At the border between ecology and evolution

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The theory of evolution by natural selection is an ecological theory – founded on ecological observation by perhaps the greatest of all ecologists (Harper, 1967).

At the frontier between ecology and evolution" - everything seems curious in this title. Ecology and evolution, biodiversity sciences[1] indeed, but ecology is a science or a set of sciences, and evolution, a theory or a historical process. Why associate a science and a theory? And is there a borderline between the two, even though they are so often associated, if only (recently) in the name SFE2 (French society for ecology and evolution), or in the names of training courses, laboratories or university departments? Such a question would probably have seemed strange to Charles Darwin, an evolutionist and ecologist if ever there was one. But in fact, ecology and evolution have slowly separated since the end of the 19th century to form distinct fields of study, which are globally little connected. However, in the last twenty years or so, explicit attempts have been made to bring them together, and terms such as "eco-evolutionary dynamics" or "eco-evolutionary loop" have flourished (Vellend, 2016; Hendry, 2017), to the point where we have come to wonder whether any study of ecology or evolution is not eco-evolutionary (*i.e.* when an ecological change leads to an evolutionary change that will, in turn, affect the ecological interactions). I will defend here the idea that this is not the case, but that we can indeed affirm that some studies are really eco-evolutionary, and that it is necessary to widen this zone of hybridization in order to understand the dynamics of biodiversity in general, and to predict its future trajectories in particular.

A (small) bit of history and definitions

The separation, or distinction, between ecology and evolution has been a subject of reflection for a century. The structuring of the "new evolutionary synthesis" in the years 1930-1940, under the leadership of theorists such as R.A. Fisher or S. Wright, and empiricists such as T. Dobzhansky or E. Mayr (see e.g. Gayon, 1992), is probably not unrelated to this, any more than is the development of conceptual bases for ecology at the same time, under the impetus of personalities such as H. Gleason or F.E. Clements (whose positions are quite opposed). This

[1] I mean biodiversity in the current sense of the term, incorporating living entities and their environments.

separatist dynamic [possibly characteristic of sciences under construction or consolidation] was not lost on the protagonists of both camps, and gave rise to recurrent attempts at rapprochement (Futuyma, 1986; Huneman, 2019). For example, one can cite the classic book of Allee et al. (1949), which devotes a consistent section to this new synthesis, but it is more of an attempt to "acclimatize" the new synthesis, to use Huneman's (2019) expression, strongly marked by the proximity between W.C. Allee and S. Wright (both professors at the University of Chicago), than a real attempt to consider ecology and evolution in a fusional vision. As a reverse pathway, from evolution to ecology, we can consider ecological genetics, whose most famous proponent is E.B. Ford, or evolutionary ecology, which appeared in the 1950s and emphasizes life-history traits and their link with population demography (Huneman, 2017). However, in both cases, it is questionable whether the environment is little more than a "tapestry" (or background) whose structure and functioning are not of fundamental importance.

Prominent figures of the 1960s (e.g., R.H. McArthur, R. Levins, R.C. Lewontin or E.O. Wilson) also made attempts to think synthetically and to construct a conceptual framework in which simple models can play a supporting role in understanding eco-evolutionary processes, from individuals to biological communities. In fact, these attempts did not change the work programs in ecology and evolution, and the scientific communities remained very compartmentalized in the period 1970 to 2000. There are, however, some attempts and successes, such as the explicit consideration of demography in evolutionary biology (e.g., Charlesworth, 1980), or models that simultaneously consider species and material dynamics and their evolutionary consequences (e.g., Loreau, 2010). An explicit evolutionary framework for explaining the complexity of biodiversity can also be noted in the writings of prominent ecologists (Levin, 2000).

