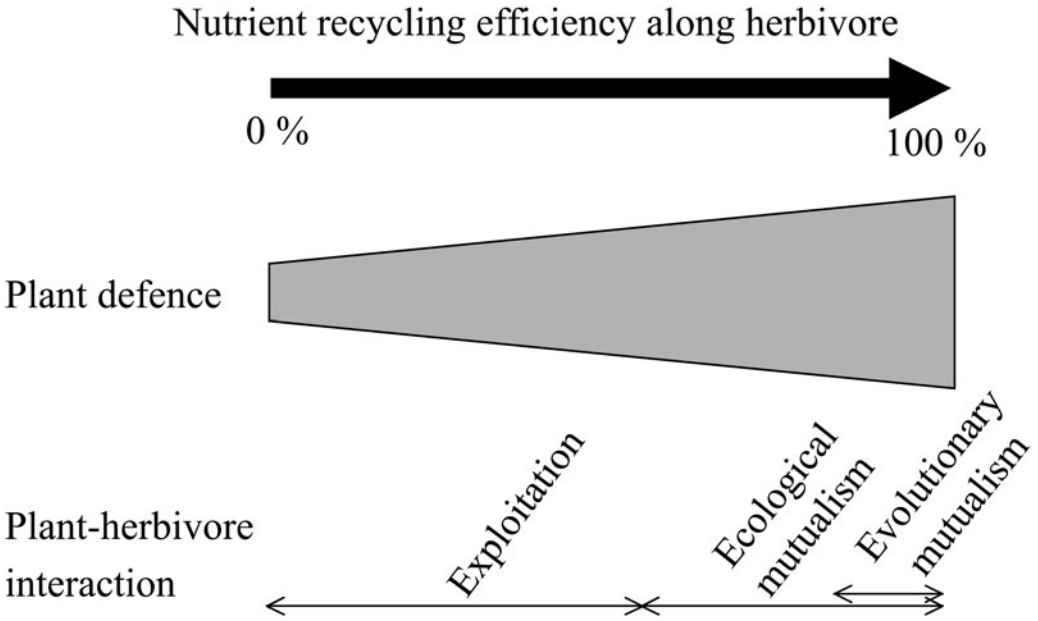

Fig. 7. – The paradox of evolution of plant antiherbivore defence: As herbivore recycling efficiency is increased, the plant–herbivore interaction becomes increasingly mutualistic (first ecologically, then evolutionarily), but plants evolve to increase their level of defence (DE MAZANCOURT et al., 2001).

conditions. Species traits and 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. Thus, merging the evolutionary, community-level and ecosystem-level perspectives, which have been increasingly separated in modern ecology, is fundamental to predict the responses of ecological systems to environmental changes, and provides mutual enrichment of the various subdisciplines. Lastly, if these theoretical considerations are correct, one implication is that conservation efforts should aim, not only to preserve species, but also to preserve the rich web of interactions in which species are imbedded in natural ecosystems, and which determine their current traits and persistence.

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Relation between Dopa Decarboxylase activity and paralytic activity in *Tenebrio molitor* and *Neobellieria bullata*

Jurgen Huybrechts, Stephen Kotanen, Arnold De Loof and Liliane Schoofs

K.U.Leuven, Laboratorium voor Vergelijkende Fysiologie en Morfologie der Dieren,
Naamsestraat 59, B-3000 Leuven

ABSTRACT. Paralysins are endogenous compounds in immature insects that cause paralysis or death in adult individuals after injection into the thorax. We have proven the universal effect of paralysins by injection of paralysins from *Neobellieria bullata* into adult *Tenebrio molitor* and vice versa. The toxic effect of the tested, 30% acetonitrile fraction from whole body homogenates depends on the stage of the insect from which the extraction was made. The activity of the paralysins shows a temporal distribution with the highest level at pupation and a second, smaller effect at eclosion.

The dopa decarboxylase (DDC) activity, measured by using a radioactive labeled substrate, in developing *N. bullata* and *T. molitor*, peaks at the most important moments in the development of the insect: at pupation but especially at eclosion.

The DDC enzyme could play an important role in the toxicity of paralysins. Relating the temporal distribution of toxic activity in both species to their correlated distribution of DDC activity shows the same pattern: DDC activity increases after stages that show high paralytic activity. Injection of β-alanine-L-tyrosine (BAY, a known paralysin of *Neobellieria bullata*) into the thorax of adult flies did not induce the DDC activity. So, this could be the key to the toxic effect of BAY, because injection of BAY into the thorax of juvenile (pupae) *Tenebrio molitor* did cause an induction of DDC activity.

KEY WORDS: dopa decarboxylase, paralysins, insects.

INTRODUCTION

Paralysins recently discovered in our lab are a new class of endogenous toxic substances found in juvenile insects that cause instant paralysis or death after injection of physiological concentrations into adults (CHIOU et al., 1998a). From *Neobellieria bullata* Parker, 1916, two paralysins were purified by means of HPLC. By means of Fast Atom Bombardment Mass Spectrometry and Nuclear Magnetic Resonance spectroscopy these substances were identified as β-alanine-L-tyrosine (BAY) and 3-OH-kynurenine (3HK). The first paralysin, BAY, (CHIOU et al., 1998b) is a dipeptide with a modified N-terminal amino acid. This paralysin was known long before but in other physiological circumstances (LEVENBOOK et al., 1969). It was named sarcophagine because it was the predominant non-protein ninhydrin-positive material in fully-grown larvae of *Neobellieria* (=*Sarcophaga*) *bullata*. Sarcophagine was found to be synthesised in the fat body and to accumulate in the larval hemolymph up to the moment of the formation of the white puparium. Thereafter, its concentration drops dramatically to almost undetectable levels. The reason for this decline is that at the moment of pupariation, hydrolases from the fat body degrade the dipeptide into the amino acids β-alanine and tyrosine, which are subsequently incorporated in the cuticle, to play a role in sclerotisation (BODNARYK & LEVENBOOK, 1969; DUNN et al., 1977). This is where DDC is implicated as this enzyme is responsible for the formation of products needed in sclerotisation. The enzyme displays a high substrate specificity in arthropods (LUNAN & MITCHELL, 1969) in contradiction to the homologous enzyme in mammals (FELLMAN, 1959; CHRISTENSON et al., 1970) where the enzyme carboxylases several aromatic amino acids. CHEN & HODGETTS (1976) studied the biochemical

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Corresponding author: J. Huybrechts,
e-mail: jurgen.huybrechts@ bio.kuleuven.ac.be