

Influence of evolution on the stability of ecological communities

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Abstract

In randomly assembled communities, diversity is known to have a destabilizing effect. Evolution may affect this result, but our theoretical knowledge of its role is mostly limited to models of small food webs. In the present article I introduce evolution in a two-species Lotka-Volterra model in which I vary the interaction type and the cost constraining evolution. Regardless of the cost type, evolution tends to stabilize the dynamics more often in trophic interactions than for mutualism or competition. I then use simulations to study the effect of evolution in larger communities that contain all interaction types. Results suggest that evolution usually stabilizes the dynamics. This stabilizing effect is stronger when evolution affects trophic interactions, but happens for all interaction types. Stabilization decreases with diversity and evolution becomes destabilizing in very diverse communities. This suggests that evolution may not counteract the destabilizing effect of diversity observed in random communities.

1 Introduction

Stability is a much discussed aspect of ecological communities, for several reasons. First, the degree of stability can often be directly assessed using temporal fluctuations of some characteristics of the community or of the densities of the different species [McCann, 2000]. Second, stability is usually thought as being tightly linked to the persistence of the system [Rosenzweig, 1971, Kondoh, 2003]. If the dynamics are unstable, populations fluctuate widely, possibly to low values that would make them vulnerable to demographic stochasticity. Stability therefore has far reaching implications for the management of exploited populations and for conservation issues. Stability also influences how communities react to disturbances, again with direct management implications.

Although many definitions of stability exist [McCann, 2000], most models use the effect of disturbances on an equilibrium to assess its stability. If the dynamics bring the system back to equilibrium, then the system is considered stable, and the inverse of the return time to the equilibrium is a measure of stability (resilience) [Pimm and Lawton, 1977, 1978]. I follow this definition and use resilience as a measure of stability. Here, the system is the community, defined by the densities of the species it includes, and the dynamics correspond to the variation of these densities in time.

Simple models (two or three species) have allowed the identification of important stability constraints. For instance, in the case of competition models based on Lotka-Volterra equations [Volterra, 1926], coexistence is stable when intraspecific competition is strong compared to interspecific competition. In predator-prey systems, stability is largely affected by the functional and numerical response of the predator [Abrams and Ginzburg, 2000]. The well-known paradox of enrichment shows that increased availability of prey may destabilize the population dynamics of predator-prey systems [Rosenzweig, 1971].

While these few-species models yield simple conditions for stability, they cannot account for another component affecting stability: diversity itself. The relationship between diversity and stability has long been supposed to be positive [Elton, 1958], but this intuition was challenged by the work of May [1973]. After May's article, finding factors to explain the stability observed in some high-diversity ecosystems became a major issue in community ecology. Food web ecology, particularly, devoted much effort to this issue. Food web stability is enhanced by the coexistence of many weak interactions with a few strong ones [McCann et al., 1998, Neutel et al., 2002], by combining different energy channels, one with fast dynamics, the other with slow dynamics [Rooney et al., 2006], or through compartmentalization [May, 1973, Krause et al., 2003]. Nestedness in mutualistic networks creates asymmetries that increase the stability of the community [Bascompte et al., 2006].

Another important issue raised by May's results relates to the assembly rules of natural communities [De Angelis, 1975]. May's study was not particularly focused on a particular type of network, links between the different components of the system being random. In nature, the links (interactions) between the different components (species) are not random. One of the major forces affecting such interactions is the coevolution of species. Whether a community assembled using evolutionary rules behaves like a random one has led to much speculation. The exact

role of evolution in community stability is still not quite clear.

Again, models that contain few species have the advantage to sometimes provide an analytical answer to this key issue. Evolution of defensive strategies often destabilizes the system while evolution of consumer attack rates has the converse effect [Abrams, 2000]. Exact effects strongly depend on the specifics of the model structure [Fussmann et al., 2007]. There is also very little empirical evidence to back up the theoretical predictions. One study on rotifer-algae interaction showed that evolution of algal defenses can affect the characteristics of population cycles [Yoshida et al., 2003].

These previous works are largely focused on trophic interactions, with little effort to examine specific other interaction types such as competition (intra or interspecific) or mutualism or to examine the interplay of different interaction types considered simultaneously. The effects of evolution on stability is largely unknown for interaction types other than trophic interactions. It is important to understand this aspect, as natural communities contain all interaction types. Moreover, models reviewed in Abrams [2000] and Fussmann et al. [2007] mostly focus on evolution under allocation costs. Costs of increased defenses are then expressed through decreases in the reproduction or growth rate, costs of increased attack rates through decreased survival, based on energetic arguments. While this is adequate for some traits, for others, costs may be expressed through ecological interactions [ecological costs, Strauss et al., 2002, Müller-Schärer et al., 2004]. Ecological costs happen when a mutation that increases a positive interaction (or decreases a negative one) but increases the negative effect of another interaction, or decreases its positive effect. For instance, traits that attract simultaneously mutualists and consumers. Such ecological costs create additional indirect feedbacks with important consequences for the community stability.

The aim of the present work is to specify how evolution influences stability, accounting for the effects of multiple interaction types, for the effects of the type of costs involved in the selection process and for the diversity of the community. I first examine the consequences of evolution on stability for different interaction types (intraspecific competition, interspecific competition, mutualism, predation) and cost types (allocation or ecological) using a 2-species Lotka Volterra model. Then, using simulations to extend the species diversity (hereafter diversity) of the community, I examine the capacity for evolution to influence stability for communities that contain all interaction types simultaneously. Finally, I discuss the importance of interaction types by making comparisons with existing food web models and I explain how the simulation results affect our perception of the diversity-stability debate.

2 Model and methods

2.1 The model and its ecological dynamics

I consider two species, whose densities are respectively noted N_1 and N_2 . To describe the dynamics of their populations, I use a simple Lotka-Volterra model in which r_i is the intrinsic growth rate of species i , and α_{ij} corresponds to the effect of an individual of species j on an individual of species i . I suppose that the population

density grows when rare in absence of the other species ($r > 0$), that intraspecific interaction is strictly competition ($\alpha_{ii} < 0$, no Allee effect). The Lotka Volterra model allows me to examine predation, competition and mutualism with the same model structure. Only the signs of the α 's need to change to generate variable types of interaction. The model describe mutualistic interactions (when α_{12} and α_{21} are positive), competitive interaction (both negative) and trophic interaction (α_{12} and α_{21} of different sign). Stable coexistence of the two species constrains the parameters to a limited range of values that depends on the interaction type. These constraints, as well as a complete description of the model, are presented in appendix A.