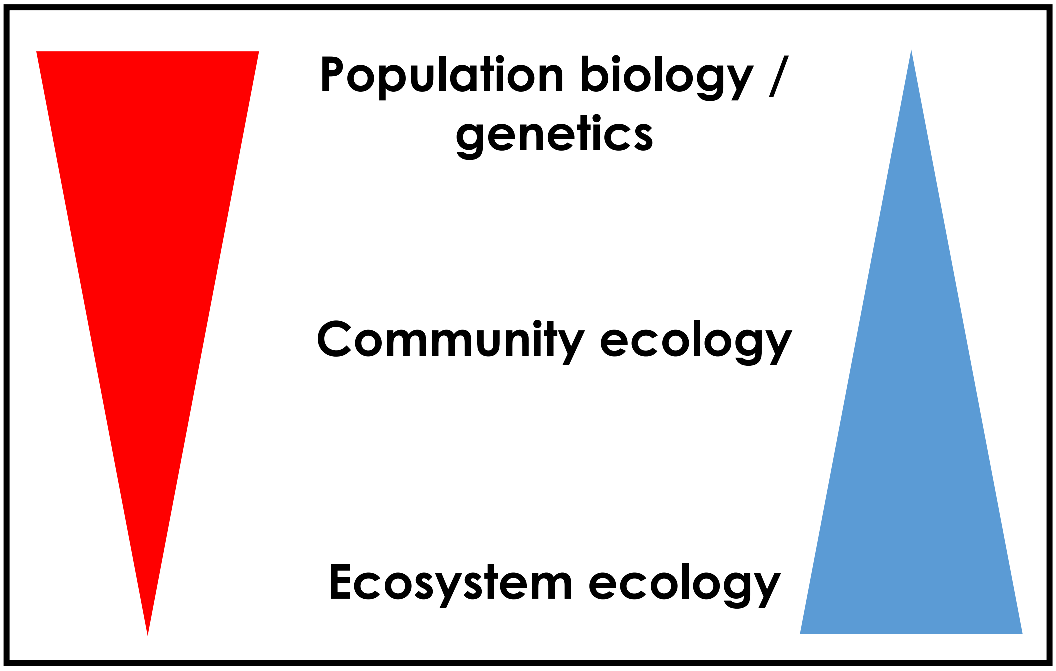

Figure 1: Simplified diagram of the decreasing impact of evolutionary theory (red triangle) in studies considering increasing levels of integration of biodiversity (blue triangle), moving from genes (population genetics) to ecosystems (ecosystem ecology). The blue triangle could also be seen as an indicator of space, with increasingly larger spatial scales (in general) toward the figure bottom.

I have talked about ecology and evolution so far without really defining them, except that they are at the heart of biodiversity sciences. Nor have the "border" been drawn. Let us start with a central point: ecology and evolution are interested in the dynamics of biodiversity, including all living organisms, in the forces and processes that drive it, in the reconstruction of its history and in the projection of its future (see Glossary). However, I would like to make a distinction here, admittedly somewhat artificial, in three vast fields of work in a partly hierarchical vision of living organisms: population biology (including genetics), community ecology and ecosystem ecology (Figure 1). Broadly speaking, we can say that population biology is concerned with evolutionary and ecological processes, from the individual level (genotype and phenotype) to the species level. Community ecology focuses rather on the assembly and dynamics of communities, and species play the central role. Ecosystem ecology is interested in the relationship between species and the environment, and perhaps even more so in environmental dynamics, in the flow of matter and energy in ecosystems. From population biology to ecosystem ecology, we thus move from a perspective where evolutionary thinking (and intraspecific diversity) plays a major role to one where ecology dominates, with a biological entry point centered on the species, or even the community (Figure 1). I insist on the fact that this is a caricatured vision, and one can note that demography has not been mentioned in these definitions. We will try to have a more nuanced approach in what follows, by exposing what separates and what brings together, before identifying what is truly eco-evolutionary.

Glossary

- Ecology: scientific ecology is a science (or set of sciences) that studies the interactions of living things with each other and with their environment. See e.g. Ricklefs & Relyea (2019) or https://en.wikipedia.org/wiki/Ecology.
- Epigenetics: the set of mechanisms or processes that modify gene expression without altering the nucleotide sequence, through reversible and transmissible (within or between generations) marking.
- Evolution: a gradual process of adaptation to the environment via (epi)genetic variation. Evolution is a theory that gave birth to the evolutionary sciences, such as evolutionary genetics or paleontology. For a detailed presentation, one can consult numerous books (e.g., David & Samadi, 2021) or an online encyclopedia (e.g., https:// https://en.wikipedia.org/wiki/Evolution).
- Ecological and evolutionary stability: we should talk about quasi-stability since no living system is stable (by definition). A system is stable if it can return to the same state (or approximately) after an environmental disturbance. This characteristic can be described by the term "resilience". Ecological equilibrium and evolutionary equilibrium are not necessarily the same thing, because evolution can lead to the emergence of new interactions between the elements of a system via mutation, for example, leading to new equilibria.
- Trait: we retain a broad meaning of phenotypic trait resulting from genetic or epigenetic expression. These traits can be molecular, individual (e.g. morphological) or more integrative such as life traits (e.g., age at first reproduction, longevity). They may also be functional, related to response to environmental factors (e.g., Violle et al., 2007; Garnier & Navas, 2013).

