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„Effects of Eco-Evolutionary Feedbacks on the Stability of Multi-Species Community Systems“

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Abstract

In the past few decades, an ever-increasing amount of empirical evidence has consistently emphasized the fact that evolutionary changes can effectively occur at an ecological rate. This realization drastically challenged the traditional isolated treatment of ecological and evolutionary systems. The inclusion of contemporary evolutionary changes into an ecological model can generate eco-evo feedbacks. These describe the interplay of ecological changes, inducing changes in evolutionary properties, which in return feed back to ecological changes, or vice versa. We first give an overview of existing works that show how eco-evo feedbacks can affect the stability of a system. In particular, we present work showing how feedbacks can stabilize an ecologically unstable system and destabilize an ecologically stable system. Moreover, they can induce permanence, reverse the direction of limit cycles and even lead to chaos. Varying the evolutionary speed can generate qualitatively different outcomes. In the second part, theoretical studies that investigate the type of feedbacks responsible for stabilizing or destabilizing a general multi-species community system are reviewed.

Zusammenfassung

In den letzten Jahrzehnten haben sich die empirischen Beweise dafür gehäuft, dass evolutionäre Veränderungen mit einer ökologischen Geschwindigkeit stattfinden können. Diese Erkenntnis stellt die traditionell isolierte Behandlung ökologischer und evolutionärer Systeme drastisch in Frage. Das Einbeziehen von schnellen evolutionären Veränderungen in ein ökologisches Modell kann sogenannte „Eco-Evo-Feedbacks“ erzeugen. Diese beschreiben das Zusammenspiel ökologischer Veränderungen, welche Veränderungen der evolutionären Eigenschaften induzieren, welche wiederum zu ökologischen Veränderungen führen oder umgekehrt. Zunächst erfolgt ein Überblick über bestehende Arbeiten, die zeigen wie sich Eco-Evo-Feedbacks auf die Stabilität eines Systems auswirken können. Insbesondere werden Arbeiten vorgestellt, die zeigen wie Eco-Evo-Feedbacks ein ökologisch instabiles System stabilisieren und ein ökologisch stabiles System destabilisieren können. Außerdem können Eco-Evo-Feedbacks Permanenz verursachen, die Richtung von Grenzzyklen umkehren und sogar Chaos auslösen. Änderungen der evolutionären Geschwindigkeit können zudem zu qualitativ unterschiedlichen Ergebnissen führen. Im zweiten Teil der Arbeit werden theoretische Studien vorgestellt, die untersuchen welche Art von Feedbacks die Stabilisierung oder Destabilisierung eines Multi-Spezies-System verursachen können.

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Introduction
Why Eco-Evo Feedbacks matter

Throughout the past century, mathematical models have repeatedly proven to be indispensable tools in studying the interactions between living organisms and unfolding the hidden mechanisms driving the diversity of ecosystems - both in the context of mathematical ecology and population genetics. The success of such models heavily relies on the right choice of level of abstraction, i.e. simplifications of reality in order to obtain a mathematically tractable problem, while at the same time incorporating all "important" factors. The definition of "important" may vary across models and depends on the desired level of accuracy. In order to pick the right choice of elements to include into the model, a thorough biological understanding of the problem is essential. Naturally, each mathematical model is only as good as the biological basis it relies on. If this basis is faulty, then the results and predictions of each mathematical model built on those biological assumptions may be flawed and need to be revised.

One of those assumptions - which is shared by a large number of mathematical models - is the fact that evolutionary changes occur on a much slower time scale than the ecological ones. Indeed, many literature works commonly adopt the terms "ecological time scale" and "evolutionary time scale" as a reference when discussing different rates of change. When talking about an ecological time scale, one usually means the time needed to observe notable changes in population densities. On the other hand, the evolutionary time scale corresponds to the time needed to observe changes in the species' traits, resp. changes in allele frequencies. For species with an intergenerational time span of one to three years - such as birds, or annual plants - the ecological time span is typically assumed to be about 100 years (Thompson 1998). This is the time scale at which most ecological studies are carried through and at which the resulting conservation decisions are based on. The evolutionary time span for such species is often assumed to be in the range of thousands to millions of years, depending on the generation length. Consequently, most ecological models completely neglect any evolutionary components since they are assumed to remain roughly unchanged during the relatively short ecological time span. Classical examples are the well known *Lotka-Volterra models* (Lotka 1920; Volterra 1928). Due to this difference, ecological and evolutionary models have mostly been treated separately throughout history. If one was interested in understanding the interactions between organisms and their environment - possibly with the objective of maintaining biological diversity found in nature - then ecological models were used. If one was interested in the processes that have caused this diversity, then the focus was laid on evolutionary models. At large, this isolated treatment of ecology and evolution was the norm and well accepted by both the biological and mathematical community.

In the past few decades, however, an increasing amount of empirical evidence consistently highlighted the fact that evolutionary changes can effectively occur at an ecological rate (Frickel et al. 2016, DeLong et al. 2016). This realization drastically challenged the traditional separation of ecological and evolutionary models. Importantly, this meant that on a contemporary time scale the ecological dynamics may be affected by rapid evolutionary changes and vice versa. It is therefore essential to incorporate evolution into the ecological models, since one might otherwise falsify the outcome and provide misleading predictions. In order to grasp the full extent of these distorted outcomes, theoretical work studying the effects of including evolutionary aspects into an ecological model is urgently needed. There are a variety of ways by which such theoretical studies can be approached, one being the investigation of so called *eco-evo feedbacks* (sometimes referred to as *eco-evolutionary feedbacks*) and their influence on the dynamics. Eco-evo feedbacks involve the reciprocal interactions between ecological and evolutionary processes. They represent the interplay of ecological changes (changes in the environment or in species abundances) that cause changes in the evolutionary traits, which in return feed back and affect the ecological properties of the system, or vice-versa. According to Govaert et al. (2019), one of the first works analyzing these feedbacks dates back to the year 1961 in a publication by Pimentel (1961). Nonetheless, for a long time most ecological studies were carried out without considering the possibility that their observed results may have been influenced by rapid evolutionary changes. It was a publication on eco-evolutionary dynamics by Fussmann et al. (2007), which revived the interest in eco-evo feedbacks among biologists and mathematical ecologists (Hendry 2016). Since then, an ever-growing number of empirical evidence for rapid evolution, as well as works studying the eco-evolutionary feedbacks have been published (Govaert et al. 2019).

There are many ecological properties in a system that can be influenced by the eco-evo feedbacks, such as stability, persistance, invasibility, permanence, directions of stable limit cycles, and many more. In this thesis, we will focus on the stability of multi-species community systems and give an overview of the few existing works that analyze the influence of these feedbacks. The goal of this thesis is the presentation of some of the most important numerical and most of all analytical results, which have advanced our knowledge of how the eco-evo feedbacks can effectively alter the stability of ecosystems. To highlight the fact that eco-evo feedbacks do truly exist, in the second chapter we will present some empirical studies which clearly show that evolutionary changes can effectively occur on a contemporary ecological time scale. The main results are presented in the third chapter. The first part of this chapter focuses on works which have analyzed the eco-evo feedbacks through numerical simulations of specific community systems, which consist of at most three species. Theoretical studies such as these - which are based on numerical simulations - are quite numerous. In contrast, analytical results on the effects of eco-evo feedbacks on system stability are hardly available with two notable exceptions by Patel, Cortez and Schreiber, which will be presented in the second part of the third chapter (Patel et al. 2018; Cortez et al. 2020). These are - at the time being - the only works which have attempted to provide analytical results on the effects of eco-evo feedbacks on system stability in general multi-species community systems. However, analytical work on specific models, typically with few species, is available (Vasseur and Fox 2011, Schreiber et al. 2011, Schreiber and Patel 2015, Patel and Bürger 2019).

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Empirical Evidence

Before tackling the theory of how eco-evo feedbacks can affect system stability, we first provide some empirical evidence of evolutionary change occurring at an ecological rate. To this end, we present a chemostat experiment (Frickel et al. 2016) which perfectly shows the coevolution of an algae-virus system at a rate congruent to the ecological dynamics. Frickel, Sieber and Becks performed the experiment by starting several chemostats all with the same isolated algae clone in order to minimize the genetic variability. After 12 days, they added a virus to the chemostats and counted virus and algae densities daily. Every other day, they removed a sample of algae and virus populations in order to keep track of the evolutionary changes. The two evolutionary properties of interests are on the one hand the resistance, resp. the susceptibility of the algae population, and on the other hand the infectivity of the virus population. At some specific time-points, several algae clones were isolated from the chemostat and each exposed to a different virus population sampled from the past up to the present. The resistance of the algae clone at a given time point was then determined by comparing the growth of the algae samples with the different viruses, to the growth of the same clone without the virus. Accordingly, the infectivity of a specific virus population was determined by the number of host clones which could be infected throughout this process.

The experiment initially led to so called arms race dynamics (ARD), where both the host and the virus alternatively adapted to the evolutionary response of the other (Figure 1). Thus, the oscillations in the first 45 days correspond to selective sweeps of new resistant algae types. Eventually the oscillations were damped out and the ARD ended with an almost general resistant algae type. The algae population did however not reach fixation due to a trade-off between resistance and growth, ultimately allowing the virus population to stabilize at some low density.

The critical observation of this experiment is that the evolutionary changes occurred at a similar rate to the ecological dynamics. At the end of chapter 3, we will return to

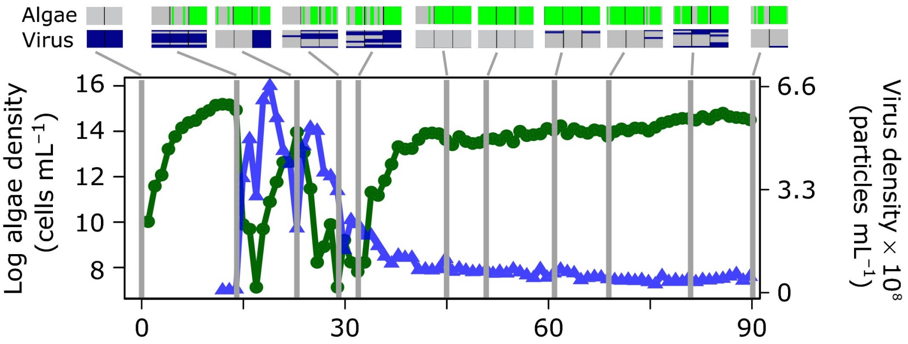

Figure 1: Illustration of the ecological and evolutionary dynamics of both algae and virus in the chemostat experiment of Frickel et al. 2016. The green dots represent the logarithms of the algae densities and the blue triangles represent the (logarithms) of the virus densities each day. The grey bars denote the time points where experiments were made in order to determine the evolutionary changes of the algae (susceptibility) and the virus (infectivity). The color coded squares above the grey bars describe the evolutionary state of the algae, resp. virus. The three squares corresponding to the algae evolution represent the susceptibility of algae from one time step in the past (first square), contemporary time point (second square), and one time step in the future to the contemporary virus. Similarly, the three squares corresponding to the virus evolution denote the infectivity of the virus at one time step in the past (first square), the contemporary time point (second square), and at one step in the future (third square) to the contemporary algae population. The color green denotes that the algae is resistant to the virus, the color blue means that the virus was able to infect the algae, and grey denotes that the algae was susceptible to the virus, resp. that the virus was unable to infect the algae.

this example with the purpose of understanding how the eco-evo feedbacks stabilized the system.

While many similar examples confirm that the evolutionary time scales are in some cases comparable to the ecological rates, it remains unclear how fast the relative ecological and evolutionary rates really are. To this end, one can consider a standard model - the so called *Lande equation* (Lande 1976) - which is commonly used to describe the change in the mean of the trait under consideration:

$$\dot{x} = h^2 \sigma^2 \frac{\partial W}{\partial x},$$

where h^2 is the heritability of the trait, σ^2 the phenotypic variance of the trait and finally W the mean fitness of the species. Using the standard definition of fitness, i.e. the per capita growth rate of the species $W = \dot{N}/N$ and using the relation $\frac{\partial}{\partial x} W = W \frac{\partial}{\partial x}(\log W)$, one obtains:

$$
\begin{aligned}
& \dot{x} = h^2\sigma^2 \frac{\partial \log W}{\partial x} W \\
\Leftrightarrow \qquad & \dot{x} = h^2\sigma^2 \frac{\partial \log W}{\partial x} \frac{\dot{N}}{N}.
\end{aligned}
$$

Finally, dividing both sides by x, results in the fact that both the ecological and evolutionary rates have the same unit and thus can be compared. All together, the critical term which relates the ecological rate $\dot{N}/N$ to the evolutionary rate is given by

$$C := \frac{h^2\sigma^2}{x} \frac{\partial \log W}{\partial x}.$$

This term can in theory be smaller or larger than 1, corresponding to slower or faster evolutionary rates compared to the ecological ones. Interestingly, strong selection (i.e. large values of $\frac{\partial}{\partial x}(\log W)$) will not guarantee fast evolutionary rates if the heritability or the variance of the trait are too low. Using this framework, DeLong et al. (2016) determined the relative evolutionary rates in 21 empirical systems with comparable ecological and evolutionary time scales, including data of algae, protists, rotifers, lizards, fish, mammals, and birds. The surprising result was that in all these systems, the evolutionary rate varied, but never exceeded the ecological ones. Indeed, the evolutionary rates were never faster than about two-thirds and on average about one-fourth of the ecological rates.

3

The Role of Eco-Evo Feedbacks on Stability

3.1 Motivation

Motivated by the significant amount of empirical evidence - suggesting that eco-evo feedbacks do effectively alter the long time behaviour of multi-species dynamics - we now approach the topic from a theoretical point of view. In particular, we would like to investigate whether and how these feedbacks affect the stability of ecosystems, i.e. the ability to withstand inevitable, but small perturbations. Advancing our understanding of the mechanisms that govern ecological stability is of utmost importance, given the rise of natural, but first and foremost anthropogenic changes, such as climate change and environmental degradation. Ecological disturbances such as these will rather likely lead to ecological responses (changes of population sizes, immigration of new species due to climate change) that change the selection pressure, resulting in an evolutionary response, which in return "feeds back" on ecological properties, or vice versa. The fundamental question whether a given ecosystem can withstand and recover from such environmental stresses - eventually allowing coexistence of all preceding species - is the key focus of many mathematical ecologists. The aim of this chapter is the presentation of existing results that elaborate the role of eco-evo feedbacks on the stability of multi-species community systems. In particular we will address the following potential questions: Can eco-evo feedbacks stabilize a system that is ecologically and/or evolutionary unstable? Is it possible to identify for each model the exact types of feedbacks (ecological, evolutionary, eco-evolutionary) that have a stabilizing/destabilizing effect?

Throughout this chapter, our main goal is the derivation of general analytical results on multi-species community systems. This seemingly innocent task will however quickly reveal itself to be surprisingly challenging. Indeed, analytical results on the effects of eco-evo feedbacks concerning the stability of general multi-species and multi-trait systems are - at the time being - hardly available, with two notable exceptions (Patel et al. 2018; Cortez et al. 2020). These results (Patel et al. 2018; Cortez et al. 2020) will be introduced in section 3.3 and 3.4 respectively. While general theory seems to be scarce, results on specific community systems are relatively common (Vasseur et al. 2011; Schreiber et al. 2011; Schreiber and Patel 2015; Mougi 2012; Cortez and Weitz 2014). Unfortunately, most of these works only provide numerical, rather than analytical results, which prevent a mechanistically understanding of the underlying eco-evo effects on stability. Nonetheless, analyzing specific community systems first, serves as a great starting point in understanding and proving the potential dependence on system stability and eco-evo feedbacks. These preliminary examples will bet limited to two or three species, with one or two evolving traits. Eventually we aim to present results on models with an arbitrary but finite number of interacting species, each of which in turn can have an arbitrary but finite number of evolving traits, which in general are subject to frequency and density dependent selection.

Before presenting the results, we first clarify what we mean by "system stability". Throughout this thesis, we will always call a system stable, if it is locally stable at an equilibrium. Local stability can be determined by calculating the Jacobian and evaluating it at the equilibrium. Finally, deriving the eigenvalues will give us the desired information on the local behaviour. In particular, if all the eigenvalues have negative real part, then the equilibrium is stable. If however one eigenvalue has positive real part, then we say that the equilibrium - and therefore the system - is unstable. If the real parts of all of the eigenvalues are non-positive with at least one eigenvalue having a negative real part, then we say that the equilibrium is neutrally stable. If the real parts of all of the eigenvalues are zero, then we call the equilibrium neutral. In addition to the notion of stability of a system, we call any matrix "stable", "unstable", "neutrally stable" or "neutral" if it's eigenvalues satisfy the previous conditions. There are of course various other ways of defining system stability. A system with a stable limit cycle around an equilibrium could for example also be considered stable, even though the equilibrium itself is unstable. Another example would be to call a system stable if it is globally stable. Indeed, since we restrict ourselves to the local analysis of isolated equilibria, we might be missing the global picture. The global dynamics can be much more complex if the system has more than one coexistence equilibrium. However, since we limit ourselves to the analysis of rather small perturbations, a local analysis - and thus, our definition of system stability - is in most cases sufficient. Unfortunately, natural perturbations can quite often be described as intense shake-ups, rather than gentle stirrings. In these cases, a good understanding of the global behaviour is highly important: The trajectories close to a locally stable equilibrium could converge to some stable limit cycle or a chaotic attractor if the perturbations are sufficiently strong. These dynamics are often highly complex and relating them to the effects of eco-evolutionary feedbacks is incredibly challenging. Fortunately, the exact ecological dynamics are in most cases of lesser importance. The more crucial part is the question, whether all species can continue to coexist after some environmental perturbation. There are various mathematical concepts involving the notion of ecological coexistence: persistence, invasibility and permanence. We briefly discuss permanence in section 3.2.2 and present a result which relates the eco-evolutionary feedbacks to permanence of a three-species apparent competition model.

3.2 Examples: Specific communities

3.2.1 2-species competition

The first example presented is a 2-species competition model by Vasseur et al. (2011), where one of the species has an evolving trait that effects the interaction coefficients. Classical non-evolutionary competition models (constant interaction coefficients), such as the *Lotka-Volterra models* (Lotka 1920; Volterra 1928) are straightforward to analyze (at least in two dimension). We start by preliminarily studying this rather simple model, with the intention of eventually comparing the results to the more general and complex evolutionary case. The equations are given by:

$$\dot{x} = r_x x(1 - c_{xy}y - c_{xx}x) \tag{3.1a}$$

$$\dot{y} = r_y y(1 - c_{yx}x - c_{yy}y), \tag{3.1b}$$

where r_x and r_y correspond to the intrinsic growth rates of species x and y respectively (Hofbauer and Sigmund 1988). The coefficients c_{xy} and c_{yx} correspond to the interspecific interaction parameters, whereas the coefficients c_x and c_y correspond to the intraspecific interaction parameters. All of the interaction terms are assumed to be non negative. Note that in the absence of species y, the system reduces to simple logistic growth of species x. For the analysis of the full model ($x \neq 0, y \neq 0$), it's sufficient to consider all possible isocline configurations. For the Lotka-Volterra competition model, the non-trivial isoclines are linear with negative slopes: $y = (1 - c_{xx}x)/c_{xy}$ for the x-isocline, and $y = (1 - c_{yx}/c_{yy})$ for the y-isocline.

Four different isocline configurations are possible as depicted in Figure 2. Each corresponds to one of three qualitatively different patterns: dominance, mutual exclusion or coexistence.

