Accepted manuscript is released with a Creative Commons Attribution Non-Commercial No Derivatives License https://creativecommons.org/licenses/by-nc-nd/4.0/

Accepted Manuscript

Environmental dimensionality

Kalle Parvinen, Ulf Dieckmann

PII:	S0022-5193(18)30122-X
DOI:	10.1016/j.jtbi.2018.03.008
Reference:	YJTBI 9385
To appear in:	*Journal of Theoretical Biology*
Received date:	3 June 2017
Revised date:	4 March 2018
Accepted date:	7 March 2018

Please cite this article as: Kalle Parvinen, Ulf Dieckmann, Environmental dimensionality, *Journal of Theoretical Biology* (2018), doi: 10.1016/j.jtbi.2018.03.008

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

ACCEPTED MANUSCRIPT

Highlights

- The number of regulating variables limits species coexistence
- Methods to determine the smallest number of regulating variables are presented
- This can be done by analyzing the dimension of a population's regulation map
- Population regulation consists of impact and sensitivity maps
- We analyze these both separately and together, highlighting their interaction

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

Environmental dimensionality

Kalle Parvinen and Ulf Dieckmann

March 14, 2018

Abstract

The number of regulating variables n in a given system is an upper bound to the number of coexisting species at equilibrium according to the competitive exclusion principle. However, it may be possible to formulate the model with a lower number of regulating variables, the smallest number of which is the dimension of the environmental feedback. Here we investigate how that dimension can be determined by analysing the two parts of environmental feedback: The impact map describes how the extant species affect the regulating variables, and the sensitivity map describes how population growth depends on the regulating variables. For the equilibrium condition it is enough to know the sign of each population growth rate, and therefore as the sensitivity map, different measures of population growth can be chosen, such as the basic reproduction number. The dimension of the environmental feedback must not depend on that choice. Different sensitivity maps can have different global dimensions, on which the definition thus cannot be based. Here we show that the local sensitivity dimension is independent of the choice, so that the concept is well-defined. The impact dimension is lower than n when the feasible set of environments is of lower dimension than n, and sensitivity dimension is lower than n when not all environmental variables affect the sign of population growth independently. Their combined effect can result in even lower environmental dimension. We illustrate such situations with examples. In conclusion, the dimension of environmental feedback gives valuable information about the potential coexistence of species.

Keywords: Population regulation; impact; sensitivity; competitive exclusion; fitness proxy

1 Introduction

Coexistence is a fundamental topic in population ecology. Darwin (1859, p. 322) wrote: “We need not marvel at extinction; if we must marvel, let it be at our presumption in imagining for a moment that we understand the many complex contingencies, on which the existence of each species depends.” The competitive exclusion principle states that complete competitors cannot coexist (Hardin, 1960). Furthermore, the number of coexisting species at equilibrium is less than or equal to the number of resources in the system (Levin, 1970; Roughgarden,

ACCEPTED MANUSCRIPT

1976). This principle is based on the fact that at equilibrium, the population growth rate of each coexisting species has to be 0, and a system of equations can in general be satisfied only if there are at least as many unknowns as equations.

The observed diversity of plankton in aquatic ecosystems, despite the seemingly small number of limiting resources, has been called as the "paradox of the plankton" (Hutchinson, 1961). Since the competitive exclusion principle in its traditional form only applies in a population-dynamical equilibrium, non-equilibrium population dynamics (cycles and chaos) may provide an explanation for the paradox (Huisman and Weissing, 1999), see also Lundberg et al. (2000). However, in such complex situations it is not so clear how one should define regulating variables.

Fitness (Metz et al., 1992) is the long-term exponential growth rate of a rare invader in some given stationary environment. A coexistence condition, which holds in general, not just in the equilibrium case, is that the fitness of each species is equal to 0. Mechanistic population models can be written in a form where the long-term growth rate of each population depends only on its demographic traits and the regulating variables through a so-called sensitivity map. These regulating variables are, again, determined by the present populations and their traits through the impact map. The environmental feedback loop (Metz and Diekmann, 1986; Metz et al., 1988; Metz and de Roos, 1992) can thus be decomposed into the impact and sensitivity maps (Meszéna et al., 2006), see also Fig. 1.

One should note that the formulation of impact and sensitivity maps is not unique: there are many different sets of variables that can be chosen as regulating variables, and the number of such variables may be different. Consider, for example, a consumer species using three resources. The average population densities of each resource in a community-dynamical attractor could be natural choices for the regulating variables. However, the resources could have equal energy contents and be equally preferable, so that the sum of these three variables would suffice to determine long-term population growth. The number of the regulating variables in a specific model formulation is therefore not necessarily minimal.

In this article we address two questions: How can one tell whether a given decomposition contains a minimal representation of the regulating variables (Heino et al., 1997)? Furthermore, what is the smallest possible number of regulating variables in a decomposition? The answer lies in analyzing the dimensions of the impact, sensitivity, and composite maps.

This article is structured as follows: in section 2 we explain how the population-regulation map can be decomposed into the impact and sensitivity maps, and sections 3 and 4 concentrate on each component. In section 5 we explain how the dimension of a map is determined, and apply this method to the impact map, the sensitivity map, and the composite map. In section 6 we provide an example with two fitness proxies that have different global dimensions. In section 7 we analyze a resource-consumer model. In section 8 we consider extensions to non-equilibrium dynamics, structured populations, and more complex environments.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

2 Decomposing the regulation map

We want to investigate how population regulation can be decomposed into the impact and sensitivity maps. In order to keep notations simple and to avoid confounding our main exposition with technical subtleties, we assume that populations are unstructured, all attractors of the studied community's population dynamics are equilibria, and that the community's environment is characterized by the population densities of the focal species. Relaxations of these assumptions are investigated in section 8.

Under the aforementioned assumptions, population models can typically be formulated either in continuous time or in discrete time, so that

$$\frac{\mathrm{d}}{\mathrm{d}t}N_i(t) = h(N_1(t), \ldots, N_k(t)) \quad \text{or} \quad N_i(t+1) = H(N_1(t), \ldots, N_k(t)), \tag{2.1}$$

where N_i is the population density (a scalar) of species i. This formulation includes how populations affect growth rates and how populations are affected by the growth rates. Note that the way (2.1) is formulated does not give any information about regulating variables; thus any number of different species could coexist in the model, in principle. For this reason, it is helpful to disentangle (2.1) into two parts, as first done in the context of physiologically structured populations (Metz and Diekmann, 1986; Metz et al., 1988; Metz and de Roos, 1992),

$$\frac{\mathrm{d}}{\mathrm{d}t}N_i(t) = f(s_i, E(t))N_i(t) \quad \text{or} \quad N_i(t+1) = F(s_i, E(t))N_i(t) \tag{2.2}$$

and

$$E(t) = \mathcal{I}(s_1, \ldots, s_k, N_1(t), \ldots, N_k(t)). \tag{2.3}$$

One should note that (2.2) and (2.3) is not just a technical decomposition, but one typically arrives in such a formulation directly, when constructing a model from individual-based mechanisms. The function f (or F) describes how sensitive population growth is to the vector of regulating variables $E \in \mathbb{E} \in \mathbb{R}^n$. That vector in turn depends on the present population density vectors through the impact mapping $\mathcal{I}$. Different species are have different individual behaviour characterized by their strategy $s \in \mathbb{S}$.

The population-regulation map is a composite map of the impact map and the sensitivity map (Fig 1). Although there are usually only a few ways one would write a decomposition, in principle there are an infinite number of ways that it can be done. The dimension of composite map is the dimension of environmental feedback. It can be characterized as the smallest possible dimension of the variable E in a decomposition (Heino et al., 1997). Presenting a decomposition with $E \in \mathbb{R}^n$ shows that the environmental dimensionality may maximally be n, but the dimension is lower than n (dimension reduction) if either the impact map or the sensitivity map is effectively of lower dimension than n. Impact dimension reduction occurs when the feasible set of environments is of lower dimension than n, and sensitivity

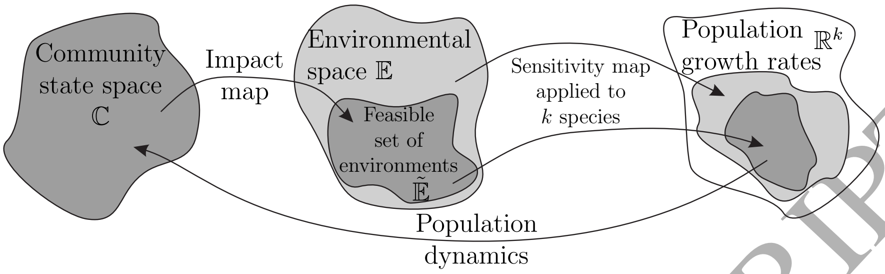

Figure 1: Environmental feedback. The impact map describes how the present species affect the environment, and the sensitivity map describes how population growth depends on the environment.

dimension reduction occurs when not all environmental variables affect population growth independently.