What separates, what brings together

Clearly highlighting what separates and brings together ecology and evolution in terms of concepts, ideas, approaches ... is not always easy because, as is often the case when dealing with sisters and brothers, what makes them diverge can also be a common point, all the more so as divergences and overlaps have evolved over time. I will limit myself to a few aspects that seem to me to be major, thus proposing a partial vision.

The nature of diversity. As mentioned above, ecology and evolution are interested in the same object, biodiversity; this means that the notion of variation, from the genotype to the ecosystem, plays a central role, because it is the fuel of the dynamics of ecological systems - ecological variation, evolutionary variation. Such variation plays a much lesser role in other areas of biology, and even less so in physics, which gives a special epistemological status to the biodiversity sciences. Of course, the emphasis is not on the same diversity, from the genotype for the geneticist to the trophic chain for the ecosystem scientist; the former, by focusing on a species, will readily dispense with interspecific relationships, whereas intraspecific diversity is not central to community or ecosystem ecology. However, over the last twenty years, there has been a strong desire for rapprochement, which takes different forms. If we look at the evolutionary side, a growing number of research programs are developing under natural conditions to fully account for environmental variation, while still often remaining focused on one species (Hendry, 2017). On the ecology side, the development of work aimed at understanding the relationship between specific diversity and ecosystem functioning now also takes intraspecific diversity into account, strongly driven by theoretical and conceptual developments (Violle et al., 2012; Vellend, 2016). Attempts to link genetic and specific diversities to explain community functioning, via the environment, is another convergence point between ecology and evolution (Lamy et al., 2017).

Selective value vs. material and energy flows. A comprehensive understanding of biodiversity dynamics can hardly ignore a common "currency". Population biology considers this to be the selective value (“fitness”), *i.e.* the number of offspring transmitted to the next generation by a gene, a genotype or an individual; a similar idea is found in community ecology, via the number of individuals produced by a species. Even if the unit considered is not the same, the dynamics is mediated by the number of units at generation N+1 produced by a unit at generation N (thus via individual dynamics), and this is what will measure the effect of natural selection or biotic interactions.

At the other end of the spectrum, ecosystem ecology has found its exchange value in flows, of matter or energy, thus much closer to physico-chemical approaches, and in particular to thermodynamic notions like entropy (and information). In the ecological psyche, this perspective is inevitably associated with the work of the Odum brothers, but also with generic hypotheses of the functioning of the earth such as Gaia (Lovelock, 1972). There will also appear here a thinking based on "complex systems" (Holling, 2001) which incorporates notions such as resilience, self-organization, complex adaptive systems, tipping point... all notions little used until recently in evolutionary biology, except in certain very theoretical approaches, and a little more in population dynamics (but see Nosil et al. 2021).

It seems difficult to directly transform a selective value into a flow, or the opposite, which do not concern the same entry into biodiversity - one rather on the biotic side and an emphasis on adaptation to the environment, the other on abiotic dynamics. However, selective value feeds on matter and energy, and the analysis of flows only makes sense for the understanding of biodiversity if these flows are embodied in units of selective value - this is even a foundation of functional ecology (Calow, 1987). One possible integration is through the simultaneous and coupled consideration of biotic and abiotic dynamics, for example by analyzing the link between physiology and selective value or via simple predator-prey models in which environmental dynamics (e.g., litter) depend on, and influence, the dynamics of predators and prey (Loreau, 2010). This type of models also allows us to understand the evolutionary dynamics of such systems.

Transmission and temporality. A key point of evolutionary theories is the transmission of genetic information (or epigenetics) from generation to generation, which depends on many processes, such as the reproductive system. These processes are themselves subject to natural selection, and therefore depend on environmental dynamics. For example, an environmental modification that reduces the density of a population, or in plants that of pollinators, can lead to a uniparental selection regime, since it becomes more difficult to find a partner to reproduce. We can thus see that environmental temporality interacts with evolutionary dynamics. However, for a long time, ecology was considered as the science of short timescales, and evolution as the science of long timescales - simply because it would take time for an evolutionary process to take place, and for a trait to become fixed. Of course, it took tens of millions of years (and many trials) for a fish to become a mammal or a bird, or for flowering plants to diversify. Of course, environmental conditions can change drastically over a very short period of time - recent climatic changes are a strong reminder of this - and can rapidly lead to variations in species occurrence in an ecosystem, or even to their disappearance.