2.2 Evolution and stability in simple systems

2.2.1 Variation of stability through time

I assume that the system is initially stable, and I study the effects of directional selection on its stability. Stability of the system is defined using the inverse of return time τ to the equilibrium after a small disturbance [resilience, see Pimm and Lawton, 1977, 1978], that scales as:

$$\tau \sim \frac{1}{-Re\lambda} \quad (1)$$

where λ is the leading eigenvalue of the jacobian matrix, the one whose real part is the larger. Because the equilibrium is stable, $Re\lambda < 0$.

I assume without loss of generality that species 1 is the evolving species and I introduce a phenotypic trait x that affects the dynamics. I assume that evolutionary changes in trait x depends on a mutation-selection process, described using an adaptive dynamics approach [Dieckmann and Law, 1996, Geritz et al., 1998]:

$$\frac{dx}{dt} = \frac{1}{2}\mu\sigma^2 N_1^*(x) \left(\frac{\partial W(x_m, x)}{\partial x_m} \right)_{x_m \rightarrow x} \quad (2)$$

Equation (2) describes the mutation process through parameters μ (mutation rate per newborn individual) and σ^2 (variance of the amplitude of mutations in terms of phenotypic effect). Therefore, $\mu\sigma^2 N_1^*(x)$ determines the total amount of variability brought by mutations. The second part of the equation describes the selection process, through the variation of fitness W of a mutant x_m whose trait is close to the trait of its parent x . In adaptive dynamics, fitness $W(x_m, x)$ is defined by the *per capita* growth rate of a rare mutant x_m in an environment set by the resident population x . Note that the direction of the variation of x through time, the direction of selection, is determined by the gradient of fitness. If the gradient is negative, x decreases, else it increases. Changes in x through evolution affects the position of the equilibrium, hence the jacobian matrix and its eigenvalues, hence the stability of the system.

In the present study, I do not follow the complete evolutionary dynamics of the system, but rather assess whether

directional selection at a given instant pushes the system toward increased stability. That is, does stability increase (decrease) when a successful mutant invades the system?

To study how evolution affects the stability of the system, I compute the time variation of the real part of the leading eigenvalue through evolutionary changes:

$$\frac{dRe_\lambda(x(t))}{dt} = \frac{\partial Re_\lambda}{\partial x} \frac{dx}{dt} \propto \frac{\partial Re_\lambda}{\partial x} \left(\frac{\partial W(x_m, x)}{\partial x_m} \right)_{x_m \rightarrow x} \quad (3)$$

Stability of the system is increased anytime Re_λ decreases due to evolution (see equation (1)).

Given the jacobian matrix at the coexistence equilibrium J^* , whose trace is $Tr(J^*)$ and determinant $Det(J^*)$, several dynamics are possible.

If $Tr(J^*)^2 \leq 4Det(J^*)$, the two eigenvalues are complex and the dynamics present dampened oscillations toward the stable equilibrium (spiral case). As shown in appendix A, spiral cases are only possible when the interspecific interaction is trophic. The real part of the leading eigenvalue is:

$$Re_\lambda(x(t)) = \frac{1}{2}Tr(J^*(x(t)))$$

When $Tr(J^*)^2 > 4Det(J^*)$, both eigenvalues are real and different and the dynamics approach the ecological equilibrium in a non-oscillatory manner (stable node). Nodes are possible for all interaction types. Then:

$$Re_\lambda(x(t)) = \frac{Tr(J^*(x(t))) + \sqrt{Tr(J^*(x(t)))^2 - 4Det(J^*(x(t)))}}{2}$$

I discuss three evolutionary scenarios hereafter:

1. Trait x is α_{11} and has an allocation cost (modification of r_1);
2. Trait x is α_{12} and has an allocation cost (modification of r_1);
3. Trait x is α_{11} and has an ecological cost (modification of α_{12}).

2.2.2 Allocation cost

In the case of an allocation cost, a mutation reinforces the positive effect of the interaction, or reduces its negative effect, at the expense of energy devoted to growth or reproduction. This type of cost is common, as many traits are energetically expensive. For instance, the production of digestibility reducing compounds or tannins by plants diverts resources from growth and reproduction [Herms and Mattson, 1992, Strauss et al., 2002, Müller-Schärer et al., 2004]. Similarly, vigilance against predators leads to reduced resource consumption therefore decreased growth or reproduction [Illius and Fitzgibbon, 1994].

When α_{11} has an allocation cost (scenario 1), any mutation that reduces the effects of intraspecific competition (that is, increases α_{11} , then less negative) decreases r_1 . Fitness of a mutant population α_{11}^m in a population whose resident trait is α_{11} is:

$$W(\alpha_{11}^m, \alpha_{11}) = r_1(\alpha_{11}^m) + \alpha_{11}^m N_1^*(\alpha_{11}) + \alpha_{12} N_2^*(\alpha_{11}) \quad (4)$$

Where r_1 is a decreasing function of the trait.

Similarly, it is possible to study the evolution of interspecific interaction α_{12} , under allocation costs (scenario 2). A mutation that decreases the negative effect of the competitor or predator or a mutation that increases the benefit of the mutualist or prey (increasing α_{12}) incurs a cost in terms of the basic growth rate r_1 . The fitness of a mutant of species 1 α_{12}^m in the resident population α_{12} is:

$$W(\alpha_{12}^m, \alpha_{12}) = r_1(\alpha_{12}^m) + \alpha_{11} N_1^*(\alpha_{12}) + \alpha_{12}^m N_2^*(\alpha_{12}) \quad (5)$$

Again, the growth rate r_1 is a decreasing function of the trait.

On figure 1, such scenarios correspond to trait 1 being r_1 and trait 2 being successively α_{11} then α_{12} . The steeper the slope at the resident trait, the larger the associated cost. Both fitness functions (4) and (5) correspond to the *per capita* growth rate of a rare mutant in the resident population [Dieckmann and Law, 1996, Geritz et al., 1998].

