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Eco-evolutionary dynamics in complex ecological communities

Flora Aubree, Vincent Calcagno

Abstract Natural ecosystems are complex assemblages composed of many species, interacting together both directly and indirectly, through their environment. The coupled population dynamics (growth, death and reproduction of species) and evolutionary dynamics (Darwinian natural selection acting on species attributes) in such systems can generate a wide range of behaviors. Ecology has long studied how ecosystem complexity should affect their stability and/or productivity, but evolutionary dynamics has received less attention. Using the mathematical framework of adaptive dynamics, we can study how ecological diversity impacts the evolutionary dynamics of ecosystems, and reciprocally, how evolutionary past can alter the diversity-functioning relationship in communities.

1 General background

Biodiversity is an important property of ecosystems that impacts several aspects of ecosystem functioning such as productivity [11], stability in the face of perturbations, and robustness to invasive species [7]. It is commonly expected that the more diverse a community, the more productive and robust it is, and there is some evidence that more diverse ecosystems provide more services [7] [8]. Studies of biodiversity-functioning (B-F) relationships are traditionally conducted from an ecological perspective, without explicit consideration of evolutionary processes, in particular Darwinian natural selec-

Flora Aubree · Vincent Calcagno
Université Côte d'Azur, INRA, CNRS, Institut Sophia Agrobiotech, 400 route des Chappes, 06903 Sophia Antipolis, France. e-mail: vincent.calcagno@inra.fr

tion and adaptation. However, it is increasingly clear that evolutionary dynamics play an important role in predicting the structure of natural communities and their response to environmental changes, even on the relatively short timescales relevant to human activities. It is therefore necessary to understand how evolutionary dynamics and ecological dynamics interact and how their interaction determines ecosystem properties. Theoretically, this requires moving from classical dynamical models in which species traits and parameters are treated as constant (or externally forced) to ones in which these parameters are themselves dynamic variables that change under the action of mutation and ecological interactions, and whose changes feedback on the ecological dynamics. Here we will briefly introduce one possible approach to this problem, and we will illustrate two applications of these concepts. The first investigates how the diversity (number of species) in a community impacts its evolutionary stability (possibility of diversification or not), with the finding that diversity often facilitates further diversification. The second explores how the evolutionary history of an ecological community (i.e., evolutionary "young" or "mature") might change the expected relationships between diversity and ecosystem functioning (productivity, resilience to perturbations and invasions).

2 Modeling framework

We consider ecosystems containing a certain number s of interacting species, each characterized by its population density n_i and one ecological trait x_i, $i \in (1,s)$. The ecological trait is taken to represent the ecological strategy of the species and determines its interactions with the environment and with the other species ("ecological niche"). Ecological dynamics are governed by a set of s ordinary differential equations of the form

$$\frac{dn_i}{dt} = r_i n_i g\left(n_1,\ldots,n_s,x_1,\ldots,x_s\right) \; i \in (1,s)\,, \tag{1}$$

with r_i the characteristic timescale of the species (intrinsic growth rate) and g some growth function.

The growth function is considered to be non-linear but sufficiently smooth, and can otherwise have different forms depending on the type of ecological interactions at play in the community (resource competition, interference, predation, etc.). An archetypal growth function is the generalized Lotka-Volterra model $1 - \frac{1}{k(x_i)} \sum_{j\in(1,s)} a(x_i,x_j) n_j$, where $k(x_i)$ is the "carrying capacity" of species i and $a(x_i,x_j)$ is the per-capita interaction coefficient of species j onto species i. Most standard scenarios for ecological interactions

can be described with appropriate functional forms for k and a, but some cannot fit the Lotka-Volterra form (see Section 4.1). It is assumed that the ecological system (1) eventually reaches a stable node as $t \to \infty$, at which some species shrink out to zero density ("extinct" species) and others equilibrate at equilibrium density n_i^*("resident" species).