However, work carried out over the last few decades has shown that ecological time and evolutionary time can overlap. For example, experimental evolutionary work (Box 1) by R. Lenski and his colleagues on the laboratory star *Escherichia coli* indicates a very rapid adaptation to environmental changes (see "For more information"). One could argue that these are organisms with a rapid life cycle (7-8 generations/day in this experiment). So let us consider organisms with slower life cycles: mosquitoes. The unfortunate "experiments" that we humans have conducted to eradicate them have systematically led to evolutionary reactions through the selection of resistance genes. Here, another argument could be developed: the selection pressure is considerable, both by the pesticide dose and by the geographical extent of the treatments. But rapid evolutionary processes have also been observed in natural populations of species with slower life cycles experiencing an environmental stress (e.g., Darwin's finches in the Galapagos; Grant & Grant, 2003), predation (e.g., guppies in Trinidad; Reznick & Travis, 2019) or hunting pressure (e.g., elephants; Allendorf & Hard, 2009). Of course, organisms with long life spans and limited fecundity will have difficulties escaping environmental variation via rapid genetic evolution, but they may have individual plasticity that can be mobilized for a short-term response. However, it should be remembered that ecology and evolution can therefore play on the same temporal scale, and that this can serve as a basis for the definition of eco-evolutionary processes.

Forces and processes. Population biology, in particular population genetics, has long formalized population functioning under the impact of forces or processes whose relative impact it seeks to understand. We can mention mutation, which generates variation, population size which directly impacts the respective effect of genetic drift and natural selection, or migration. This framework is found in models from the 1930s onwards, with a more or less great influence given to the spatial structuring of populations (Fisher, 1930; Wright, 1931).

Such a frame appears in ecology only in the 1960s (McArthur & Wilson, 1967), and has been revived more recently (e.g., Hubbell, 2001; Vellend, 2016); here we speak of speciation that brings new species into existence, ecological drift, interspecific competition, or migration. Thus, "natural" analogies can be detected between the levels of populations in species and species in biological communities. These kinds of ideas have also been generalized to ecosystems, with the notion of meta-ecosystems, including not only species migration, but also matter and energy flows (Loreau, 2010).

In fact, these approaches led authors to propose using these analogies to understand the dynamics of biodiversity jointly at different levels of integration of living organisms according to environmental conditions that will, for example, act directly on the population dynamics of all species (Vellend, 2016; Hendry, 2017; McPeek, 2017). Consider site size as an environmental parameter: a larger site will be able to support larger populations, within species, as well as more species, because it may offer more resources or different microenvironments, or is more stable over time and/or more easily reached by migrants. With larger populations, there will be, on average, a higher evolutionary potential, and thus a possibility of maintaining ecological and evolutionary stability in the face of environmental change. Every analogy has its limits - here, natural selection at the population level (interactions between alleles) cannot take the same forms as the variety of interspecific interactions (mutualism, parasitism, competition, predation ...). But it remains that we have a comparative entry between evolution and ecology, via forces and processes, which act at different levels of integration.