3 The sensitivity map

In this section we establish a formal link between the sensitivity map and the concept of fitness.

3.1 Fitness

Long-term coexistence of species requires the existence of a community-dynamical attractor in which all these species are present. In case of unstructured populations at an equilibrium, the instantaneous growth rates of all species are 0, $f(s_i, E) = 0$ (or $F(s_i, E) = 1$) for all i. For non-equilibrium attractors, such as cyclic orbits, the instantaneous growth rates are not 0. For structured populations, we do not have just one rate per each state (describing reproduction within that state and death), but also rates corresponding to transitions (and reproduction) between states. At equilibrium, these rates need not to be 0, but their total effect must be 0. Since we want to discuss extensions to non-equilibrium dynamics (Section 8.1) and also to structured populations (Section 8.2), we formulate the coexistence condition using more general terms. In a community-dynamical attractor none of the coexisting species can increase or decrease in density in the long run, and their long-term growth rates are 0. These long-term growth rates are familiar from evolutionary theory, and in particular the theory of adaptive dynamics (Metz et al., 1992), where they are called fitness: Let $N(s, t, N_0|E)$ denote the solution of

$$\frac{\mathrm{d}}{\mathrm{d}t}N(t) = f(s, E(t))N(t) \quad \text{or} \quad N(t+1) = F(s, E(t))N(t) \tag{3.1}$$

with the initial condition $N(0) = N_0$, where instead of (2.3), the environment E is given as an argument. Provided that the limit exists, fitness

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

$$r(s,E)=\lim_{T\to\infty}\frac{1}{T}\ln\frac{\|N(s,T,N_0|E)\|}{\|N_0\|} \tag{3.2}$$

is the long-term exponential growth rate of a species with strategy s in the environment E. Especially, when E is set by the community-dynamical attractor of the coexisting species, the long-term growth rate of each species present in the community is zero. In general, a necessary condition for coexistence is that $r(s_i,E)=0$ for all i in the environment $E=\{E(t),t\geqslant 0\}$ set by all the coexisting species characterized by s_i together. Since we assume equilibrium dynamics, the environment E does not depend on time. From now on we in addition assume that $E\in\mathbb{R}^n$.

The sensitivity map describes how population growth depends on the regulating variables. Therefore, the sensitivity map can be defined as fitness (3.2) applied to species $s_1,\dots,s_k$. Next we discuss so-called fitness proxies in order to obtain a more general definition.

3.2 Fitness proxies

Fitness measures population growth in real time, but also other measures are widely used. For example, the basic reproduction ratio or lifetime reproductive success is the expected number of offspring that an individual will on average get during its lifetime, and thus measures growth between generations. The same concept is used in the context of infectious diseases, where it is the average number of new infections caused by one infectious individual (Diekmann et al., 1990; Heesterbeek, 1992; Dieckmann and Heesterbeek, 2000), often denoted by R_0. The population will grow, or the infection will spread, if and only if the basic reproduction ratio is greater than 1. In structured metapopulation models, the metapopulation reproduction ratio R_m (Metz and Gyllenberg, 2001; Gyllenberg and Metz, 2001; Parvinen, 2006) measures analogously growth between dispersal generations instead of actual generations. When the investigated model has more than one birth state, the reproduction ratio typically is the dominant eigenvalue of the next-generation matrix $\mathbf{M}$. According to Metz and Leimar (2011), $-\det(I-\mathbf{M})$ can often be used as a local fitness proxy.

For simple models it is typically easy to calculate fitness and different fitness proxies. However, in many other models, calculating fitness is very difficult, but calculating a specific fitness proxy is relatively easy. To enable our analysis to the vast literature on fitness proxies, we now clarify how to define sensitivity maps based on fitness proxies. This raises the important question how to define the dimension of those maps in a way that does not depend on a particular choice of a fitness proxy.

For the invasion potential and coexistence, it is enough to know the sign of fitness. From this perspective, we define any function $\hat{r}(s,E)$ that is both continuous with respect to s and E and satisfies the condition

$$\text{there exists a constant } c \text{ so that } \hat{r}(s,E)\lesseqqgtr c \Leftrightarrow r(s,E)\lesseqqgtr 0 \text{ for all } s \text{ and } E, \tag{3.3}$$

ACCEPTED MANUSCRIPT

as a fitness proxy for the fitness function $r(s, E)$. Fitness can often be expected to be continuous and smooth with respect to s and E, and therefore we expect the same from fitness proxies. This is the case for mechanistic models, in which small changes in traits have small effects in behaviour and growth, and thus small effects in fitness. The constant c is the neutral value of the fitness proxy $\hat{r}(s, E)$. There are many naturally arising fitness proxies with a neutral value that is not 0, such as the basic reproduction ratio R for which $c = 1$. It would be easy to make an order-preserving transformation, like $\ln R$, producing a function that is sign-equivalent with fitness. The definition above, however, allows us to call R a fitness proxy, as well as $\ln R$. Since any fitness proxy can be used to determine whether the population density of a species in a given environment will grow or not, we can define that any fitness proxy applied to species $s_1, \dots, s_k$ is a sensitivity map.

4 The impact map

In general, the impact map is a mapping from the community state space $\mathbb{C}$ to the environment space.

$$\mathcal{I} : \mathbb{C} = \bigcup_{k=1}^{\infty} \mathbb{S}^k \times \mathbb{P}^k \to \mathbb{E} \subset \mathbb{R}^n, \tag{4.1}$$

where $\mathbb{S}$ is the strategy space and $\mathbb{P}$ is the population state space (for unstructured models, $\mathbb{P} = \mathbb{R}$). In other words, one needs to know the strategies and population states (sizes) of all extant species to be able to determine the present state of the environmental variables. As stated in section 2, we concentrate on equilibria, and assume $\mathbb{E} \subset \mathbb{R}^n$. Because the numbering of present species is arbitrary, some symmetry properties naturally arise. Furthermore, a species with population size (vector) 0 does not affect the environment, and the effect of two equal species is the same as one species with a combined population. These principles result in relations of the following type,

$$\begin{aligned}\mathcal{I}(s_1, s_2, s_3; N_1, N_2, N_3) &= \mathcal{I}(s_2, s_1, s_3; N_2, N_1, N_3),\\ \mathcal{I}(s_1, s_2, s_3; N_1, N_2, 0) &= \mathcal{I}(s_1, s_2; N_1, N_2),\\ \mathcal{I}(s, s; N_1, N_2) &= \mathcal{I}(s; N_1 + N_2).\end{aligned} \tag{4.2}$$

The image of the impact map $\tilde{\mathbb{E}} = \mathcal{I}(\mathbb{C})$ will be called the feasible set of environments. Note that the feasible set of environments $\tilde{\mathbb{E}}$ is not necessarily the whole environment space (see Fig. 1).

ACCEPTED MANUSCRIPT

5 Dimension of the population regulation

5.1 Dimension of a function

A function $f : \mathbb{A} \to \mathbb{B}$ is a mapping from the domain $\mathbb{A}$ to the codomain $\mathbb{B}$. For each $a \in \mathbb{A}$, $f(a) \in \mathbb{B}$. The set $f(\mathbb{A}) = \{f(a) | a \in \mathbb{A}\}$ is called the image of the function f. The dimension of the image is the dimension of the function (Durinx et al., 2008, Appendix E). The image is a subset of the codomain, $f(\mathbb{A}) \subset \mathbb{B}$, but is not necessarily equal to the whole codomain. A function for which $f(\mathbb{A}) = \mathbb{B}$ is called a surjection. The impact and sensitivity maps are typically not surjections.

The Jacobian matrix of a map is defined as

$$J_f(\hat{a}) = \left. \begin{pmatrix} \frac{\partial}{\partial a_1} f(a_1, \ldots, a_n) \\ \frac{\partial}{\partial a_2} f(a_1, \ldots, a_n) \\ \vdots \\ \frac{\partial}{\partial a_n} f(a_1, \ldots, a_n) \end{pmatrix}^{\mathrm{T}} \right|_{(a_1, \ldots, a_n) = \hat{a}} . \tag{5.1}$$

When $a \approx \hat{a}$, the linearization $f(a) \approx f(\hat{a}) + J_f(\hat{a})(a - \hat{a})$ is a good approximation of the function f, and furthermore, the rank of the matrix $J_f(\hat{a})$ gives the local dimension of the image, and thus also the local dimension of the function f (assuming that f is at least twice boundedly differentiable). This is less than or equal to the dimension of the domain $\mathbb{A}$. We find it useful to investigate the maximal local dimension of the image, and will call that the dimension of the map

$$\dim f = \max_{\hat{a} \in \mathbb{A}} \operatorname{rank}\, J_f(\hat{a}). \tag{5.2}$$

See Appendix B for various methods for determining the rank of a matrix.