The above described ecological dynamics are supplemented by a process of evolutionary dynamics, whereby the species trait values x change through time under the action of Darwinian natural selection. In principle this implies at least adding to (1) a set of s equations for dx_i/dt. In practice, we use a slow-fast approximation known as adaptive dynamics [4], that we briefly introduce here. It is assumed that each species produces, at some (low) rate, mutant individuals with slightly deviant trait value $x_m = x_i + \delta$, where x_i is the trait of the parent and δ is a random deviate with zero mean and vanishingly small variance. Since mutants are initially very rare they do not have a significant impact on the ecological dynamics of the resident species, and since mutations are infrequent, the resident species have time settle at their equilibrium abundances n_i^*. If the initial density of a mutant population is n_m, we define the *invasion fitness* of the mutant as

$$f(x_m) = \lim_{n_m \to 0} \left(\frac{1}{n_m} \frac{dn_m}{dt} \right) , \tag{2}$$

If $f(x_m) < 0$ the mutant population declines and disappears, whereas if $f(x_m) > 0$ mutants increase in abundance and settle in the community ("invade"). One advantage of this approach is that fitness naturally emerges from the ecological dynamics specified in (1). Note that fitness is context dependent and depends on the composition of the entire community.

Mutant invasion implies that the whole system may be pushed to a totally different equilibrium. However, since mutants are almost identical to their parental species, mutant invasion generically results in a substitution of the parental species by the mutant population. In these conditions, species traits evolve continuously through time, at a rate proportional to the *selection gradients*, defined as

$$\nabla(x_i) = \left. \frac{df(x_m)}{dx_m} \right|_{x_m = x_i} \quad i \in (1, s) , \tag{3}$$

If $\nabla(x_i) > 0$, evolution makes the species trait increase through time, if $\nabla(x_i) < 0$ it makes it decrease.

The process describes gradual directional changes in species traits. Because of the slow-fast approximation, as trait values evolve the system tracks the (moving) ecological equilibrium defined from (1). As evolution proceeds, some species may go to extinction, i.e., the equilibrium may collide

with the boundary of their persistence domain. Another possibility is that some species reach a so-called *singular strategy* at which the selection gradient vanishes. In this case different possibilities exist. One is that the species reaches a fitness maximum, and its trait value thus represents an evolutionary end point (no further change). Another is that the species reaches a fitness minimum, in which case mutants on both sides (or at least on one side in some degenerate cases) can invade. In this case it is possible that mutant invasion does not imply mutant substitution: the mutant population may coexist with the resident population, and the two populations may subsequently diverge in trait space, thus effectively splitting the initial parental species into two daughter lineages. After a branching event, we need to add one equation to (1). This type of singular strategies are called *branching points*, and the process of branching is regarded as a model of species formation through ecological interactions (ecological diversification). It is possible to classify the different types of evolutionary dynamics around a singular strategy using the two derivatives $d^2 f(x_m)/dx_m^2$ and $d\nabla(x_i)/dx_i$.

In the following applications we will use a set of different ecological models (particular instances of (1)) to avoid model-specific conclusions.

3 How diversity impacts evolutionary diversification

3.1 Context and methods

It is well-understood, theoretically, that the more species in an ecological system, the less likely it should be for the system to settle at a dynamically stable equilibrium, and the less stable the equilibrium, if any, would be. A seminal paper by May [14], using the theory of random matrices, provided a general argument for this and elicited a long and fruitful debate on the relationships between species diversity and different types of ecological stability. The debate remained in the field of ecology though, and evolutionary stability, i.e., the tendency of evolutionary attractors to be fitness maxima (stable) or fitness minima (unstable), and thus the possibility of diversification, was disregarded. In parallel, evolutionary biology proposed the controversial hypothesis that species diversity could stimulate further diversification (the "diversity-begets-diversity" hypothesis), but this was not investigated using ecological theory.