2.2.3 Ecological cost

Although allocation costs are often used, they do not apply to all traits. For instance, production of some toxins by plants does not seem to reduce growth or reproduction, but their efficiency toward generalist herbivores is balanced by attraction of specialist herbivores [qualitative defenses, Müller-Schärer et al., 2004]. Mobility of prey is efficient against mobile predators but increases vulnerability to sit-and-wait predators [Rosenheim et al., 2004]. A plant trait that attract pollinators such as colorful flowers, may also be used as a cue for herbivores [Strauss et al., 2004]. For such traits, whenever evolution increases the positive effect of an interaction (or decreases its negative effect), it decreases the benefits of another interaction or worsen its negative effects. It is for instance possible that changes in traits that determine α_{11} will incur costs in terms of interspecific interaction rate α_{12} (scenario 3). The fitness function of a mutant α_{11}^m in a resident population whose trait is α_{11} is:

$$W(\alpha_{11}^m, \alpha_{11}) = r_1 + \alpha_{11}^m N_1^*(\alpha_{11}) + \alpha_{12}(\alpha_{11}^m) N_2^*(\alpha_{11}) \quad (6)$$

In equation (6), α_{12} is a decreasing function of α_{11} .

On figure 1, such ecological costs correspond to trait 1 being α_{12} and trait 2 being α_{11} . The steeper the slope

of this function at the resident trait, the larger the associated cost.

2.3 Evolution and stability in diverse communities

May [1973] showed that more diverse communities of given connectance C and diversity k were likely stable provided:

$$s\sqrt{kC} < 1 \quad (7)$$

with s the maximum interspecific interaction rate (all intraspecific competition rates α_{ii} are -1). I use this criterion to generate communities with different diversities k ($C = 0.1$, $s = 0.2$, $k \in \{5, 10, 15, 20, 30, 100\}$). References to diversity hereafter correspond to species diversity k , not to the diversity of interaction types. For each matrix, all non-zero interactions are drawn from a uniform distribution on the interval $[-s, s]$, meaning that on average 25% of these interactions are mutualistic, 25% competitive and 50% trophic interactions. For each matrix, I compute the position of the equilibrium for all populations. Note that May's stability criterion (7) has been shown to be less mathematically general than initially thought [Cohen and Newman, 1984]. I check that all densities are positive at equilibrium and that it is locally stable ($Re_\lambda < 0$).

I then consider each non-zero interaction of the matrix, including intraspecific competition, and draw a mutant at random in each case. Considering an initial rate of α_{ij} where i is the evolving species, the trait of the mutant is $\alpha'_{ij} = \alpha_{ij} + \epsilon$, where ϵ has a fixed absolute value representing the amplitude of mutation (0.001) and a sign determined by the fitness gradient (using extended version of fitness equations (4),(5) in allocation scenarios and of (6) in ecological scenarios). This ensures that such a mutant has a selective advantage on the resident population, likely replacing it. A random number determines the curvature b of the trade-off function ($b \in [-3, 0]$). If the scenario corresponds to an allocation cost, the intrinsic growth rate of the mutant is $r'_i = r_i + b\epsilon$. If the scenario corresponds to an ecological cost, I successively draw a mutant for all interactions species i has with other species k of the community $\alpha'_{ik} = \alpha_{ik} + b\epsilon$. For each mutation, I compute the new equilibrium population densities and the stability Re_λ . $\Delta Re_\lambda = Re_\lambda - Re_{\lambda'}$ assesses the effects of evolution on stability. If it is positive, evolution increases the stability of the system (equation (1)), else stability is decreased.

I use these simulations to answer two questions:

1. Do the results of the two-species system apply to more diverse communities?
2. Does the probability of stabilization depend on the diversity of the community?

I have used 140000 simulated communities to study allocation costs (over 8 million mutation events) and 880000 simulated communities to study the ecological costs (over 20 million mutation events). These numbers emerge from the following procedure:

- For each cost scenario and each diversity, I started with 10000 communities;

- I then doubled the number of communities until this doubling did not change the stabilization/destabilization probabilities reported hereafter by more than 1%.

Therefore, 1% corresponds to the possible error around the probability values presented on the figures below.

3 Results

3.1 Evolution and stability in simple systems

By replacing equations (4), (5) or (6) in equation (3), it is possible to determine analytically the effects of evolution on the stability of the system for the traits and trade-offs described above. I examine here scenario 2. Results for scenarios 1 and 3 are presented in appendix B.

Figure (2)A shows the effect of evolution of a phenotypic trait that affects a mutualistic interaction ($\alpha_{12} > 0$) on stability when there is an allocation cost (e.g., benefit to a mutualist with respect to the interaction incurs a cost in terms of reproduction). A successful mutant increases stability when the cost value is either very low or very high and decreases stability when it is intermediate. At very large costs, phenotypic trait is counterselected. Because stability is decreasing with the trait value, evolution stabilizes the system. Conversely, low costs select for higher values of the phenotypic trait. Because stability is there an increasing function of the trait value, evolution also stabilizes the system. In between, evolution destabilizes the system because higher values of the phenotypic trait are selected while stability is a decreasing function of the trait value. Limits between the different cases correspond to the values R_1 and R_2 at which the fitness gradient $\left(\frac{\partial W(\alpha_{12}^m, \alpha_{12})}{\partial \alpha_{12}^m}\right)_{\alpha_{12}^m \rightarrow \alpha_{12}}$ and function $\frac{\partial Re\lambda}{\partial \alpha_{12}}$ change sign. Graphically, on figure (2)A, evolution increases stability when the product of the two curves is negative (equation (3)), else it decreases it. Note that for this particular case (mutualism and allocation costs), R_2 is always larger than R_1 (appendix B).

Using a similar method, I study the influence of evolution on stability for the other interaction types (panel B). Important differences exist depending on the types of stable dynamics that is affected by evolution (spiral or node). For node cases, the effects of evolution on stability is different at extreme vs intermediate values of the cost as it was in the mutualistic case (panel A). When dynamics are spiral, evolution is always stabilizing when the evolving species is a prey or weak predator (weak effect on its prey: $\alpha_{21} > \alpha_{11}$), always destabilizing if it is a strong predator ($\alpha_{21} < \alpha_{11}$). This is because roots R_1 and R_2 are confounded in such instances. Note that relative position of the two roots is fixed within each node case. All computations are presented in appendix B.