Since the population-regulation map is a composite map of the impact map and the sensitivity map, it is often helpful to investigate both parts in order to find its dimension.

5.2 Impact dimension

The impact map $\mathcal{I} : \mathbb{C} \to \mathbb{E}$ describes how the present community determines the environment. However, it may be that not all points in the environment space $\mathbb{E}$ can be realized, and thus the image $\tilde{\mathbb{E}} = \mathcal{I}(\mathbb{C})$ is not necessarily the same as $\mathbb{E}$. Together with the dimension of the sensitivity map (fitness proxy), the impact dimension needs to be taken into account when determining the dimension of the population-regulation map.

Here we only consider unstructured models, so that the community state consists of the present k strategies together with their population sizes $N_i \in \mathbb{R}$. The impact vectors are defined as

$$I_i = \frac{\partial}{\partial N_i} \mathcal{I}(s_1, \ldots, s_k; N_1, \ldots, N_k). \tag{5.3}$$

ACCEPTED MANUSCRIPT

The dimension of the impact map is the maximal rank of its Jacobian matrix (5.2) over $\mathbb{C}$. The dimension of the regulation map is at most the dimension of the impact map.

5.3 Sensitivity dimension

To determine the coexistence condition, as well as the potential of a mutant strategy to invade, it is enough to know the sign of fitness. Therefore, one can investigate any fitness proxy. We define the sensitivity function as a fitness proxy function applied to k species,

$$r(s_1, \ldots, s_k; E) = (r(s_1, E), \ldots, r(s_k, E)). \tag{5.4}$$

The environment $E \in \mathbb{E}$ in (3.2) contains all the necessary information for the fitness calculation, but it may not be expressed in the most compact form. For chaotic dynamics, or for cyclic dynamics of continuous-time models, the environment space $\mathbb{E}$ would typically be infinite-dimensional. Here we assume that $\mathbb{E} \subset \mathbb{R}^n$, which is typical for equilibria, and for discrete-time models with cycles of length L (which can be interpreted as equilibria of an L-iterated map).

It may now be possible to write the fitness (proxy) in the form

$$r(s, E) = \hat{r}(s, g(E)) \text{ for all } s, \text{ where } g : \mathbb{R}^n \to \mathbb{R}^m, m < n, \tag{5.5}$$

which means that a lower-dimensional environmental variable suffices. In order to determine the sensitivity dimension, first note that the sensitivity vector (environmental gradient) of the fitness function for the species characterized by s is

$$S(s, E) = \nabla_E r(s, E) = \left(\frac{\partial}{\partial E_1}, \ldots, \frac{\partial}{\partial E_n}\right) r(s, E). \tag{5.6}$$

By collecting k sensitivity vectors into a matrix, we obtain the Jacobian matrix of (5.4), which is also called the sensitivity matrix,

$$\mathbf{S}(k, E) = (S(s_1, E), S(s_2, E), \ldots, S(s_k, E))^{\mathrm{T}}. \tag{5.7}$$

The global dimension (5.2) of the sensitivity map (5.4) is the maximal rank of the sensitivity matrix over all species combinations and environments,

$$\dim r = \max_{E \in \mathbb{E}, k \in \mathbb{N}, s_i \in \mathbb{S}, i=1,\ldots,k} \operatorname{rank} \mathbf{S}(k, E) \tag{5.8}$$

The latter rank is the same as the maximal number of linearly independent sensitivity vectors. This number is naturally less than or equal to n, which is the dimension of the environment vector E. It is therefore enough to check the rank of $S(k, E)$ for $k \leqslant n$. If n sensitivity vectors are in general linearly dependent, and thus $\det \mathbf{S}(n, E) = 0$, the environment is of lower dimension than n. It depends on the model how easy or difficult it is to write the fitness function using a lower-dimensional environmental variable. An example of such a procedure is presented in Parvinen and Dieckmann (2013). We thus have the following result

ACCEPTED MANUSCRIPT

- In case $\mathbb{E} \subset \mathbb{R}^n$, the environmental dimension is lower than n, if and only if the rank of a fitness proxy function $r(s_1, \dots, s_n; E) = (r(s_1, E), \dots, r(s_n, E))$ is lower than n for all $E \in \mathbb{E} \subset \mathbb{R}^n$ and $s_i \in \mathbb{S}$, $i = 1, \dots, n$.

It would be tempting to claim that the global rank of any fitness proxy function would directly give the effective dimension of the environment. However, different fitness proxies can have different global ranks (J.A.J. Metz, personal communication). To demonstrate this fact, in section 6 we present a model for which the global rank of the fitness function r is 2, but the rank of a fitness proxy, the basic reproduction ratio R, is 1.

In the example above, the analysis of the rank of the fitness function r does not seem to indicate that the environment is effectively of a lower dimension. However, one should note that it is only the sign of the fitness function that matters, which brings us to the following conclusions for this subsection:

- The effective dimension (Metz et al., 2008) of the sensitivity map for given strategies $s_1, \dots, s_k$ is the lowest possible global rank of a fitness proxy function $\hat{r}(s_1, \dots, s_k; E)$, $E \in \mathbb{E}$.

- Another method to determine the effective dimension is to restrict attention to the set $\mathbb{E}_0 = \{E \,|\, r(s_1, E) = r(s_2, E) = \cdots = r(s_n, E) = 0\}$ and determine the rank of one, freely chosen fitness proxy function $\hat{r}(s_1, E)$, $\hat{r}(s_2, E), \dots, \hat{r}(s_n, E)$, $E \in \mathbb{E}_0$.

- This rank is given by the number of linearly independent sensitivity vectors. This number is independent of the choice of fitness proxy, because sensitivity vectors at $r = 0$ are perpendicular to the tangent plane of the zero-contour surface, and the zero-contour surface is by definition independent of the choice of fitness proxy.

- The dimension of the regulation map is at most the dimension of the sensitivity map.

A procedure for checking whether the effective dimension of the feedback loop is one dimensional, directly related to the above considerations, can be found in Appendix A of Dieckmann and Metz (2006).

5.4 Regulation dimension

So far we have investigated the impact map and the sensitivity map (for fitness proxies). The impact map is a map from the community state space $\mathbb{C}$ to the environmental space $\mathbb{E}$, and it captures how the present populations affect the environmental variables. For a given strategy, the fitness (proxy) is a map from the environmental space $\mathbb{E}$ to the set of real numbers $\mathbb{R}$, and it describes how a rare population with this strategy grows in the present environment. The population-regulation map is the composite map of the impact and sensitivity maps (Fig. 1). More precisely, for a given set of strategies, $(s_1, \dots, s_k)$,

$$f : \mathbb{R}^k \to \mathbb{R}^k, \quad f_i(N_1, \dots, N_k) = r(s_i, \mathcal{I}(s_1, \dots, s_k; N_1, \dots, N_k)). \tag{5.9}$$

ACCEPTED MANUSCRIPT

Robust coexistence of given k strategies is only possible if the dimension of f is k. Because f is a composite map, its dimension is at most the dimension of the impact map, and at most the dimension of the sensitivity map. For each, the dimension is at most n, the dimension of environmental space $\mathbb{E}$, and thus it is only meaningful to study values $k \leqslant n$. In general, the effective regulation dimension is lower than n (dimension reduction) if either not all items in the environmental space can be realized, or not all components of the environment variable affect fitness independently.

The function $f : \mathbb{R}^k \to \mathbb{R}^k$ is k-dimensional if and only if $\det(\mathbf{A}_k) \neq 0$, where the matrix

$$\mathbf{A}_k = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1k} \\ a_{21} & a_{22} & \cdots & a_{2k} \\ \vdots & \vdots & \ddots & \vdots \\ a_{k1} & a_{k2} & \cdots & a_{kk} \end{pmatrix}, \quad a_{ij} = S_i \cdot I_j \tag{5.10}$$

is the product of two matrices consisting of impact vectors (5.3) and sensitivity vectors (5.6). In vector form this is

$$\mathbf{A}_k = \mathbf{S}^{\mathrm{T}}\mathbf{I} = \begin{pmatrix} S_1, & S_2, & \ldots, & S_k \end{pmatrix}^{\mathrm{T}} \begin{pmatrix} I_1, & I_2, & \ldots, & I_k \end{pmatrix}. \tag{5.11}$$

The vectors I_j and S_i have dimension n, and there are k each of them. Therefore, the matrices $\mathbf{I}$ and $\mathbf{S}$ are not necessarily square matrices.