We thus analyzed whether an ecological system of s species, as modeled in section 2, is more or less likely to be evolutionary unstable, i.e., to evolve toward branching points rather than fitness maxima, as the number of species s increases. To this end we simulated the evolutionary dynam-

ics of ecological communities, starting from different initial levels of initial diversity, from monomorphic ($s = 1$) to diverse ($s = 5$). We did this using three contrasted forms of ecological interactions, modeled as three different forms of the growth function g, all of the Lotka-Volterra family: symmetric competition of resources, asymmetric competition with interference, and a competition-colonization trade-off scenario, where better competitors are poorer at colonizing empty patches [1,12]. For each model, we systematically varied two key parameters controlling the modalities of ecological interactions [3].

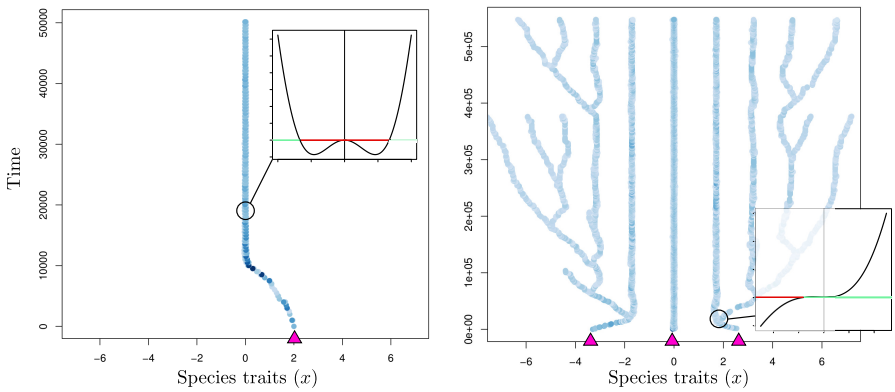

Fig. 1 Diversity triggers diversification. Two example simulations are shown. Starting from one initial species, a fitness maximum is attained and no further evolution occurs (*left*). For exactly the same parameters, bringing in an initial diversity of three species unlocks the possibility of adaptive diversification and repeated evolutionary branchings occur and diversity explodes (*right*). Figure from [3].

3.2 Results

We found that for many parameter sets, adaptive diversification was impossible when starting from one species (i.e., evolutionary trajectories halted at fitness maxima) but became possible after some initial level of diversity was brought into the system (Fig. 1). For a given parameter set, in all three models, there generally existed a minimum level of diversity above which evolutionary branching became possible. In other words, increasing ecological diversity may unlock the possibility of further adaptive diversification, in a form of auto-catalysis. By studying the curvature of the fitness func-

tion around the evolutionary singularities ($d^2 f(x_m)/dx_m^2$), and how it varies as s increases, we could identify three components of natural selection that explained the evolutionary bifurcations (i.e., loss of evolutionary stability). From the three models we observed two general mechanisms explaining the positive effect of diversity on diversification, one operating mostly at low diversity levels and the other at higher diversity levels [3].

It is usually thought that a positive effect of diversity on diversification necessitates specific processes such as niche construction, cross-feeding or ecological facilitation. Our results indicate that the same standard ecological principles that predict a negative effect of diversity on diversification, can just as well predict a diversification-promoting effect of diversity. This might provide an explanation to patterns observed at different scales, such as the delayed onset of lizard adaptive radiations on some islands, or recent findings that diversification correlates positively with initial diversity in experimental microbial communities [3]. Importantly, they suggest that the loss of ecological diversity may drive ecosystems below the threshold level for diversification, compromising the recovery of diversity, even in the long term.

4 How evolutionary history impacts the diversity-functioning relationship

4.1 Context and methods

Studies of biodiversity-functioning (B-F) relationships are traditionally conducted from an ecological perspective, without explicit consideration of evolutionary processes. Yet, it is clear that by altering the trait distribution and thus species interactions, evolutionary history (intended here as the history of coevolution of species within an ecosystem) may have a non-negligible role in determining the existence, magnitude and shape of B-F relationships. Several studies have already been undertaken in that direction, looking at the impact of fast evolution on ecosystem properties [6], of environment changes on robustness [16] or of the species coevolution on ecological stabilities [10].