I undertake similar computations for scenarios 1 (evolution of α_{11} with allocation costs) and 3 (evolution of α_{11} with ecological costs). Details of the computations and a general table presenting all results may be found in appendix B. Qualitative patterns when changing from one cost type to another are generally robust. Relative position of R_1 and R_2 is not determined generally. However, for a given interaction type and cost type this relative position is usually fixed. R_1 is then often smaller than R_2 . R_2 is sometimes be positive, variation of stability with

the trait is then monotonic. In general, when mutations that benefit the interaction have very large costs in terms of reproduction (scenario 1 and 2) or in terms of the effects of another interaction (scenario 3), evolution leads to stabilization more often than intermediate or low costs.

In some instances, the interaction type and cost type allow a complete prediction of the effect of evolution on stability. This is for instance true for spiral dynamics associated with allocation costs (figure 2B). Extreme costs (close to zero or very negative) lead to stabilization when interspecific interaction is mutualistic associated with allocation costs (figure 2A) or when costs are ecological and interaction is competition (Appendix B, table 1).

Because of all these specifics, effects of interaction type are not easy to distinguish. However, one general finding is that evolution in the context of trophic interactions results more often in increased stability. This is because spiral dynamics are then more often stabilized by evolution (evolving prey or weak predator) than destabilized (strong predators). Evolution associated with trophic interaction is then overall more positive for stability compared to other interaction types (figure (2), panel B).

This exercise examine pairwise interactions and highlights the effects of evolution on stability for different interaction and cost types. However, an important determinant of stability is the diversity of the community. The two-species system does not allow any indirect effects as it does not include multiple interaction pathways. Another important reason to investigate this diversity aspect is that increased diversity, in isolation of other processes, destabilizes the system [May, 1973]. If diversity leads to an increased probability that evolution stabilizes the community dynamics, this evolutionary effect would counteract the destabilizing effect suggested by May.

3.2 Evolution and stability in diverse communities

Figure 3A shows the effects of evolution on stability when the cost is expressed in terms of allocation. Many mutations do not produce any change in stability (black area), especially when diversity is low. Though mutations affect eigenvalues of the system, they do not necessarily modify the leading eigenvalue that determines local stability. This is particularly true because the low connectance produces compartmentalized communities. When communities are larger, such “no change” events become less likely. In diverse communities, a mutation changes the equilibrium populations of more species, through indirect effects within the community. As more species are affected, the “no change” situations become less likely.

Results for ecological costs are summarized on the panel B of figure 4. Interestingly, I found little qualitative difference between ecological and allocation costs. Again, many mutations do not change the stability of the community, especially for small communities. The fact that the type of cost little affects the role of evolution is consistent with similar observations made earlier on the simple model that qualitative patterns regarding stability are usually quite similar across cost types.

Figure 3 shows the global effect of evolution that is to say that it involves all mutations within the community, regardless of the interaction type they affect. However, the simulated communities are made of different interaction

types (intraspecific competition, interspecific competition, mutualism and predation). It is possible that the probability of stabilization or destabilization depends on the interaction type that is directly affected by the mutation. To clarify this aspect, I discard simulations that did not produce any change in stability (i.e., no change in Re_λ) and study the ratio between the number of mutations that increased stability to the number of mutations that decreased it, depending on the interaction type they affect. Results are summarized on figure 4.

Except at highest diversities, all curves lie above one, indicating that evolution tends to stabilize communities, regardless of the type of interaction. The larger the community the less the stabilizing effect of evolution. For very large communities, evolution does little to increase stability or even decreases it, for the highest diversity level. The stabilizing effect of evolution is meaningful for communities up to 20 or 30 species. Figure 4 also shows that the stabilizing effect of evolution strongly depends on interaction types at such low diversity levels. Evolution of mutualistic or trophic interactions much more often increases stability compared to evolution of competitive interaction. That evolution of trophic interaction more often leads to increased stability is consistent with the observations from the two-species model (figure 2 panel B). It is important to note that differences among interaction types are strong at low diversity, but become small as diversity increases, so that these differences appear to be context dependent. Again, all these results are similar for allocation and ecological costs.

As for the two-species model though, quantitative differences exist between allocation and ecological costs. Figure 3 shows that evolution under ecological costs is less likely to be neutral than under allocation costs. This is because ecological costs induce a shift in two interactions, therefore more populations are directly affected by the mutation. Such mutations therefore cause more indirect effects. Figure 4 panel A shows that many more mutations lead to stabilization than to destabilization for allocation costs at low diversity. Although it remains true for ecological costs (figure 4, panel B), this stabilizing effect is less strong, the ratio being smaller overall. The stabilization effect is then much stronger for mutualistic and trophic interaction, while evolution of intraspecific competition leads less often to stabilization compared to allocation costs. Contrary to figure 4 panel A, one of the curves (interspecific competition) is constantly below one on figure 4 panel B, meaning that evolution that affects interspecific competition tends to destabilize the community under ecological costs regardless of the diversity of the community.

4 Discussion

Results presented above have some interesting implications for the diversity-stability debate. May [1973] showed that increased diversity possibly yields decreased stability, measured, as here, using the real part of the leading eigenvalue of the jacobian matrix. The aim of the simulations presented here is to understand whether selective pressures push the communities toward increased stability or not. Because natural communities contain hundreds of species, the simulation results presented here (figure 4) indicate that evolution destabilize the system at such

diversity, thereby reinforcing the effect observed by May, not preventing it. This destabilization effect does not depend on the interaction type affected by the mutation nor of the cost type associated to it.

Previous studies have suggested that accounting for food web constraints to build such communities often leads to more stable communities [De Angelis, 1975, Allesina and Pascual, 2008]. Several food web models use evolutionary assembly to let diversity and community structure emerge through the mutation-selection process [Caldarelli et al., 1998, Loeuille and Loreau, 2005, Rossberg et al., 2006, Loeuille and Loreau, 2006, Ito and Dieckmann, 2007]. These evolutionary rules often lead to assemblages in which population dynamics are stable [Loeuille and Loreau, 2009, Loeuille, 2010]. These models are based on trophic interactions. The results presented here suggest that in a broader context, within communities containing all interaction types, evolution of trophic interactions is often more stabilizing compared to evolution of other interaction types, but that this difference, very large at low diversity, decreases at high levels of diversity. At levels of diversity that are relevant for natural communities, evolution destabilizes the system regardless of the type of interaction.