For $k = n$, the matrices $\mathbf{I}$ and $\mathbf{S}$ are square matrices, and the function $f : \mathbb{R}^n \to \mathbb{R}^n$ is n-dimensional if and only if

$$\det(A_n) = \det(\mathbf{S}^{\mathrm{T}}\mathbf{I}) = \det(\mathbf{S})\det(\mathbf{I}) \neq 0, \tag{5.12}$$

which means that both the impact map and the sensitivity map have dimension n. For $k < n$, such a result holds only in one direction. The dimension of the composite map may be the same as the lower of the dimensions of the impact and the sensitivity maps, but it is also possible that the dimension is further reduced. This occurs if the image of the impact map has higher-than-zero-dimensional intersection with the nullspace of the fitness function. Next, we will investigate such situations for $n = 3$.

5.5 Example of dimension reduction

Consider a situation in which $\mathbb{E}$ is three-dimensional, but both the impact map and the sensitivity map are (at most) two-dimensional. This means that one of the components of the impact vector is a linear combination of the others, say $I_1(s) = cI_2(s) + dI_3(s)$ for all s. The same holds for the sensitivity vectors for some other component, say $S_3(s) = aS_1(s) + bS_2(s)$. Both $\det(\mathbf{S}_3) = \det(\mathbf{I}_3) = 0$, so that $\det(\mathbf{A}_3) = 0$, and the dimension of the composite map is obviously less than 3. But is it 1 or 2? For answering this question, we consider

$$\det(\mathbf{A}_2) = (bc - a - d) \begin{vmatrix} I_2(s_1) & I_3(s_1) \\ I_2(s_2) & I_3(s_2) \end{vmatrix} \begin{vmatrix} S_1(s_1) & S_2(s_1) \\ S_1(s_2) & S_2(s_2) \end{vmatrix}. \tag{5.13}$$

ACCEPTED MANUSCRIPT

The $\det(\mathbf{A}_2) = 0$ if either of the determinants on the right-hand side are equal to 0, but this means that either the impact map or the sensitivity map is only one-dimensional. However, it is also true that $\det(\mathbf{A}_2) = 0$ if $bc - a - d = 0$. In that case, the regulation dimension is 1, although both impact and sensitivity maps are two-dimensional. If the parameters a, b, c, and d could be chosen freely and independently, the probability of choosing values such that $bc - a - d = 0$ is 0. However, these values depend on the properties of the model under investigation, and it may very well be that in some models $bc - a - d = 0$ generally holds. A trivial example is $a = b = c = d = 0$, which means that one component of the environmental variable, E_1, is such that it is not affected by the populations, but it affects the growth of populations (such as average annual rainfall), and another component, E_3, is affected by the populations, but it does not affect the growth of the populations (such as water quality downstream from the habitat of the populations), and thus E_2 completely suffices to describe the environment.

Next consider the case in which it is the third component that is a linear combination of the others for both impact and sensitivity: $I_3(s) = cI_1(s) + dI_2(s)$ and $S_3(s) = aS_1(s) + bS_2(s)$. In this case,

$$\det(\mathbf{A}_2) = (1 + ac + bd) \begin{vmatrix} I_1(s_1) & I_2(s_1) \\ I_1(s_2) & I_2(s_2) \end{vmatrix} \begin{vmatrix} S_1(s_1) & S_2(s_1) \\ S_1(s_2) & S_2(s_2) \end{vmatrix}. \tag{5.14}$$

Again, $\det(\mathbf{A}_2) = 0$ if either of the determinants on the right-hand side is 0, so that either the impact map or the sensitivity map is one-dimensional. For two-dimensional impact and sensitivity maps, a further dimension reduction happens if $1 + ac + bd = 0$. A simple example of such a case is $r(s, E) = z(E_1) + E_2 - E_3$, so that $a = 0$ and $b = -1$, but actually $E_2 = E_3$, so that $c = 0$ and $d = 1$. Investigating the impact and sensitivity maps separately, they appear two-dimensional, but with the knowledge $E_2 = E_3$, we observe that fitness depends only on E_1, so regulation is one-dimensional. This example may seem trivial, but in complex models this kind of phenomena may be difficult to detect without proper analysis.

6 Example of fitness proxies with different global ranks

Consider a species which harvests a resource with density Z_1. The strategy s of an individual determines the effective harvesting rate $f(s)$. Assume that the per capita birth rate of an individual with a harvesting strategy s is $f(s)\beta(Z_1)$, where β is an increasing function of Z_1. Harvesting exposes the species to predation so that the per capita death rate of an individual with a harvesting strategy s is $g(s)\mu(Z_2)$, where μ is an increasing function of the predator population density Z_2. We assume that the functions f and g are not linearly dependent. The density of individuals with strategy s_i changes according to

$$\frac{\mathrm{d}}{\mathrm{d}t} N_i = (f(s_i)\beta(Z_1) - g(s_i)\mu(Z_2))N_i. \tag{6.1}$$

Furthermore, assume that the resource population grows according to

ACCEPTED MANUSCRIPT

$$\frac{\mathrm{d}}{\mathrm{d}t}Z_1 = \alpha_1 - \left(\delta_1 + \sum_{i=1}^{k} f(s_i)N_i\right) Z_1, \tag{6.2}$$

so that new resource is added to the system with rate α_1, and the natural decay rate of the resource is δ_1. The predator population density is assumed to grow according to

$$\frac{\mathrm{d}}{\mathrm{d}t}Z_2 = \left(\alpha_2 + \sum_{i=1}^{k} g(s_i)N_i\right) Z_2 \left(1 - \frac{Z_2}{K}\right) - \delta_2 Z_2. \tag{6.3}$$

Predators also have resources other than the focal species, so that their birth rate is positive even in the absence of it. Predator birth is only possible into empty sites, which are found with the probability $(1 - Z_2/K)$. Finally, predator death rate is δ_2. Assume also that resource and predator dynamics occur on a fast timescale, so that they are always at equilibrium, denoted by E_1 and E_2. Therefore we obtain the impact map (assuming $\alpha_2 > \delta_2$)

$$\begin{aligned}&\mathcal{I}(s_1, \ldots, s_k, N_1, \ldots, N_k)\\ &\quad= \left(\underbrace{\frac{\alpha_1}{\delta_1 + \sum_{i=1}^{k} f(s_i)N_i}}_{E_1}, \underbrace{K\left(1 - \frac{\delta_2}{\alpha_2 + \sum_{i=1}^{k} g(s_i)N_i}\right)}_{E_2}\right).\end{aligned} \tag{6.4}$$

6.1 Fitness has global dimension 2

According to (6.1), the fitness of a rare invader with strategy s is

$$r(s, E) = f(s)\beta(E_1) - g(s)\mu(E_2). \tag{6.5}$$

The sensitivity vectors (5.6) are

$$S_i = \nabla_E r(s_i, E) = \left(f(s_i)\beta'(E_1), -g(s_i)\mu'(E_2)\right). \tag{6.6}$$

The determinant of the sensitivity matrix for two species is

$$\begin{aligned}\det(\mathbf{S}_2) &= \begin{vmatrix} f(s_1)\beta'(E_1) & -g(s_1)\mu'(E_2) \\ f(s_2)\beta'(E_1) & -g(s_2)\mu'(E_2) \end{vmatrix}\\ &= \left[f(s_2)g(s_1) - f(s_1)g(s_2)\right]\beta'(E_1)\mu'(E_2),\end{aligned} \tag{6.7}$$

which is generally non-zero, unless the functions f and g are linearly dependent. The global rank of the sensitivity map (based on fitness) is thus 2.

6.2 Basic reproduction ratio has global dimension 1

The basic reproduction ratio is the expected number of offspring per individual during its lifetime. In a constant environment, an individual with strategy s has death rate $g(s)\mu(E_2)$, and thus its expected lifetime is $1/[g(s)\mu(E_2)]$. During its lifetime the individual will produce offspring with the rate $f(s)\beta(E_1)$, and thus we get

$$R(s, E) = \frac{f(s)}{g(s)} \cdot \frac{\beta(E_1)}{\mu(E_2)}. \tag{6.8}$$

Obviously, $R(s, E) > 1$ if and only if $r(s, E) > 0$, and therefore $R(s, E)$ is a fitness proxy. The expression $\beta(E_1)/\mu(E_2)$ clearly acts as a one-dimensional environment. The sensitivity vectors are

$$S_i = \nabla_E r(s_i, E) = \frac{f(s)}{g(s)\mu(E_2)} \cdot \left(\beta'(E_1), -\frac{\beta(E_1)}{\mu(E_2)}\mu'(E_2)\right). \tag{6.9}$$

For different strategies s these vectors are the same except for the multiplier $f(s)/[g(s)\mu(E_2)]$ in front, which means that they are linearly dependent. This also shows that the global rank of R is 1.

6.3 Sensitivity dimension

Instead of investigating the determinant (6.7) for all E, we should concentrate on the E, for which $r(s_i, E) = 0$. This results in $g(s_i) = f(s_i)\beta(E_1)/\mu(E_2)$, so that (6.7) becomes $\det(\mathbf{S}_2) = 0$. Furthermore, the sensitivity vectors (6.6) become

$$S_i = \nabla_E r(s_i, E) = f(s_i) \left(\beta'(E_1), -\frac{\beta(E_1)}{\mu(E_2)}\mu'(E_2)\right), \tag{6.10}$$

and they are all linearly dependent, which also shows that the rank of the function r is 1 in the subset of the environmental space satisfying the equilibrium condition. Note also that the vectors in equations (6.9) and (6.10) have the same direction.

6.4 Impact dimension

When strategies $s_1, \ldots, s_k$ with population densities N_1, …, N_k are present, the impact vector of the population with strategy s_i is

$$I_i = \left(-\frac{\alpha_1}{\left(\delta_1 + \sum_{j=1}^{k} f(s_j)N_j\right)^2} f(s_i),\ K\frac{\delta_2}{\left(\alpha_2 + \sum_{j=1}^{k} g(s_j)N_j\right)^2} g(s_i) \right). \tag{6.11}$$

The impact determinant with two strategies is

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

$$\det(\mathbf{I}_2) = -\frac{\alpha_1}{\left(\delta_1 + \sum_{j=1}^{k} f(s_j)N_j\right)^2} K \frac{\delta_2}{\left(\alpha_2 + \sum_{j=1}^{k} g(s_j)N_j\right)^2} \begin{vmatrix} f(s_1) & g(s_1) \\ f(s_2) & g(s_2) \end{vmatrix} \neq 0, \tag{6.12}$$

unless the functions f and g are linearly dependent, which is assumed not to be the case. The impact dimension thus equals two.

6.5 Regulation dimension

Although the impact dimension is 2, the regulation dimension cannot be higher than the sensitivity dimension, 1. In conclusion, one strategy at most can be present in a population-dynamical equilibrium, and it is the strategy with largest $f(s)/g(s)$ that wins the competition.

7 Example of a consumer-resource model

Now consider a model with multiple resources Z_j, which grow according to the differential equation $\mathrm{d}Z_j/\mathrm{d}t = f_j(Z_j)$ in the absence of consumers. Consumers deplete resources with a linear functional response, so that in the presence of consumers, the resources grow according to

$$\frac{\mathrm{d}}{\mathrm{d}t} Z_j = f_j(Z_j) - Z_j \sum_i \beta_j(s_i) N_i. \tag{7.1}$$

Resource dynamics is assumed to occur on a fast timescale, so that they are always at equilibrium, denoted by E_j, satisfying

$$f_j(E_j) - E_j \sum_i \beta_j(s_i) N_i = 0. \tag{7.2}$$

Consumed resources are turned into consumer biomass with an efficiency that may depend on the consumer strategy (some consumption may be wasteful, see (Leimar et al., 2013)). In addition, the death rate μ may depend on the strategy. Therefore, consumer populations grow according to

$$\frac{\mathrm{d}}{\mathrm{d}t} N_i = \gamma N_i \sum_j \alpha_j(s_i) E_j - \mu(s_i) N_i. \tag{7.3}$$

The consumers affect each other only via the resources. Note that in standard resource-consumer models one would typically have $\alpha_j(s) = \beta_j(s)$.

7.1 Fitness, sensitivity, and impact

Based on (7.3), the fitness of a rare invader with strategy s is

$$r(s, E) = \gamma \sum_j \alpha_j(s) E_j - \mu(s), \tag{7.4}$$

provided that the resident system is at an equilibrium. The sensitivity vectors (5.6) are obtained by differentiation,

$$S_i = \nabla_E r(s_i, E) = \gamma \left(\alpha_1(s_i), \ldots, \alpha_n(s_i)\right). \tag{7.5}$$

At an equilibrium, we have $\mathrm{d}E_j/\mathrm{d}t = 0$. By applying the implicit function theorem on (7.2) we obtain the impact vector

$$\begin{aligned} I_i &= \left(\frac{-\beta_1(s_i)E_1}{f_1'(E_1) - \sum_i \beta_1(s_i)N_1}, \ldots, \frac{-\beta_n(s_i)E_n}{f_n'(E_n) - \sum_i \beta_n(s_i)N_n} \right) \\ &= \left(-\beta_1(s_i)z_1, \ldots, -\beta_n(s_i)z_n\right), \end{aligned} \tag{7.6}$$

where $z_j = -E_j / \left[f_j'(E_j) - \sum_i \beta_j(s_i)N_i\right] = -E_j / \left[f_j'(E_j) - f_j(E_j)/E_j\right]$. The latter equality follows from the equilibrium condition. In a stable positive equilibrium we have $z_j > 0$. This means that the impact vectors are linearly independent if and only if the vectors $(\beta_1(s_i), \ldots, \beta_n(s_i))$ are. Extinct resources ($E_j = 0$) obviously do not contribute to the dimension of the environment. Next we use the resource-consumer model to illustrate the dimensions of the impact and the sensitivity map, and their effect on the dimension of population regulation in the case of three resources with growth functions $f_j(E_j) = j - E_j$, $j = 1, 2, 3$.

7.2 Three-dimensional impact and sensitivity resulting in three-dimensional regulation

A choice of functions that easily results in coexistence of three strategies is

$$\alpha_i(s) = \exp\left(-\frac{(s-a_i)^2}{\sigma_\mathrm{a}}\right), \quad \beta_i(s) = \exp\left(-\frac{(s-a_i)^2}{\sigma_\mathrm{b}}\right), \quad \mu(s) = \mu, \tag{7.7}$$

provided that the strategies resulting in maximal resource use (a_1, a_2, and a_3) are sufficiently different, and the parameters σ_a and σ_b are small enough. By choosing $s_i = a_i$ we would even obtain evolutionarily uninvadable coexistence of three strategies.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

7.3 Two-dimensional impact and/or sensitivity resulting in two-dimensional regulation

The impact map will have a dimension lower than 3, if the functions β_i are assumed to be linearly dependent. This occurs, for example, if we assume (7.7) to hold except for $\beta_2(s) = (\beta_1(s) + \beta_3(s))/2$. Now the determinant of the impact matrix for three strategies is

$$\det(\mathbf{I}_3) = -z_1 z_2 z_3 \begin{vmatrix} \beta_1(s_1) & \frac{1}{2}(\beta_1(s_1) + \beta_3(s_1)) & \beta_3(s_1) \\ \beta_1(s_2) & \frac{1}{2}(\beta_1(s_2) + \beta_3(s_2)) & \beta_3(s_2) \\ \beta_1(s_3) & \frac{1}{2}(\beta_1(s_3) + \beta_3(s_3)) & \beta_3(s_3) \end{vmatrix} = 0, \tag{7.8}$$

so that the impact dimension is indeed less than 3. Two impact vectors, $(-\beta_1(s_1)z_1,\ -(\frac{1}{2}(\beta_1(s_1)+\beta_3(s_1))z_2,\ -\beta_3(s_1)z_3)$ and $(-\beta_1(s_2)z_1,\ -(\frac{1}{2}(\beta_1(s_2)+\beta_3(s_2))z_2,\ -\beta_3(s_2)z_3)$, are linearly independent, if

$$\begin{vmatrix} \beta_1(s_1) & \beta_3(s_1) \\ \beta_1(s_2) & \beta_3(s_2) \end{vmatrix} \neq 0, \tag{7.9}$$

which is guaranteed by (7.7) when $s_1 \neq s_2$. Therefore the impact dimension is equal to two. As in the previous subsection, (7.7) holds for α_i, and the sensitivity map is three-dimensional. Overall, the population-regulation map is two-dimensional.

Analogously, the sensitivity map will have a dimension lower than 3, if the functions α_i are assumed to be linearly dependent. We can, for example, assume that (7.7) holds except for $\alpha_2(s) = (\alpha_1(s) + \alpha_3(s))/2$, so that

$$\det(\mathbf{S}_3) = \begin{vmatrix} \alpha_1(s_1) & \frac{1}{2}(\alpha_1(s_1) + \alpha_3(s_1)) & \alpha_3(s_1) \\ \alpha_1(s_2) & \frac{1}{2}(\alpha_1(s_2) + \alpha_3(s_2)) & \alpha_3(s_2) \\ \alpha_1(s_3) & \frac{1}{2}(\alpha_1(s_{31}) + \alpha_3(s_{13})) & \alpha_3(s_3) \end{vmatrix} = 0. \tag{7.10}$$

Two sensitivity vectors, $(\alpha_1(s_1),\ \frac{1}{2}(\alpha_1(s_1)+\alpha_3(s_1)),\ \alpha_3(s_1))$ and $(\alpha_1(s_2),\ \frac{1}{2}(\alpha_1(s_2)+\alpha_3(s_2)),\ \alpha_3(s_2))$, are linearly independent, provided that

$$\begin{vmatrix} \alpha_1(s_1) & \alpha_3(s_1) \\ \alpha_1(s_2) & \alpha_3(s_2) \end{vmatrix} \neq 0, \tag{7.11}$$

which under the current assumptions holds for $s_1 \neq s_2$. The impact map with (7.7) remains three-dimensional. Also in this case the dimension of population regulation is two, and at most two strategies can coexist.

Let us next assume that (7.7) holds except for $\beta_2(s) = (\beta_1(s) + \beta_3(s))/2$ and $\alpha_2(s) = (\alpha_1(s) + \alpha_3(s))/2$, so that both (7.8) and (7.10) hold. As we have already concluded, both impact and sensitivity maps are then two-dimensional. Now

$$\det(\mathbf{A}_2) = -\frac{1}{4}(z_2 z_3 + z_1 z_2 + 4 z_1 z_3) \begin{vmatrix} \alpha_1(s_1) & \alpha_3(s_1) \\ \alpha_1(s_2) & \alpha_3(s_2) \end{vmatrix} \begin{vmatrix} \beta_1(s_1) & \beta_3(s_1) \\ \beta_1(s_2) & \beta_3(s_2) \end{vmatrix} \neq 0, \tag{7.12}$$

unless at least two resources are extinct. Note that both determinants in (7.12) are non-zero for $s_1 \neq s_2$, and thus the population regulation is two-dimensional.

7.4 Two-dimensional impact and sensitivity resulting in one-dimensional regulation

The two-dimensional impact map together with a two-dimensional sensitivity map does not always result in two-dimensional population regulation. Further dimension reduction occurs if the image of the impact map has higher-than-zero-dimensional intersection with the nullspace of the fitness function. Consider a special case, in which

$$\begin{aligned} \alpha_1(s) &= 0.1, \quad \beta_1(s) = 0, \\ \alpha_2(s) = \beta_2(s) &= \exp\left(-\frac{(s-a_2)^2}{2\sigma_{\mathrm{a}}}\right), \\ \alpha_3(s) &= 0, \quad \beta_3(s) = 0.3. \end{aligned} \tag{7.13}$$

This means that the environmental variable E_1 is not affected by the consumers, but it does affect the growth of consumers (like annual rainfall). The environmental variable E_3 is affected by the consumers, but does not affect the growth of the consumers. Since both matrices $\mathbf{I}_3$ and $\mathbf{S}_3$ contain a column of zeros, their determinants are 0, and the impact and sensitivity maps are of dimension lower than three. For $s_1 \neq s_2$, the impact vectors $(0, -\beta_2(s_1)z_2, -0.3z_3)$ and $(0, -\beta_2(s_2)z_2, -0.3z_3)$ are linearly independent ($z_2 > 0$,$z_3 > 0$), so the impact map is two-dimensional. Analogously, the sensitivity vectors $(0.1, \alpha_2(s_1), 0)$ and $(0.1, \alpha_2(s_2), 0)$ are linearly independent for $s_1 \neq s_2$, and thus the sensitivity map is two-dimensional. Since

$$\mathbf{A}_2 = \begin{pmatrix} -\beta_2(s_1)z_2\alpha_2(s_1) & -\beta_2(s_1)z_2\alpha_2(s_2) \\ -\beta_2(s_2)z_2\alpha_2(s_1) & -\beta_2(s_2)z_2\alpha_2(s_2) \end{pmatrix} \text{ and } \det(\mathbf{A}_2) = 0, \tag{7.14}$$

population regulation is one-dimensional, and only one strategy may persist at a time.

8 Extensions

In section 2 we assumed that all population-dynamical attractors are equilibria, populations are unstructured, and that there is no explicit dynamics of resources or other species on the same time-scale as the dynamics of the focal species. Next we discuss the relaxing of each of these assumptions in turn.

8.1 Non-equilibrium attractors

When analyzing the potential for species coexistence in a specific model, one typically first tries to find population-dynamical equilibria and study their population-dynamical stability. Non-equilibrium attractors are more difficult to find and analyze, but are nevertheless common in models. Next we study which parts of the theory investigated in this article can be extended to non-equilibrium attractors.

ACCEPTED MANUSCRIPT

Fitness (3.2) is the long-term exponential growth rate $r(s, E)$ of a rare invader with strategy s in the environment E (Metz et al., 1992). In (3.2), $N(s, T, N_0|E)$ is the population state of a species with strategy s at time T under the assumption that its population state at time 0 was N_0. In order to determine $N(s, T, N_0|E)$, one needs to know the instantaneous environment $E(t)$ from time 0 to T. In order to determine the limit (3.2), one needs to know the instantaneous environment $E(t)$ for all $t \geqslant 0$. Such an infinite-dimensional object does not provide a useful upper bound for species coexistence, except in the following special cases, in which we assume that each $E(t) \in \mathbb{R}^n$:

- As already discussed before, if the community-dynamical attractor of the resident is an equilibrium, $E(t)$ does not depend on time t, so that the environment is n-dimensional.
- If the model is defined in discrete time, and the community-dynamical attractor is a cycle of finite length T, (3.2) becomes

  $$r(s, E) = \frac{1}{T} \ln \frac{\|N(T, N_0|E)\|}{\|N_0\|}. \tag{8.1}$$

  The environment E consists of vectors $E(0), E(1), \ldots, E(T-1)$, where each $E(t) \in \mathbb{R}^n$. Altogether $n \cdot T$ variables are needed, and thus the environment is finite-dimensional. These variables naturally form a matrix, and with a suitable indexing, they can be formulated as a vector $\hat{E} \in \mathbb{R}^{nT}$. Using such a vector formulation, sensitivity dimension of (8.1) can be analyzed using methods presented in section 5.3. Analyzing impact dimension is also straightforward.
- Even for a complex community-dynamical attractor, the environment can in some cases be expressed with a finite variable. For example, this may be the case, if fitness is a function of average resource densities, or some other time-averages over the community-dynamical attractor. For an example of such a model, see Parvinen and Dieckmann (2013). Analyzing sensitivity dimension becomes then straightforward. It may, however, be difficult to define the impact map for such models.

8.2 Structured populations

In section 2, the population dynamics (2.1) and (2.2) was defined for unstructured populations, so that N_i is the population density (a scalar) of species i. For structured population models, in which individuals differ in their developmental stage, or for metapopulation models describing populations in different habitat patches, a single density does not suffice to fully describe the state of a population. In complex models, the population state can be a complicated object. Consider a structured model, for which (2.1) and (2.2) apply, and the population state for species i is a finite-dimensional real vector $N_i \in \mathbb{R}^u$. For such models, $f(s_i, E)$ is a u-dimensional square matrix. At equilibrium, $f(s_i, E)N_i = 0$, so that the dominant eigenvalue of the matrix $f(s_i, E)$ must be 0 for each i. For discrete-time models, $F(s_i, E)N_i = N_i$, so

ACCEPTED MANUSCRIPT

that the dominant eigenvalue of the matrix $F(s_i, E)$ must be one for each i. The dominant eigenvalue is the fitness, when the population-dynamical attractor is an equilibrium, so that the dimension of the sensitivity map can be determined using methods presented in section 5.3.

The impact map for structured models is more complicated than for unstructured models. It is not enough just to know the total population size of each species. The population's structural composition necessarily affects the environmental variable E, but since each N_i is an eigenvector corresponding to the dominant eigenvalue of $f(s_i, E)$ (or $F(s_i, E)$), the environmental variable E affects the population's structural composition. Therefore analyzing the impact dimension is more complicated than for unstructured models, and is an interesting topic for future research.

8.3 Complex environments

Real ecosystems form complex food-webs. For simplicity, one often restricts attention to a small set of species, the focal species. Population dynamics of other species can be assumed to be so slow that their population densities remain constant, or so fast that their population densities are always at equilibrium set by the focal species. There is thus time-scale separation between the population dynamics of focal species and other species, and the population densities of the focal species fully determine the environment, so that population dynamics of the focal species can be formulated as in (2.1) and (2.2). These formulations do not apply, when there are other species present with dynamics in the same time-scale as the focal species. If such species are present, population models defined in continuous time can be of type

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} N_i(t) &= h_i(N_1(t), \ldots, N_k(t), Z_1(t), \ldots, Z_p(t)), \\ \frac{\mathrm{d}}{\mathrm{d}t} Z_j(t) &= \hat{h}_j(N_1(t), \ldots, N_k(t), Z_1(t), \ldots, Z_p(t)). \end{aligned} \tag{8.2a}$$

An analogous formulation in discrete time is

$$\begin{aligned} N_i(t+1) &= H_i(N_1(t), \ldots, N_k(t), Z_1(t), \ldots, Z_p(t)), \\ Z_j(t+1) &= \hat{H}_j(N_1(t), \ldots, N_k(t), Z_1(t), \ldots, Z_p(t)), \end{aligned} \tag{8.2b}$$

where, for unstructured populations, N_i is the population density (a scalar) of focal species i, and the scalars Z_j are population densities of other species or resources.

For finding equilibria when $p > 0$, it is not enough that just the population densities N_i of the focal species are constant. In addition, the densities Z_j need to remain constant. Assuming that N_i are constant, we can often solve for the equilibria of Z from (8.2). If for each population state $(N_1, \ldots, N_k)$ a unique (stable) equilibrium $(Z_1, \ldots, Z_p)$ exists, the equilibrium condition can be formulated as $f(s_i, E) = 0$ (or $F(s_i, E) = 1$) for all $i = 1, \ldots, k$ together with $E = \mathcal{I}(s_1, \ldots, s_k, N_1, \ldots, N_k)$, where the impact map is now defined such that

ACCEPTED MANUSCRIPT

the densities Z_j are assumed to be at the equilibrium. The same formulation applies, if instead of one equilibrium, there are several (finitely many) equilibria, as long as we separately specify in which branch of solutions of the equilibrium Z resides. Impact dimension and sensitivity dimension can then be analyzed as described in sections 5.2 and 5.3

9 Discussion

In this article, we have investigated the dimension of population regulation in order to better understand the potential for species coexistence. The decomposition of the population-regulation map into the impact and sensitivity maps is essential in our analysis (Metz and Diekmann, 1986; Metz et al., 1988; Metz and de Roos, 1992; Meszéna et al., 2006). The former describes how a community affects its environment (regulating variables), and the latter how population growth depends on the regulating variables. In such a formulation, the number of regulating variables gives an upper bound for the number of coexisting species.

We have also investigated methods for analyzing the dimensions of the impact map, the sensitivity map, and their composite map, i.e., the regulation map. Because the sensitivity map is obtained by applying any fitness proxy to a given number of species, the sensitivity dimension must not depend on the choice of the proxy. We have demonstrated that the global ranks of two different fitness proxies (for the same model) can be different. It is therefore critical to restrict attention to the neutral contour, which is a subset of the environmental space in which fitness is 0. The local rank of any fitness proxy on the neutral contour is independent of the choice of the fitness proxy, and this is the proper way to define the sensitivity dimension. Furthermore, we have demonstrated how the regulation dimension is reduced either because of dimension reduction in the impact map (not all parts of the environmental space can be realized), or in the sensitivity map (the sign of fitness does not depend on all subspaces of the environmental space), or from their combined effect (the image of the impact map has higher-than-zero-dimensional intersection with the nullspace of the fitness function).

Our work is related to the vast literature on the competitive exclusion principle (e.g., Hardin, 1960; Levin, 1970; Roughgarden, 1976), and the environmental feedback loop (Metz and Diekmann, 1986; Metz et al., 1988; Metz and de Roos, 1992). Meszéna et al. (2006) also found it useful to decompose the regulation map into impact and sensitivity maps, and their work is especially relevant here. See also Barabás and Meszéna (2009) and Barabás et al. (2014). Their main focus was on robustness – a measure describing the potential for coexistence when the regulation dimension is known. Our emphasis here has been on determining the regulation dimension.

We have concentrated on analyzing the dimension of population regulation in order to determine the potential for coexistence. As already mentioned, that dimension gives an upper bound for the number of coexisting species. However, the following requirements may additionally hinder the coexistence of species. First, the dimension of the population-regulation cycle does not guarantee the existence of an equilibrium with as many strategies with posi-

ACCEPTED MANUSCRIPT

tive population densities (feasibility). Second, for long-term coexistence, it is necessary that the equilibrium is stable in the population-dynamical sense (stability). Third, the domain of attraction of the coexistence equilibrium in the population state space may be small (attainability). Fourth, the ecological equilibrium may not be stable against mutant invasions, so that the number of species in an evolutionarily stable strategy coalition is lower than the dimension of the population-regulation cycle (evolutionary stability).

In this article, we have concentrated on models of unstructured populations, and mainly investigated equilibrium dynamics. For discrete-time models with finite cycles of population dynamics, the methods used here can be applied to the iterated map. For chaotic dynamics and cyclic population-dynamical attractors in continuous-time models, the environmental space needed to determine the sign of fitness may easily be infinite-dimensional. In some cases (e.g., Parvinen and Dieckmann, 2013) a finite-dimensional object (or even a one-dimensional one, resulting in optimizing selection) may suffice, despite complex population dynamics. Analyzing the impact dimension may be complicated, but methods for analyzing the sensitivity dimension can nevertheless be applied in such cases. For models of structured populations (Durinx et al., 2008; Szilágyi and Meszéna, 2009), the same consideration applies. When the sign of fitness – which can be given, e.g., by the dominant eigenvalue of a matrix (such as the next-generation matrix in the notation of Durinx et al. (2008)) – depends on a finite-dimensional environmental variable, the sensitivity dimension can be analyzed as before. For the impact map, however, it is not enough just to know the total population size of each species; we also need to understand the population's structural composition, so analyzing the impact dimension is more complicated. Furthering understanding of the impact dimension in both cases mentioned above is an interesting challenge for future research.

To conclude, we have investigated the dimension of the impact map, the sensitivity map, and the regulation map in order to understand the potential for species coexistence. Although we have concentrated on models of unstructured populations at equilibrium, many of the methods are applicable more widely, for more complex population-dynamical attractors and for models of structured populations. We hope these methods will help other researchers in understanding biodiversity.

Acknowledgements

The authors wish to thank Hans Metz for numerous discussions throughout our careers, and for many detailed comments about this work.

References

Barabás, G. and G. Meszéna (2009). When the exception becomes the rule: the disappearance of limiting similarity in the Lotka-Volterra model. *J. Theor. Biol 258*, 89–94.

Barabás, G., L. Pásztor, G. Meszéna, and A. Ostling (2014). Sensitivity analysis of coexistence in ecological communities: theory and application. *Ecol. lett. 17*, 1479–1494.

ACCEPTED MANUSCRIPT

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* John Murray, London, U.K.

Dieckmann, U. and J. A. J. Metz (2006). Surprising evolutionary predictions from enhanced ecological realism. *Theor. Popul. Biol. 69*, 263–281.

Diekmann, O. and J. A. P. Heesterbeek (2000). *Mathematical Epidemiology of Infectious Diseases: Model Building, Analysis and Interpretation.* Wiley-Blackwell.

Diekmann, O., J. A. P. Heesterbeek, and J. A. J. Metz (1990). On the definition and the computation of the basic reproduction ratio R_0 in models for infectious-diseases in heterogeneous populations. *J. Math. Biol. 28*, 365–382.

Durinx, M., J. A. J. Metz, and G. Meszéna (2008). Adaptive dynamics for physiologically structured population models. *J. Math. Biol. 56*, 673–742.

Gyllenberg, M. and J. A. J. Metz (2001). On fitness in structured metapopulations. *J. Math. Biol. 43*, 545–560.

Hardin, G. (1960). Competitive exclusion principle. *Science 131*, 1292–1297.

Heesterbeek, J. A. P. (1992). R_0. Ph. D. thesis, University of Leiden, The Netherlands.

Heino, M., J. A. J. Metz, and V. Kaitala (1997). Evolution of mixed maturation strategies in semelparous life histories: the crucial role of dimensionality of feedback environment. *Trans Roy Soc London B 352*, 1647–1655.

Huisman, J. and F. J. Weissing (1999). Biodiversity of plankton by species oscillations and chaos. *Nature 402*, 407–410.

Hutchinson, G. E. (1961). The paradox of the plankton. *Am. Nat. 95*, 137–145.

Leimar, O., A. Sasaki, M. Doebeli, and U. Dieckmann (2013). Limiting similarity, species packing, and the shape of competition kernels. *J. Theor. Biol 339*, 3–13.

Levin, S. A. (1970). Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat. 104*, 413–423.

Lundberg, P., E. Ranta, V. Kaitala, and N. Jonzen (2000). Coexistence and resource competition. *Nature 407*, 694.

Meszéna, G., M. Gyllenberg, L. Pásztor, and J. A. J. Metz (2006). Competitive exclusion and limiting similarity: a unified theory. *Theor. Popul. Biol 69*, 68–87.

Metz, J. A. J. and A. M. de Roos (1992). The role of physiologically structured population models within a general individual-based modeling perspective. In D. L. DeAngelis and L. J. Gross (Eds.), *Individual-based models and approaches in ecology*, pp. 88–111. Routledge, Chapman & Hall.

Metz, J. A. J., A. M. de Roos, and F. van den Bosch (1988). Population models incorporating physiological structure: a quick survey and an application to size structured population dynamics in waterfleas. In B. Ebenman and L. Persson (Eds.), *Size-structured populations: ecology and evolution*, pp. 106–124. Berlin, Springer.

Metz, J. A. J. and O. Diekmann (1986). *The dynamics of physiologically structured populations*, Volume 68 of *Lecture Notes in Biomathematics*. Springer Verlag.

Metz, J. A. J. and M. Gyllenberg (2001). How should we define fitness in structured metapopulation models? Including an application to the calculation of ES dispersal strategies. *Proc. R. Soc. London B 268*, 499–508.

Metz, J. A. J. and O. Leimar (2011). A simple fitness proxy for structured populations with continuous traits, with case studies on the evolution of haplo-diploids and genetic dimorphisms. *J. Biol. Dyn 5*, 163–190.

Metz, J. A. J., S. D. Mylius, and O. Diekmann (2008). When does evolution optimize? *Evol. Ecol. Res. 10*, 629–654.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz (1992). How should we define ”fitness” for general ecological scenarios? *Trends Ecol. Evol. 7*, 198–202.

Parvinen, K. (2006). Evolution of dispersal in a structured metapopulation model in discrete time. *Bull. Math. Biol. 68*, 655–678.

Parvinen, K. and U. Dieckmann (2013). Self-extinction through optimizing selection. *J. Theor. Biol 333*, 1–9.

Roughgarden, J. (1976). Resource partitioning among competing species – a coevolutionary approach. *Theor. Popul. Biol. 9*, 388–424.

Szilágyi, A. and G. Meszéna (2009). Limiting similarity and niche theory for structured populations. *J. Theor. Biol. 258*, 27–37.

A Appendix: Proxy transformations

To demonstrate the richness of potential fitness proxies, we introduce the concept of a proxy transformation.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

A.1 Definition of a proxy transformation

For any specific model, there are typically only a few ways that one would normally derive fitness proxies such as the basic reproduction number. One should note, however, that for any model, there is an infinite number of fitness proxy functions. Once one fitness proxy $\hat{r}_1(s,E)$ with neutral value c_1 is known, we can use a proxy transformation to obtain others. A general transformation is

$$\hat{r}_2(s,E) = a(s,E)\left(\hat{r}_1(s,E) - c_1\right) + c_2, \tag{A.1}$$

where $a(s,E)$ is a positive function that is continuous with respect to E, at least when $\hat{r}_1(s,E) \neq c_1$. Specifically, if we have two different fitness proxies $\hat{r}_1(s,E)$ and $\hat{r}_2(s,E)$ with neutral values c_1 and c_2, respectively, the function $a(s,E)$ in the proxy transformation (A.1) is defined by

$$a(s,E) = \frac{\hat{r}_2(s,E) - c_2}{\hat{r}_1(s,E) - c_1}, \text{ when } \hat{r}_1(s,E) - c_1 \neq 0. \tag{A.2}$$

Since the numerator and denominator are sign-equivalent, the function $a(s,E)$ gets positive values when it is defined, and it is continuous with respect to E, because the fitness proxies are. When the denominator is 0, we can, in principle, define the value of $a(s,E)$ to be any finite (preferably positive) number, and (A.1) still holds. When the denominator is 0, so is the numerator, and thus the limit $\lim_{\hat{E}\to E} a(s,\hat{E})$ may be calculated using the rule of l'Hospital. We conclude that the limit exists if the fitness proxies are continuously differentiable with respect to E (for a counterexample, see r_4 and a_4 in Fig. 2), but the limit can also be 0 (as for a_2 in Fig. 2b) or ∞ (as for a_3 in Fig. 2b).

A.2 Examples of proxy transformations

Consider the model $\mathrm{d}N_i(t)/\mathrm{d}t = sE(t)N_i(t)$, for which the fitness at an ecological equilibrium is $r(s,E) = s\,E$. For example, the following functions are sign-equivalent with $r(s,E)$, so that they are fitness proxies with a neutral value of 0,

$$\begin{aligned} r_2(s,E) =& s\,E^3, \\ r_3(s,E) =& s\ \mathrm{sign}(E)\,|E|^{1/2}, \\ r_4(s,E) =& \begin{cases} s\,2E, & E \geqslant 0 \\ s\,E/2, & E < 0 \end{cases}. \end{aligned} \tag{A.3}$$

The function r_4, however, is not continuously differentiable at $E = 0$. These functions and the corresponding proxy transformations are illustrated in Figure 2.

ACCEPTED MANUSCRIPT

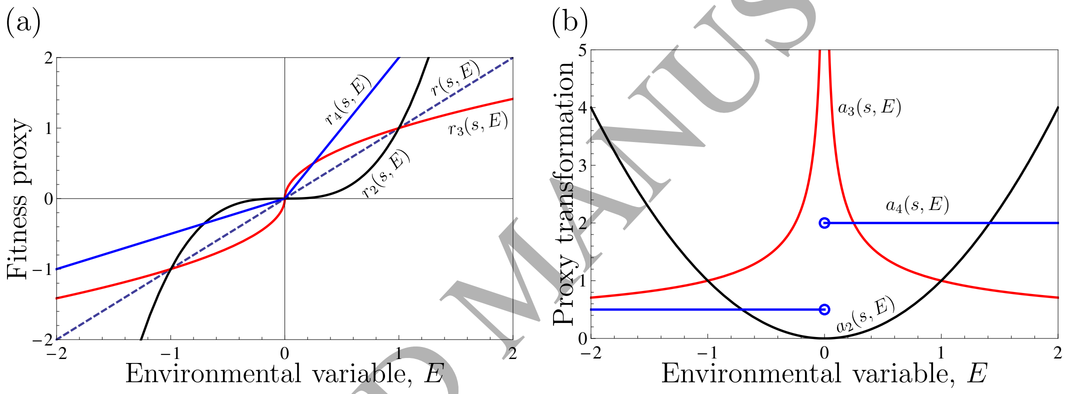

Figure 2: Proxy transformations. (a) Illustration of fitness and fitness proxies, and (b) the function $a(s,E)$ in the proxy transformation (A.1) corresponding to equation (A.3), in which case E is one-dimensional. Panel a illustrates that the fitness proxies (with a neutral value of 0) are sign-equivalent with fitness (dashed line). Panel b illustrates that the function $a(s,E)$ in the proxy transformation (A.1) is positive, when $\hat{r}_1(s,E) - c_1 \neq 0$, but the limit does not need to exist, and when it does, it may also be 0 or infinite. The situation is illustrated for the strategy $s = 1$.

ACCEPTED MANUSCRIPT

B Matrix rank

For the benefit of the reader, here we list some textbook facts about the rank of a matrix. There are various equivalent ways to determine the rank of a $m \times n$ matrix $\mathbf{M}$, including the following:

1. The number of linearly independent row vectors of $\mathbf{M}$.
2. The number of linearly independent column vectors of $\mathbf{M}$.
3. The dimension of the image of the linear mapping $f : \mathbb{R}^n \to \mathbb{R}^m$, $f(x) = \mathbf{M}x$.
4. The number of columns n minus the dimension of the kernel of f (rank–nullity theorem).
5. The number of non-zero singular values in a singular value decomposition, which is also the same as the number of non-zero eigenvalues of the matrix $\mathbf{M}\mathbf{M}^*$ and $\mathbf{M}^*\mathbf{M}$, where the star stands for the conjugate transpose.

For square matrices one can consider the relation of its rank and eigenvalues. If $\mathbf{M}$ is a square matrix of dimension n, and has n distinct eigenvalues, the number of non-zero eigenvalues (which must be either n or $n-1$) equals the rank of the matrix. This property does not hold in general, and the existence of eigenvalue 0 only tells us that the matrix does not have a full rank. For example the matrix

$$\mathbf{A} = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix} \tag{B.1}$$

has two linearly independent row (and column) vectors, so it has rank 2. Since it is an upper triangular matrix, the diagonal elements are eigenvalues, and they are all 0, so that no non-zero eigenvalues exist. For the matrix $\mathbf{A}$ given by (B.1), the matrix

$$\mathbf{A}\mathbf{A}^* = \mathbf{A}^*\mathbf{A} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 0 \end{pmatrix} \tag{B.2}$$

is a diagonal matrix with two nonzero eigenvalues on the diagonal, corresponding to the rank of the matrix $\mathbf{A}$. We hope this example helps in avoiding the pitfall of confusing the rank of the matrix with the number of non-zero eigenvalues of the matrix itself.

ACCEPTED MANUSCRIPT