Here we propose to study whether B-F relationships could depend on the evolutionary history of ecosystems. Specifically, we will generate two types of communities: **random** ("young") and **coevolved** ("mature"). In random communities species traits are drawn independently from an entropy-maximizing distribution. In coevolved communities, trait values are set at a (co-)evolutionary equilibrium, finding trait combinations that cancel all se-

lection gradients (eq.3) and are local attractors of evolutionary trajectories. This permits one to contrast communities with no evolutionary history at all with maximally coevolved (mature) ones. We did this for different levels of species richness s (1-10) and under five scenarios of ecological interactions (eq.3) representative of known species coexistence mechanisms. In addition to the three scenarios used in section 3 we considered two non-Lotka-Volterra scenarii: the tolerance-fecundity trade-off scenario [15] and the size-structured trophic chain scenario [9]. Three types of B-F relationships are then quantified: (a) **Total productivity** defined as the sum over species of the positive contributions to net growth rate (eq.1) ; (b) **Temporal stability** defined here as the asymptotic resilience (closest to zero eigenvalue of the Jacobian matrix of (1)); and (c) **Robustness to invasion** is assessed by two metrics: the probability of establishment of invasive species with random trait x_e (invasion resistance), and, for successful invasions, the expected number of resident species that are driven to extinction (invasion tolerance). For a range of parameter values, the B-F relationships were systematically compared between random and co-evolved communities.

4.2 Results

B-F relationships were affected by evolutionary history in all five scenarii. In random communities, productivity, as expected, increased with diversity in most cases, with the notable exception of the CC trade-off scenario (Figure 2). A history of coevolution had quantitative and qualitative effects on the diversity-productivity (D-P) relationships. Quantitatively, D-P relationships had smaller amplitudes in mature communities compared to random ones, to the point of being almost undetectable in the tropic chain scenario, and they have a much more concave shape. Qualitatively, coevolution can reverse the slope of the D-P relationship, as observed in the CC trade-off scenario. Overall, evolutionary history strongly affects the expected D-P relationship, with a general tendency of D-P relationships to be shallower, and more consistently positive in mature communities compared to random communities.

Asymptotic resilience decreased with diversity in all scenarii, as expected in such models, and irrespective of evolutionary history. In the CC, TF and trophic chain interactions, there was no appreciable difference in the shape of the diversity-stability (D-S) relationships. However, the shape change induced by the past evolutionary history in the niche and body size scenarii was notable. It changed from convex to sigmoid, respectively, in mature and random communities, and led to more stability for mature communities at

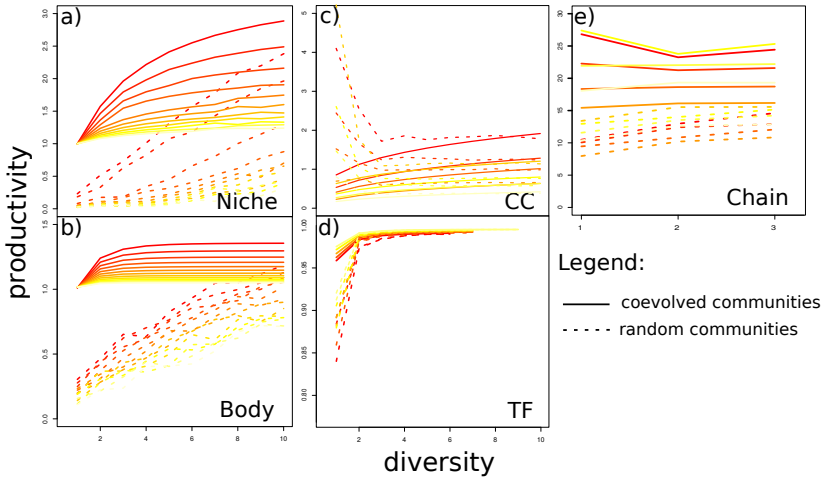

Fig. 2 Productivity for the (a) *niche*, (b) *body size*, (c) *CC trade-off*, (d) *TF trade-off* and (e) *trophic chain* scenarii. Colors stand for the different model parameters varied.

high diversity. It resulted that the fast decrease for mature communities at low diversity slowed down at higher diversity, while the contrary occurred for random communities.

Invasion resistance was not drastically influenced by past evolutionary history: the invasion probability, which was decreasing with diversity as expected, was only slightly smaller in coevolved communities (except in the CC scenario where it was slightly higher). By contrast, for the invasion tolerance results clearly showed that coevolved communities were much less perturbed by invasive species than random ones: almost no species disappeared for all species richness explored, and the invasive species remained at a very low abundance compared to resident species. To the contrary, random communities lost a lot of species when invaded and the invasive species was more abundant. In sum, past evolutionary history did not impact clearly the probability of invasion, but changed considerably the response to an effective invasion.

To conclude, all scenarii of ecological interaction and all the observed functional properties were sensitive to the past evolutionary history. Natural unperturbed ecosystems and young (or recently perturbed) ecosystems did not behave and react the same. Those studies confirm that evolutionary history should be a parameter to consider while studying ecosystem functioning.

5 Conclusion

As is visible in the examples presented here, ecological and evolutionary dynamics have reciprocal interactions, and it may be insufficient to study them individually. Adaptive dynamics provides a useful method to incorporate adaptive evolution into ecological models and expand our theoretical understanding the dynamics of ecosystems. The approaches presented here can be expanded to relax some critical assumptions, such as the rarity of mutations and slow-fast approximation [2], the absence of spatial structure [13], the scalarity of species traits [5] and beyond.

References

1. Calcagno, V., Mouquet, N., Jarne, P., and David, P.: Coexistence in a metacommunity: the competition-colonization trade-off is not dead. Ecology Letters, **9**(8), 897-907 (2006)
2. Calcagno, V., Dubosclard, M. and de Mazancourt, C.: Rapid exploiter-victim coevolution: the race is not always to the swift. The American Naturalist, **176**(2), 198-211 (2010)
3. Calcagno, V., Jarne, P., Loreau, M., Mouquet, N. and David, P.: Diversity spurs diversification in ecological communities. Nature Communications. **18** (2017)
4. Dercole, F. and Rinaldi, S.: Analysis of evolutionary processes: the adaptive dynamics approach and its applications: the adaptive dynamics approach and its applications. Princeton University Press. (2008)
5. Doebeli, M., and Ispolatov, I.: Complexity and diversity. Science, **328**(5977), 494-497 (2010)
6. Fussmann, G. F., Loreau, M. and Abrams, P. A.: Eco-evolutionary dynamics of communities and ecosystems. Functional Ecology, **21**: 465-477 (2007)
7. Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J. and Wardle, D. A.: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs, **75**: 3-35 (2005)
8. Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S. & Loreau, M.: High plant diversity is needed to maintain ecosystem services Nature. Nature Publishing Group, **477**, 199- (2011)
9. Loeuille, N. & Loreau, M.: Evolutionary emergence of size-structured food webs. National Academy of Sciences, **102**, 5761-5766 (2005)
10. Loeuille, N.: Influence of evolution on the stability of ecological communities. Ecology Letters, **13**: 1536- (2010)
11. Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D. A.: Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges Science. American Association for the Advancement of Science, **294**, 804-808 (2001)

12. Livingston, G., Matias, M., Calcagno, V., Barbera, C., Combe, M., Leibold, M. A., and Mouquet, N.: Competition-colonization dynamics in experimental bacterial metacommunities. Nature communications, **3**, 1234 (2012)
13. Massol, F., Calcagno, V., and Massol, J.: The metapopulation fitness criterion: proof and perspectives. Theoretical population biology, **75**(2-3), 183-200 (2009)
14. May, R. M.: Will a large complex system be stable?. Nature, **238** (5364), 413 (1972)
15. Muller-Landau, H. C.: The tolerancetextendashfecundity trade-off and the maintenance of diversity in seed size. National Academy of Sciences, **107**, 4242-4247 (2010)
16. Strona, G. & Lafferty, K. D.: Environmental change makes robust ecological networks fragile. Nature Communications, **7**, 12462- (2016)