One of the reasons used to explain stability in evolutionary assembled food web models is the fact that evolution yields a skewed distribution of interaction strength [Kondoh, 2003, Loeuille and Loreau, 2009, Loeuille, 2010]. The coexistence of many weak interactions with few strong ones is known to increase stability within food webs [McCann et al., 1998]. The results of the two-species model suggest that evolution always stabilizes spiral dynamics when the evolving species is a prey or a predator with a weak interaction (figure 2B). This suggests that not only weak trophic interactions stabilize the system but when they exist, their evolution increases the stability, at least at low diversity levels.

Outside of the study of trophic interactions, I know few works that explicitly study the effects of evolution on stability. A competition model showed that evolution may drive to more or less stability [Zeineddine and Jansen, 2005], in agreement with the two-species model. In an assembly model based on competition, coevolution of species increases stability, measured as the resistance to disturbances [Rummel and Roughgarden, 1983]. Present simulations suggest that stabilization is likely, except when evolution is constrained by ecological costs or when diversity is high. In mutualistic networks, coevolution has been suggested to yield nested structures that enhance stability [Bascompte et al., 2003, 2006]. Results presented here show that even in the absence of nested structures, evolution of mutualistic interactions *per se*, in randomly structured communities, has an overall stabilizing effect, but only for communities that contain few species. At diversity levels that are relevant for natural communities, evolution of mutualistic interactions is more often destabilizing.

For all their merits, all these previous works are based on a single type of interaction, disregarding the diversity of interactions present in natural communities. I feel it is important to understand how the interplay of different interaction types affect our perception of community ecology, as the addition of these other interaction types modifies the structure of feedback loops that determines stability in complex systems. A clear advantage to focus on food webs or mutualistic networks is that such networks are well described and we know how they differ from random

networks [e.g., Montoya and Solé, 2003, Stouffer et al., 2007]. There are no such generalities regarding the structure of networks containing all interaction types. In the absence of this empirical knowledge, I do not see any reason to prefer a given structure as a starting point, so I chose to start from randomly assembled communities. The object of the study is not the random structure itself, but the difference (due to evolution) between the two communities (before and after invasion by the successful mutant). How this difference depends on the initial structure is an interesting question that goes beyond this study. Similar comparative methods starting from May's results have been employed earlier to identify key constraints of stability [De Angelis, 1975, Allesina and Pascual, 2008].

I use a fixed connectance ($C = 0.1$) and fixed maximum interaction strength. For food webs, connectance is known to be usually in the interval $[0.01, 0.38]$, most usually in the lower values of the interval, and to decrease with diversity [Beckerman et al., 2006]. It is unknown whether this value and pattern apply to communities when all kinds of interactions are considered. Food web connectance is computed using some degree of species aggregation ("tropho species", e.g, Martinez, 1991), meaning that species who share predators and preys are grouped. When communities are built using many kinds of interaction, connectance will be defined differently. It is unsure whether connectance values and the connectance-diversity decreasing relationship will remain outside the food web context. In the case of the present model, increasing connectance necessarily decreases the proportion of neutral mutations (black in figure3), that do not affect stability, because each mutation then affects more species in the food web via indirect effects. I do not see any mechanism through which changes in connectance would affect the other simulation results.

I focus here on the effect of replacing a given phenotype by a better-suited mutant, using an adaptive dynamics approach. I do not study the whole evolutionary dynamics, but simply focus on the effect of directional selection at a given instant. In such conditions, assessing the fitness gradient is sufficient and the results are expected to be similar to what would be found by quantitative genetic or evolutionary stable strategy models [Abrams, 2001]. A critical assumption is that invasion of the mutant leads to replacement of the resident population. When mutations are small and rare, as assumed here, this is true for many kinds of ecological models [Geritz, 2005], including the ones I use here. In natural systems however, this may not always be true.

Evolution is only one of many factors that influence population dynamics. It is more likely to play a role when it happens fast, as replacement of the resident by the mutant takes little time. This replacement timescale depends on the magnitude of the fitness gradient. Results for extreme cost situations (b close to 0 or very negative) are therefore likely to be all the more relevant for natural communities. Such costs more often lead to stabilization through evolution (appendix B, table 1).

Many one or few-species models linking evolution and stability exist (for a review, see Abrams, 2000, Fussmann et al., 2007). Most of them focus on trophic interactions. These studies reveal the importance of many factors such as non-linearity of the description of the interaction or of the fitness function [Abrams and Matsuda, 1997, Abrams, 2000, Schreiber and Vejdani, 2006, Doebeli and Koella, 1995], spatial components (refuges: Hochberg and

Holt, 1995, patch choice: van Baalen and Sabelis, 1993) or physiological structure [Ferrière and Gatto, 1993]. Some results support the ones I report here. For instance, that evolution of prey under allocation costs increases stability has already been noted elsewhere [Abrams and Matsuda, 1997, Abrams, 2000].

The present work studies the effects of evolution on stability depending on three factors: interaction type, cost type and diversity. A very important aspect is the fact that differences among interaction and cost types depend strongly on the diversity of the community. At low diversity they are quite large, but at high diversity, they do not exist any more. Because most of our knowledge on the relationships between evolution and stability builds on low diversity models, it is important to investigate whether their results also hold in more diverse communities, experimental or theoretical.

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Figure 1: Costs constraining evolution. (1) Large cost. The trade-off function linking trait 1 and trait 2 is steep. The cost (slope b of the tangent) is very negative. Mutants on trait 2 (stars) differs much in terms of trait 1 compared to their parent (circle). (2) intermediate cost. The slope is shallower so that a mutation on trait 2 does not yield a large difference in terms of trait 1. (3) weak costs. The slope is close to zero. Mutation on trait 2 little affects trait 1.