Box 1. Approaches and tools for a dialogue

Ecology and evolution have been separated since the end of the 19th century in terms of approaches and tools, for example with a much greater emphasis on the study of biodiversity in the "natural environment" and on physico-chemical analyses for ecology and on experimental approaches in the laboratory or molecular biology for evolution. Considerable convergence has occurred in recent years, in connection with conceptual and technological developments, which seem to us to open up areas of dialogue on common objects of study. Indeed, these approaches and tools require a high level of technical competence given their increasing sophistication, and therefore the creation of places (*sensu lato*) for transmission and exchange (e.g., work groups, dedicated training courses, etc.). They also require more and more team work and projects integrating multiple approaches, or even exchanges between disciplines (inter-, trans-, multi-...). We can think of molecular and chemical methods, sensors, statistical methods (including artificial intelligence) or data mining. I will develop here the case of experimentation.
A fundamental question, when one is interested in the functioning and dynamics of biodiversity, is to know if the controlled experimental approach is sufficient or if it is necessary to work "in nature". On the one hand, we consider the real environment undergone by the organisms, on the other hand we wish to have control over the environment. This old debate is far from over (see e.g. Hendry, 2019), echoing reductionist *vs*. holistic perspectives, but also the possibility of a hypothetical-deductive approach, and there is certainly no single answer. Moreover, research programs are increasingly jointly incorporating a range of approaches from microcosms under controlled laboratory conditions, especially for organisms with short generation times, to ensembles of field sites undergoing ambient environmental conditions (including the human environment), through instrumented experimental devices such as the Ecotron or the use of sensors to monitor biotic or abiotic parameters (Le Galliard & Montoya, 2017). In this perspective, rather than opposing laboratory and field, the trend is to develop long-term approaches, known as evolution or experimental ecology. While they do not exhaust the reductionist / holistic debate, they do allow for a more integrative understanding of the processes at play in a temporal perspective and an explicit consideration of the different levels of variation, for example intra-individual *vs*. interspecific, and of the appearance of new variation through mutation (or even speciation if we can wait long enough). They also make it possible to integrate various environmental forcing into ecology and evolution studies, such as climate change or the arrival of new variants or species, or the spatial structuring of biodiversity in a more or less fragmented form.

I have only touched on an (important) subset of what could integrate, or unlink, ecology and evolution. Other aspects that play a significant and growing role in this integration could have been mentioned. In the first place, natural selection and niche are strongly linked, natural selection emerging from ecological interactions, and I also did not insist much on the notion of space. One can also think of the notion of trait - in its sense of phenotypic trait resulting from genetic or epigenetic expression. Subject to selection and expressing plasticity, it can respond to environmental variation, from the individual to the ecosystem level, and regulate intra- and interspecific competitive relationships (see for example Garnier & Navas, 2013 in ecology; Roff, 1992 in evolutionary biology). Moreover, a trait can also be directly related to selective value or material and energy flows (Violle et al., 2007), providing a common entry point into the "population biology / community ecology / ecosystem ecology" triptych mentioned above. From a more pragmatic point of view, common tools and approaches have a role to play in the eco-evolutionary dialogue (Box 1). Phylogenetics could fall into this category; used for more than half a century to reconstruct kinship relationships between populations or species (Felsenstein, 2004), ecophylogenetics has developed with the idea of detecting ecological signals in the phylogenetic patterns of species communities, as a result of both evolutionary history and ongoing ecological interactions (Cavender-Bares et al., 2009; Mouquet et al., 2012). The results are quite disappointing, however, as these signals are weak.

Eco-evolution, really?

If the above explains why and how ecology and evolution are interested in the dynamics of biodiversity, when is it important to develop an eco-evolutionary thought and framework? As a first approach, we can categorize current approaches into (i) evolutionary studies, often "species-centric", focusing on genetic variation and introducing a dose of environment into their approaches; (ii) ecological studies that consider evolutionary impact (or mechanisms), focusing on biological communities or ecosystems; (iii) (probably rarer) integrative work. All three approaches are valid, both from a basic research perspective and when it comes to managing biodiversity (Sarrazin & Lecomte, 2016). In fact, any study of biodiversity is in the absolute sense eco-evolutionary since its dynamics and structure depend on ecological and evolutionary processes.

However, do we really need evolutionary thinking to explain species-environment relationships here and now (small spatial scale and short timescale)? Symmetrically, does the understanding of long-term evolutionary processes require a detailed ecological knowledge? Can we not refer evolution to long time and ecology to short time? In a way, decouple the time scales, as theorists sometimes do, by assuming a weak selection regime, such that population dynamics have time to equilibrate before a new mutation appears and potentially disrupts this equilibrium (e.g., Lion 2018). What place and need then for eco-evolutionary studies? Following Bassar et al.'s (2021) proposal, we will consider a dynamic to be truly eco-evolutionary when ecological and evolutionary processes are contemporaneous, *i.e.* when they are positioned in the same temporality or unfold at the same pace. This emphasizes reciprocal interactions between ecology and evolution on the same time scale, while noting that it is not always easy to appreciate this contemporaneity.

A growing number of studies can be considered eco-evolutionary, and we will take the example of guppies (*Poecilia reticulata*) in Trinitad (West Indies), a study conducted over the past 40 years by D. Reznick and colleagues (Reznick & Travis, 2019) based on a combination of field work (Fig. 2), mesocosm and molecular approaches. Guppies belong to fish communities in which the predation they experience, e.g. by cichlids, is low or high, both upstream and downstream of rivers; marked differences were noted, in response to predation for a range of traits (reproduction, morphology ...). The selection pressure is in fact due to the difference in density in the populations; the density is indeed much higher when predation is low. The high density in populations with low predation reduces food availability, and vice versa, leading to an existence adapted to these food conditions (e.g. smaller size). Under these conditions, primary productivity is also affected, as are the dynamics of other fishes that compete with guppies (*Rivulus hartii*). We can thus clearly see here the eco-evolutionary loop that operates on the scale of a few tens of generations, involving the different levels of biodiversity, mentioned at the beginning of the article, populations, communities and ecosystems.

Figure 2. A waterfall on the El Cedro River in Trinidad (West Indies) that separates fish communities where predation on guppies is high (downstream) from communities where predation is more limited. Predation not only leads to trait changes in guppies, but also to changes in ecosystem functioning. This is one of the sites where D. Reznick introduced guppies (upstream) in 1981 to study their evolution in the absence of predation. Photo credit: Joshua Goldberg.

We can also found examples where the starting point is not populations and evolutionary biology but rather the relationship between biodiversity and ecosystem functioning (BEF; e.g., are species-richer ecosystems more productive?) to integrate the evolutionary process. This is the case of a study conducted in the long-term grassland plant experiment ("the Jena experiment"; see "Read more"). The treatments included a variable diversity of species per experimental plot, in particular monocultures versus polycultures. The BEF relationship was shown to strengthen over generations, which may result from complementarity between species in resource use in polycultures. The study by Zuppinger-Dingley et al. (2014) suggests that this strengthening could also result from selection for niche differentiation between species via phenotype differentiation (e.g., leaf size in plants) - referred to as "character displacement" in the literature. Here, selection was based on the (epi)genetic variation of the plants that were selected to constitute the first generation of the experiment, leading to a reduction in interspecific competition. In this example, the eco-evolutionary loop is thus based on selection that leads to differential resource use.

As a conclusion

Ecology and evolution offer a necessary framework for understanding the structure and dynamics of biodiversity, a complex subject if ever there was one. Probably not a theory at all (do we really need one, despite Lawton (1999)?), but much more than a set of case studies ... via a spatio-temporal perspective, theories of adaptation and interactions of species, among themselves and with their environment. It seems important to keep a distinction between ecology and evolution, to let them develop in their respective niches, to refine and to increase their complexity in order to analyze and understand biodiversity. To use the metaphor of the brother and sister again, ecology and evolution, as they have grown older and matured, have come closer together, understanding each other better, as is often the case (one hopes) with siblings, even if they should interact more strongly. This rapprochement has taken shape over the last two decades on a theoretical and empirical basis, via data mining and the development of common tools; and the term eco-evolutionary is used in a common way, so common that it has come to lose a real meaning, perhaps to the point of tending to make us believe that in ecology and evolution, everything is in everything. It is proposed here to stick to a stricter definition of what is eco-evolutionary, based on a common temporality, while amplifying a dialogue through the development of common concepts, integrated (integrative) approaches jointly examining the complexities of ecological systems through collective work. Neither holism nor reductionism ... the right amount of parsimony to deconstruct these complexities and their dynamics.

If ecology and evolution are necessary to understand the dynamics of biodiversity (this is the focus of this article), they are not sufficient. In particular, I have not addressed the contribution of the humanities and social sciences, for example through the notion of socio-ecosystems or the rise of the "environmental humanities". Eco-evolutionary integration also seems to me to be an interesting way of addressing key points of the relationship of humans to the world. Evolution has taught us where we came from, how we fit into the history of life on Earth, or how we relate to the world (for example, through various value systems). Ecology forces us to think about our relationship to biodiversity, questions us about which ecosystem engineers we are, for better and (I fear) for worse. Eco-evolution can help us to project our futures, and to get out of the vortex of environmental destruction in which we have put ourselves - I believe in it in my most optimistic phases.

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For more information
Ecotron websites: https://www.anaee-france.fr/service/ecotrons
On the experiment of R. Lenski and collaborators: https://en.wikipedia.org/wiki/E._coli_long-term_evolution_experiment
On the Jena experiment: http://the-jena-experiment.de

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