Dominance: As the name suggests, one species dominates the other. Let's assume w.l.o.g that x is dominant. In this case, y goes extinct, reducing the dynamics of x to simple one-dimensional logistical growth. As a consequence, x converges to its carrying capacity $K_x = 1/c_{xx}$. This pattern always prevails when both isoclines do not intersect in the positive quadrant. In this case, the species with the "higher" isocline is dominant. In Figure 2, (a) corresponds to dominance of species x over y and (b) corresponds to dominance of species y over x. Biologically, this means that both species share the same limited resource, which according to the so called

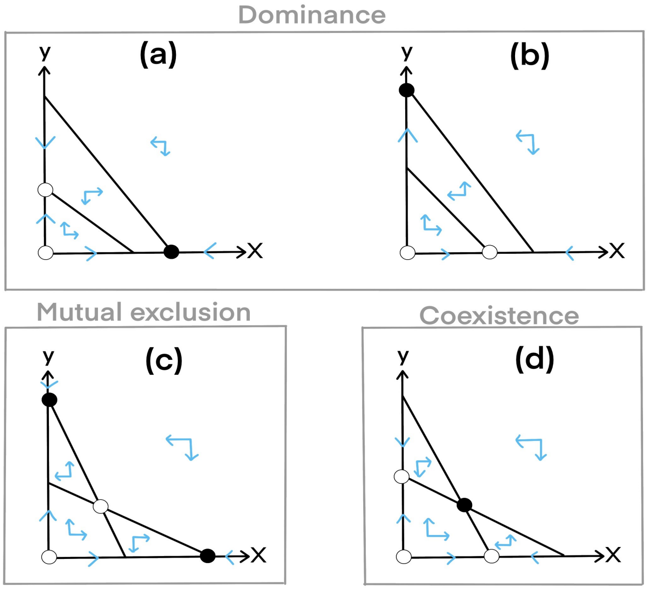

Figure 2: Four possible isocline configurations of (3.1). Unstable equilibria are represented by white circles, whereas asymptotically stable equilibria are represented by black circles. (a) and (b) correspond to dominance of one species over the other. (c) corresponds to the case of mutual exclusion. (d) corresponds to the case of coexistence.

competitive exclusion principle (sometimes referred to as *Gause's law*) always drives the weaker competitor to extinction.

Mutual exclusion: If interspecific competition is stronger than competition among conspecifics, this could once more lead to the extinction of one of both interacting species. Mathematically speaking, this corresponds to the case where the isoclines intersect below the carrying capacity of both species (Figure 2c), leading to an unstable interior equilibrium and two asymptotically stable boundary equilibria. Depending on the initial frequencies of both species, the long-term outcomes will be differently: Either they converge towards the carrying capacity of x and extinction of y, or vice versa.

Coexistence: The most interesting case (from an ecologist's perspective) is of course coexistence. This is possible if the intraspecific competition between conspecifics outweighs the competition with the other species. Mathematically speaking, this corresponds to the case where the isoclines cross above the carrying capacity of both species (Figure 2d), leading to two unstable saddles on the boundary and a globally stable interior equilibrium at the intersection of the isoclines. Biologically, this means that - unlike in the case of dominance - each species has its own private resource. This is also known as the process of *niche differentiation* or the *principle* *of limiting similarities*, and is critical in promoting the high biodiversity found in certain areas of the world.

Niche differences can arise through various ways, such as by using different environmental areas or consuming specialized foods. While the theory about niche differentiation enabling coexistence seems clear, empirical demonstrations of the latter have proven itself to be much more challenging. While perfectly obvious examples confirming the theory are easy to think of (Figure 3), there are exceptions to the rule: *Hispine beetles* have been obeserved to eat the same food and share the same habitat, without showing any evidence of intra- or interspecific aggression, while according to the theory, they should be subject to interference competition (Strong 1982). This inconsistency between theory and empirical observations suggest that for a deeper understanding of coexistence in natural communities, additional non-ecological factors may have to be considered as well.

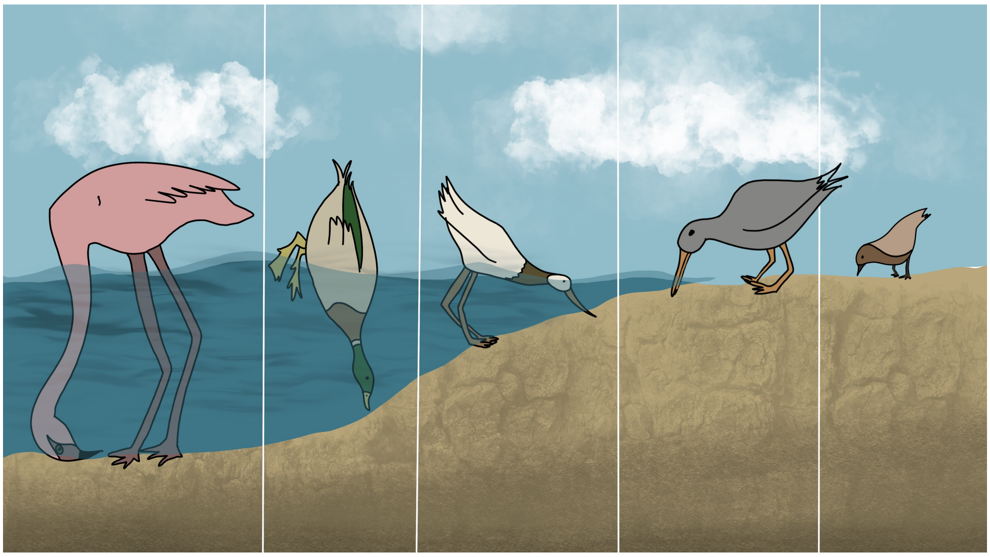

Figure 3: Example of niche differentiation in nature. The five different bird species in the illustration share the same habitat, while each have their individual niches. In this particular example, the niche differences correspond to the different levels in the sand where they search their prey and on which they feed on. This allows them to coexist peacefully without the risk of extinction of any of the involved species.

Adding an evolutionary component

Following Vasseur et al. (2011), we now present an alternative mechanism allowing coexistence, which assumes the additional existence of an evolutionary process

occurring on a congruent time scale.
In classical character displacement theory, similar competing species evolve through traits that create niche differences, ultimately allowing coexistence. Classical examples are the diverse beak forms (and functions) of the Galápagos finches (also known as *Darwin's finches*). Other examples, such as that of the Hispine beetles however, show that these niche differences do not necessarily need to occur in real coexisting communities. As an alternative explanation, Vasseur et al. considered traits that are subject to so called *neighbor-dependent selection*: when rare (most "neighbors" are heterospecifics), a species experiences stronger selection on traits associated to interspecific competition, and when abundant (most "neighbors" are conspecifics), it experiences stronger selection on traits involved in intraspecific competition. This means that - in contrast to character displacement - the involved traits are not niche axes, but allow stable coexistence by permanently shifting the respective dominance, depending on the relative abundance of either species (eco-evo feedbacks). Importantly, this implies that the involved species won't develop niche differences and therefore cannot coexist in the absence of evolution according to Gause's law. In other words, the eco-evo feedbacks allows coexistence, in an otherwise ecologically unstable system.

To begin with, Vasseur et al. assumed that only one of the two involved species has an evolving trait, which in the following will be referred to as the *variable species* and denoted by N_v. Accordingly, the other species will be referred to as the *fixed species* and denoted by N_f. Furthermore, they assumed that the traits under consideration all have a genetic basis, and that there exists a trade-off which ensures that the optimal traits for dominance in a conspecific neighborhood (intraspecific competition) preclude dominance in a heterospecific neighborhood (interspecific competition). The trait for dominance in a conspecific neighborhood are now called x and the other trait y. As depicted in Figure 4, the fitness landscape changes depending on the relative abundances of the species. In a conspecific neighborhood, fitness is maximized for low values of x (θ_c) and high values of y. In a heterospecific neighborhood, fitness is maximized for high values of x (θ_H) and low values of y. Since both traits are negatively correlated, it is therefore sufficient to only consider trait x for the analysis.

For the ecological part, one can once more use a Lotka-Volterra competition model. In contrast to (3.1), now the mean interspecific interaction terms ($\overline{c}_{fv}(\overline{x}), \overline{c}_{vf}(\overline{x})$) and the mean intraspecific interaction term of the variable species ($\overline{c}_{vv}(\overline{x})$), continuously depend on the mean trait $\overline{x}$. Only the conspecific interaction parameter of the fixed

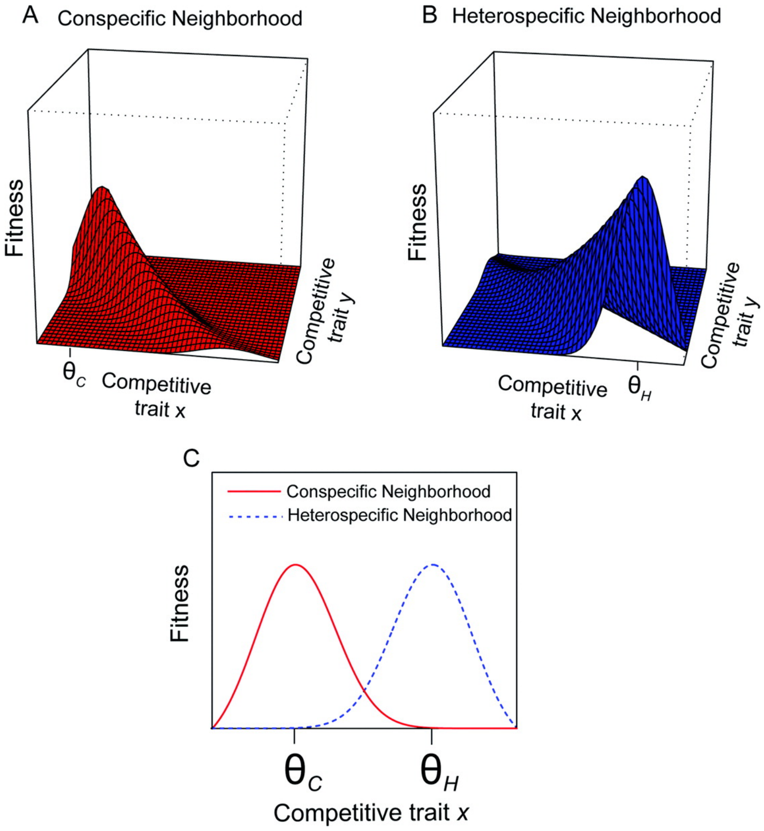

Figure 4: Illustration of the fitness landscapes in a neighborhood dominated by conspecifics (A) and heterospecifics (B). In a conspecific neighborhood (A), the fitness is maximized for small values of the trait x and large values of the trait y. In a heterospecific neighborhood, the opposite is the case: the fitness is maximized for high values of x and low values of y. Due to this trade-off, it is sufficient to only consider x for the analysis as depicted in (C), where the fitness in a conspecific (resp. heterospecific) neighborhood is maximized for $x = \theta_C$ (resp. $x = \theta_H$). (Vasseur et al. 2011)

species (c_{ff}) remains constant. All together, gives:

$$\dot{N}_f = r_f N_f (1 - \overline{c}_{fv}(\overline{x}) N_v - c_{ff} N_f) \tag{3.2a}$$

$$\dot{N}_v = r_v N_v (1 - \overline{c}_{vf}(\overline{x}) N_f - \overline{c}_{vv}(\overline{x}) N_v), \tag{3.2b}$$

The evolutionary dynamics are described in terms of the mean trait $\overline{x}$ and follow the so called *Lande equation* (Lande 1976), which is, essentially, equivalent to the so-called *breeder's equation*:

$$\dot{\overline{x}} = h^2 \sigma^2 \cdot \frac{\partial}{\partial \overline{x}} \Big(\frac{\dot{N}_v}{N_v} \Big). \tag{3.3}$$

Explanation of the equations

To begin with, one needs to note that in the equations (3.2), the mean of the competition terms were used as coefficients, as opposed to the competition terms themselves. For this, Vasseur et al. adopted the typical assumption for quantitative traits, namely that x is normally distributed with mean $\overline{x}$ and variance σ^2. Thus, the mean interaction coefficients are given by the integral

$$\overline{c}_{ij}(\overline{x}) = \int_{-\infty}^{\infty} c_{ij}(x) \cdot \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{-(-x - \overline{x})^2}{2\sigma^2} \right) dx. \tag{3.4}$$

Here $c_{ij}(x)$ denote the interaction coefficients as a function of the quantitative trait x. Finally, multiplying them with the according distribution function and integrating across all possible trait values gives the desired mean competition coefficients used in equations (3.2). For a detailed analysis, the exact form of the interaction coefficients $c_{ij}(x)$ still need to be specified. Ultimately, they should resemble the graphs of Figure 4C, i.e. they should be continuous in the trait x and attain a local minimum or maximum at some finite value for x. The most obvious approach is to simply consider Gaussian functions, however any similar functions with the same critical points work fine as well. Since the interaction parameter of the fixed species c_{ff} remains constant, only the terms c_{fv}, c_{vf} and c_{vv} need to be considered:

$$c_{fv}(x) = a_1 + \exp\left(\frac{-(x-\theta_H)^2}{2\tau^2}\right) \tag{3.5a}$$

$$c_{vf}(x) = 1 + a_1 - \exp\left(\frac{-(x-\theta_H)^2}{2\tau^2}\right) \tag{3.5b}$$

$$c_{vv}(x) = 1 + a_1 - \delta - (1-2\delta)\cdot\exp\left(\frac{-(x-\theta_C)^2}{2\tau^2}\right). \tag{3.5c}$$

Note that both c_{vf} and c_{vv} are upside-down Gaussian functions with a minimum at θ_H and θ_C respectively. Minimizing $c_{vv}(x)$ in a conspecific neighborhood is always the best strategy for the variable species, since this is equivalent to minimizing intraspecific competition. Thus, $x = \theta_C$ corresponds to the optimal trait value for the variable species in a conspecific neighborhood. Similar is true if the neighborhood is dominated by heterospecifics: In this case, the optimal strategy for the variable species is to minimize $c_{vf}(x)$ and maximize $c_{fv}(x)$, since this corresponds to dominance of N_v over the fixed species. For simplicity, it is assumed that $c_{vf}(x)$ and $c_{fv}(x)$ attain their critical points at the same value $x = \theta_H$. Thus, θ_H corresponds to the optimal trait value for the variable species in a heterospecific neighborhood. A further assumption is that all three Gaussian functions have the same width τ. Finally, a_1 determines the extreme values of the respective functions and δ determines the relative rate at which the coefficient c_{vv} changes with the trait.

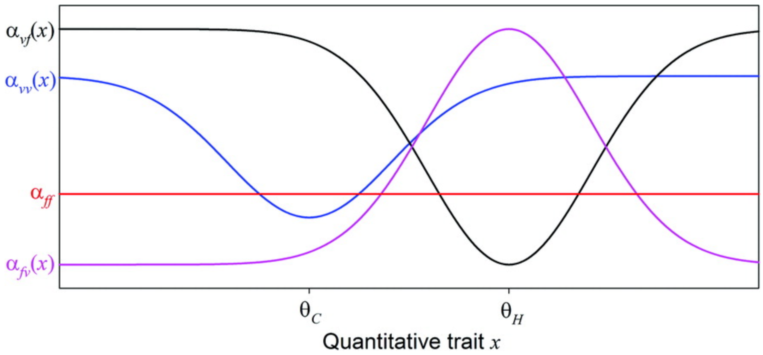

Figure 5: Interspecfic interaction terms as function of the quantitative trait x. Note that $\alpha_{ij}(x) = c_{ij}(x)$. At $x = \theta_C$, the interaction term c_{vv} is minimized which means that the variable competitor is best-adapted in a neighborhood of conspecifics. At $x = \theta_H$, the coefficient c_{vf} is minimized whereas c_{fv} attains its maximal value, which means that the variable competitor is optimally adapted in a neighborhood dominated by heterospecifics. (Vasseur et al. 2011)

Combining equations (3.3) and (3.5), and solving the integral results in the following representation of the mean interaction coefficients used in the model:

$$\overline{c}_{fv}(\overline{x}) = a_1 + \left(\frac{\tau}{\sqrt{\tau^2+\sigma^2}}\right)\exp\left(\frac{-(\overline{x}-\theta_H)^2}{2\tau^2+2\sigma^2}\right) \tag{3.6a}$$

$$\overline{c}_{vf}(\overline{x}) = 1 + a_1 - \left(\frac{\tau}{\sqrt{\tau^2+\sigma^2}}\right)\exp\left(\frac{-(\overline{x}-\theta_H)^2}{2\tau^2+2\sigma^2}\right) \tag{3.6b}$$

$$\overline{c}_{vv}(\overline{x}) = 1 + a_1 - \delta - (1-2\delta)\cdot\left(\frac{\tau}{\sqrt{\tau^2+\sigma^2}}\right)\exp\left(\frac{-(\overline{x}-\theta_C)^2}{2\tau^2+2\sigma^2}\right). \tag{3.6c}$$

For a better understanding of the evolutionary equation, we need to clarify what the Lande equation actually describes. In its most general form, the Lande equation is given by $R = \sigma_G^2 S$. Here R refers to the change in the mean of the quantitative trait. S is the so called selection differential: $S < 0$ if N_v benefits from lower values of the trait and $S > 0$ if selection favors higher values of the trait. In equation (3.3), S is given by the derivative of the per capita growth rate of N_v w.r.t. the mean trait $\overline{x}$ (fitness gradient), which obviously satisfies the previous properties. Finally, σ_G^2 is the heritable component of the phenotypic variance, which determines the rate at which the mean trait changes as a response to the selection differential S. Indeed, the phenotypic variance can be written as $\sigma^2 = \sigma_G^2 + \sigma_E^2$, where σ_G^2 is its heritable genetic component and σ_E^2 is the environmental component. The parameter $h^2 = \sigma_G^2/\sigma^2$ is called the heritability of the trait. Using this, Lande's equation can be rewritten as $R = h^2\sigma^2 S$. This representation of the change of the mean trait is useful when studying the consequences of varying the evolutionary speed of the system, which can then simply be done by changing the value of the heritability parameter h^2.

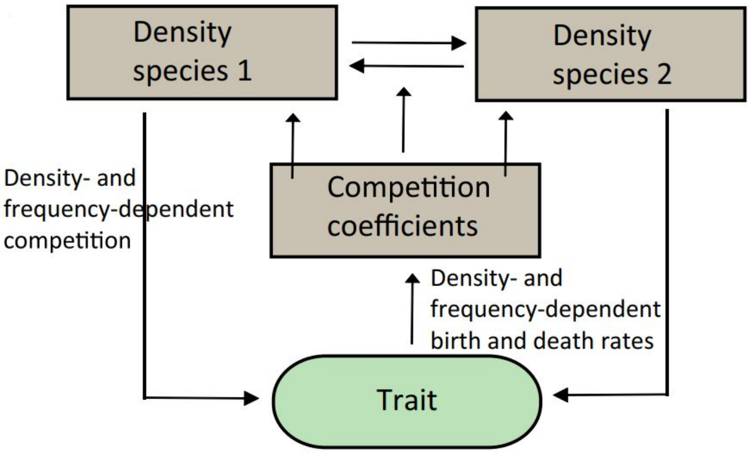

Figure 6: Graphical representation of the model in Vasseur et al. 2011. (Figure from Govaert et al. 2019)

Numerical analysis of the model

As with most eco-evo models, the full dynamical behavior cannot be determined by mathematical analysis. Therefore Vasseur et al. (2011) helped themselves with numerical methods to understand the underlying effects of the eco-evo feedbacks. As a preliminary step, they ignored the evolutionary dynamics and analyze the outcomes of the pure ecological Lotka-Volterra model, while varying the value of the mean trait $\overline{x}$. To this end, they restricted the domain of $\overline{x}$ to $[\theta_C, \theta_H]$. Indeed, if the variable species lives in a neighborhood of conspecifics, then its per capita growth rate is proportional to $1 - \overline{c}_{vv}(\overline{x})$, thus selection on the trait decreases $\overline{c}_{vv}(\overline{x})$. As a consequence, $\overline{x}$ converges towards θ_C. On the other hand, if the variable species lives in a neighborhood dominated by heterospecifics, then its per capita growth rate is proportional to $1 - \overline{c}_{vf}(\overline{x})N_f$, thus selection on the trait decreases $\overline{c}_{vf}(\overline{x})$. Similar to the previous case, $\overline{x}$ will converge towards θ_H. Hence, the mean trait $\overline{x}$ is bounded by θ_C and θ_H, and one can assume w.l.o.g. that $\theta_C < \theta_H$. Furthermore, Vasseur et al. assumed that the competitive parameters depend on the mean trait $\overline{x}$ in such a way that the variable species dominates in a heterospecific environment if $\overline{x} = \theta_H$, and the fixed species dominates if $\overline{x} = \theta_C$. A violation of this assumption leads to the dominance of one of both species over the entire domain $[\theta_C, \theta_H]$. As depicted in Figure 2, dominance corresponds to the case where the isoclines do not intersect in the positive quadrant. The species with the higher isocline dominates and drives the other to extinction. Since in this case, dominance is reversed at the endpoints of the selection domain, the isoclines will have to intersect at some intermediate value $\overline{x}^* \in (\theta_C, \theta_H)$. Three possible outcomes can emerge depending on the shape and position of the interaction functions (Figure 7): coexistence, neutrality and mutual exclusion.

The intersection of the isoclines with the N_f axes are given by $1/c_{ff}$ and $1/c_{vf}$. Since both isoclines eventually change positions, there exists a value $\overline{x}_f$ at which $1/c_{ff} = 1/c_{vf}$. The same is true for the intersections of the iosoclines on the N_v axes, which are given by $1/c_{vv}$ and $1/c_{fv}$. The trait value satisfying $1/c_{vv} = 1/c_{fv}$ will accordingly be called $\overline{x}_v$. The ecological outcome at intermediate mean trait values depends on the relative positions of $\overline{x}_f$ and $\overline{x}_v$: (1) if $\overline{x}_f < \overline{x}_v$, the isoclines will intersect above the carrying capacity of both species and as a result, one gets coexistence at a stable interior equilibrium (Figure 7b); (2) if $\overline{x}_f = \overline{x}_v$, the outcomeis neutrality (Figure 7c); (3) if $\overline{x}_f > \overline{x}_v$, the isoclines will intersect below the carrying capacity of both species and the outcome is mutual exclusion (Figure 7d). Importantly, this implies that the ecological outcome at intermediate values depends on the relative

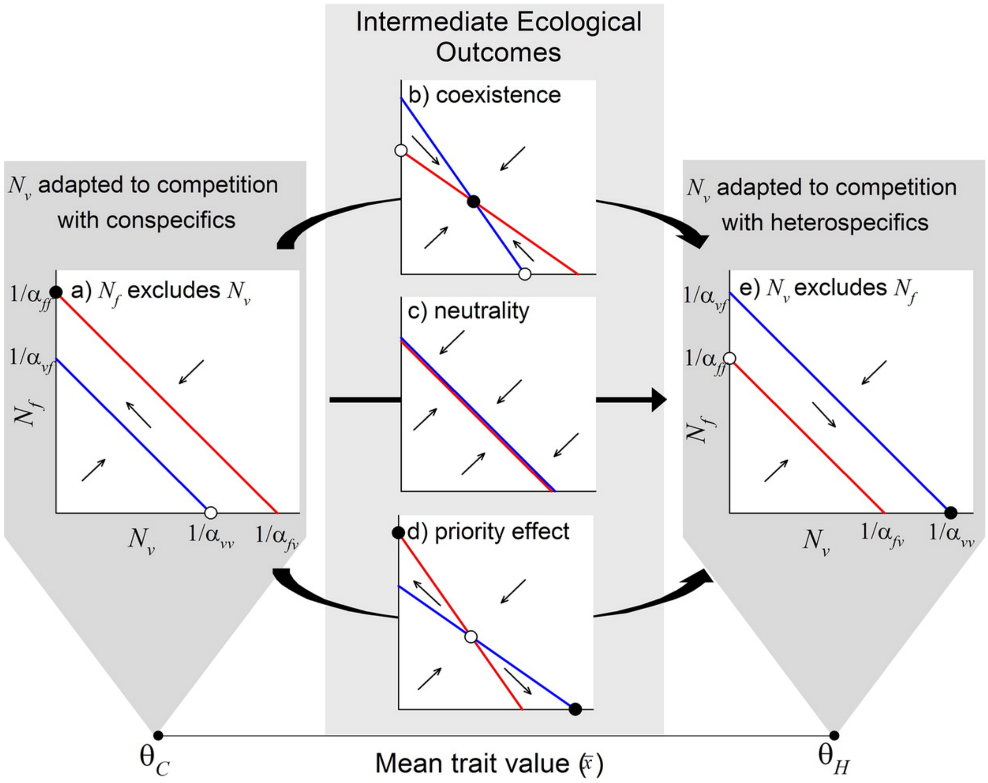

Figure 7: Isocline configurations for different mean trait values $x \in [\theta_C, \theta_H]$. Note that $\alpha_{ij} = c_{ij}$. At the boundary points θ_C and θ_H the isoclines reverse their relative positions. Consequently, the isoclines intersect (in the positive quadrant) for some intermediate value of x. This can happen in three different ways depicted in (b), (c) and (d). Panel (b) illustrates an intersection at a single point, resulting in coexistence at a globally stable equilibrium. The second panel (c) shows the case of neutrality where a continuum of equilibria appear. In the third case (d), the isoclines intersect at a single point, resulting in an unstable interior saddle equilbrium and two stable boundary equilibria, leading to the extinction of one of both species, depending on their initial densities. (Vasseur et al. 2011)

positions of the intersections of $c_{ff}(\overline{x})$ and $\overline{c}_{vf}(\overline{x})$, and of $\overline{c}_{vv}(\overline{x})$ and $\overline{c}_{fv}(\overline{x})$. By the choice of the interaction functions, it is guaranteed that each two functions intersect exactly once in the selection domain (i.e. $\overline{x}_f$ and $\overline{x}_v$ are well defined), provided that $0 \leq \delta \leq 0,5$. As depicted in Figure 8, varying the fixed parameter c_{ff} can lead to a reversal of the relative positions of $\overline{x}_f$ and $\overline{x}_v$. Thus, the ecological outcome can be changed solely by varying c_{ff}.

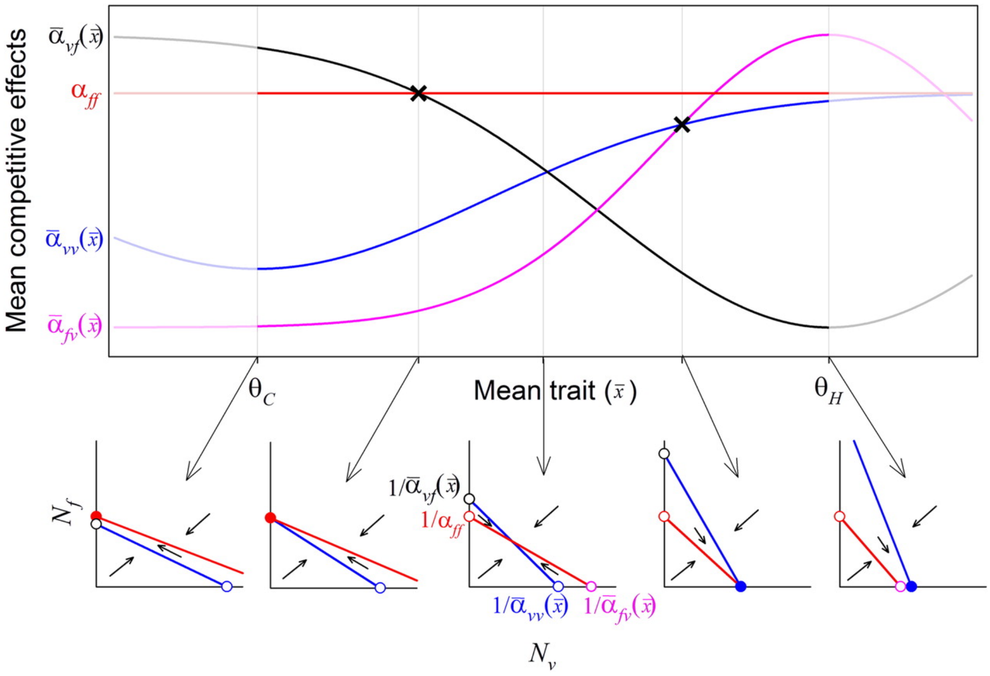

Figure 8: Mean interspecific interaction terms as function of the mean trait $\overline{x}$ in the case of $\overline{x}_f < \overline{x}_v$. Note that: $\overline{\alpha}_{ij} = \overline{c}_{ij}$. The isocline configurations are depicted for several values of the mean trait $\overline{x}$. Since $\overline{x}_f < \overline{x}_v$, there exists some intermediate value of the mean trait such that the isoclines intersect in a way which results in a coexistence equilibrium. (Vasseur et al. 2011)

Next, Vasseur et al. included the evolutionary dynamics and simulated the model for three different values of c_{ff}, corresponding to coexistence, neutrality and mutual exclusion in the purely ecological model (Figure 9). To this end, they assumed that a small number of individuals of the fixed species ($N_f(0) = 0,01$) invade a population of the variable species ($N_v(0) = 1/\overline{c}_{vv}(\overline{x})$) which is optimized for a neighborhood of conspecifics ($\overline{x}(0) = \theta_C$).

If the intermediate ecological outcome for a fixed mean trait is coexistence, then the mean trait in the full eco-evo dynamics converges towards an optimum at which stable coexistence is possible once again (Figure 9a-c). If the intermediate ecological outcome for a fixed mean trait is neutrality or mutual exclusion, then the mean trait

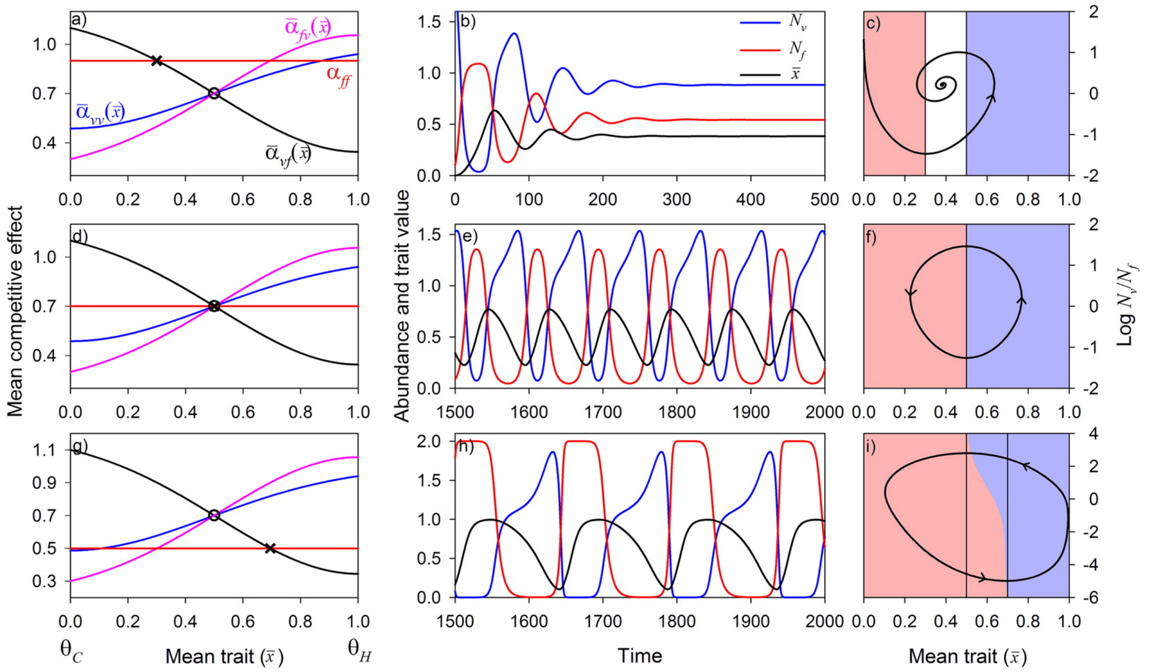

Figure 9: Simulations of the eco-evolutionary model each corresponding to one of the three possible intermediate ecological outcomes depicted in Figure 7. (a)-(c) correspond to a value of c_{ff} which lead to coexistence in the ecological model; (d)-(f) correspond to a value of c_{ff} which lead to neutrality in the ecological model; (g)-(i) correspond to a value of c_{ff} which lead to mutual exclusion in the ecological model. Notation: $\alpha_{ij} = c_{ij}$. (Vasseur et al. 2011)

oscillates within the selection domain, leading to alternating periods of dominance of either species. Thus, in both cases, the species converges towards a stable limit cycle (Figure 9d-i). A crucial observation is - as predicted in the beginning of this section - that the eco-evo feedbacks allow coexistence in an ecologically unstable system (Figure 9g-i). This phenomena can be understood as a form of so called *intransitive competition*. Typically, in competition systems, there is a clear transitive hierarchy in dominance among species: A dominates B or vice versa. Coexistence is only possible if A and B have their own individual niches. In contrast, systems with intransitive competition are not hierarchical: A dominates B, B dominates C and C dominates A. Thus, there is no strongest or weakest species, just as in a rock-paper-scissors game (Soliveres and Allan 2018). Typically, intransitive competition requires at least three species to form such a loop. This outcome is however no violation to the rule since the variable species can be simply interpreted as two different species: The variable species adapted to heterospecifics wins against the fixed species, the fixed species wins against the variable species adapted to conspecifics, and finally the variable species adapted to conspecifics wins against the same species adapted to heterospecifics.

Conclusion

This model serves as a perfect demonstration of how eco-evo feedbacks can stabilize an ecologically unstable system and provides a possible explanation for the coexistence of species without niche differences, such as the Hispine beetles. Thus, Gause's law need not always be satisfied in natural communities. As a matter of fact, a more recent study suggests that species coexisting while sharing the same limited resource might even be advantageous in a changing environment (Prinzing et al. 2017). The reason is that sharing the same niche might help promote mutualist exchange, niche expansion and hybridization among the interaction species, which in return helps them to resist natural perturbations.

3.2.2 Eco-evo feedbacks can destroy coexistence in simple predator-prey models

In this and the following subsections, we briefly present some further examples on how the eco-evo feedbacks can influence a system besides stabilizing it. The proofs of the main results are omitted since the aim should simply be to highlight the importance of feedbacks.

In the model of Vasseur et al. (2011), the eco-evo feedbacks promoted coexistence in a system that would otherwise lead to the extinction of one of the involved species. We now show that this does not always have to be the case. Indeed, as a first example, we present a coexisting predator prey system, where incorporating an evolutionary trait leads to the extinction of at least one of both species. As a basis, we start with a simple Lotka-Volterra predator prey system without intraspecific competition:

$$\dot{N} = N(r - c_{NM}M) \tag{3.7a}$$

$$\dot{M} = M(c_{MN}N - d), \tag{3.7b}$$

where N is the density of the prey, M the density of the predator, $r > 0$ is the intrinsic growth rate of the prey, $c_{NM} > 0$ and $c_{MN} > 0$ are parameters describing the interaction between the predator and the prey, and finally $d > 0$ is the death rate of the predator. This model was originally used by Vito Volterra to explain the increased number of sharks and rays in the sea after the first world war, when fishing had been interrupted for a few years. A detailed analysis of this model can be found in Hofbauer and Sigmund (1988). The phase plane of this model consists of a continuum of periodic orbits around a unique coexistence equilibrium (Figure 10). Initial conditions that are "far" away from this equilibrium result in oscillations that get dangerously close to the x, resp. y axis. Consequently, slight perturbations of the model may lead to the extinction of one of both species. If we however start with initial conditions that are reasonably close to the equilibrium, both species will be able to coexist.

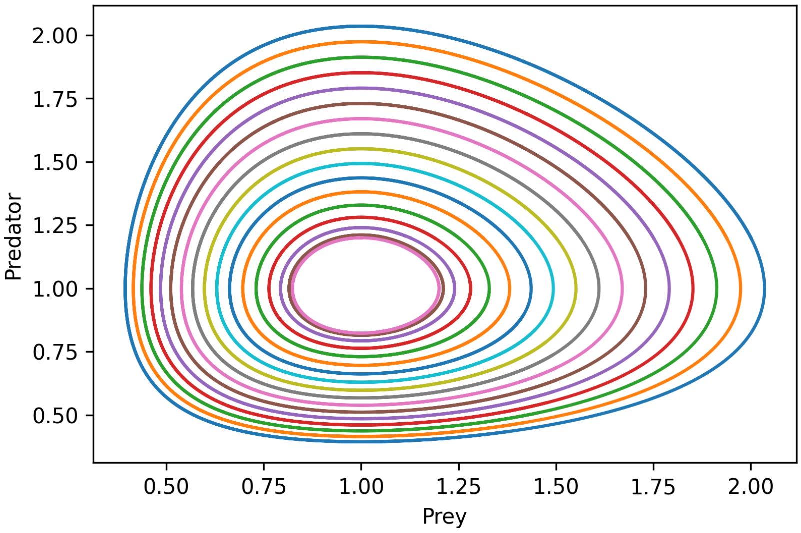

Figure 10: Illustration of the continuum of periodic orbits that appear in the phase portrait of a Lotka-Volterra predator prey system without intraspecific competition.

Next, we include an evolutionary component to the model. For this, we assume that the predator has an evolving trait that determines both its attack and death rate. We assume that there is a trade off, such that trait values which are beneficial in the interaction with the prey, result in a lower life expectancy, and thus a higher death rate. Conversely, trait values which increase the life expectancy, result in a decrease of the attack rate. If we describe the change of the mean trait $\overline{x}$ using the Lande equation as in Vasseur et al. (2011), this gives:

$$\dot{N} = N(r - f(\overline{x})M) \tag{3.8a}$$

$$\dot{M} = M(g(\overline{x})N - h(\overline{x})) \tag{3.8b}$$

$$\dot{\overline{x}} = \sigma_G^2 \cdot \frac{\partial}{\partial \overline{x}}\Big(\frac{\dot{M}}{M}\Big), \tag{3.8c}$$

where the interaction terms $f(\overline{x})$ and $g(\overline{x})$ and the death rate of the parameter $h(\overline{x})$ are now functions of the mean trait $\overline{x}$. The term σ_G^2 denotes the genetic variance of the trait. By our assumption, an increase in the mean trait results in an increase of the functions f, g and h, i.e. $\partial f/(\partial \overline{x}) > 0$, $\partial g/(\partial \overline{x}) > 0$ and $\partial h/(\partial \overline{x}) > 0$. The simplest functions satisfying these conditions are linear functions $f(\overline{x}) = c_{NM}\overline{x}$, $g(\overline{x}) = c_{MN}\overline{x}$ and $h(\overline{x}) = d\overline{x}$, with $c_{NM}, c_{MN}, d > 0$. Plugging this into our model gives us:

$$\dot{N} = N(r - c_{NM}\overline{x}M) \tag{3.9a}$$

$$\dot{M} = M(c_{MN}\overline{x}N - d\overline{x}) \tag{3.9b}$$

$$\dot{\overline{x}} = \sigma_G^2 \cdot (c_{MN}N - d). \tag{3.9c}$$

Plotting the phase portrait of this new model reveals that the incorporation of an evolutionary trait in this way destroys the continuum of periodic cycles found in the ecological model and replace them with growing oscillations that spiral out and asymptotically approach the boundary (Figure 11). Eventually, the densities of both the predator and the prey reach values close to zero. Thus, slight perturbations either lead the predator, or both the predator and the prey to extinction.

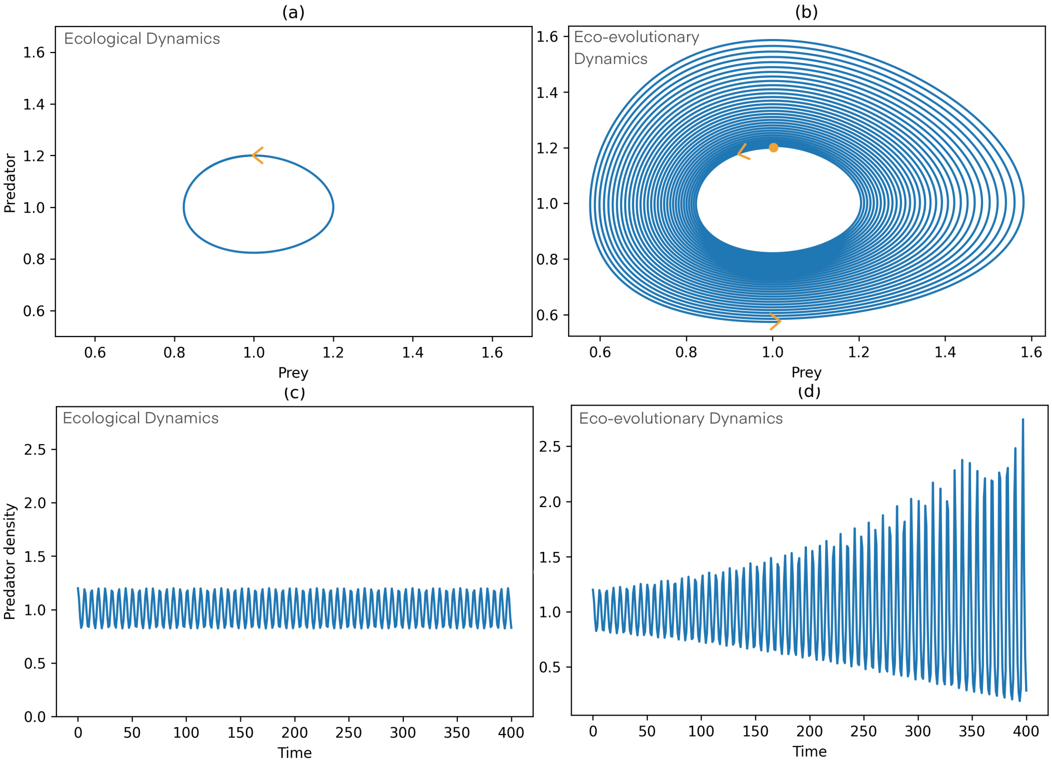

Figure 11: Comparison between the dynamics of the ecological model (a),(c) and of the model with an evolving predator (b),(d). The parameter values are $r = c_{NM} = c_{MN} = d = 1$. All four plots start with the same initial conditions $(N, M) = (1, 1.2)$. In (a) and (c), both species coexist while exhibiting periodic oscillations. In (b) and (d), the full eco-evolutionary dynamics are considered with $\sigma_G^2 = 0.01$. The eco-evolutionary dynamics in (b) and (d) oscillate with growing amplitude and progressively approach the boundary, resp. zero., which increases the risk of extinction.

3.2.3 Rich eco-evo dynamics in a three-species apparent competition model

The second example we present is a 3-species apparent competition model by Schreiber et al. (2011). The model is based on a Lotka-Volterra system of two prey species with densities N_1 and N_2, which are consumed by a single evolving predator with density P. Ignoring the evolutionary component, the system reduces to a purely ecological model of the type:

$$\dot{N}_1 = r_1 N_1 (1 - \frac{N_1}{K_1}) - \alpha N_1 N_2 - a_1 N_1 P \tag{3.10a}$$

$$\dot{N}_2 = r_2 N_2 (1 - \frac{N_2}{K_2}) - \beta N_1 N_2 - a_2 N_2 P \tag{3.10b}$$

$$\dot{P} = P(e_1 a_1 N_1 + e_2 a_2 N_2 - d). \tag{3.10c}$$

Takeuchi and Adachi (1983) showed that if $\alpha\beta < 1$, then three different outcomes are possible: (1) Global convergence towards a coexistence equilibrium of all three species; (2) Global convergence towards an equilibrium which only supports the prey species, and thus results in the extinction of the predator; (3) Global convergence towards an equilibrium supporting the predator and a single prey, resulting in the extinction of the second prey. All together, convergence towards a globally stable equilibrium is guaranteed in all three cases.

The model of Schreiber et al. (2011) is exactly of this type with $\alpha = \beta = 0$, i.e. the direct competition between both preys is ignored. However, they added an evolutionary component to model and assumed that the predator's attack rate $a_i(x)$ on species i continuously depends on some trait x of each individual predator. The trait x is assumed to be normally distributed with mean $\overline{x}$ and variance σ^2. The attack rates are maximized at some optimal trait value $x = \theta_i$. More precisely, they described them as a Gaussian function $a_i(x) = \alpha_i \exp -\frac{(x-\theta_i)^2}{2\tau_i^2}$, where α_i is the maximal attack rate and τ_i measures the speed at which the attack rates decline when moving away from the optimal trait value θ_i. Thus, if $\theta_1 \neq \theta_2$, then there is a trade-off s.t. the predators which are specialized on prey 1 are not best-adapted for feeding on prey 2 and vice versa. Similar to the previous model of Vasseur, they now averaged the attack rates

$$\overline{a}_i(\overline{x}) = \int_{-\infty}^{\infty} a_i(x)p(x,\overline{x})\,dx = \frac{\alpha_i\tau_i}{\sqrt{\sigma^2+\tau_i^2}} \exp -\frac{(\overline{x}-\theta_i)^2}{2(\sigma^2+\tau_i^2)},$$

where $p(x,\overline{x}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp -\frac{(x-\overline{x})^2}{2\sigma^2}$ is the density of the normal distribution. All together, the ecological dynamics are given by

$$\dot{N}_i = r_iN_i(1-\frac{N_i}{K_i}) - \overline{a}_i(\overline{x})N_iP \tag{3.11a}$$

$$\dot{P} = P(e_1\overline{a}_1(\overline{x})N_1 + e_2\overline{a}_2(\overline{x})N_2 - d), \tag{3.11b}$$

where r_i are the intrinsic growth rates of the preys, K_i are their carrying capacity, d is the death rate of the predator and the parameters e_i determine how the prey consumption is linked to the growth of the predator. As in Vasseur et al. (2011), the evolutionary dynamics are described using the Lande equation

$$\dot{\overline{x}} = \sigma_G^2\frac{\partial\overline{W}}{\partial\overline{x}}, \tag{3.12}$$

where $\overline{W} = \sum_{i=1}^{2} e_i\overline{a}_i(\overline{x})N_i - d$ is the average per capita growth rate of the predators' population, and σ_G^2 is the genetic heritable component of the phenotypic variance of the trait. Intuitively, selection tends to increase the fitness of the corresponding species. However, since the fitness functions depend continuously on the trait x - which might change over time - the fitness functions changes as well, leading to eco-evo feedbacks. These feedbacks affect the overall outcome in different ways, depending on the degrees of heritability $h^2 = \sigma_g^2/\sigma^2$ and phenotypic variance σ.

For $\sigma^2 = 0.04$, the densities of all three species converge towards a stable equilibrium (Figure 12a,b). This is consistent with the system behaviour in the case of no evolution as shown by Takeuchi and Adachi (1983). However, if the value of the phenotypic variance is decreased to $\sigma^2 = 0,01$, then interesting dynamics can be observed by slightly shifting the heritage parameter h^2. For small values such as $h^2 = 0.1$, the densities of all three species remain stable at an equilibrium. Slightly increasing the heritability to $h^2 = 0.25$ results in all three species exhibiting sustained oscillations reminiscent of chaotic behavior (Figure 12d). This shows that, the eco-evo feedbacks can induce oscillations in a system which would otherwise converge towards a globally stable equilibrium in the case of no evolution.

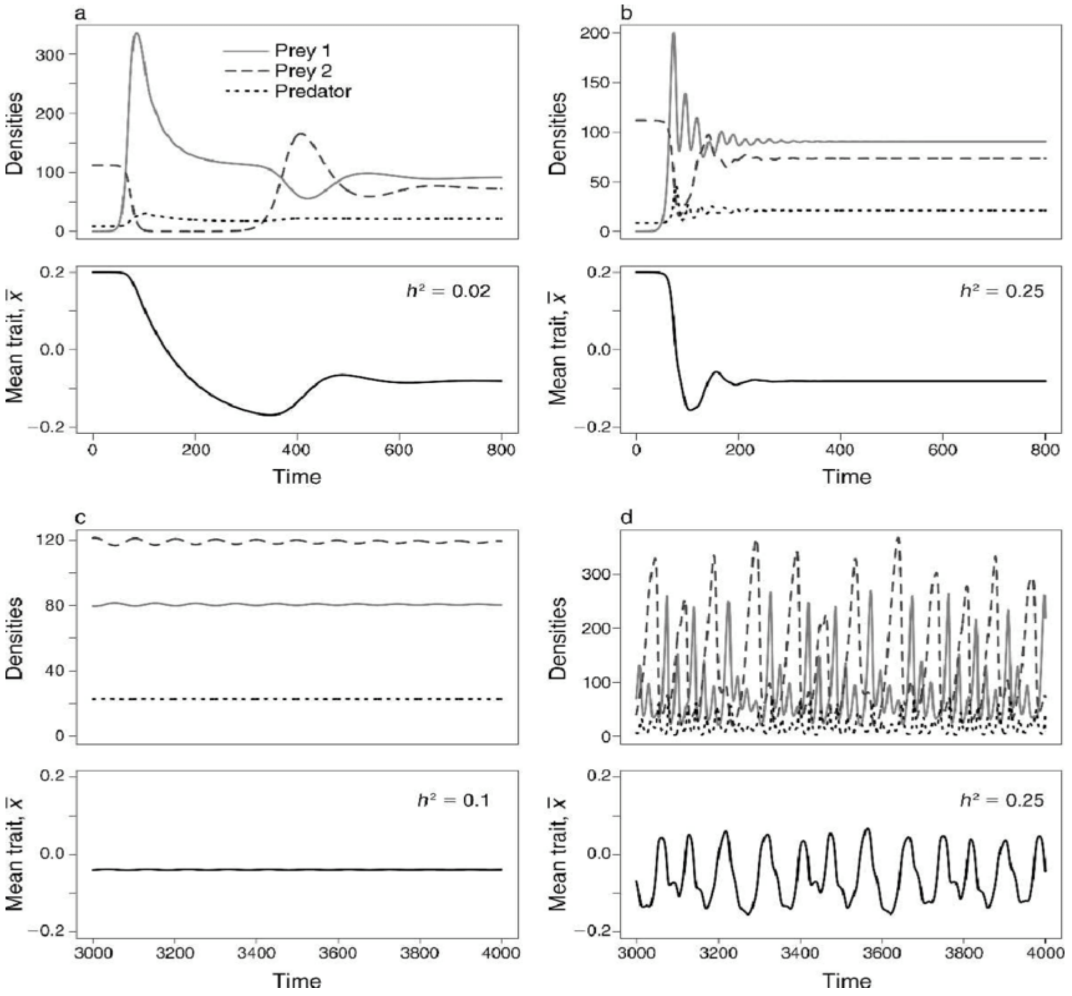

Figure 12: Different system behaviours are possible in the evolutionary apparent competition model of Schreiber et al. 2011. The panels (a) and (b) illustrate the introduction of the superior prey 1 (i.e. $r_1/\alpha_1 > r_2/\alpha_2$) in a system consisting of the predator and prey 2, where $\sigma^2 = 0.04$. In (a), $h^2 = 0.02$ was chosen, whereas in (b) $h^2 = 0.25$ was chosen. In both cases, the densities first exhibit oscillations which are eventually damped out and the system stabilizes at a new coexistence equilibrium. In panels (c) and (d), the long term dynamics of the system consisting of all three species are illustrated for $\sigma^2 = 0.01$. In panel(c), the heritability parameter has value of $h^2 = 0.1$. Here the densities remain stable at a coexistence equilibrium. In panel (d), the heritability parameter is increased to a value of $h^2 = 0.25$. Here both the densities of all species and the mean trait $\overline{x}$ exhibit oscillations.

3.2.4 Interlude: Permanence

As mentioned in the beginning of this chapter, throughout this thesis, we restrict ourselves to the analysis of small perturbations. For this purpose, a local analysis around the equilibrium is acceptable. In nature however, powerful perturbations are not uncommon. Consequently, the global dynamics can be quite complex and a local analysis won't be sufficient anymore. Fortunately, in most cases we are not interested in the exact dynamics. The question whether all species can survive in the long term after strong disturbances is more important. To this end, we now introduce the notion of *permanence* (Hofbauer and Sigmund 1988).

Consider the dynamical system

$$\dot{N}_i = f_i(N, x) \quad \forall i \in \{1, ..., n\}$$

of n species, whose densities are captured in $N = (N_1, N_2, ..., N_n)$, which depend on l evolutionary traits $x = (x_1, ..., x_l)$. We call the system *permanent* if there exists some positive constant $\delta > 0$ s.t. $N_i(0) > 0 \quad \forall i \in \{1, ..., n\}$ implies

$$\delta < \liminf_{x \to \infty} N_i(t) \leq \limsup_{x \to \infty} N_i(t) \leq \frac{1}{\delta} \quad \forall i \in \{1, ..., n\}.$$

To illustrate how the eco-evo feedbacks can affect permanence in a system, we once again consider the 3-species apparent competition model from the previous example. The main result which we would like to present is from Schreiber and Patel (2015) and states that under some conditions - in particular in the case of intermediate trade-offs - the eco-evo feedbacks in this model can indeed induce permanence.

Theorem 3.1: Condition for permanence

(i). If the following holds

   (a) $\frac{r_i}{\overline{a}_i(\theta_j)} > \frac{r_j}{\overline{a}_j(\theta_j)}(1 - \frac{d}{\overline{a}_j(\theta_j) e_j K_j})$ for $i = 1, 2$ and $i \neq j$

   (b) $\overline{W}(K_1, K_2, \overline{x}^*) > 0$ for all $\overline{x}^* \in Q := \{\overline{x} \in \mathbb{R} | \frac{\partial W}{\partial x}(K_1, K_2, \overline{x}) = 0\}$

   then the system is permanent in $\mathbb{R}^3_+ \times \mathbb{R}$.

(ii). If the inequality in (a) is reversed for $i = 1$ (resp. $i = 2$), then the equilibrium $(\frac{d}{e_1 \overline{a}_1(\theta_1)}, 0, \frac{r_1(1 - \hat{N}_1/K_1)}{\overline{a}_1(\theta_1)}, \theta_1)$ (resp. $(0, \frac{d}{e_2 \overline{a}_2(\theta_2)}, \frac{r_2(1 - \hat{N}_2/K_2)}{\overline{a}_2(\theta_2)}, \theta_2)$) is stable. As a consequence, there exist initial positive population densities $(N_1(0) N_2(0) P(0) > 0)$ s.t. one of both prey species goes extinct. Thus, the system is not permanent.

(iii). If the inequality in (b) is reversed for some $\overline{x}^*$, then the equilibrium $(K_1, K_2, 0, \overline{x}^*)$ is stable. As a consequence, there exist initial positive population densities $((N_1(0)N_2(0)P(0) > 0))$ s.t. the predator population eventually goes extinct. Thus, the system is not permanent.

Condition (a) means that prey 1 needs to have a positive per capita growth rate when the predator is specialized on prey 2 (i.e. $\overline{x} = \theta_2$) and vice versa. The second condition (b) means that the predator needs to have a positive per capita growth rate at all extrema of its fitness function, when both prey species are at their carrying capacity. As a consequence of this theorem, one can show that if the carrying capacities of the preys are high, then permanence is only possible at intermediate trade-offs $|\theta_2 - \theta_1|$. This can nicely be illustrated in the case $\frac{r_1}{\overline{a}_1(\theta_1)} > \frac{r_2}{\overline{a}_2(\theta_2)}$ (i.e. prey 1 is "superior" to prey 2). In this case, the relation

$$\frac{r_1}{\overline{a}_1(\theta_2)} > \frac{r_1}{\overline{a}_1(\theta_1)} > \frac{r_2}{\overline{a}_2(\theta_2)} > \frac{r_2}{\overline{a}_2(\theta_2)}(1 - \frac{d}{\overline{a}_2(\theta_2)e_2K_2}),$$

is satisfied, thus condition (a) is always satisfied for $i = 1$ independent of the trade-off. As a consequence, prey 1 will never go extinct. In order to relate the trade-off to permanence of the system, one therefore only needs to consider the second prey and the predator, and check for which values of the trade-off they can survive. As a start, one can begin with prey 2 and assume that there is no trade-off, i.e. $\theta_1 = \theta_2$. Using the assumption that the carrying capacity K_1 is sufficiently large, one can easily check that the inequality (a) is inverted for species 2. Thus, in the case of no trade-off, prey 2 goes extinct. Increasing the trade-off results in a decrease of $\overline{a}_2(\theta_1)$, and thus in an increase of $\frac{r_2}{\overline{a}_2(\theta_1)}$, which is precisely the left hand side of condition (a) for $i = 2$. As a result, condition (a) for species 2 is more easily satisfied for larger trade-offs. As a next step, condition (b) for the predator is considered. Since the per capita growth rate of the predator depends on the strength of the trade-off, the same holds for its extremas, which are collected in the set Q. In particular, in the case of $\tau_1 = \tau_2$, one can show that for $|\theta_2 - \theta_1| \leq 2\sqrt{\sigma^2 + \tau^2}$ the predator's fitness (as a function of $\overline{x}$, where both preys are assumed to be at their carrying capacity) is a unimodal function with a single maximum. Thus, for condition (b) only a single inequation needs to be verified since Q only consists of a single point. Increasing the trade-off, i.e. $|\theta_2 - \theta_1| > 2\sqrt{\sigma^2 + \tau^2}$, usually results in the fact that the fitness function (again as a function of $\overline{x}$, and both preys at their carrying capacity) will have two maxima near $\overline{x} = \theta_1$ and $\overline{x} = \theta_2$. Consequently, a minimum will appear between both maxima.

Finally, for sufficiently large trade-offs, the fitness function will be negative at this minimum, resulting in the extinction of the predator population (part (iii) of the theorem). To summarize, if prey 1 is superior to prey 2 and the carrying capacity K_1 is sufficiently high, then weak trade-offs lead to the extinction of prey 2 and strong trade-offs lead to the extinction of the predator. As a consequence, permanence is only possible at intermediate trade-offs.

3.2.5 Types of predator-prey cycles

As a last example to highlight the importance of eco-evo feedbacks, we investigate the types of cycles which may appear at unstable equilibria of predator-prey systems. Intuitively, cycles in such systems consist of peaks in prey abundance which precede peaks of predator abundance. If the predators are scarce, the prey will naturally increase in abundance. Consequently, an increase of prey abundance corresponds to an increase of food resource for the predators, which in turn allows them to increase in abundance as well. Once the predators have reached some critical capacity, the prey population won't be able to grow anymore, leading to a decrease of their abundance, followed by a decrease of the predators' abundance. Plotting this in the phase plane results in counterclockwise cycles. Classical models, such as the *Lotka-Volterra* predator-prey models (Lotka 1920; Volterra 1928) share this prediction. Indeed, empirical examples such as the predator-prey interactions of lynx and snowshoe hare in Canada exhibit exactly such counterclockwise cycles where a rise in hare abundance is followed by a rise in lynx abundance (Figure 13A). However, other types of cycles have been observed as well: e.g. antiphase cycles in a rotifer-algae system (Figure 13B) or cryptic cycles (i.e. the preys' density remains constant while the predator population exhibits cycles) in a phage-bacteria system (Figure 13C). The question remains, how such counter intuitive types of cycles occur. One possible explanation are the eco-evo feedbacks. Indeed, theoretical studies have shown that including an evolutionary component to both the predator and the prey can lead to antiphase and cryptic cycles (Mougi 2012). Cortez and Weitz went a step further and showed that the coevolution between the predator and the prey can even completely reverse the cycle, leading to clockwise cycles in the phase plane where peaks of predator abundance precede peaks of prey abundance (Cortez and Weitz 2014).

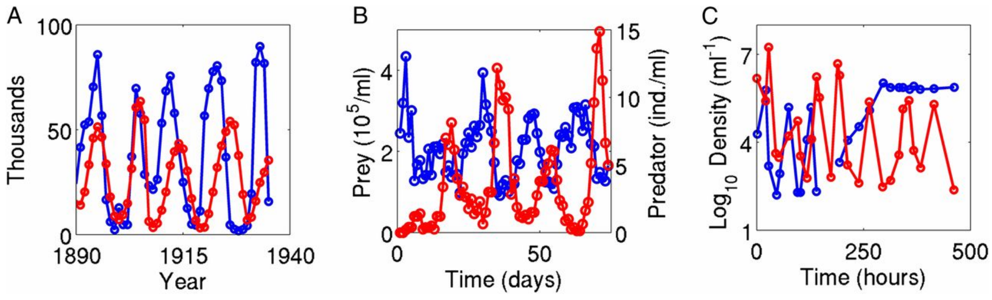

Figure 13: Illustration of different types of cyclic behaviours in exploiter-victim system (Cortez and Weitz 2014). (A) Counterclockwise lynx-hare cycles (Elton and Nicholson 1942); (B) Antiphase rotifer-algal cycles (Becks et al. 2010); (C) Cryptic phage-bacteria cycles (Bohannan and Lenski 1999)

3.2.6 Varying evolutionary speed

Empirical evidence shows that evolution - while occurring on a congruent time scale - can occur at various rates relative to the ecological processes (DeLong et al. 2016). Of course these relative differences need to be appropriate and not taken to the extreme limits, since otherwise the model can be reduced to pure ecological or evolutionary dynamics, and therefore eliminating the indirect effects of eco-evo feedbacks. Nonetheless, it seems essential to investigate whether and how changes in the evolutionary speed can affect the outcomes of eco-evo feedbacks in the previous models. We present results for the two-species competition model of Vasseur et al. (2011) and the three-species apparent competition model of Schreiber et al. (2011). In both cases, this can be achieved by varying the heritability parameter h^2, which essentially determines the rate of the evolutionary response to the selection differential of the quantitative trait under consideration.

2-species competition

Vasseur et al. (2011) investigated the potentially different outcomes of their model, when varying the heritability h^2 in a range from 0 to 1. They did this for five qualitatively different parameter cases, corresponding to following ecological outcomes: (a) a large intermediate coexisting region; (b) a small intermediate coexisting region; (c) neutrality at some intermediate trait value; (d) a small intermediate mutual exclusion region; (e) a large intermediate mutual exclusion region (Figure 14). In the first case (a), the heritability has almost no effect on the outcome. For nearly all values of h^2, both species converge towards an equilibrium allowing stable coexistence. However, if h^2 is close to 0, the evolutionary trait won't be able to evolve fast enough. Consequently, during the initial phase of invasion of the fixed species, the variable species won't adapt quickly enough to fight of the dominance of the latter and go extinct. In the case of a small intermediate coexisting region (b), the situation is quite a different one. For a start, the extinction threshold is much higher than in the previous case. The reason is that the trait values allowing coexistence are further away from the initial state $\overline{x}(0) = \theta_C$. Therefore, reaching this region in a sufficiently short amount of time requires a higher heritability. Further increasing the evolutionary speed eventually leads to an overshooting of the coexistence equilibrium, leading to a Hopf bifurcation. Thus, coexistence is still possible, however not at an equilbrium, but now in form of a stable limit cycle due to evolutionary overcompensation. In the last three cases (c)-(e), the extinction threshold is much higher than in the first two cases. This makes sense since these cases correspond to ecologically unstable dynamics, therefore coexistence requires a much higher rate of change of the evolutionary trait. Further increasing the heritability h^2 has a relatively small effect: increasing the evolutionary speed leads to a faster turnover of the species' dominance, resulting in slightly shorter cycles.

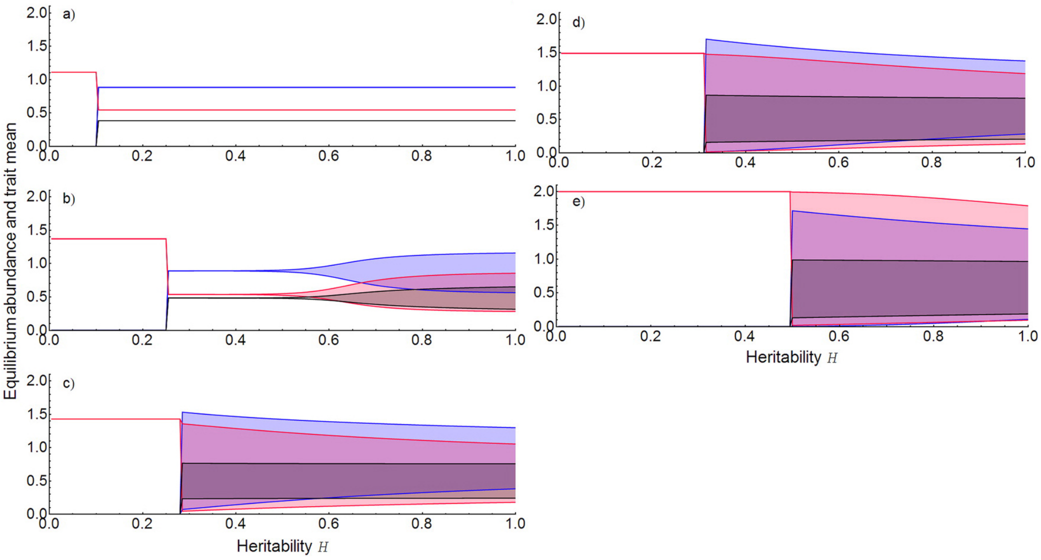

Figure 14: Bifurcation diagram for the two species competition model of Vasseur et al. 2011, showcasing the effects of increasing the heritability parameter $H = h^2$ and thus the evolutionary speed of the evolving species in different cases: (a) a large intermediate coexisting region; (b) a small intermediate coexisting region; (c) neutrality at some intermediate trait value; (d) a small intermediate mutual exclusion region; (e) a large intermediate mutual exclusion region. The fixed species is represented in red, the variable species in blue and the mean trait in black. The shaded regions correspond to oscillations of the species, resp. mean trait. Low heritability parameters lead to the extinction of the variable species in all five cases. Increasing the heritability first leads to coexistence at a stable equilibrium in (a) and (b). Further increasing the heritability parameter leads to a Hopf bifurcation in (b), resulting in periodic orbits. In (c), (d) and (e), increasing the heritability leads to oscillations allowing coexistence.

3-species apparent competition

The second example we consider is the three-species apparent competition model which was previously presented, both in the context of feedback induced oscillations (Schreiber et al. 2011) and permanence (Schreiber and Patel 2015). As a matter of fact, we already presented a result of Schreiber et al. (2011) which showed how changes in the heritability can affect the system behavior. Indeed, if the phenotypic variance remains fixed at $\sigma^2 = 0.01$, then slight changes in the heritability h^2 drastically affects the behaviour of the model, changing it from a stable equilibrium to sustained oscillations (Figure 12). Schreiber et al. (2011) showed that further increasing the heritability can result in even more complex behaviour such as chaos (Figure 15). Comparing this result to the outcome of the purely ecological model (Takeuchi and Adachi 1983) - where only convergence towards a globally stable equilibrium was possible - shows the importance of including the evolutionary dynamics in the case of congruent ecological and evolutionary time scales. Neglecting the evolutionary component - and therefore the effects of eco-evo feedbacks - can in some cases severely distort the outcome of the dynamics and lead to false predictions.

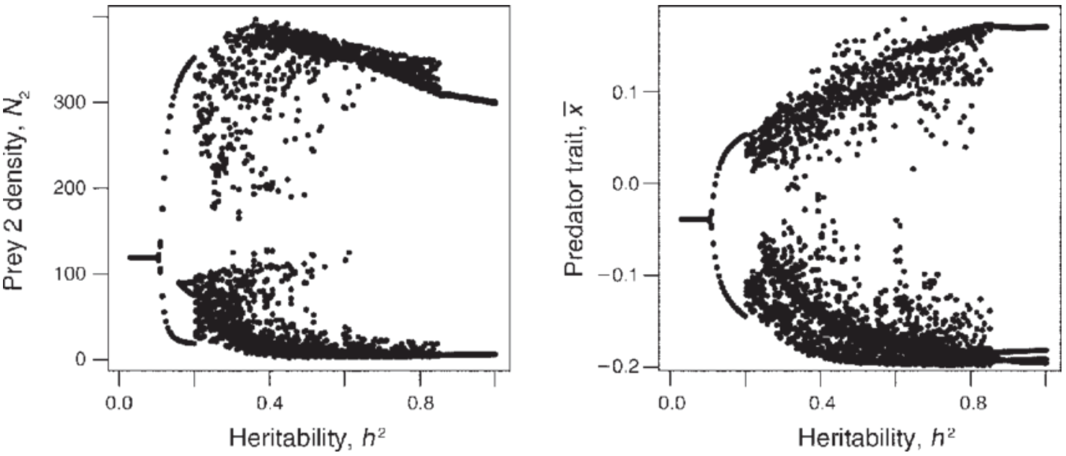

Figure 15: Bifurcation diagram for one of the preys and the predator's trait in the apparent competition model of Schreiber et al. 2011, showcasing the effects of increasing the heritability parameter h^2 and thus the evolutionary speed of the predator's trait. Both the prey's density and the predator's trait converge towards a stable equilibrium for small values of h^2. Increasing the parameter first leads to a Hopf bifurcation resulting in oscillations. Further increasing the heritability eventually leads to chaos for both the prey's density and the predator's trait.

3.3 General theory for slow and fast evolution

3.3.1 Stability conditions

Nearly all existing work on the effects of eco-evo feedbacks on system stability focus on small, specific communities with at most two evolving species (Vasseur et al. 2011, Schreiber et al. 2011, Vasseur and Fox 2011). Moreover, due to the complex mathematical tractability of indirect feedbacks, most of these works rely on numerical rather than analytical methods, which prevents a deep understanding of the underlying effects. In recent years, several mathematicians have committed themselves to the task of developing a general theory that provides analytical results on the dependency of eco-evo feedbacks and system stability in general coupled ecological and evolutionary systems. Their first result (Patel et al. 2018), will be presented in this chapter and concerns the case of slow and fast evolution compared to the ecological time scale. After all, empirical data (DeLong et al. 2016) as well as theoretical results (Vasseur et al. 2011, Schreiber et al. 2011) have consistently highlighted the existence and importance of the relative eco and evo time scales, when investigating the effects of eco-evo feedbacks on system stability. Of course, as stated earlier, these time scales - while being different - should still be comparable. For slow evolution, this could be the case if there is low genetic variance which slows down the evolution of the trait under consideration. Importantly, this difference in time scales should not be taken to the limit, which in the extreme case would lead to negligible trait adaptation, and thus reduction of the coupled system to a simple ecological process. On the other hand, fast evolution can occur in a community with a high population turnover, but with limited resources, which ultimately prevents the growth of the population. Again, it's important to note that this difference should not be taken to the limit, which in the extreme case would lead to a constant population size and thus reducing the coupled system to a simple evolutionary model of the involved traits.

We now present a general model of a multi-species community with evolving traits by Patel et al. (2018), which we will be used for the analysis. For this, Patel et al. assumed to have k interacting species and l evolving traits. Denoting the densities of the species by $N_1, ..., N_k$ and the trait values by $x_1, ..., x_l$, results in the following model

$$\dot{N}_i = N_i f_i(N, x) \tag{3.13a}$$

$$\dot{x}_j = \varepsilon g_j(N, x), \tag{3.13b}$$

where both N and x are vectors such that: $N = (N_1, ..., N_k)$ and $x = (x_1, ..., x_l)$. The functions f_i are the per capita growth rates of the species, which depend on the densities of all involved species and their traits. The selection functions g_i describe how the selection pressure - imposed by the densities of all species and their traits - affects the evolution of the traits. The parameter ε determines that rate of adaptation of the traits. Thus, a small ε corresponds to the case of slow evolution, whereas a large ε corresponds to fast evolution compared to the ecological time scale. No further assumptions on the type of functions f_i and g_j are made, in order to keep the model as general as possible.

In the following, Patel et al. assumed that their model is at an equilibrium $(\hat{N}, \hat{x})$ and investigated the consequences of perturbations. In other words, they wanted to determine the local stability of this equilibrium by studying the eigenvalues of the Jacobian J evaluated at $(\hat{N}, \hat{x})$:

$$J = J(\hat{N}, \hat{x}) = \begin{pmatrix} A & B \\ \varepsilon C & \varepsilon D \end{pmatrix},$$

where the submatrices A, B, C and D are given by

$$A = \Big(\partial(N_i f_i)/\partial N_j\Big), \quad B = \Big(\partial(N_i f_i)/\partial x_j\Big), \quad C = \Big(\partial g_i/\partial N_j\Big), \quad D = \Big(\partial g_i/\partial x_j\Big).$$

The matrix A describes how the growth rate of species i changes with the density of species j. The matrix B describes how the growth rates change w.r.t. the various traits. C describes how the selection function of trait i changes with the density of species j. And finally, D describes how the selection functions change w.r.t. the other traits. The main goal is to investigate the effects which the eco-evo feedbacks have on the stability of the equilibrium. However, Patel et al. went one step further and tried to determine the individual roles of all of the direct and indirect effects on the stability. The direct effects are those captured by the submatrices A, B, C and D. The matrix A corresponds to the direct effects which the ecological processes have on the species density, and D captures the direct effects which the evolutionary processes have on the traits. Thus, A and D correspond to the Jacobian of the uncoupled ecological and evolutionary processes respectively. In an uncoupled system (i.e. $B = C = 0$), the Jacobian is a block matrix. Thus by simple linear algebra, the equilibrium is stable iff it is stable in both the ecological and evolutionary process respectively. Local stability is determined by the eigenvalues of J. More precisely, if the largest real part of the eigenvalues of the Jacobian - also called, the stability modulus $s(J)$ - is negative, then the equilibrium is asymptotically stable and thus resistant to small perturbations. In the case of the uncoupled system, this mean that $s(J) < 0 \Leftrightarrow \Big(s(A) < 0 \wedge s(D) < 0\Big)$.

Since the aim is to investigate the effects of the indirect eco-evo feedbacks, from now on a coupled system ($C \neq 0$ and $B \neq 0$) is assumed. In this case, the stability of the equilibrium additionally depends on indirect eco-evo feedbacks. There are two types of such feedback loops which Patel et al. investigated: eco-evo-eco and evo-eco-evo feedbacks. The eco-evo-eco feedbacks incorporate the subsequent effects of changes in the population densities that lead to a change of some evolutionary traits, which in return alter the densities of the species. These three steps are captured by the matrix $BD^{-1}(-C)$. The matrix C describes the effects of ecological changes on the evolutionary dynamics and thus corresponds to the first step of the eco-evo-eco feedbacks. In the second step, the evolutionary traits respond to these changes and converge towards a new equilibrium. Thus the first and second steps are given by the matrix $D^{-1}(-C)$. Finally, changes in the evolutionary traits lead to changes in the species densities, which is captured by the matrix B. The evo-eco-evo feedbacks can be described analogously and are captured by the matrix $CA^{-1}(-B)$.

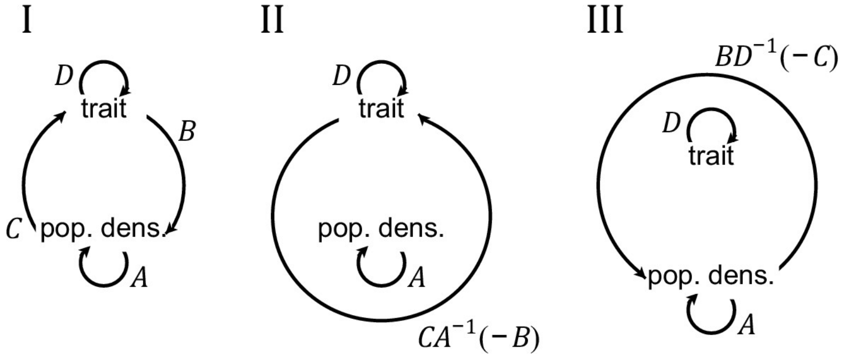

Figure 16: Representation of the most important feedbacks in a model with congruent ecological and evolutionary time scales. (I-III) The clockwise arrows represent the direct evolutionary resp. ecological feedbacks which the trait, resp. ecological populations have on themselves. (I) The counterclockwise arrows represent the feedbacks which the ecological parameteres have on the evolutionary ones and vice versa. (II) The counterclockwise arrow denotes the combined evo-eco-evo feedbacks. (III) The counterclockwise arrow denotes the combined eco-evo-eco feedbacks. (From Patel et al. 2018)

The main results of this section (and of Patel et al. (2018)) are stated in the next two theorems. For this, one needs to assume that the equilibrium $(\hat{N}, \hat{x})$ under consideration is hyperbolic (i.e. no eigenvalues with zero real part) so that the

Hartman-Grobman theorem holds. This guarantees that the orbits of the dynamical system near the equilibrium are topologically equivalent to those of the linearized system.

Theorem 3.2: Stability condition for slow evolution

Suppose J, A, B, C and D are as defined above and $\varepsilon > 0$. Then, for a sufficiently small ε, the following holds:

$$s(A) < 0 \quad \text{and} \quad s(CA^{-1}B + D) < 0 \quad \Rightarrow \quad s(J) < 0$$

Proof. Patel et al. (2018) made use of some standard perturbation methods to prove that the solutions λ of the eigenvalue equation $Ju = \lambda u$ have negative real part if ε is sufficiently small.

For this, they used the following perturbation expansions:

$$J = J_0 + \varepsilon J_1 + O(\varepsilon^2) \tag{3.14a}$$

$$u = \begin{pmatrix} v_0 \\ w_0 \end{pmatrix} + \varepsilon \begin{pmatrix} v_1 \\ w_1 \end{pmatrix} + O(\varepsilon^2) \tag{3.14b}$$

$$\lambda = \lambda_0 + \varepsilon \lambda_1 + O(\varepsilon^2), \tag{3.14c}$$

with $J_0 = \begin{pmatrix} A & B \\ 0 & 0 \end{pmatrix}$ and $J_1 = \begin{pmatrix} 0 & 0 \\ C & D \end{pmatrix}$.

Plugging this into the eigenvalue equation and ignoring higher order terms gives:

$$J_0 \begin{pmatrix} v_0 \\ w_0 \end{pmatrix} + J_0 \begin{pmatrix} v_1 \\ w_1 \end{pmatrix} \varepsilon + J_1 \begin{pmatrix} v_0 \\ w_0 \end{pmatrix} \varepsilon = \lambda_0 \begin{pmatrix} v_0 \\ w_0 \end{pmatrix} + \lambda_0 \begin{pmatrix} v_1 \\ w_1 \end{pmatrix} \varepsilon + \lambda_1 \begin{pmatrix} v_0 \\ w_0 \end{pmatrix} \varepsilon.$$

By comparing the coefficients of ε^0 one gets the following two equations:

$$Av_0 + Bw_0 = \lambda_0 v_0 \tag{3.15a}$$

$$0 = \lambda_0 w_0. \tag{3.15b}$$

Comparing the coefficients of ε^1 additionally gives:

$$Av_1 + Bw_1 = \lambda_0 v_1 + \lambda_1 v_0 \tag{3.16a}$$

$$Cv_0 + Dw_0 = \lambda_0 w_1 + \lambda_1 w_0. \tag{3.16b}$$

Case 1: $\lambda_0 \neq 0$

In this case, equation (3.15)(b) implies that $w_0 = 0$. By setting $w_0 = 0$ in (3.15)(a), one can see that λ_0 is an eigenvalue of A. Because of the assumption $s(A) < 0$, this implies in particular that $\mathrm{Re}(\lambda_0) < 0$. Since this holds for any eigenvalue $\lambda = \lambda_0 + \varepsilon\lambda_1 + O(\varepsilon^2)$ of J, it follows that $s(J) < 0$ if ε is sufficiently small.

Case 2: $\lambda_0 = 0$

In this case one needs to look at the higher order terms λ_1. From equation (3.15)(a), one gets $v_0 = A^{-1}(-Bw_0)$. Plugging this into equation (3.16)(b) leads to $(CA^{-1}(-B) + D)w_0 = \lambda_1 w_0$. Thus, λ_1 is an eigenvalue of $CA^{-1}(-B) + D$. By assumption, all eigenvalues of $CA^{-1}(-B) + D$ have negative real part, thus the same holds for λ_1. Since this holds for any eigenvalue $\lambda = \varepsilon\lambda_1 + O(\varepsilon^2)$ of J, it follows that $s(J) < 0$ if ε is sufficiently small.

□

Before interpreting this result, we state an analogous theorem from Patel et al. (2018) in the case of fast evolution:

Theorem 3.3: Stability condition for fast evolution

Suppose J, A, B, C and D are as defined above and $\varepsilon > 0$. Then, for a sufficiently large ε, the following holds:

$$s(D) < 0 \quad \text{and} \quad s(A + BD^{-1}(-C)) < 0 \quad \Rightarrow \quad s(J) < 0$$

Proof. Simply define $J_0 = \begin{pmatrix} 0 & 0 \\ C & D \end{pmatrix}$ and $J_1 = \begin{pmatrix} A & B \\ 0 & 0 \end{pmatrix}$. The computations are now similar to those in the previous proof.

□

Interpretation of the theorems

The most important consequence of Theorem 3.2, is that the evo-eco-evo feedbacks are critical for the stability in the case of slow evolution. To better illustrate this, Patel et al. (2018) considered the case of k interacting species, but with only one slowly evolving trait. In this case, the condition of Theorem 3.2 can be written as: (1) $s(A) < 0$ and (2) $cA^{-1}b + d < 0$, where both c and b are vectors, and d is a scalar. Condition (1) corresponds to the fast ecological response: After some initial perturbation away from the equilibrium $(\hat{N}, \hat{x})$, the ecological dynamics will follow approximately the linear dynamics given by the matrix A, i.e., $\dot{\tilde{N}} \approx A\tilde{N}$, where $\tilde{N} = N - \hat{N}$ is the deviation from the equilibrium. Thus, if this condition is not satisfied, the solutions quickly diverge away from the equilibrium. Since the evolutionary dynamics are assumed to be slow, they won't be able to compensate this effect, eventually resulting in an overall unstable equilibrium. For this reason, this first condition is always necessary to guarantee the stability of J. The second condition (2) corresponds to the slow evolutionary response. It consists of the combined effect of the direct evolutionary feedbacks (d) and the indirect evo-eco-evo feedbacks $(cA^{-1}b)$. In the case of one single evolving trait, (2) states that the sum of the corresponding matrices (here scalars) should be negative. Thus, the more negative the evo-eco-evo term is, the more negative the whole sum will be, i.e. the more the evo-eco-evo feedbacks will have a stabilizing effect. Similar is true if $cA^{-1}b$ is positive: In this case, the evo-eco-evo feedbacks have a destabilizing effect. Intuitively, this condition describes the combined effects of (a) the trait slowly changing as a direct evolutionary response to the perturbation, and (b) the indirect effects which arise as a fast ecological response to these evolutionary changes and thus affecting the selection pressure, which in return feeds back to an indirect slow evolutionary response.

Using the stability condition of Theorem 3.2, four qualitatively different situations are possible in an ecologically stable system $(s(A) < 0)$:

(i) evolutionary stable and overall stable equilibrium

(ii) evolutionary stable and overall unstable equilibrium

(iii) evolutionary unstable and overall unstable equilibrium

(iv) evolutionary unstable and overall stable equilibrium

A system is "overall stable" if all of the eigenvalues of the Jacobian have negative real part (i.e. $s(J) < 0$). On the other hand, "evolutionary stable" means that the eigenvalues of the Jacobian of the evolutionary subsystem have negative real part (i.e. $s(D) < 0$) The cases (ii) and (iv) are of particular interest since they emphasize the importance of the indirect evo-eco-evo feedbacks in the case of slow evolution. In case (ii), the evo-eco-evo feedbacks destabilize a system which is both ecologically and evolutionary stable. Accordingly, in case (iv), the evo-eco-evo feedbacks stabilize a system which is evolutionary unstable in the absence of the ecological dynamics.

Concerning Theorem 3.3 it's interesting to note that no particular assumptions on the fitness functions g_j and f_i were stated, and thus a simple rearrangement and renaming of the functions leads to the exact same mathematical situation as in Theorem 3.2. Therefore, the proof of Theorem 3.3 follows directly from Theorem 3.2. The difference is that now the evolutionary stability is essential since it is the faster process. The second condition corresponds to the combined effect of the direct ecological and the indirect eco-evo-eco responses to some initial perturbation. Thus the key finding of these theorems is that the indirect eco-evo-eco feedbacks are critical for the stability in the case of fast evolution, whereas the evo-eco-evo feedbacks are essential in the case of slow evolution.

3.3.2 Application

As an application of the theory of Patel et al. (2018), we go back to the two-species competition model of Vasseur, which showed that the eco-evo feedbacks can indeed stabilize an ecologically unstable system. For this, Patel et al. looked at a system which - depending on the mean trait values - can either have ecological dominance or mutual exclusion. Mathematically, this corresponds to the case where $s(A) > 0$. In order to apply the general theory, one needs to assume to either have fast or slow evoution. Thus, Patel et al. assumed to have fast evolution compared to the ecological process, so that they could eventually apply Theorem 3.3. Interestingly, the whole analysis can be done, solely by looking at the signs of the individual entries of the Jacobian. Since the competition model under consideration contains only two species, A will be a 2×2 matrix with only negative entries, D a scalar, and both B and C will be vectors. Furthermore, since the aim is to apply Theorem 3.3, Patel et al. assumed to have an evolutionary stable system, which corresponds to $D = s(D) < 0$. For the signs of the vectors B and C they use the properties of the trait of the variable species. For this, note that the Jacobian was evaluated at an equilibrium, thus the first entry of B is zero. The second entry of B corresponds to the change in the fixed species when varying the mean trait. Since increasing the mean trait value decreases the fitness of the fixed species, this entry is negative. Finally, due to the selection pressure, an increase of the variable species leads to a decrease in the mean trait value, while an increase of the fixed species leads to an increase in the mean trait value. All together, the submatrices have the following signs:

$$A = \begin{pmatrix} - & - \\ - & - \end{pmatrix}, \qquad D = (-)\,, \qquad B = \begin{pmatrix} 0 \\ - \end{pmatrix}, \qquad C = \begin{pmatrix} - & + \end{pmatrix}.$$

The eco-evo-eco feedbacks are given by:

$$BD^{-1}(-C) = \begin{pmatrix} 0 \\ - \end{pmatrix} (-) \begin{pmatrix} - & + \end{pmatrix} = \begin{pmatrix} 0 \\ + \end{pmatrix} \begin{pmatrix} - & + \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ + & - \end{pmatrix}.$$

Next, one needs to study the sum $A + BD^{-1}(-C)$. Since this is a 2x2 matrix, it's stability can be determined solely by looking at its trace and determinant. More precisely, a 2x2 matrix is stable iff its determinant is positive and its trace is negative. The matrix A by itself is unstable by assumption. One therefore needs to investigate what happens if $BD^{-1}(-C)$ is added. Obviously, this makes the trace "more negative", but how is the determinant affected? For this one can consider:

$$\det(A) = \det \begin{pmatrix} - & - \\ - & - \end{pmatrix} = ① - ② \quad \text{and}$$

$$\det(A + BD^{-1}(-C)) = \det \begin{pmatrix} - & - \\ \pm & - \end{pmatrix} = ③ - ④,$$

where ① $= A_{11} \cdot A_{22}$, ② $= A_{12} \cdot A_{21}$, ③ $= (A+BD^{-1}(-C))_{11} \cdot (A+BD^{-1}(-C))_{22}$ and ④ $= (A + BD^{-1}(-C))_{12} \cdot (A + BD^{-1}(-C))_{21}$. Note that ①, ② and ③ are positive. Furthermore, ③ is larger than ①, since the lower right entry of $A+BD^{-1}(-C)$ is more negative than A_{22}. For ④ there are two possibilities: either ④ is positive and smaller than ②; or ④ is negative. In both cases, the determinant of $A+BD^{-1}(-C)$ is larger than the determinant of A, which means that the eco-evo feedbacks always have a stabilizing effect. If ④ is negative, then the determinant will be positive, which according to Theorem 3.3 implies that the eco-evo-eco feedbacks stabilize the system. Thus, Patel et al. (2018) analytically confirmed the results of Vasseur et al. (2011) in the case of fast evolution.

3.4 General theory for comparable eco and evo time scales

3.4.1 Stability conditions in special cases

General analytical conditions for stability in the case of comparable ecological and evolutionary time scales (i.e. intermediate rates of evolution) are much harder to obtain and barely available. However there are a few special cases for which similar stability results as in the previous section can be derived. Both results which we present are based on the general model of Patel et al. (2018).

Stability condition for a single evolving trait

The first result is from Patel et al. (2018) and gives a sufficient condition for instability in the case of k interacting species, but only one evolving trait. It holds for all intermediate rates of evolution and states that if the system is ecologically stable and overall unstable for slow evolution, then it is overall unstable for every $\varepsilon > 0$. Thus, the Jacobian is given by:

$$J = \begin{pmatrix} A & b \\ \varepsilon c & \varepsilon d \end{pmatrix},$$

where b, c are vectors and d is a scalar.

Theorem 3.4: Stability condition for a single evolving trait

Suppose J, b, c, d are as defined above and $\varepsilon > 0$. Then, the following holds $\forall \varepsilon > 0$:

$$s(A) < 0 \quad \text{and} \quad s(d + cA^{-1}(-b)) > 0 \quad \Rightarrow \quad s(J) > 0$$

Proof. One can assume w.l.o.g. that the number of interacting species k is even (otherwise, simply invert all of the inequalities in the proof). Note that the determinant of a matrix is equal to the product of its eigenvalues. Together with the assumption $s(A) < 0$ (i.e. that all the eigenvalues of A have negative real part) and the fact that there is an even number of species, this implies that $\det(A) > 0$. Next, Patel et al. assumed that $\varepsilon > 0$ is very small. Using the assumption $s(d + cA^{-1}(-B)) > 0$ and applying the stability condition from the last section for slow evolution, one gets that the system is overall unstable, i.e. $\det(J_\varepsilon) > 0$. Finally, the sign of $\det(J_\varepsilon)$ is invariant for all ε. This implies that $\det(J) = \det(J_\varepsilon) > 0$ for every $\varepsilon > 0$.

□

Stability condition for symmetric Jacobian matrices

Similar stability conditions for k interacting species and l evolving traits are in general difficult to obtain. However, if we limit ourselves to the quite strong assumption that the Jacobian J is symmetric, then we can derive nice stability conditions for comparable eco and evo time scales with $\varepsilon = 1$. The result relies on Sylvester's law of inertia, which we state without proof:

Lemma 3.5: Sylvester's law of inertia

Let $A \in \mathbb{R}^{n\times n}$ be a symmetric matrix and $S \in GL(n, \mathbb{R})$ an invertible matrix. Then A and S^TAS have the same number of positive and negative eigenvalues.

The statement of this lemma is interesting in the sense that it does not assume S to be unitary, in which case the statement would be trivial (since in that case, A and S^TAS would be unitary equivalent, which implies that they are similar). Importantly, this law states that A is stable iff S^TAS is. To apply this result to the Jacobian, we therefore need to assume that J is symmetric and of the following form:

$$J = \begin{pmatrix} A & B \\ B^T & D \end{pmatrix},$$

where A and D are symmetric matrices.

With the help of this lemma we can derive the following general stability condition:

Theorem 3.6: Stability condition for symmetric Jacobian

Suppose that J is symmetric and defined as above. Then, the following are equivalent:

(i) J is stable

(ii) $s(A) < 0$ and $s(D + B^T A^{-1}(-B)) < 0$

(iii) $s(D) < 0$ and $s(A + BD^{-1}(-B^T)) < 0$

Proof. We start by showing the first equivalence (i)⇔(ii) using Sylvester's law of inertia. Ideally one would like to derive a Cholesky decomposition of the type $J = L^T DL$, where D is a diagonal matrix. However due to the limited information we have on the feedback matrices, the following factorization is the best we can do:

$$\begin{aligned} J &= \begin{pmatrix} I & 0 \\ B^T A^{-1} & I \end{pmatrix} \begin{pmatrix} A & 0 \\ 0 & D + B^T A^{-1}(-B) \end{pmatrix} \begin{pmatrix} I & A^{-1}B \\ 0 & I \end{pmatrix} \\ &= \begin{pmatrix} I & A^{-1}B \\ 0 & I \end{pmatrix}^T \begin{pmatrix} A & 0 \\ 0 & D + B^T A^{-1}(-B) \end{pmatrix} \begin{pmatrix} I & A^{-1}B \\ 0 & I \end{pmatrix}. \end{aligned}$$

Note that the matrices A and D are symmetric as a consequence of J being symmetric. Thus, A^{-1} is symmetric. Next, $B^T A^{-1}(-B)$ is symmetric, which can easily be checked by calculating the transposed: $(B^T A^{-1}(-B))^T = (-B)^T (A^{-1})^T B = B^T A^{-1}(-B)$. Finally, $D + B^T A^{-1}(-B)$ is symmetric as a sum of symmetric matrices. Together, this implies that the block-diagonal matrix in the factorization is symmetric. Now we can use Sylvester's law of inertia which states that the block diagonal matrix is stable iff the Jacobian is. Since the eigenvalues of a block-diagonal matrix are given by the eigenvalues of the individual blocks, the Jacobian is stable iff both blocks are stable, thus the statement follows.

For the equivalence (i)⇔(ii), we use the following similar decomposition:

$$\begin{aligned} J &= \begin{pmatrix} I & 0 \\ D^{-1}B^T & I \end{pmatrix} \begin{pmatrix} A + BD^{-1}(-B^T) & 0 \\ 0 & D \end{pmatrix} \begin{pmatrix} I & BD^{-1} \\ 0 & I \end{pmatrix} \\ &= \begin{pmatrix} I & BD^{-1} \\ 0 & I \end{pmatrix}^T \begin{pmatrix} A + BD^{-1}(-B^T) & 0 \\ 0 & D \end{pmatrix} \begin{pmatrix} I & BD^{-1} \\ 0 & I \end{pmatrix}. \end{aligned}$$

The block-diagonal matrix is symmetric by similar arguments as above. Therefore we can apply Sylvester's law of inertia which finally gives us the second equivalence.

□

An important consequence of this theorem is that in the case of comparable relative time scales ($\varepsilon = 1$), the eco-evo feedbacks cannot stabilize a system which is ecologically or evolutionary unstable. Indeed, the theorem states that a stable equilibrium requires both $s(A)$ and $s(D)$ to be negative. In contrast to the previous results, this stability condition is both sufficient and necessary. Therefore, in addition to the conditions for stability, the theorem provides conditions for instability too. A surprising implication is that sufficiently strong eco-evo feedbacks can destabilize a system which is both ecologically and evolutionary stable. Indeed, the more "positive" $B^T A^{-1}(-B)$ and $BD^{-1}(-B^T)$ get, the more $s(D + B^T A^{-1}(-B))$ and $s(A + BD^{-1}(-B^T))$ become positive, i.e. the more the eco-evo feedbacks will have a destabilizing effect. As an example, consider the real valued 2×2 Jacobian $J = \left(\begin{smallmatrix} a & b \\ b & d \end{smallmatrix}\right)$. Let's assume that the system is both ecologically and evolutionary stable, i.e. $a < 0$ and $d < 0$. The eco-evo-eco feedbacks are now given by $bd^{-1}(-b) = b^2(-d^{-1}) > 0$. This term is positive independent of the value of b (since we assume that J is real valued). Thus, $s(a+bd^{-1}(-b)) = a+bd^{-1}(-b)$ can be positive if the term $bd^{-1}(-b)$ is sufficiently large, resp. the eco-evo-eco feedbacks are sufficiently strong. In this case, the system becomes unstable according to (ii) of Theorem 3.6. As a result, the eco-evo-eco feedbacks can destabilize a system which is both ecologically and evolutionary stable. Similarly, using $ba^{-1}(-b) = b^2(-a) > 0$ and $s(d + ba^{-1}(-b)) = d + ba^{-1}(-b)$, we can see that sufficiently strong evo-eco-evo feedbacks can destabilize the system according to (iii) of Theorem 3.6. To summarize, if J is symmetric and $\varepsilon = 1$, then: (1) the eco-evo feedbacks cannot stabilize an ecologically or evolutionary unstable system; (2) the eco-evo feedbacks can destabilize a system which is both ecologically and evolutionary stable.

As a warning note, one should mention that the assumption of a symmetric Jacobian is quite restrictive and therefore not applicable in a realistic ecological model. Indeed, in most ecological models with multiple species, the interacting species influence each other in different ways, which results in a non-symmetric Jacobian. Nonetheless this result is interesting since it shows that a generalization (for all $\varepsilon > 0$) of the previous results of slow and fast evolution - namely that eco-evo feedbacks can stabilize an unstable system - is not possible. On the other hand, this theorem does not exclude the existence of a general instability condition, implying that eco-evo feedbacks can destabilize a stable system. Thus, this theorem is in no contradiction to the result of Patel et al. (2018) concerning a single evolving trait.

3.4.2 Identifying the influence of eco-evo feedbacks on stability

While the relative rates of ecological and evolutionary dynamics can indeed differ (DeLong et al. 2016), in many empirical studies, the rates have been observed to occur on a similar time scale (Haafke et al. 2016, Frickel et al. 2016, etc.). Stability conditions similar to those of Theorem 3.2 and 3.3 are however not possible for arbitrary intermediate evolutionary time scales (arbitrary $\varepsilon > 0$), as shown by Theorem 3.6. To this end, a new approach is needed to identify the effects of eco-evolutionary feedbacks in the case of arbitrary evolutionary rates. In this section, we will present a general method by Cortez et al. (2020), which is useful to identify the influence of the ecological, evolutionary and eco-evolutionary feedbacks on the stability of empirically parametrized models. Applying this method to a large amount of empirical data may grant a substantial insight on the underlying effects of the eco-evolutionary feedbacks on system stability.

The method is based on a similar multi-species model as the one used in the case of slow and fast evolution. The densities of the species will be denoted by $N_1, ..., N_k$, the trait values by $x_1, ..., x_l$, the functions f_i are the growth rates of the species, and finally the selection functions g_i describe the effects of the selection pressure on the evolution of the traits:

$$\dot{N}_i = f_i(N, x) \tag{3.17a}$$

$$\dot{x}_j = g_j(N, x). \tag{3.17b}$$

A notable difference compared to (3.13) of the previous section are the missing ε in the trait equations in order to include the cases of intermediate evolutionary rates.

Transformation of empirical models into the general form

The aim of this method is to take mathematical models which are parametrized using empirical data and apply the theory to understand how the feedbacks affect the stability in this particular case. Therefore, the first crucial step in the method is to transform the parametrized models into the above form (3.17). Since this form is quite general, in many cases, no transformations need to be done and this step can be skipped. Nonetheless, one limitation of this model is the assumption of a continuous trait. Indeed, many empirical studies use discrete trait models: In contrast to the general model of Cortez et al. (2020) - where the dynamics are given by separate equations of the species density $\dot{N}$ and its trait $\dot{x}$ - discrete trait models describe the evolution in a single species, in terms of the dynamics of a discrete number of its clones C_i. Each clone corresponds to an individual of this species with a different trait value. In order to convert it into a continuous trait model, one starts by defining $N = \sum_i C_i$, which corresponds to the ecological variable in the general form. The differential equation $\dot{N}$ is derived by applying the chain rule: $\dot{N} = \sum_i \dot{C}_i$. For the evolutionary variables, the frequencies of the different clones are used: $x_i = C_i/N$. Again, using the chain rule, this results in following differential equation in the general model: $\dot{x}_i = (N\dot{C}_i - C_i\dot{N})/N^2$.

Complementary pairs of subsystems

Once the model is transformed into the general form, the stability analysis can begin. To this end, one needs to determine the Jacobian J and evaluate it at a coexistence equilibrium $(\hat{N}, \hat{x})$. The central idea of the method is to compare the stability of the Jacobian to the stability of well chosen complementary pairs of a subsystem. A subsystem describes the dynamics of a subset of ecological and evolutionary variables, while the other variables remain fixed at their equilibrium values. If the set of variables of two subsystems are disjoint and their union contains all of the variables of the original model, then they form a complementary pair of subsystems. Furthermore, the stability of a subsystem is determined by its Jacobian, which is always a submatrix of J.

Note that the concept of subsystems is not new. In the previous section on slow and fast evolution Patel et al. (2018) looked at subsystems too, namely the ecological and evolutionary subsystems (we will from now on refer to this as the eco-evo subsystem pair). This approach was useful to determine how the feedbacks between the ecological and evolutionary variables affect the stability of the system. In this section, Cortez et al. (2020) generalized this idea. After all, feedbacks need not only occur between the ecological and evolutionary subsystems. Indeed, in some cases, the main stabilizing forces turn out to be the feedbacks between completely different complementary pairs of subsystems.

To illustrate how such subsystem pairs provide information on the relation between eco-evolutionary feedbacks and system stability, it's worth looking at some examples. First, consider the eco-evo subsystem pair. If the ecological an evolutionary dynamics were decoupled, the stability of the system would solely be determined by the stabilities of the respective subsystems. This can be explained by looking at the Jacobian, which in the decoupled case corresponds to a block diagonal matrix. By simple linear algebra, the stability of the Jacobian is therefore determined by the stability of both submatrices. If one now considers a coupled ecological and evolutionary system, then the Jacobian does not have a block diagonal form anymore, and the stability additionally depends on the feedbacks between both subsystems. If the Jacobian is stable and at least one of the subsystems unstable, then the feedbacks between the subsystems are stabilizing. If the Jacobian is unstable and both subsystems stable, then the feedbacks have a destabilizing effect. This concept can be generalized to arbitrary complementary pairs of subsystems. To see this, simply rearrange the variables and use the same arguments as above. Another way to illustrate this is to consider the characteristic polynomial of the Jacobian. For simplicity reasons, Cortez et al. (2020) considered a four dimensional system with three species N_1, N_2, N_3 and one evolving trait x_1. The Jacobian of this system is given by:

$$J = \begin{pmatrix} \partial f_1/\partial N_1 & \partial f_1/\partial N_2 & \partial f_1/\partial N_3 & \partial f_1/\partial x_1 \\ \partial f_2/\partial N_1 & \partial f_2/\partial N_2 & \partial f_2/\partial N_3 & \partial f_2/\partial x_1 \\ \partial f_3/\partial N_1 & \partial f_3/\partial N_2 & \partial f_3/\partial N_3 & \partial f_3/\partial x_1 \\ \partial g/\partial N_1 & \partial g/\partial N_2 & \partial g/\partial N_3 & \partial g/\partial x_1 \end{pmatrix}.$$

If one denotes the submatrices corresponding to each subsystem by M_S, where S is the set of variables in this subsystem and the determinant of the submatrices by $|M_S|$, then the characteristic polynomial can be expressed as:

$$p(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4,$$

where

$$\begin{aligned} a_1 &= -(|M_{N_1}| + |M_{N_2}| + |M_{N_3}| + |M_{x_1}|) \\ a_2 &= |M_{N_1N_2}| + |M_{N_1N_3}| + |M_{N_1x_1}| + |M_{N_2N_3}| + |M_{N_2x_1}| + |M_{N_3x_1}| \\ a_3 &= -(|M_{N_1N_2N_3}| + |M_{N_1N_2x_1}| + |M_{N_1N_3x_1}| + |M_{N_2N_3x_1}|) \\ a_4 &= |J|. \end{aligned}$$

The Routh-Hurwitz criterion gives necessary and sufficient conditions for the stability of the Jacobian. Unfortunately, this conditions can get quite complex for large matrices. Therefore Cortez et al. (2020) only used the necessary condition, which states that all coefficients of the characteristic polynomial a_1, a_2, a_3, a_4 must be positive. To see how the stability of the Jacobian relates to the stability of subsystems, they additionally computed the characteristic polynomial of $M_{N_1N_2N_3}$:

$$q(\lambda) = \lambda^3 + b_1\lambda^2 + b_2\lambda + b_3,$$

where

$$\begin{aligned} b_1 &= -(|M_{N_1}| + |M_{N_2}| + |M_{N_3}|) \\ b_2 &= |M_{N_1N_2}| + |M_{N_1N_3}| + |M_{N_2N_3}| \\ b_3 &= -|M_{N_1N_2N_3}|. \end{aligned}$$

As before, a necessary condition for the stability of $M_{N_1N_2N_3}$ is $b_i > 0$ for all i. Furthermore due to Routh-Hurwitz, a necessary condition for a neutrally stable subsystem or a neutral subsystem with purely imaginary eigenvalues is $b_i \geq 0$ for all i, with at least one positive b_i . Note that for each i, b_i is a partial sum of a_i. This is true for the characteristic polynomial of any subsystem. Thus, if the subsystem is stable, neutrally stable or neutral with purely imaginary eigenvalues, then the b_i are non-negative and some of them positive, which implies that the coefficients a_i become more positive. Therefore, stable, neutrally stable or neutral subsystems with purely imaginary eigenvalues have a stabilizing effect on the whole system. In the case of a neutral subsystems with only zero eigenvalues, the coefficients b_i are all zero. Therefore, such subsystems have no direct effect on the overall stability of the system. If however at least one coefficient b_i is negative - this is the case for unstable subsystems - then at least one of the coefficient a_i gets more negative. Therefore, unstable subsystems have a destabilizing effect on the whole system.

Motivated by these arguments, the next step in the method of Cortez et al. (2020) is to choose a pair of complementary subsystems and determine its stability. If both subsystems are stabilizing and the whole system is unstable, then this implies that the feedbacks between the subsystems have a destabilizing effect. If at least one of both subsystems is destabilizing and the whole system is stable, then this implies that the feedbacks are stabilizing the system. Altogether, if the stability of the Jacobian differs from what is predicted from the stabilities of the complementary subsystem pair, then the feedbacks between the subsystems do influence the stability of the whole system.

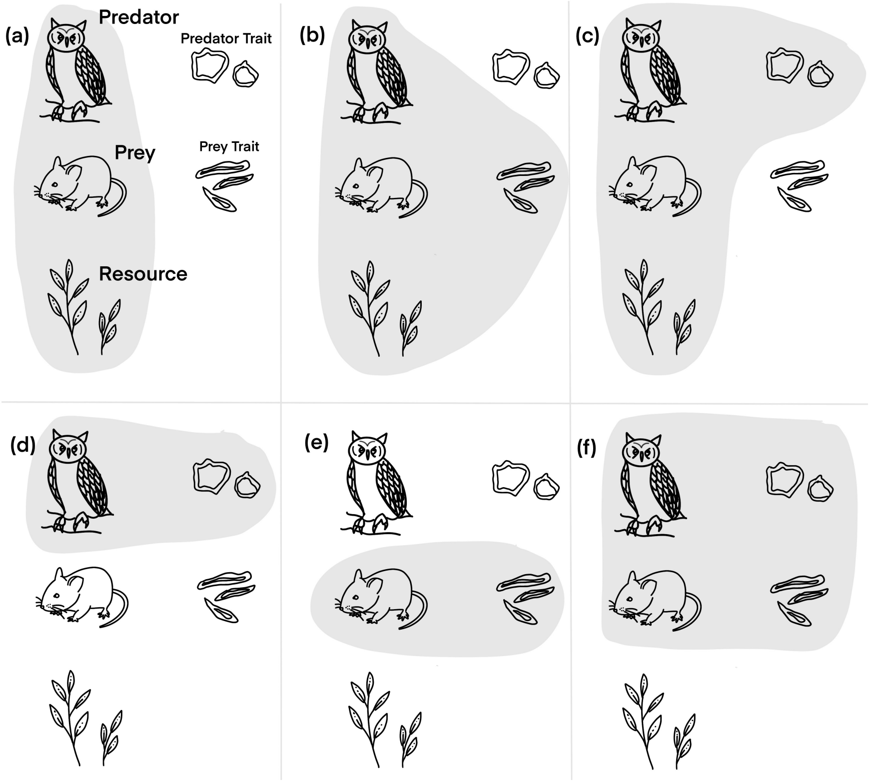

Figure 17: Different complementary subsystem pairs in a system consisting of a resource and two evolving species, a predator and a prey. The colored area in grey represents a subsystem. The complementary subsystems consist of the species/traits which are not grey. The subsystems in grey are: (a) the ecological subsystem consisting of the predator, prey and resource; (b) The complementary subsystem to the subsystem consisting of the predator's trait; (c) The complementary subsystem to the subsystem consisting of the prey's trait; (d) The eco-evolutionary subsystem of the predator; (e) The eco-evolutionary subsystem of the prey; (f) The complement to the subsystem which only contains the resource.

Which complementary pairs of subsystems to choose?

There are a large number of possible pairs of subsystems one can study. Cortez, Schreiber and Patel decided to focus on four types of complementary subsystems, chosen for their biological significance. The first pair consists of the ecological and evolutionary subsystems (Figure 17a). Analyzing the stability of this pair allows to determine which effects the ecological, evolutionary and eco-evolutionary feedbacks involving all species have on the whole system. The second subsystem pairs they studied are the subsystems consisting of the evolutionary traits of a single species and its complement (Figure 17b,c). This allows the identification of the influence of evolutionary feedbacks of a single species. As a third type of subsystem pairs, Cortez et al. considered the subsystems consisting of the ecological and evolutionary variables of a single species and its complement (Figure 17d,e). Determining the stability of these subsystem pairs will help to identify the effects of the feedbacks within each species. Finally, the last subsystem pairs they considered are the subsystems containing all of the variables (species and traits) within a single trophic level and its complement (Figure 17d,e,f). By analyzing the stability of those subsystem pairs, Cortez et al. (2020) managed to identify the effect of the feedbacks within each trophic level.

Applying the method to empirically parametrized models

To illustrate how to apply the theory to an empirically parametrized model, we return to the algae-virus experiment (Frickel et al. 2016) presented in chapter 2. In addition to the chemostat experiment, Frickel, Sieber and Becks derived a mathematical model, which they parametrized using the data of the experiment. The ecological variables in the model are the resource S which continuously flows into the chemostat, the algae $B = (B_1, B_2, B_3, B_4)$ which feed on the resource and the virus $P = (P_1, P_2, P_3)$ which can infect the algae. The variables B_i and P_j correspond to different algae and virus types such that P_i can infect B_j if and only if $j \leq i$. Consequently, B_1 is susceptible to all three virus types and B_4 corresponds to a general resistant host. The change in resource S is given by

$$\dot{S} = DS_0 - c\sum_{i=1}^{4} g_i(S)B_i - DS,$$

where S_0 denotes the constant inflow of resource concentration in the chemostat, D is the dilution rate specific to the chemostat, which determine both the rate of in-and outflow of the resource, $g_i(S)$ is the functional response of algae type i which describes the consumption of the resource by B_i and c is a parameter describing the resource conversion efficiency. The functional response of algae type i is given by $g_i(S) := a_i S/(H + S)$, where a_i is the growth rate of B_i and H is the so called half-saturation constant of the algae. The growth rates a_1 and a_4 were measured in the experiment. Due to a trade-off between resistancy and growth rate, it followed that $a_1 > a_N$. Assuming a linear trade-off (which is suggested by the data), the growth rates of a_2 and a_3 were derived as $a_i := (a_4 - a_1)(i - 1)/3 + a_1$. In order to derive equations for the change of algae and virus densities, one first needs to clarify how the mutations can occur. Frickel et al. (2016) assumed that mutations are only possible towards the neighboring type, i.e. the algae type B_i can have offspring B_{i-1}, B_i or B_{i+1} (for $1 < i < 4$), B_1 can only have offspring of type B_1 or B_2, B_4 can only have offspring of type B_4 or B_3, the virus type P_1 can have offspring of type P_1 and P_2, P_2 can have any other virus type as offspring and finally P_3 can only have P_3 or P_2 as offspring. Furthermore Frickel et al. assumed that mutations occur at rate ε. If two mutations are possible - meaning the algae or virus type has two neighbors - then each mutation is equally likely and occurs at a rate $\varepsilon/2$. With this in mind, Frickel et al. (2016) described the mutation rates by two tridiagonal matrices

$$M_B = \begin{pmatrix} (1-\varepsilon) & \varepsilon/2 & 0 & 0 \\ \varepsilon & (1-\varepsilon) & \varepsilon/2 & 0 \\ 0 & \varepsilon/2 & (1-\varepsilon) & \varepsilon \\ 0 & 0 & \varepsilon/2 & (1-\varepsilon) \end{pmatrix}$$

for the algae types, where $(M_b)_{ij}$ denotes the rate of mutation from type j to type i, and accordingly

$$M_P = \begin{pmatrix} (1-\varepsilon) & \varepsilon/2 & 0 \\ \varepsilon & (1-\varepsilon) & \varepsilon \\ 0 & \varepsilon/2 & (1-\varepsilon) \end{pmatrix}$$

for the virus types. The rates of change of algae densities are now given by:

$$
\begin{aligned}
\dot{B}_1 &= \Big[(1-\varepsilon)g_1(S)B_1 + \frac{\varepsilon}{2}g_2(S)B_2\Big] - \Phi(P_1+P_2+P_3)B_1 - DB_1 \\
\dot{B}_2 &= \Big[\varepsilon g_1(S)B_1 + (1-\varepsilon)g_2(S)B_2 + \frac{\varepsilon}{2}g_3(S)B_3\Big] - \Phi(P_2+P_3)B_2 - DB_2 \\
\dot{B}_3 &= \Big[\frac{\varepsilon}{2}g_2(S)B_2 + (1-\varepsilon)g_3(S)B_3 + \varepsilon g_4(S)B_4\Big] - \Phi P_3 B_3 - DB_3 \\
\dot{B}_4 &= \Big[\frac{\varepsilon}{2}g_3(S)B_3 + (1-\varepsilon)g_4(S)B_4\Big] - DB_4
\end{aligned}
$$

where Φ is the viral adsorption rate which is constant among all virus types. Note that each equation can essentially be divided into three parts. The first part (in brackets) denotes the gain in abundance of the respective algae type. For fixed i, this term includes the offspring of B_i which have not mutated and the offspring of B_{i-1} and B_{i+1} where the according mutation rate towards type i is taken into account. The second part of the equation denotes the infected algae types which are removed from the system. Since B_4 is resistant to all three virus types, this term is missing in the fourth equation. Finally, the term BD_i denotes the outflow of algae in the chemostat, which is determined by the dilution rate D. The change of virus densities can be described in a similar way as:

$$
\begin{aligned}
\dot{P}_1 &= \beta\Phi\Big[(1-\varepsilon)B_1P_1 + \frac{\varepsilon}{2}(B_1+B_2)P_2\Big] - \Phi B_1P_1 - DP_1 \\
\dot{P}_2 &= \beta\Phi\Big[\varepsilon B_1P_1 + (1-\varepsilon)(B_1+B_2)P_2 + \varepsilon(B_+ + B_2 + B_3)P_3\Big] - \Phi(B_1+B_2)P_2 - DP_2 \\
\dot{P}_3 &= \beta\Phi\Big[\frac{\varepsilon}{2}(B_1+B_2)P_2 + (1-\varepsilon)(B_1+B_2+B_3)P_3\Big] - \Phi(B_1+B_2+B_3)P_3 - DP_3,
\end{aligned}
$$

where β is the number of new virus particles which are created during the lysis of an infected host cell. Note that each equation consists of three parts. The first part corresponds to the gain in abundance of the virus types. In the case of P_1 for example: Virus particles of type P_1 are either created upon lysis of a host cell infected with the P_1 virus when no mutation occurred, or they are created upon lysis of host cell infected with the P_2 virus when a mutation from type 2 to type 1 occured. In the first case, $\Phi B_1 P_1$ corresponds to the number of B_1 which are infected by P_1. Multiplying this term with β gives the number of virus particles created by the infected hosts and finally multiplying the result by $(1-\varepsilon)$ gives the number of new virus particles of type P_1 created during this process. In the second case, $\Phi(B_1+B_2)P_2$ are the number of B_1 and B_2 which are infected by P_2. This term needs again to be multiplied by β, and since one is only interested in offspring of type P_2 one still need to take into account the corresponding mutation rate which in this case is $\varepsilon/2$. Both cases together give the first part of the equation for P_1. The other equations can be explained analogously. The second part in each equation corresponds to the virus particles which have infected a host and are removed from the system. Finally, as in the equations for the source and algae, one needs to subtract a term DP_i which corresponds to the outflow of virus particles in the chemostat.

By introducing an additional matrix

$$A = \begin{pmatrix} 1 & 1 & 1 \\ 0 & 1 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix},$$

Frickel et al. (2016) rewrote the whole system in a more compact form as

$$\dot{S} = DS_0 - c\sum_{i=1}^{4} g_i(S)B_i - DS \tag{3.20a}$$

$$\dot{B} = M_B(g(S) * B) - (\Phi AP) * B - DB \tag{3.20b}$$

$$\dot{P} = M_P\beta(\Phi A^T B) * P - (\Phi A^T B) * P - DP, \tag{3.20c}$$

where $g(S) := (g_1(S), g_2(S), g_3(S), g_4(S))$ and $*$ denotes the component-wise multiplication.

In order to apply the theory one needs to transform this model into a continuous trait model of the form (3.17). The equation for S remains unchanged. For the ecological equations, Cortez et al. (2020) introduced the new variables $\hat{B} = B_1 + B_2 + B_3 + B_4$ and $\hat{P} = P_1 + P_2 + P_3$, which correspond to the total algae, resp. virus densities. The evolutionary variables are then denoted by $x_1 = B_1/\hat{B}$, $x_2 = B_2/\hat{B}$, $x_3 = B_3/\hat{B}$, $x_4 = P_1/\hat{P}$ and $x_5 = P_2/\hat{P}$. To determine the equilibria and stability of the system, one still needs to decide on the values of the parameters used in the model. Based on the empirical observations of the chemostat experiment, Frickel, Sieber and Becks used the values depicted in table 1.

Table 1: Parameter values used in the transformed model

Parameter	Biological meaning	Value
D	Chemostat dilution rate	$0,1$
S_0	Inflow resource concentration	30
a_1	Algae maximum growth rate of ancestor B_1	$0,25$
a_N	Algae maximum growth rate of ancestor B_4	$0,15$
H	Algae Half-saturation constant	1
c	Algae conversion efficiency	$2,3 \cdot 10^{-5}$
Φ	Virus adsorption rate	$7,5 \cdot 10^{-8}$
β	Virus burst size	100
ε	Mutation rates	10^{-3}

Parameter values from Frickel et al. (2016)

Inserting this into the transformed continuous trait model, gives $(S, \hat{B}, \hat{P}, x_1, x_2, x_3, x_4, x_5) = (2.01, 1210000, 0.00884, 0.726{\cdot}10^{-4}, 0.00224, 889000, 0.973 \cdot 10^{-5}, 0.005)$ as the equilibrium. This is consistent with the observation of the chemostat experiment, where virus population eventually stabilized at a low density. Next, one needs to determine the stability of the Jacobian at this equilibrium. According to the computations of Cortez et al. (2020), the Jacobian J is given by:

$$\begin{pmatrix}
-0,564 & 2,32 \cdot 10^{-6} & 0 & -1,85 & -1,24 & -0,618 & 0 & 0 \\
20200 & 0 & -0,00101 & 80,1 & -26800 & -53300 & 187 & 181 \\
0 & 0,0736 & 0 & 7,97 \cdot 10^{6} & 7,97 \cdot 10^{6} & 7,93 \cdot 10^{6} & -18500 & -17900 \\
0,0000967 & 0 & -6,56 \cdot 10^{-10} & -1,18 \cdot 10^{-6} & 0,000268 & 0,00039 & -1,37 \cdot 10^{-6} & -1,32 \cdot 10^{-6} \\
7,93 \cdot 10^{-7} & 0 & -5,38 \cdot 10^{-12} & 0,0000167 & -0,0222 & 6,44 \cdot 10^{-5} & 4,83 \cdot 10^{-6} & -1,09 \cdot 10^{-8} \\
2,44 \cdot 10^{-5} & 0 & -1,656 \cdot 10^{-10} & -0,0001 & 0,000022 & -0,0441 & 0,000149 & 0,000149 \\
0 & 0 & 0 & 2,26 \cdot 10^{-5} & -6,46 \cdot 10^{-5} & -8,69 \cdot 10^{-5} & -0,0208 & 4,06 \cdot 10^{-5} \\
0 & 0 & 0 & 0,00897 & 0,00897 & -0,0356 & 0,000083 & -0,0201
\end{pmatrix}$$

The eigenvalues of J are $(\lambda_1, \lambda_2, \lambda_3, \lambda_4, \lambda_5, \lambda_6, \lambda_7, \lambda_8) = (-0.463, -0.00437 \pm 0.0792i, -0.1, -0.0365, -0.0204, -0.0207, -0.0222)$. Thus, the real part of all eigenvalues are negative, which means that the equilibrium is stable. This is again consistent with the observation in the chemostat experiment, where both the algae and virus densities eventually converged towards a stable coexistence equilibrium. In order to determine which feedbacks influenced this result, Cortez et al. (2020) checked the stabilities of various complementary pairs of subsystem. The results are summarized in table 2.

In this example, all of the subsystems are either stable or neutrally stable, and therefore have a stabilizing effect on the whole system. Since J is stable as well, the stabilities of the subsystems are in no contradiction to the overall stability of the system. Thus, in this example one cannot specify if the feedbacks between the subsystems have a stabilizing effect. The most one can say is that if they are destabilizing, then this effect is not strong enough to destabilize the whole system.

Table 2: Stabilities of complementary pairs of subsystems in Frickel et al. 2016

Subsystem	Variables	Eigenvalues	Stability*
Eco	$S, \hat{B}, \hat{P}$	-0.463, -0.1, -0.000905	S
Evo	$x_1, x_2, x_3, x_3, x_4, x_5$	-0.5·10^{-8}, -0.0439,-0.0222, -0.0203, -0.0208	S
Host evo	x_1, x_2, x_3	$-5.0610 \cdot 10^{-8}$, 0.0222, -0.0441	S
Complement	$S, \hat{B}, \hat{P}, x_4, x_5$	-0.463, -0.1, -0.000905, -0.0208, -0.0201	S
Host eco-evo	$\hat{B}, x_1, x_2, x_3$	0, $-5.06 \cdot 10^{-8}$, -0.0222, -0.0441	NS
Complement	$\hat{S}, \hat{P}, x_4, x_5$	0, -0.564, -0.0207, -0.0201	NS
Virus evo	x_4, x_5	-0.0208, -0.0201	S
Complement	$S, \hat{B}, \hat{P}, x_1, x_2, x_3$	-0.463, -0.00436± 0.0792i, -0.1, -0.0368, -0.0222	S
Virus eco-evo	$\hat{P}, x_4, x_5$	0,-0.0208, -0.0201	NS
Complement	$S, \hat{B}, x_1, x_2, x_3$	-0.463, -0.102, -0.044, -0.0222, -5.01 ·10^{-8}	S

[∗] The letter S means that all of the eigenvalues of the subsystem have negative real part and thus the subsystem is *stable.* On the other hand, NS is short for *neutrally stable* and means that the real part of the eigenvalues are all non-positive, at least one of the eigenvalues has negative real part and at least one of the eigenvalues is 0. (Table from Cortez et al. (2020))

In order to understand how eco-evo feedbacks can affect system stability, one needs to repeat this process for a large number of empirically parametrized models and hope to observe patterns. Cortez, Patel and Schreiber did exactly this and replicated the approach on an additional 8 models for which empirically obtained parameter values were available. All of the included models were of the type exploiter-victim (e.g. predator-prey, pathogen-host, parasite-host), where the densities either converged towards a stable coexistence equilibrium or exhibited sustained oscillations around an unstable equilibrium. Analyzing those models can therefore grant further insights on which type of feedbacks cause sustained oscillations and which type of feedbacks cause convergence towards a stable equilibrium. The results of Patel, Cortez and Schreiber are summarized in table 3. Across the nine models, four exhibited sustained oscillations around an unstable equilibrium and four models converged towards a stable equilibrium. The stabilities of the different subsystems differed depending on the trophic level (exploiter or victim) and the type of subsystem (eco, evo or eco-evo). The most noticeable difference can be observed when comparing the ecological and the evolutionary subsystems: In all but one model, the ecological subsystems were stable, whereas the evolutionary subsystems were only stable in four out of nine models. Another noticeable difference can be seen when comparing the eco, evo and eco-evo subsystems of the exploiter to the eco, evo and eco-evo subsystems of the victim species: For the exploiter species, the subsystems were stable, neutrally stable or neutral in all but one model, whereas for the victim species, the subsystems where stable in only four models.

In order to understand how the feedbacks between the subsystem affected the stability of the system, Cortez et al. (2020) compared the stabilities of complementary subsystem pairs. They divided the models into two groups and started with the four models with an unstable equilibrium. The ecological subsystem was stable in three models, whereas the evolutionary subsystem was stable in all four models. Thus, the feedbacks between the ecological and evolutionary subsystems were either destabilizing or they were stabilizing, however not strong enough to stabilize the whole system. The evo, eco and eco-evo subsystems of the exploiter species were stable or neutrally stable in all four models, whereas their complement was unstable in all four models. This means that the feedbacks between the subsystems of the exploiter and their complement were either destabilizing or stabilizing, however not strong enough to stabilize the whole system. Finally, the eco, evo and eco-evo subsystems of the victim species were unstable in all four of the models exhibiting cycles and their complementary subsystems were stable or neutrally stable in three models. As before, this implies that the feedbacks between the victim subsystems and their complements were either destabilizing or they were stabilizing, however insufficiently strong to stabilize the whole system. Next, Cortez et al. (2020) looked at the five models with a stable equilibrium. In three models, all of the subsystems were stable or neutrally stable. Thus, in these cases, the feedbacks were either stabilizing or they were destabilizing, however insufficiently strong to destabilize the whole system. In one of the five models, all subsystems but one were stable. In this system, the feedbacks between the exploiter eco subsystem and its complement were sufficiently strong to stabilize the whole system. Finally in the last of the five stable models, all of the complementary subsystem pairs contained exactly one unstable subsystem. Thus, the feedbacks between all of the five subsystem pairs had a stabilizing effect which was sufficiently strong to stabilize the whole system.

Table 3: Effects of complementary pairs of subsystems on system stability in parametrized models

Article	Evolving Species	System Behaviour	Stability of Eco and Evo Subsystems	Stability of Victim Evo Subsystem	[1]Stability of Victim Eco or Eco-Evo Subsystem	Stability of Exploiter Evo Subsystem	[2]Stability of Exploiter Eco or Eco-Evo Subsystem
Becks et al. 2010	prey	cyclic	S-U	U-S	U-NS		NS-U
Frickel et al. 2016	both	stable	S-S	S-S	NS-NS	S-S	NS-S
Haafke et al. 2016	both	cyclic	U-U	U-U	U-NS	NS-U	NS-U
Kasada et al. 2014	prey	stable	S-U	U-S	U-NS		N-U
Wei et al. 2011	both	stable	S-S	S-NS	S-NS	N-S	N-S
Yoshida et al. 2003	prey	cyclic	S-U	U-S	U-NS		NS-U
Hiltunen et al. 2014	prey	cyclic	S-U	U-S	U-S		S-U
Bolker et al. 2010	parasite	stable	S-S		S-NS	S-S	NS-S
Duffy et al. 2012	host	stable	S-S	S-S	S-S		U-S

[∗] The letters S, U, N and NS denote a stable, unstable, neutral and neutrally stable system respectively. In the column "Stability of Eco and Evo Subsystems", the first letter corresponds to the stability of the ecological and the second to the evolutionary subsystem. In all other columns, the first letter corresponds to the stability of the subsystem mentioned above and the second corresponds to the stability of the complementary subsystem.
[1] If the victim (prey or host) in the model is not evolving, then the Victim Eco subsystem was used. Otherwise the Victim Eco-Evo subsystem was used.
[2] If the exploiter (predator, virus or parasite) in the model is not evolving, then the Exploiter Eco subsystem was used. Otherwise the Exploiter Eco-Evo subsystem was used. (Table from Cortez et al. (2020))

4

Conclusion and Future Research

Conclusion

The evergrowing number of empirical and theoretical works studying the influence of eco-evolutionary feedbacks on system stability shows that the traditional separation of ecology and evolution is artificial and needs to be revised. Indeed, laboratory experiments (Frickel et al. 2016; DeLong et al. 2016) and data collections of natural communities (DeLong et al. 2016) consistently show that rapid evolution on a contemporary ecological time scale is possible. The immense amount of empirical evidence suggests that a drastic rethinking is needed. The incorporation of evolutionary aspects into ecological systems is imperative and needs to be the norm of modern ecological modeling. Purely ecological models without any evolutionary elements may generate false explanations and predictions, with potentially severe consequences in areas such as natural resource management or wildlife conservation. This concern is well-founded and strengthened by a number of theoretical works that show the extent of how neglecting the eco-evo feedbacks can distort our perceived reality (Vasseur et al. 2011; Schreiber et al. 2011; Schreiber and Patel 2015; Mougi 2012; Cortez and Weitz 2014; Patel et al. 2018).

Eco-evo feedbacks can stabilize ecologically unstable systems and allow coexistence in competitive communities without the creation of niche differences (Vasseur et al. 2011). This contradicts Gause's law that states that in such cases, the weaker competitor should always be driven to extinction. Inconsistencies of Gause's law are however not new. Indeed, many empirical examples of natural communities, such as that of the Hispine Beetles have coexisted despite Gause's law predicting the contrary (Strong 1982). The eco-evo feedbacks merely serve as a possible explanation for this phenomenon. Other theoretical work has shown that eco-evo feedbacks can lead to permanence (Schreiber and Patel

2015), drive antiphase or cryptic cycles in predator-prey models (Mougi 2012), completely reverse the cycle directions in predator-prey models (Cortez and Weitz 2014) or destabilize an ecologically stable system, leading to sustained oscillations or even chaotic behaviour (Schreiber et al. 2011). While this thesis was mostly focused on the effects that eco-evo feedbacks have on the stability of systems, all this work shares a common interest, that is the accentuation of the vast amount of unintuitive outcomes when taking the evolutionary aspects and thus the eco-evo feedbacks into account. It is therefore essential to always at least consider the possibility that the observed behaviours in ecological models may be influenced by eco-evo feedbacks.

Nonetheless, simply including evolutionary aspects into the model may not be sufficient and in some cases still lead to false outcomes. As a matter of fact, the relative speed of the evolutionary and ecological variables are highly important and can greatly influence the outcomes as well (Vasseur et al. 2011; Schreiber et al. 2011). Slow evolutionary rates translate to weak eco-evo feedbacks that may not be sufficient to exhibit a notable difference in the outcome. Increasing the evolutionary rates increases the possibility of observing the effects of eco-evo feedbacks, e.g. stabilizing an equilibrium and allowing coexistence in an otherwise unstable ecological system (Vasseur et al. 2011). Further increasing the evolutionary speed in a system with a stable equilibrium can lead to an overpowering of the eco-evo feedbacks, resulting in an overshooting of the equilibrium, which is made visible by sustained oscillations around the equilibrium (Vasseur et al. 2011; Schreiber et al. 2011) or even chaotic behaviour (Schreiber et al. 2011). The importance of analyzing the stabilizing properties of eco-evo feedbacks at different evolutionary rates is backed up by theoretical studies (Patel et al. 2018; Cortez et al. 2020).

Indeed, depending on the evolutionary rates, different kinds of feedbacks are essential in stabilizing a system (Patel et al. 2018). The indirect evo-eco-evo feedbacks are critical in the case of slow evolution, whereas eco-evo-eco feedbacks are essential in the case of fast evolution. This result is the first of its kind. Unlike most of the previous works, which have limited themselves to numerical results in systems consisting of only a few species, this work provided analytical conditions that greatly advance our mechanistically understanding of how the eco-evo feedbacks can stabilize a system. Furthermore, this result was pioneering in the sense that it was stated in the context of general community systems with an arbitrary but finite number of interacting species and evolving traits. Analytical results such as these are highly important and decisively improve our knowledge on the fundamental question in eco-evolutionary dynamics of how eco-evo feedbacks can influence the stability of an ecological system.

Similar analytical conditions - which determine the type of feedbacks that are crucial for stabilizing a system - are, however, not possible in the case of intermediate evolutionary rates (Theorem 3.6). Thus, in order to determine the exact types of feedbacks that stabilize a system, alternative methods are needed.

One possibility is to determine the stability of different complementary pairs of subsystems in empirically parametrized models and compare the predicted stability of the subsystems to the actual stability of the Jacobian at an equilibrium (Cortez et al. 2020). This method gives us even further insights into the types of feedbacks that have a stabilizing effect and - in contrast to the result of Patel et al. (2018) - can even determine which feedbacks are destabilizing. One limitation of this method is, however, that its success relies on the quantity of empirically parametrized models available. On the plus site, this method can continuously give us additional information on the types of feedbacks that are stabilizing, resp. destabilizing, as the number of models that are parametrized using empirical data grows.

Another possibility to determine the effects of eco-evo feedbacks in the case of intermediate evolutionary rates - as proposed by Patel et al. (2018) - is the use of so called *loop analysis*, a method developped by Levins (2020). Similar to the method by Patel et al. (2018), loop analysis allows the identification of the specific feedback loops which are responsible for destabilizing the equilibrium. This is done by using special stability conditions depending on the length of the feedback loop, and checking whether they are satisfied or not. One disadvantage of this method is however that the number of loops, and thus the number of stability conditions rapidly grows as the number of species and traits increases.

Future Research

While the presented work has greatly improved our understanding of the effects of eco-evo feedbacks on the stability of systems, the full nature of the underlying mechanisms driving the feedbacks, and in particular the question if and how they stabilize or destabilize a system seem still far away. Most studies which have analyzed the influence of eco-evo feedbacks on stability provide numerical results and are limited to two to three species with at most one evolving trait. Simulations of larger community systems with several evolving traits would certainly be interesting. Ultimately, however, analytical results will always be favorable since they provide a better understanding of the underlying effects resulted by the feedbacks. Unfortunately, such studies are - at the time being - barely available with the two exceptions of Patel et al. (2018) and Cortez et al. (2020).

While Patel et al. (2018) succeeded to determine which types of feedbacks are essential for stabilizing a system in the case of slow and fast evolution, similar results that determine the types of feedbacks that are essential for destabilizing a system in the case of slow and fast evolution are not available and would be interesting to see in future works. Furthermore, stability conditions as in Patel et al. (2018) for arbitrary intermediate ecological rates would significantly improve our understanding of the relation between eco-evo feedbacks and system stability. Unfortunately, such conditions are in general not possible (Theorem 3.6). Thus, if one would still wish to obtain similar stability conditions for intermediate evolutionary rates, one would need to sacrifice the generality of the model used in Patel et al. (2018) and focus on more specific cases.

One possibility would be to restrict the number of species or the number of traits to one or two. After all, Patel et al. (2018) did precisely this and consequently succeeded to provide an instability condition in the case of intermediate evolutionary rates. Alternatively, one could try to keep the generality of the model while focusing on only one kind of interaction between the involved species. Indeed, the properties of competition, mutualism and predator prey models are often considerably different. Focusing on a single type of interaction could therefore greatly simplify the analysis of an eco-evolutionary system. A third possibility would be to consider other types of eco-evo feedbacks. Patel et al. (2018) restricted themselves to the investigations of the feedbacks between the ecological and evolutionary subsystem. Cortez et al.

(2020), however, showed that feedbacks between other kinds of subsystems can have systematically different effects on the stability of the system. Future works investigating the effects of eco-evo feedbacks on stability in systems with intermediate evolutionary rates could therefore try to develop similar results to that of Patel et al. (2018) while focusing on the feedbacks between the subsystems presented in Cortez et al. (2020).

In contrast to a general stability condition, Theorem 3.6 does not exclude the existence of a general instability condition for intermediate evolutionary rates, as the example of Patel et al. (2018) with one single evolving trait shows. Generalizations of this result for multiple traits would be interesting to see in the future.

As a matter of fact, the publication of Cortez et al. (2020) provides a method that could potentially answer most of the above questions. However, the success of this method depends at large on both the quality and the quantity of the empirically parametrized models available. In this study, only nine models were analyzed. These were the only models parametrized with empirical data, which Cortez, Patel and Schreiber managed to find. The small number of models and the fact that all of those models were of the exploiter-victim type, drastically weakened the relevance of the resulting observations. The few empirically parametrized models available are insufficient to provide a deeper insight, determining the influence of the different types of feedbacks in a general system. However, due to the increasing recognition of rapid evolution on an ecological time scale and the evergrowing number of theoretical studies highlighting the importance of incorporating evolutionary aspects into ecological models, more and more biological studies and collection of data - both in the laboratory and in natural environments - are expected to appear in the near future. In this case, the work of Cortez et al. (2020) can be applied to a larger set of data, eventually advancing our understanding of the dependency of eco-evo feedbacks and the stability of multi-species community systems.

Most works presented in this thesis were focused on the local stability around an isolated equilibrium. The global dynamics can however often be substantially more complex. Indeed, investigating the effects of eco-evo feedbacks on the global dynamics in a general model is practically unfeasible. Fortunately, the question whether all species can continue to coexist after some initial perturbation is more important than the analysis of the exact dynamics. Thus, results on permanence are in most cases sufficient. Analytical work on the effects of eco-evo feedbacks on permanence in a 3-species apparent competition model is available (Schreiber and Patel 2015). Future works could therefore follow a similar approach and investigate the effects of eco-evo feedbacks on permanence in models with different kind of interactions.

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