The figure is enlarged around the resident trait, but in adaptive dynamics, mutation amplitudes are supposed to be very small. In such conditions, trade-off curves and their tangents are almost confounded. Trade-off curve is only drawn for (1), for illustration purposes. Note that the model does not make any hypothesis on the exact shape of the trade-off function. Traits 1 and 2 depend on the scenario. For allocation costs scenarios, trait 2 is alternatively α_{12} then α_{11} while trait 1 is r_1 . For ecological costs, trait 2 is α_{11} and trait 1 is α_{12} .

Figure 2: Effects of evolution of α_{12} on stability under allocation trade-offs. Panel A shows the gradient of fitness ($\left(\frac{\partial W(\alpha_{12}^m, \alpha_{12})}{\partial \alpha_{12}^m}\right)_{\alpha_{12}^m \rightarrow \alpha_{12}}$, grey) and the variations of the real part of the leading eigenvalue with α_{12} , $\frac{\partial Re\lambda}{\partial \alpha_{12}}$, depending on the cost. Interaction between species 1 and 2 is mutualistic. Evolution increases stability when the product of the two values is negative (see equation 3), that is to say below R_1 (white disk) or above R_2 (black disk), the roots of $\left(\frac{\partial W(\alpha_{12}^m, \alpha_{12})}{\partial \alpha_{12}^m}\right)_{\alpha_{12}^m \rightarrow \alpha_{12}}$ and $\frac{\partial Re\lambda}{\partial \alpha_{12}}$ respectively. Between R_1 and R_2 , evolution decreases the stability. Parts of the cost axis for which evolution is stabilizing are solid, the part where it is destabilizing is dashed. Parameters: $r_1 = 0.1$, $r_2 = 1$, $\alpha_{12} = \alpha_{21} = 0.9$, $\alpha_{11} = -1$, $\alpha_{22} = -2$. Panel B shows how evolution affects stability along the cost axis depending on the type of dynamics (node or spiral), on the interaction type, and on the role of the evolving species (prey or weak predator: $\alpha_{21} > \alpha_{11}$, strong predator: $\alpha_{21} < \alpha_{11}$). Branches of the dendrogram show the alternatives for each of the scenarios. For the spiral case, the two roots are confounded. See appendix B for details.

Figure 3: Proportion (%) of mutations that leads to stabilization (white), destabilization (grey) and no change (black) in stability depending on the diversity of the community. Evolution is constrained by allocation costs for panel A and by ecological costs for panel B.

Figure 4: Stabilization effects of evolution in complex communities, when costs are expressed in terms of allocation (panel A) or in terms of ecological interactions (panel B). Different lines are used to show the ratio between the number of selected mutations that lead to increased stability and the ones that lead to decreased stability, depending on the interaction types the mutation affected (A=all interactions, I=intraspecific competition, M=mutualism, O=interspecific competition, P=trophic interaction).

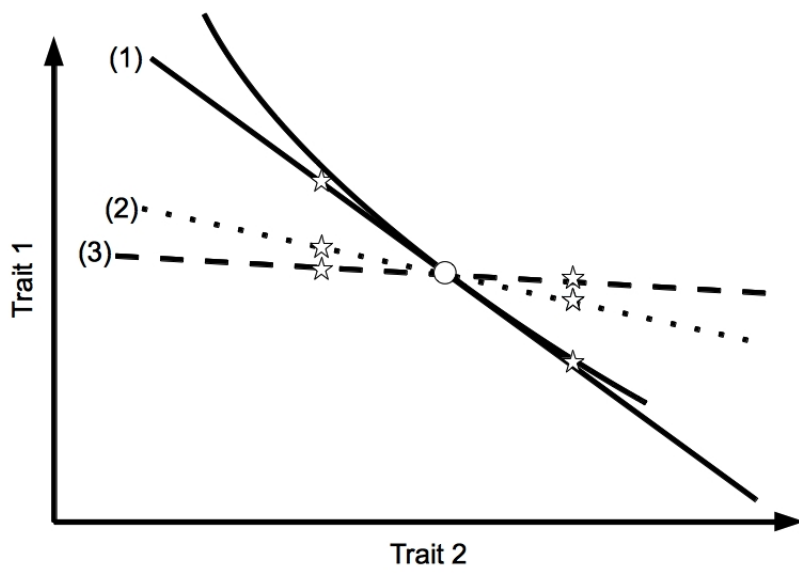


Figure 1:

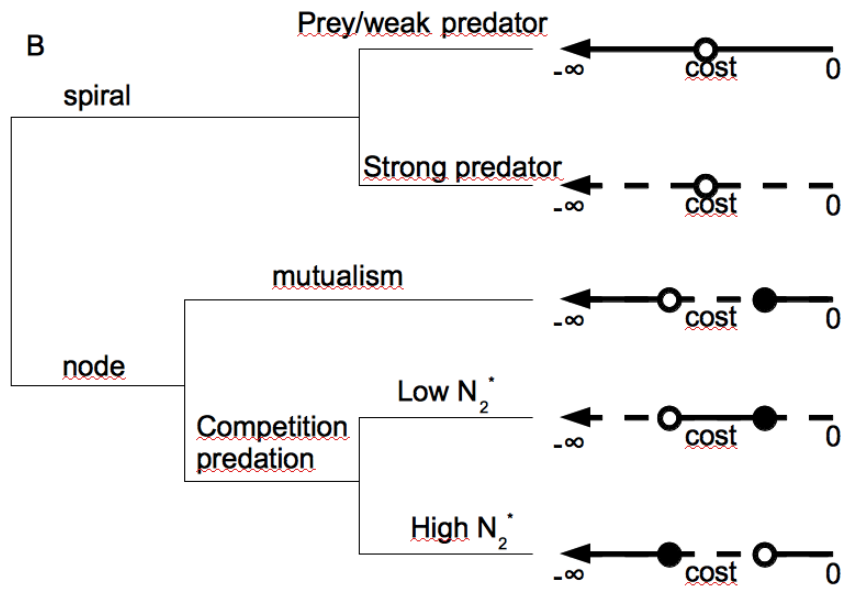
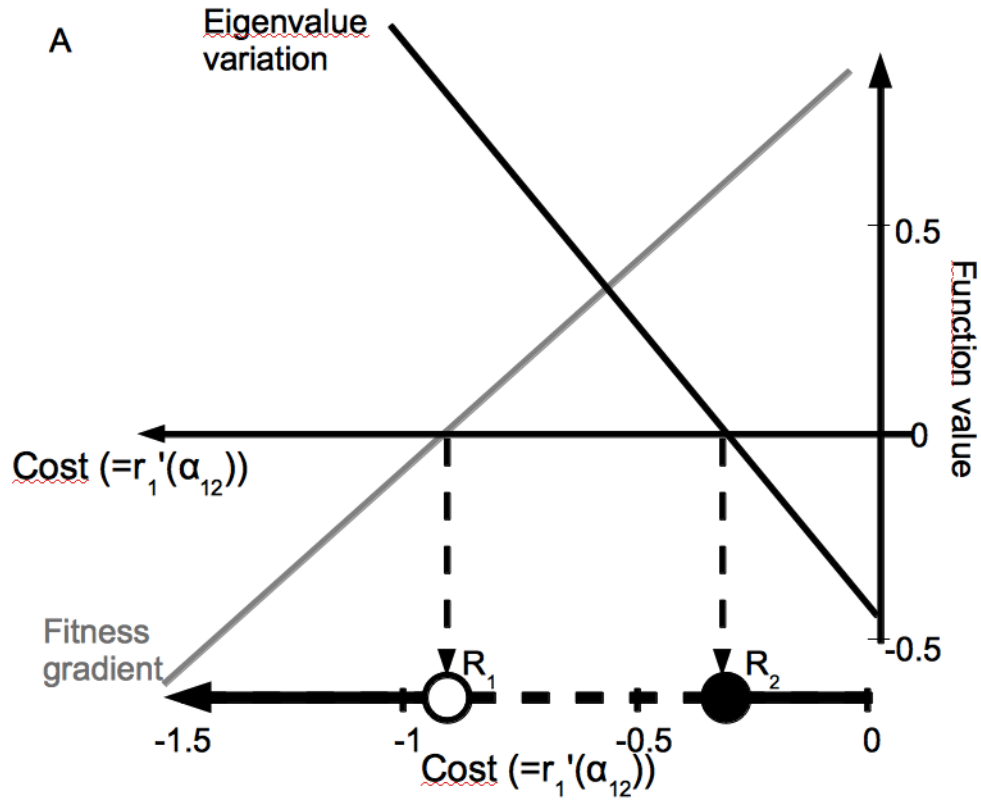
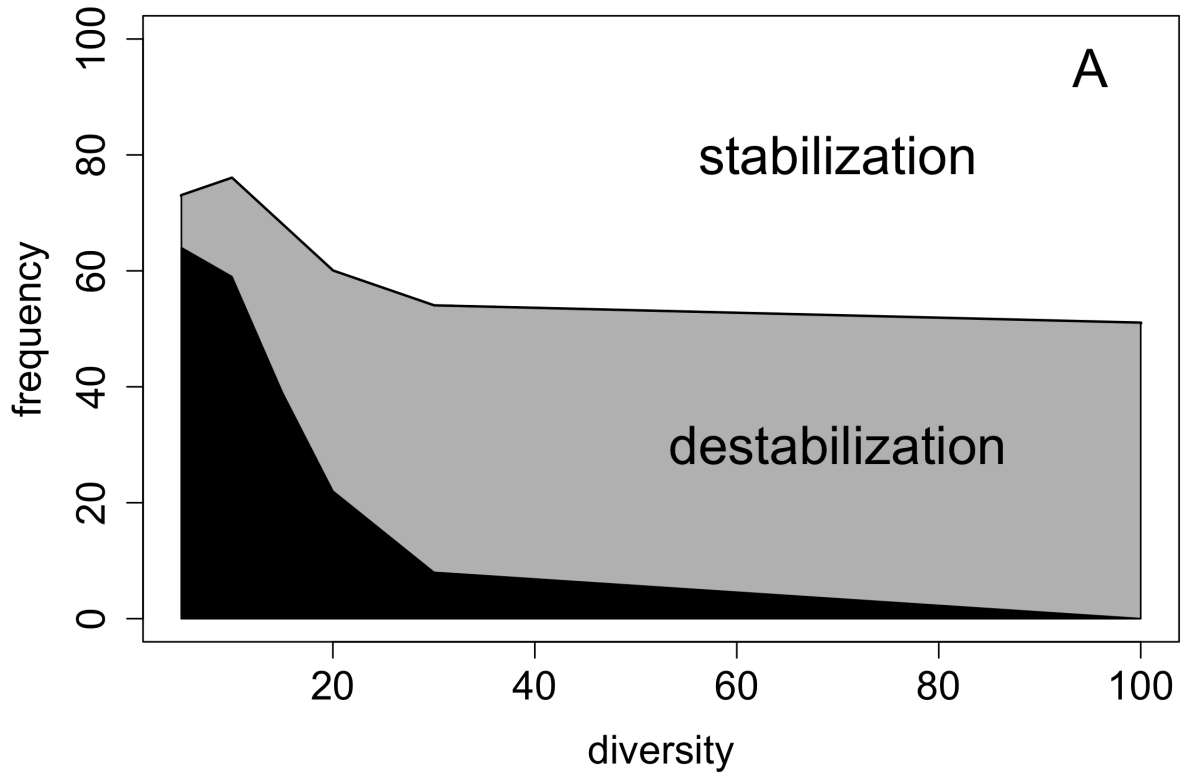


Figure 2:

Allocation costs



Ecological costs

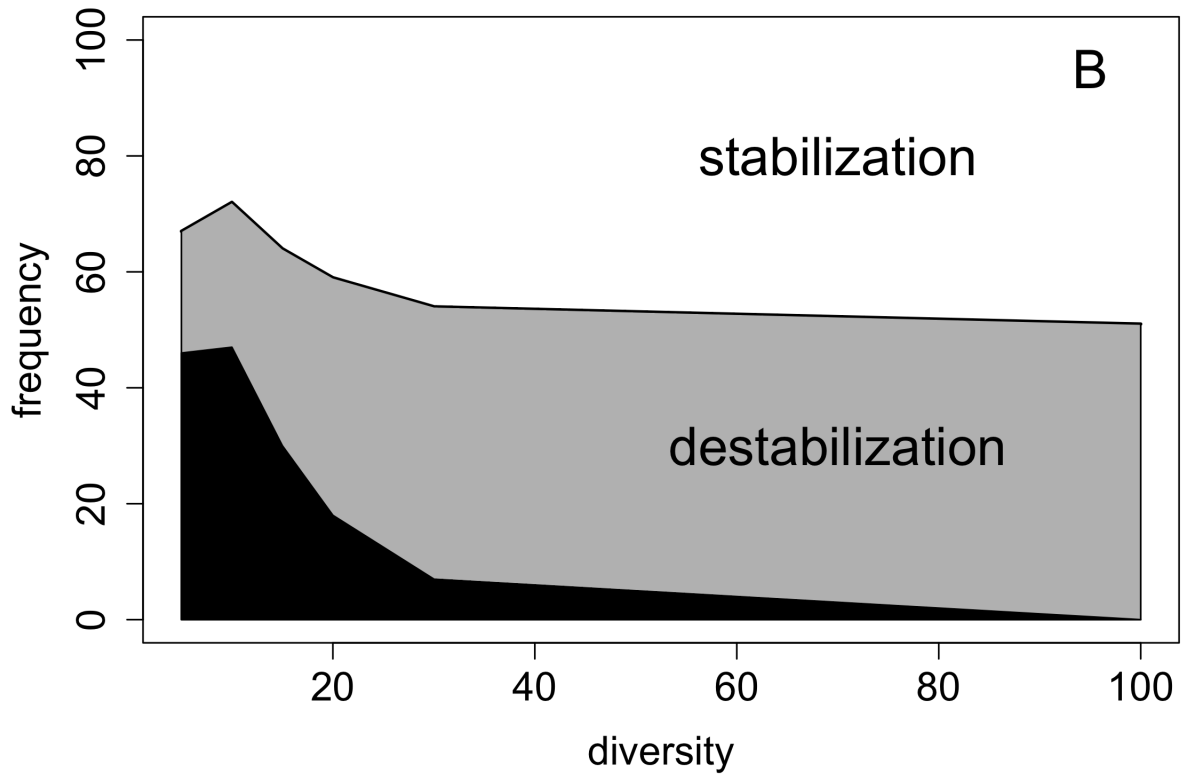


Figure 3:

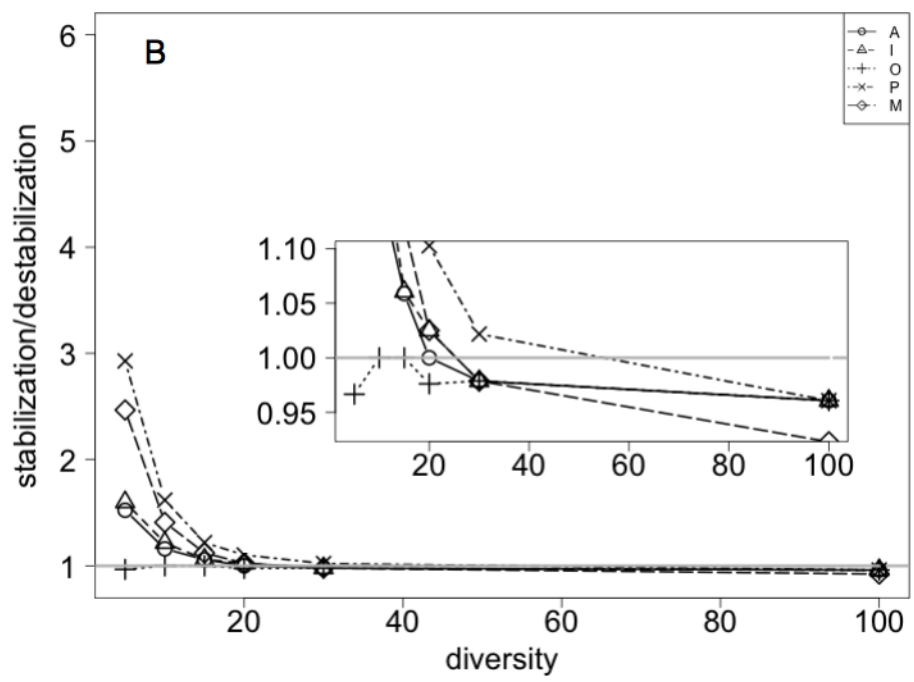
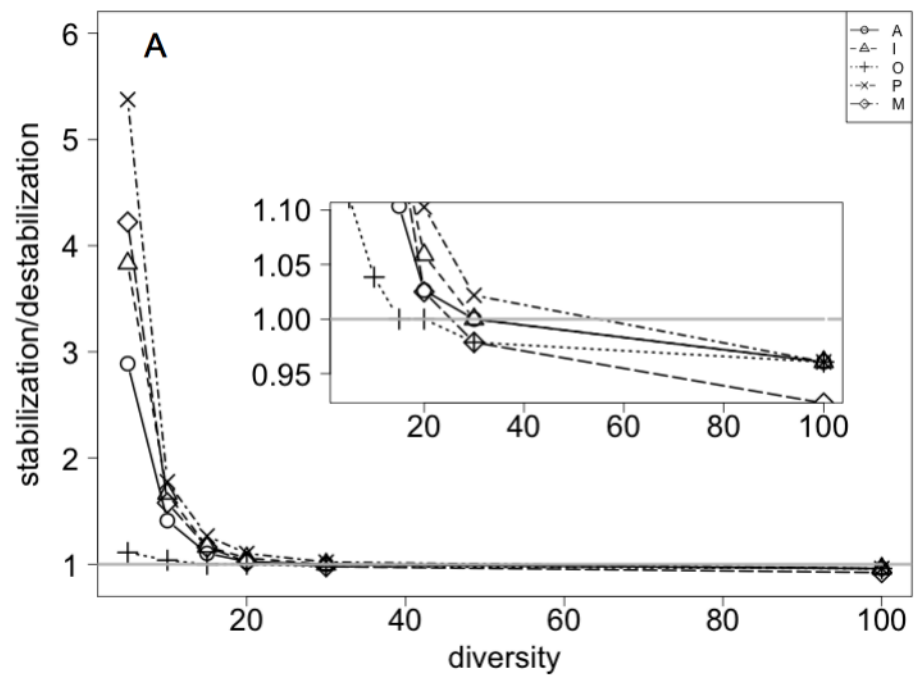


Figure 4: