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Interim Report IR-99-045

Species diversity and population regulation: the importance of environmental feedback dimensionality

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 38

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Species diversity and population regulation: the importance of environmental feedback dimensionality

Géza Meszéna
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1 The Dimension-Diversity Theorem

The idea of "optimizing" evolution is confined to the case of one-dimensional population regulation in the sense of Metz et al. (1996). If the population is limited by a single factor, one of the competing strategies inevitably wins the competition. This situation is referred to as "competitive exclusion." In more general cases, the selection becomes frequency-dependent and leads often to evolutionary branching (Geritz et al., 1997, 1998). In line with the ideas of MacArthur and Levins (1964), Levin (1970), and Heino et al. (1997), we exploit here the regulation dimensionality further by stating that the number of coexisting strategies are majorated by the number of regulating dimensions like resources, etc. This statement is true even for spatially structured and fluctuating/oscillating, but stationary populations (Section 2). The connection between this statement and the notion of niche will be clarified by investigating the situation in which some of the environmental dimensions are barely distinguishable from the point of view of the organism in Section 4. We will recapitulate the adaptive dynamics theory of Geritz et al. (1997, 1998) in terms of environmental feedbacks in Section 5, and show that evolutionary branching is nothing more than a kind of niche-segregation process. The connection between dimension of the trait space and dimension of the environmental regulation is discussed in Section 6. No mathematical rigor is intended.

Consider a number K of coexisting species. The long-term average growth rates (averaged over the time scale of demographic and environmental fluctuation and/or periodicity) of the ith species, as defined in Metz et al. (1992), Ferrière and Gatto (1995) have to be zero:

$$r_i = 0 \qquad \text{for } i = 1, 2, ..., K. \tag{1}$$

This "equilibrium" condition is the most important restriction on the shape of the s functions of adaptive dynamics. (See again: Geritz et al. 1997, 1998, and for individual-based justification of these issues: Dieckmann and Law, 1996.) The validity of it is *not* restricted to an equilibrium population in a fixed-point attractor. The long-term growth rate *must* be zero for fluctuating/oscillating populations, as well, provided that the population size remains bounded for a long period of time (see Box 2).

BOX 1: DIMENSION-DIVERSITY THEOREM

$$K \leq N$$

where K is the number of coexisting populations and N is the dimension of the environmental feedback (population regulation).

Biologically, feedback mechanisms must exist to ensure zero long-term average growth rate: resource shortage, increased predation (infection) rate or anything else must on average decrease the growth rate when the population becomes very large or increase it when the population becomes very small. We use a terminological convention by supposing that all interactions between the individuals are channeled through environmental variables. That is, we refer the environment of an *individual* as "environment."

In this sense, the feedbacks have to operate through environmental variables that we will collect into the vector $\boldsymbol{E}$. Eq. (2) is a system of K equations for these variables:

$$r_i(\boldsymbol{E}) = 0 \qquad \text{for } i = 1, 2, ..., K. \tag{2}$$

Generically, it can be solved only if

$$K \leq N = \dim \boldsymbol{E}. \tag{3}$$

That is, the number of coexisting populations can not be larger than the number of feedback dimensions of the environment. Environmental variables not affected by the populations, like temperature, illumination, etc., do not count. We will refer to these variables as "external" ones. See Box 3 for the formal definition of the feedback dimension.

The validity of Eq. (3) is very general, it relies on nothing else than the assumption of stationarity. Examples of counting these dimensions will be given in the next two sections for equilibrium and non-equilibrium populations, respectively. Feedback dimension is often infinite. For instance, a resource continuum constitutes an infinite dimensional resource space. However, living beings have a limited capability to distinguish between these dimensions. So, in some sense, the number of dimensions from their point of view remains bounded, as we will see in a mathematical form in Section 4 and in Box 9.

2 Counting Feedback Dimensions

If the environment and the population is constant, that is, they are in a fixed-point attractor, $\boldsymbol{E}$ is the instantaneous description of the feedback environment. The "canonical" example for such feedback dimension is density of a resource, organic or inorganic. An increase of the population size decreases the resource density which,

BOX 2: HOW EXACTLY IS $r = 0$?

Consider a species existing for at least $T = 10^4$ years. Denote the number of individuals of this species (in the whole area of its distribution) at the beginning and at the end of this period by N_0 and N_1, respectively. Suppose, that

$$0.01 < \frac{N_1}{N_0} < 100,$$

that is, density fluctuation doesn't exceed two orders of magnitude. This assumption implies that the long-term average growth rate

$$r = \frac{\ln \frac{N_1}{N_0}}{T}$$

satisfies the inequality

$$|r| < 4.6 \cdot 10^{-4},$$

that is, $r = 0$ is obeyed with a precision unprecedented in theoretical biology. Our assumptions were mild. If the population was present for a longer period and/or its population size didn't change by a factor of 100, our conclusion would be even stronger.

in turn, decreases the growth rate of the population. It is a well-known statement that in the case of pure resource competition, the number of coexisting populations is limited by the number of resources (MacArthur and Levins, 1964, Tilman, 1982).

There are regulating factors other than resources (Levin, 1970). Population regulation can work through predators, as well. An increase of the prey population size increases the predator density which, in turn, decreases the growth rate of the prey (Tilman, 1982). Suppose, for instance, that in a prey-predator system, preys are limited exclusively by the predators and the predators are limited exclusively by their resources, the preys. We can conclude that the number of predator species and the number of prey species must be equal. The conclusion is different if the preys are also limited by their own resources. In the latter case, the number of predator species must not exceed the number of prey species while the number of prey species must not exceed the number of resources plus the number of predator species. Infection behaves similarly: The higher the population density is, the higher the rate of infection will be. Consequently, higher density increases mortality.

Note that the environmental feedback variables (resources, etc.) are not necessarily represented in a model explicitly. For instance, if the environmental state is instantaneously determined by the population size, the feedback can be expressed directly as the density dependence of the growth rate. In this case, we opt to parameterize the environment of the individuals by the size of the population. Even in this case, the key question remains, whether the growth rate of the competing populations feel the *aggregated* size of the populations (for instance, because they share

BOX 3: DEFINITION OF FEEDBACK DIMENSION

Let E denote the space of stationary environments E_{attr} that can occur in community dynamical attractors. The effective dimension of the environmental feedback to a family of "species" distinguished by a parameter $x \in X$ is the smallest number k for which there exist smooth functions

$$\psi : E \to \Re^k \quad \text{and} \quad \beta : X \times \Re^k \to \Re$$

such that

$$\text{sign } r(x, E_{\mathrm{attr}}) = \text{sign } \beta(x, \psi(E_{\mathrm{attr}}))$$

where $r(x, E_{\mathrm{attr}})$ denotes the long-term growth rate of a rare strategy x with a background community in its attractor E_{attr}.

a resource) or whether they depend on different combinations of the populations sizes.

Generally, any kind of (direct or indirect) interaction between individuals may have a regulating effect. Witting (1997) coined the term "interference regulation" for feedbacks caused by direct interactions, like conflict, mutual support, etc., between individuals. We regard this type of feedback as environmentally mediated, too. This is not just a mathematical construct. From the point of view of a specific female individual trying to raise offspring, "availability of help" is a real environmental parameter that significantly affects her fitness.

Age-structured dynamical population models, if they consider population regulation at all, usually pick-up one of the age-groups as the "critical" one and postulate that population regulation is confined into this age-group (Charlesworth, 1980). Even if more (or all) age groups are regulated, and all of this regulation is dependent on the density of a single age group or a single combination of the age group densities, it is still a one-dimensional feedback. In the general case, however, different age group densities feed back separately, leading to a multidimensional density regulation (Loreau and Ebenhöh, 1994, and Heino et al., 1997). This multidimensionality is often related to resource diversity: The larval and adult stage of the same insect usually consume different resources.

Metapopulation is an another kind of structured population. It is natural to suppose that there are separate density feedbacks in each patch (that is that there are separate resource pools in the patches). Patches are not necessarily separated by migration barriers. If the environment consists of colder and warmer regions, for instance, it is a two-dimensional environment even if there is a single resource: The resource in the cold region and the resource in the warm region may be exploited by different populations. (Note that patchiness is often generated by the population interactions itself. This phenomenon is especially important in maintaining floral diversity.)

Such a metapopulation model (a clonal equivalent of Levin's soft selection model)

BOX 4: HISTORICAL REMARKS

MacArthur and Levins (1964) were the first to suggest that the number of coexisting species is limited by the number of ecological resources they live on. Later, their attention turned to the continuous resource distribution (niche space) where the "limiting similarity" was the analogous statement: the number of species is limited by the fact that the niches must not overlap too much (MacArthur and Levins, 1967). Despite that the existing mathematical background of limiting similarity is poor at best (Abrams, 1983 reviews the topic without clear conclusions), the concept of niche has become the "main organizing concept of ecology" (Leibold, 1995). May (1973, 1974) expounds the theory that is nearest to our discussion, but May's is limited to the resource continuum framework. (See Box 9 for further explanation.) The issue of a finite number of (discrete) resources was rejuvenated and publicized by Tilman (1982). While May predicted adverse effect of fluctuation on diversity, Levins (1979), and Kisdi and Meszéna (1993, 1995) noted that a fluctuating resource has to be counted as more than one resource, and that it can maintain diversity.

While Levin (1970) has already extended the idea by introducing the notion of "limiting factors," the topic is still referred as "resource competition theory" in most of the cases. Nowadays, a significant part of the ecologist community criticizes this theory. They emphasize, among other things, the role of spatial organization and temporal fluctuation. The demise of competition theory led to skepticism with the mechanistic explanation of diversity in general. See Den Boer (1986) for a very skeptical review, and Leigh (1990) for an optimistic one.

Christiansen and Loeschcke (1980, 1987) considered the "multiple resource" situation as a source of frequency-dependent (disruptive) selection in genetical population models. However, most of the models of frequency-dependent selection dealt with another source of frequency-dependence: animal conflicts (evolutionary game theory). Geritz et al. (1987, 1988) provided a general framework to handle frequency-dependent selection, which led to the notion of evolutionary branching. However, the connection between community ecology and evolutionary branching/speciation remains to be seen.

is presented in Geritz et al. (1998). Note that in the hard selection version of the very same model, the feedback is one-dimensional. What makes the difference? In the case of hard selection, we consider strategies that differ in the number of seeds they produce. The seed pool is supposed to be common, and in the case of hard selection, the size of this pool is the only feedback variable. Conversely, in the soft selection situation, strategies differ in the competitive ability of the seedlings. The feedback

BOX 5: COEXISTENCE IN FLUCTUATING ENVIRONMENTS

Consider a pair of strategies with instantaneous growth rates

$$r_1(t) = \xi(t) - a[n(t) - K_1] - b[n(t) - K_1]^2$$

$$r_2(t) = -c(n(t) - K_2)$$

where $n(t) = n_1(t) + n_2(t)$ is the added density of the two species at time t and $\xi(t)$ is an ergodic random external environmental parameter with expectation zero ($\overline{\xi}(t) = 0$).

If the environment is constant, that is, if $\xi = 0$, the population dynamics converge to a stable fixed point. The feedback is one-dimensional, as $n(= \mathit{const.})$ is the only relevant feedback variable. K_1 and K_2 are the carrying capacities for the two species. Competitive exclusion applies, and the species with higher carrying capacity will outcompete the other one.

However, in the presence of external fluctuation ($\xi \neq 0$), densities will fluctuate as well. It is easy to see that the long-term growth rates depend only on the average $\overline{n}$ and the variance $V(n)$ of the added density $n(t)$:

$$\overline{r_1} = -a(\overline{n} - K_1) - b(\overline{n} - K_1)^2 - V(n)$$

$$\overline{r_2} = -c(\overline{n} - K_2).$$

Is coexistence of these two strategies possible? Mutual invasibility is a sufficient condition for coexistence, so we will check this condition. Suppose that strategy 1 is rare. Strategy 2 is not affected by the fluctuation, so it will reach an equilibrium population with density $n = K_2$. Strategy 1 can grow in this background if $K_1 > K_2$, because $\overline{n} = K_2$ and $V(n) = 0$. Consider now the opposite extreme, when strategy 2 is the rare one. The population of strategy 1 is fluctuating, that is, $V(n) > 0$, implying $\overline{n} < K_1$. The condition of growing for strategy 2 is $\overline{n} < K_2$. One can conclude that the condition of mutual invasibility is:

$$\overline{n}_1 < K_2 < K_1$$

where $\overline{n}_1$ means the average density of species 1 when established without presence of species 2 (Kisdi, Meszéna, 1993). There is not an easy way to calculate $\overline{n}_1$; it is determined solely by the parameters of species 1 and $\overline{n}_1 < K_1$. So, one can choose K_2 according to this condition to ensure coexistence.

variables are the summed competitive abilities of the seeds fallen into a given patch – that is the feedback dimension equals the number of patches. Consequently, there is no evolutionary branching in the hard selection model, while it does exist in the soft selection case. Observe again that the regulating dimension depends on the strategy class considered (see Box 3).

BOX 6: ONLY IN LINEAR MODELS?

Armstrong and McGehee (1976) demonstrated coexistence of two populations on a single resource. The model was a nonlinear one with oscillating population dynamics. They concluded that diversity is limited by the number of resources in linear models only. As we argue here, stationarity rather than linearity is the real issue. If the population dynamics oscillate, so does the resource, that is, the single resource has to be counted as multiple environmental feedback dimensions. This phenomenon was investigated further by Adler (1990) and Jansen and Sevenster (1997). The problem doesn't exist in linear models in which, according to the considerations of Box 5, the time average of the oscillating density is the single feedback variable.

If the environment and/or the populations are fluctuating or oscillating, the situation is more complicated but not entirely different. (This oscillation/fluctuation can be driven either by an external factor or by the internal dynamics of the ecosystem. See Loreau [1989] for an example of the first kind and references in Box 6 for examples of the second kind.) As a standard assumption in adaptive dynamics, we suppose that the time scale of (ecological) fluctuation/oscillation is much shorter than the evolutionary time scale. With this very strong, but meaningful assumption, Eq. (1) is still valid for the growth rate averaged over the fast time-scale. However, $\boldsymbol{E}$ is no longer the *instantaneous* description of the environment. This vector must incorporate all the statistical parameters of the environmental fluctuation affecting long-term population growth. Box 5 contains an example (Kisdi and Meszéna, 1993), in which the average and the variance of the aggregated population size are the only statistical parameters affecting population growth. As this feedback is two-dimensional, at most, two populations can coexist. This model is very artificial, but the idea is more general: Growth rate can be expressed by the statistical moments of the environmental variable. Even a spatially extended *and* fluctuating ecosystem can be described with the statistical moments of the spatial correlation functions. The reader can find a good summary of “moment methods” in Bolker et al., 1999. The main issue is “moment closure,” that is, to find a good approximate description using a *finite* number of moments.

So, there are many cases in which environmental dimensionality N is finite and can be counted unequivocally by counting the resources, predators, infectors, patches, age groups, relevant statistical moments, etc. Our Dimension-Diversity Theorem limits the number of coexisting populations in these situations. Counting dimensions requires careful analysis of the feedback pattern, however. One can not count the dimensions in the “empty” environment and “predict” the number of coexisting species without considering the possible types of population interactions. The original version of the resource competition theory raised false expectations by suggesting that it is enough to count the “resources.” Unfortunately, one can not count the number of patches before considering the populations living in them if the patchiness is generated by the populations, and so on.

Environmental dimensionality is infinite in many cases: The well-known "resource continuum" is the simplest example. Heterogeneous environment is not necessarily formed by discrete, but homogenous patches. Instead, an (external) environmental variable may have a continuous geographic variability leading to infinite dimensional feedback. It may not be possible to describe environmental fluctuation in a finite dimensional way. Interference regulation may or may not behave in a finite dimensional way. Asymmetric competition – where the larger animal has an advantage over the smaller one – is a good example of infinite dimensional regulation. In this case, the size distribution of the population, an infinite dimensional mathematical object, is the feedback variable. Asymmetric competition of seeds with different size (Geritz, 1995, Geritz et al., 1999) leads to an exciting branching pattern that is a result of interplay between asymmetric competition and patchiness generated by the population.

While the Dimension-Diversity Theorem is not applicable, there is a limitation on the number of coexisting species even in the infinite dimensional situations. This will be the subject of Section 4 after some homework in Section 3.

3 Interactions between Populations and the Environment

Eq. (2) represents the environmental dependence of the population growth rate. To proceed further, we have to close the feedback loop by specifying the environmental impact of the populations. To make life easier, we will restrict the generality of the treatment. For the rest of this paper, we will suppose that the population is unstructured, the environment is constant, and the population dynamics converge to a fixed-point attractor. However, we think that our conclusions remain valid for the general case. Boxes 7 and 10 give hints for the generalization.

With these assumptions, the environmental condition $\boldsymbol{E}$ in a given moment is determined instantaneously by the population sizes n_1, n_2, ..., n_K of the species present:

$$\boldsymbol{E} = \boldsymbol{E}(n_1, n_2, ..., n_K) \tag{4}$$

and Eq. (2) provides the K number of equilibrium conditions for the K number of population sizes.

The vector

$$\boldsymbol{e}^i = -\frac{\partial r_i}{\partial \boldsymbol{E}} \tag{5}$$

measures the environmental sensitivity of the ith population while the vector

$$\boldsymbol{f}^i = \frac{\partial \boldsymbol{E}}{\partial n_i} \tag{6}$$

measures the per capita environmental impact of the same population. Vectors $\boldsymbol{e}^i$ and $\boldsymbol{f}^i$ together represents the two-way interaction between the population and the

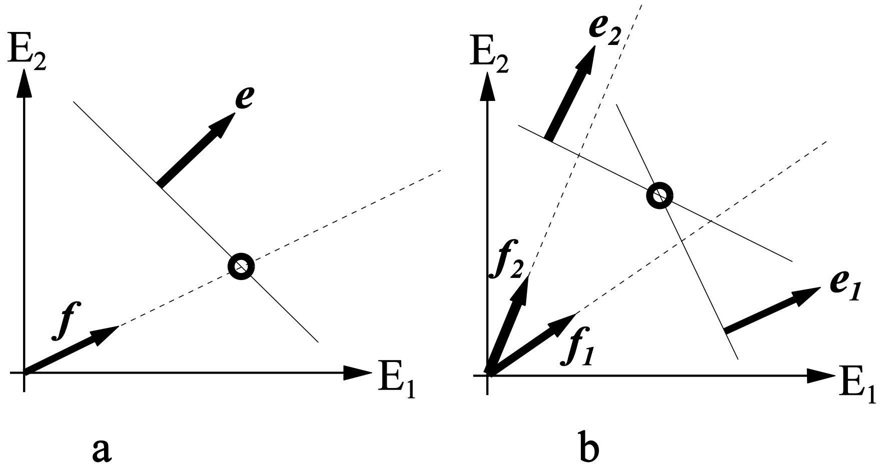

Figure 1: Equilibrium of a single (a) or two coexisting populations (b) in a two-dimensional environment (linear approximation). The solid lines are the Zero Net Growth Isocline-s (ZNGI). The equilibrium points are denoted by the small circles. In Fig. 1a, the environmental equilibrium point is the intersection between the ZNGI and the direction of the environmental impact vector $\boldsymbol{f}$. In Fig. 1b, the intersection of the two ZNGIs is the equilibrium point that must lie within the wedge between the two environmental impact vectors.

environment. We will refer to them as sensitivity ($\boldsymbol{e}$) and impact ($\boldsymbol{f}$) vectors. (The minus sign for $\boldsymbol{e}^i$ is chosen for later convenience.)

Leibold (1995) emphasized the need to distinguish between the impact niche and the requirement niche. Our impact and sensitivity vectors match exactly to this dual notion of niche. Most of the niche models mix the two meanings by using a single "resource utilization function."

If the environment dependence and environmental impact is linear, one can write:

$$r_i(\boldsymbol{E}) = r_i^0 - \boldsymbol{e}^i \cdot \sum_{j=1}^{N} \boldsymbol{f}^j n_j \tag{7}$$

leading immediately to Lotka-Volterra type competition between the populations. If the dependencies are nonlinear, Eq. (7) is still valid as a local approximation. In the linear case, but not in general, r_i^0 can be identified by the growth rate of the ith species in the virgin environment. This linearization will be used in Section 5 for discussion of small evolutionary steps during which the environmental change remains small. In the rest of the present section, it will be employed for illustrative purposes.

Fig. 1 shows one (a) and two (b) populations in a two-dimensional environmental space. The Zero Net Growth Isocline (ZNGI, Tilman, 1982) of a strategy is the set of environmental conditions in which the strategy is in equilibrium $(r_i(\boldsymbol{E}) = 0)$. ZNGIs are straight lines perpendicular to the gradient vector $-\boldsymbol{e} = \frac{\partial r}{\partial \boldsymbol{E}}$, which points to the direction of steepest increase of the growth rate in the environmental space. For the sake of clarity, we choose a parameterization in which all components of the sensitivity vectors are positive in the small neighborhood we are interested in:

$$\boldsymbol{e}^i > 0. \tag{8}$$

($\boldsymbol{e}^i \cdot \boldsymbol{f}^i > 0$ is required for the ith population to be regulated, so at least some components of the impact vectors have to be positive, as well.) This choice of sign means that a population has a positive growth rate below its ZNGI, and a negative growth rate above it.

For one species in the two-dimensional environment,

$$\boldsymbol{E} = \frac{\partial \boldsymbol{E}}{\partial n} n = n\boldsymbol{f}, \tag{9}$$

that is, the direction $\boldsymbol{f}$ gives the possible environmental conditions. The equilibrium environment is the crossing point of the ZNGI with the direction of $\boldsymbol{f}$. Likewise, for two species,

$$\boldsymbol{E} = \frac{\partial \boldsymbol{e}}{\partial n_1} n_1 + \frac{\partial \boldsymbol{E}}{\partial n_2} n_2 = n_1 \boldsymbol{f}^1 + n_2 \boldsymbol{f}^2, \tag{10}$$

so the wedge between the two $\boldsymbol{f}$s forms the set of allowable conditions corresponding to positive population sizes. The crossing point of the two ZNGIs is the equilibrium point.

Observe the different nature of the equilibrium conditions in the two cases! However, conditions for invasion of a rare mutant are identical for one and two residents. A rare mutant can or can not grow if its own ZNGI is above or below the equilibrium point, respectively. This observation will be used heavily in Section 5.

The ZNGIs of two populations must intersect each other within the wedge of the two $\boldsymbol{f}$ vectors for positive equilibrium densities, that is, for real coexistence. Observe that if either the two $\boldsymbol{f}$ vectors or the two $\boldsymbol{e}$ vectors are very similar to each other in direction, this condition is difficult to meet: only a very narrow range of the r^0 values allow coexistence. The coexisting populations must differ in environmental impact AND in environmental sensitivity to coexist. The smaller the difference is in either respect, the smaller the chance of coexistence. (This statement is in accordance with the argumentation in Abrams, 1988, but it is slightly different from the conclusion of Leibold, 1995, who supposed no effect of the impact vectors on the existence of the equilibrium point.) We will express this in a general form in the next section.

4 Limiting Similarity

Limiting similarity, the idea that niches of coexisting populations must not be too similar, has an obvious connection to the Dimension-Diversity Theorem. Niche means a collection of resources. Different species live on different resources when living in different niches. Technically, however, a niche, as a subset of a continuous niche space, is an infinite collection of resources in an infinite dimensional resource space, so the Dimension-Diversity Theorem is not directly applicable. However, in a real-life biological example, a bird may not be able to distinguish between seeds of a very similar size in the seed-size continuum. The environment is never *really*

BOX 7: GENERALIZATION FOR ARBITRARY POPULATION DYNAMICS

Let n_j denote the total, averaged size of the jth population summed over all individual states and locations and averaged over the fluctuation time-scale. We reintroduce population size dependence Eq. (4) with the following “thought experiment” interpretation:

1. Keep n_j constant artificially at a given value by an appropriate rate of random removal/addition of individuals.
2. Allow the populations-environment process to relax for a sufficient time period.
3. Observe the statistics of the environmental process. These statistics are denoted by $\boldsymbol{E}$.

The “equilibrium” condition Eq. (2) determines the total averaged population sizes at zero removal rate, that is during the normal life. With natural smoothness assumptions, our conclusions follow for the general case.

See also Box 10.

infinitely dimensional from the point of view of a population. We are looking for the mathematical representation of this idea.

Let us rewrite Eq. (2) as

$$r_i(\boldsymbol{E}(n_1, n_2, ..., n_K), \epsilon) = 0 \qquad \text{for } i = 1, 2, ..., K \tag{11}$$

with an external environmental parameter ϵ. One can express the equilibrium densities, as a function of the parameter ϵ, by implicit function theorem if the Jacobian

$$J = \det\left(\frac{\partial r_i}{\partial n_j}\right) = \det(\boldsymbol{e}^i \cdot \boldsymbol{f}^j) \tag{12}$$

is different from zero. The Jacobian J appears in the denominator of the expression, so, if the absolute value $|J|$ is small, the equilibrium densities are very sensitive to the parameter ϵ.

This sensitivity means, among other things, that for only a small range will the parameter ϵ allow all of the equilibrium densities calculated from Eq. (11) to be positive. That is, these populations can coexist only in a small range of this parameter. Even if the parameter value happens to be favorable for the coalition in a given moment, a small external disturbance will lead to the collapse of it. See Box 8 for an explicit probabilistic argument.

It is clear, that $J = 0$ for $N < K$ because neither the rows nor the columns of the Jacobian matrix can be linearly independent in this case. That is, coexistence of K number of species in an $N < K$ dimensional environmental space requires a non-generic choice of the external parameters, a conclusion that coincides with the Dimension-Diversity Theorem.

BOX 8: PROBABILITY OF COEXISTENCE

We will show that probability of coexistence becomes small for small Jacobian J. Instead of Eq. (11), we write

$$r_i(\boldsymbol{E}(n_1, n_2, \ldots, n_K)) - \delta_i = 0$$

where the vector $\boldsymbol{\delta}$ represents the perturbation in the external environment. Suppose a probability distribution of $p(\boldsymbol{\delta})$ for this external parameter. We are interested to know the probability $P(\boldsymbol{n} > 0)$ that all the equilibrium densities (as determined by the value of $\boldsymbol{\delta}$) are positive:

$$P(\boldsymbol{n} > 0) = \int_{\boldsymbol{n}>0} p\left(\boldsymbol{\delta}(\boldsymbol{n})\right) \left| \det \left(\frac{\partial \boldsymbol{r}}{\boldsymbol{n}} \right) \right| d\boldsymbol{n}.$$

Seemingly, this probability goes to zero in the limit $J \to 0$.

When will the Jacobian $|J|$ be small? Let us rewrite it in the form

$$J = \det(\boldsymbol{e}^i \cdot \boldsymbol{f}^j) = (\boldsymbol{e}^1 \wedge \boldsymbol{e}^2 \wedge \ldots \wedge \boldsymbol{e}^K) * (\boldsymbol{f}^1 \wedge \boldsymbol{f}^2 \wedge \ldots \wedge \boldsymbol{f}^K) \tag{13}$$

where $\wedge$ means “wedge product,” or “outer product,” a generalization of the vector product of the three-dimensional vectors for arbitrary dimensions. The absolute value of the wedge product is the K dimensional volume of the paralellepiped defined by the vectors involved. It vanishes if not all of the vectors are linearly independent. For two vectors,

$$|\boldsymbol{u} \wedge \boldsymbol{v}| = |\boldsymbol{u}| \cdot |\boldsymbol{v}| \sin(\boldsymbol{u}, \boldsymbol{v}) \tag{14}$$

where $(\boldsymbol{u}, \boldsymbol{v})$ denotes the angle between the vectors $\boldsymbol{u}$ and $\boldsymbol{v}$. (See the Appendix for a short introduction to the wedge product.)

If either two of the sensitivity vectors ($\boldsymbol{u} = \boldsymbol{e}^i$ and $\boldsymbol{v} = \boldsymbol{e}^j$) or two of the impact vectors ($\boldsymbol{u} = \boldsymbol{f}^i$ and $\boldsymbol{v} = \boldsymbol{f}^j$) becomes nearly parallel, the Jacobian becomes small proportionally to the sine of the angle between these vectors, making coexistence improbable. That is, coexistence of species too similar to each other is not favored. We think that this is the general notion of the “limiting similarity” concept.

It is disfavored also if a species tries to occupy a niche that is very similar to a linear combination on the niches of other species, because the wedge product becomes very small in this case, too. A species can not choose a combination of other species’ diet as its own diet.

It is important to stress that the coexistence of niches with great similarity is improbable rather than impossible. One can easily construct theoretical counterexamples to limiting similarity just by introducing some degeneracy into the model. This is the reason, why “limiting similarity” earned a bad reputation in theoretical ecology though it works well in reality.

Note that the scalar product

$$\boldsymbol{u} \cdot \boldsymbol{v} = |\boldsymbol{u}| \cdot |\boldsymbol{v}| \cdot \cos(\boldsymbol{u}, \boldsymbol{v}) \tag{15}$$

BOX 9: RESOURCE CONTINUUM -
THE CANONICAL EXAMPLE FOR NICHE

Let us recapitulate the standard theory of limiting similarity with a one-dimensional resource continuum. The environmental state $\boldsymbol{E}$ is described by the function $\boldsymbol{E}(x)$, which denotes a shortage of resource type x caused by the populations. Linearity is supposed and Eq. 7 becomes

$$r_i(\boldsymbol{E}) = r_i^0 - \int \boldsymbol{e}^i(x) \sum_j \boldsymbol{f}^j(x) n_j dx$$

where $\boldsymbol{f}^i(x)$ is the consumption of and $\boldsymbol{e}^i(x)$ is the sensitivity to resource type x of the strategy l. As no distinction between resource sensitivity and resource impact is made, $\boldsymbol{e}^l(x) = \boldsymbol{f}^l(x)$ is chosen. This is the "resource utilization function." The "overlap integral" of it, corresponding to the scalar product of the sensitivity/impact vectors,

$$\boldsymbol{e}^i \cdot \boldsymbol{e}^j = \boldsymbol{f}^i \cdot \boldsymbol{f}^j = \int \boldsymbol{f}^i(x) \boldsymbol{f}^j(x) dx$$

measures the niche overlap/similarity. The higher the niche overlap is, the smaller the parameter range allowing coexistence is (May, 1973, 1974). All of our formulas are applicable. (See the Appendix for the definition of scalar and wedge product of functions.)

is large when the wedge product is small, and vice versa. So, similarity between the (impact, or requirement) niches can be expressed by the high scalar product of the corresponding vectors, as well. This is the description that is directly related to the traditional theory of limiting similarity in the context of resource continuum (Box 9).

It is known that in an adaptive dynamics context, similar strategies can not coexist except in the vicinity of a singular strategy (Geritz et al., 1997, 1998, Frans Jacobs, unpublished). This vicinity just corresponds to a special fine-tuning of the parameters, so our results here are consistent with the adaptive dynamics theory. Now, we turn to this theory and investigate the adaptive process in terms of feedback variables.

5 Adaptive Dynamics with Feedback Variables

Let us recapitulate the local adaptive dynamical theory of Geritz et al. (1997, 1998) for two environmental dimensions. We consider strategies that differ in a single trait. (As it will be shown in the last section, it is always enough to consider two environmental variables for local analysis of adaptive dynamics in one-dimensional trait spaces.) We will rely on geometric intuition exclusively. The formulas will be

BOX 10: TIME-SCALE SEPARATION

If we restrict our interest to small evolutionary steps (as we do in adaptive dynamics), we have to deal with mutant growth rates only slightly different from zero. The slowly growing mutant population equilibrates its structure and sample environmental stochasticity during its initial growth; this is why the long-term growth rate works as a fitness measure. Similar things can be said for a small change of the external environmental parameter ε in Section 4: as the long-term averaged growth rates remain near zero, the population size averaged over the fluctuation/relaxation time scales changes slowly.

That is, in all cases of interest of this paper, there are two, separate time scales of the population dynamics: the fast fluctuation/relaxation time scale and the slow, population growth/decrease time scale. The two time scales can be investigated separately. In this paper, n denotes the slow variable: the total population size averaged over the fast time scale. We do not lose generality if we do not consider the fast time scale, the population relaxation, and environmental variability, explicitly. However, one has to include the statistical description of the environmental variables into the feedback variable $\boldsymbol{E}$. (See Box 5.) This description will represent the fast time scale at the level of slow dynamics. (See also Box 7.)

Note that the existence of a third time scale is also supposed in adaptive dynamics: The rate of mutation is required to be slow even compared to the population growth time scale.

published elsewhere, or the user can redo them as an exercise.

We restrict our interest to local analyses like local fitness gradient and singular point classification so that we can apply the linear approximation of Eq. (7). ZNGIs of the strategies form a one-dimensional set of straight lines. Locally, this set can be viewed as a straight line rolling on a curve, which we will refer to as Boundary. This curve can be convex (Fig. 2a) or concave (2b) as viewed from the origin of the environmental space. In the convex case, the ZNGI lines can not cross into the region above the Boundary. That is, in the region above the Boundary, no strategy can be in equilibrium. Similarly, in the concave case, the region below the Boundary can not contain an equilibrium state.

One can plot the growth rate as a function of the strategy in every point of the environmental space. We may be interested either in the vicinity of a local fitness maximum or a vicinity of a local fitness minimum. These cases correspond to the convex and concave Boundary, respectively (Fig. 3.) In the vicinity of a fitness maximum and at very high environmental values, no strategy can survive. The empty region above the convex Boundary corresponds to this Hell. In a vicinity of a fitness minimum and at low environmental values (below the concave Boundary, in the Eden), every strategy survives.

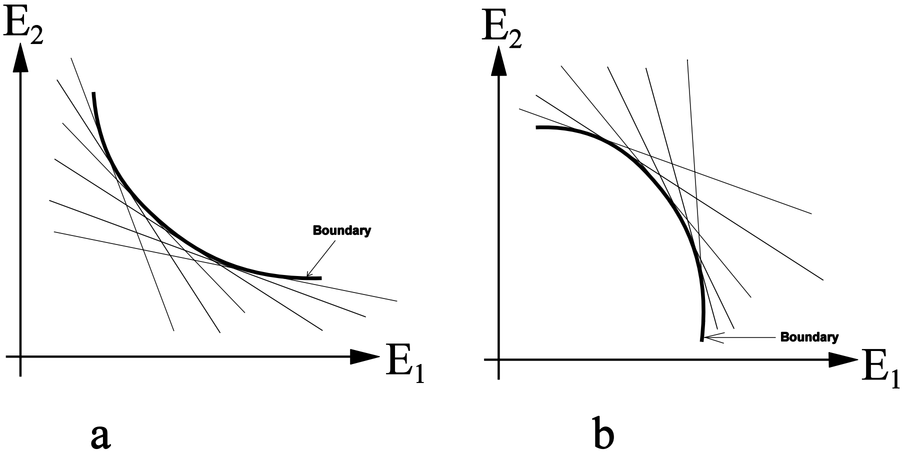

Figure 2: ZNGIs of a one-dimensional set of strategies is represented by lines rolling on a convex (a) or a concave (b) curve.

Observe the following: In Fig. 3a, corresponding to a vicinity of a fitness maximum (that is, in the vicinity of an ESS), coexistence of two strategies can be invaded by a third one with a strategy between the strategies of the two. On the other hand, in Fig. 3b, corresponding to a vicinity of a fitness minimum, the strategy between can not invade.

Fig. 4 shows how directional selection operates. The trick to reading these figures is simple: One has to check to see if the resource equilibrium point of the established strategy is above or below the ZNGI line of the mutant strategy. One can observe that the direction of the evolution is determined by the relative position of the equilibrium point of the established strategy relative to the touching point of its ZNGI and the Boundary. A corollary is that a strategy is singular if its equilibrium point coincides to the touching point. If strategy s_2 in Fig. 3ab is singular in this sense, it is an ESS in Fig. 3a, but not in Fig. 3b. In a dimorphic population formed by strategies s_1 and s_2, the strategies evolve toward each other near an ESS (Fig. 3a), but evolve away from each other near an evolutionary unstable singularity (in Fig. 3b), as it is known in the adaptive dynamics theory.

In Fig. 5 one can study convergent stable and convergent unstable singular points.

In Fig. 6 we investigate evolution of strategy s in the presence of a distinct strategy d. The ZNGI of strategy d does not necessarily touch the Boundary valid in the small neighborhood of strategy s. The equilibrium point of coexistence of strategy d and any descendant of strategy s must lie on the ZNGI of d. That is, the two-dimensional environmental space is constrained to a one-dimensional space by the presence of another strategy. (In other words, one of the two environmental dimensions is occupied by the strategy d.) If the s ZNGI touches the Boundary at the crossing point of the d ZNGI and the Boundary, then the strategy s is singular. Otherwise, s evolves toward the singular strategy if the Boundary is convex (ESS, Fig. 6a) and away from it if the Boundary is concave (non-ESS, Fig. 6b). There-

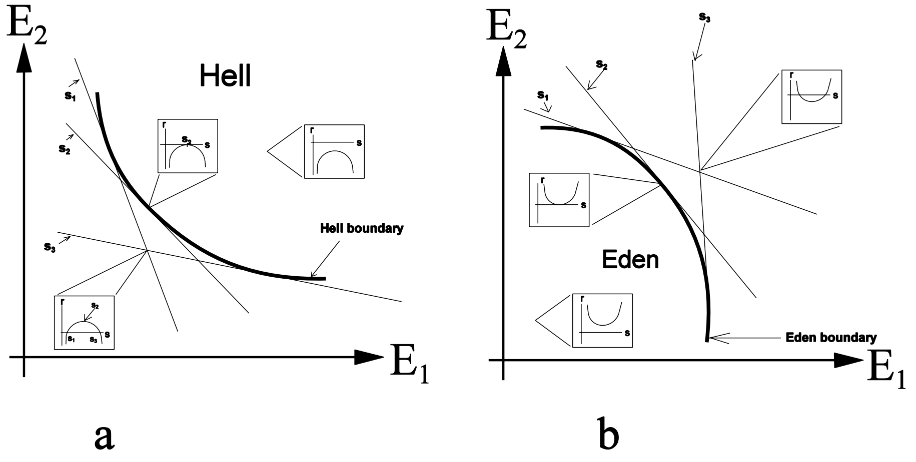

Figure 3: Near to a local fitness maximum (a) or minimum (b). The small plots represent the fitness curve in a given point of the environmental space.

fore, evolution and convergent stability are equivalent for strategy s, and no further branching is possible. (Being otherwise would be a violation of the Dimension-Diversity Theorem!)

6 Trait Dimensions and Feedback Dimensions

Additional to the feedback dimension N, there is an another relevant dimension parameter of the evolutionary process, the dimension of the trait space, denoted here by M. They are both independent parameters of a model. However, they have an intimate relationship: If either the trait space or the environmental space has a fixed dimensionality, then the number of *important* dimensions in the other space is limited. We have two statements:

Statement A. Only an $M+1$ dimensional subspace of the environmental space is relevant for *local, monomorphic* evolution.

Statement B. The strategies, having had a chance to survive the selection process, are contained in a $N-1$ dimensional sub-manifold of the trait-space.

That is, if we are sure, by any reason, that the feedbacks are controlled by a limited number of environmental variables, we need not consider but a limited number of trait variables. On the other hand, if our model has a limited number of trait dimensions, only a limited number of environmental variables have local importance.

It is very important to stress that Statement A is valid only locally. A corollary of it is that, at most, $M+1$-fold branching is possible. However, if the total number of environmental dimensions are higher, this local constraint excludes neither further branchings from occurring nor the coexistence of more than $M+1$ (different enough) strategies. Statement B is valid in a local as well as in global sense: One may consider the strategy set reachable from the currently established populations by a

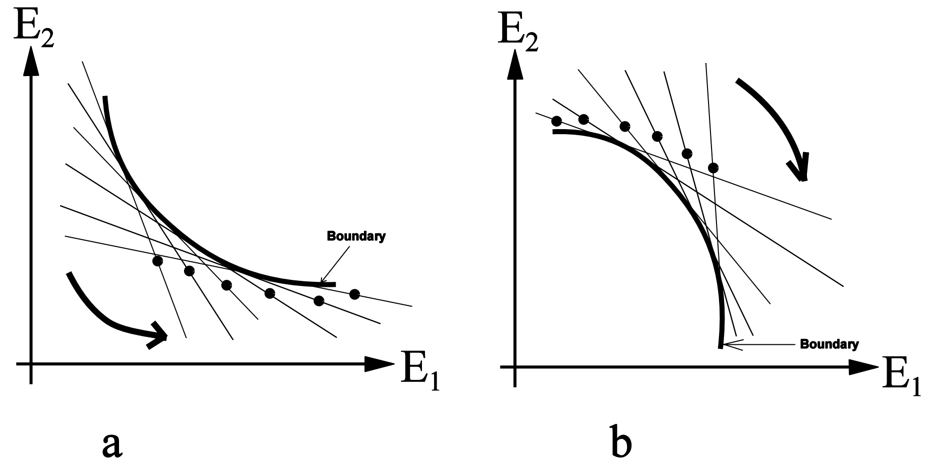

Figure 4: Directional selection with convex (a) and concave (b) boundary. The equilibrium point is denoted by a dot on the ZNGI of the respective strategy. The arrows show the direction of rotation of the ZNGI line as consequence of the trait substitution process.

small number of mutation steps or the full set of possible strategies.

To prove Statement A, it is enough to enumerate the relevant environmental dimensions. The environmental state can change either by a small change in the population density or by a small change of the strategy x. The first possibility corresponds to a single direction in the environmental space: the direction of the environmental impact vector $\boldsymbol{f}(x)$. The second possibility represents M number of directions determined by the partials $\frac{\partial \boldsymbol{f}(x)}{\partial x}$. So, $M+1$ is the number of directions into which the system can change locally. Note that if one is interested in the environmental change to the kth order, then one has to consider $kM+1$ environmental dimensions in a similar fashion. For singular point classification, it is sufficient to calculate the second partial derivative with respect to the mutant strategy and the first partial derivative with respect to the resident strategy. Consequently, $M+1$ environmental dimensions are enough for this purpose. But higher order derivatives and, consequently, more dimensions are needed for bifurcation theory. To prove Statement B it is useful to consider the function

$$r_{max}(\mathbf{E}) = \max_{x \in \boldsymbol{X}} r(x, \mathbf{E}) \tag{16}$$

representing the growth rate of the *best* strategy in a given environment. $\boldsymbol{X}$ is the strategy set considered. We suppose that the trait space is compact and the function r is continuous, so this maximum exists and, as the reader can prove easily, the function r_{max} is continuous as well. (The optimal strategy itself is *not* a continuous function of the environmental state, because the absolute maximum switches from one local maximum to an another one at some points in the environmental space.)

The set

$$\mathbf{Hell} = \{\mathbf{E} | r_{max} < 0\} \tag{17}$$

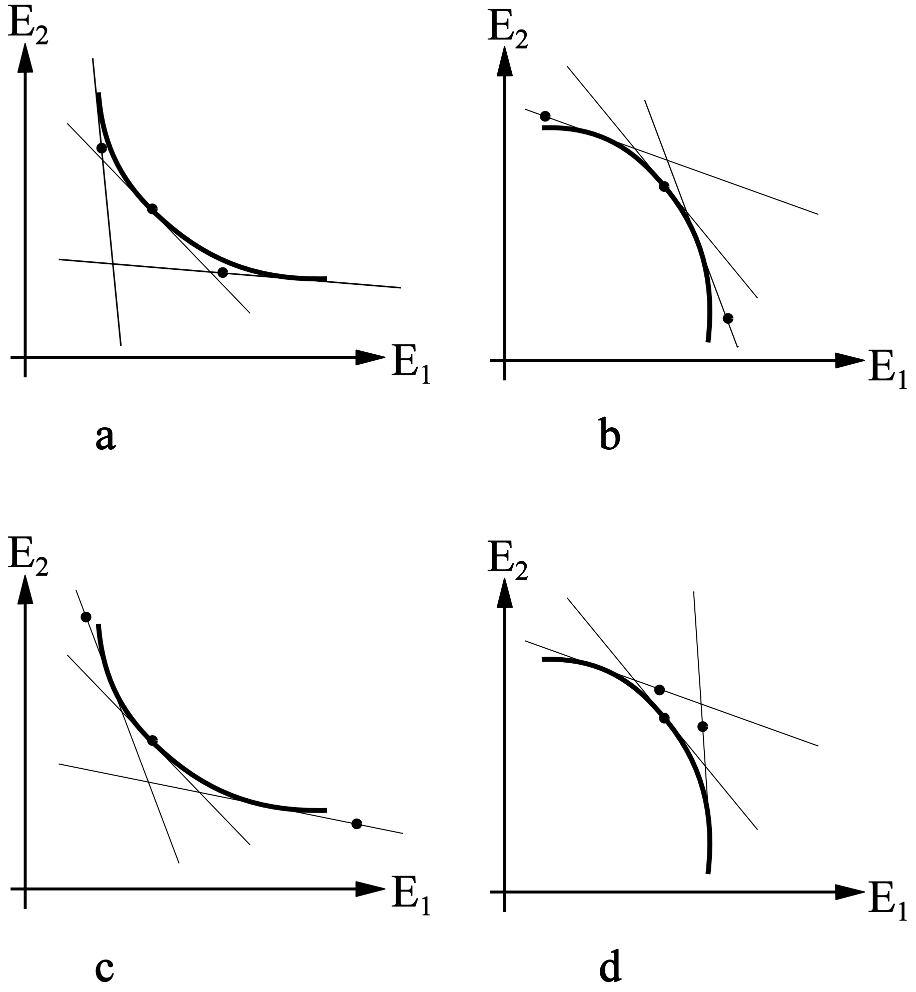

Figure 5: a: convergent stable ESS; b: convergent stable non-ESS (branching point); c: convergent unstable ESS; d: convergent unstable non-ESS. The dots on the ZNGI lines denote the equilibrium points of the respective strategies.

is the subset of the environmental conditions that excludes any population's survival. The boundary of the Hell

$$\textbf{Boundary} = \{\mathbf{E}|r_{max} = 0\}, \tag{18}$$

which is generically a dimension $N - 1$ sub-manifold of the environmental space, contains the possible equilibrium environmental conditions. (Hell and Boundary was used in Section 5 in a local sense.) For each environmental point, there is a single strategy or, generically, a discrete set of strategies, which is the optimal one at the given environmental conditions. The strategies, which are optimal in at least one of the points of the $N - 1$ dimensional environmental sub-manifold, form the interesting $N - 1$ dimensional sub-manifold of the strategy space.

These statements tell us that discussion of the $N = 2$, $M = 1$ case in Section 5 is more general than it seems. There is no need either for considering more

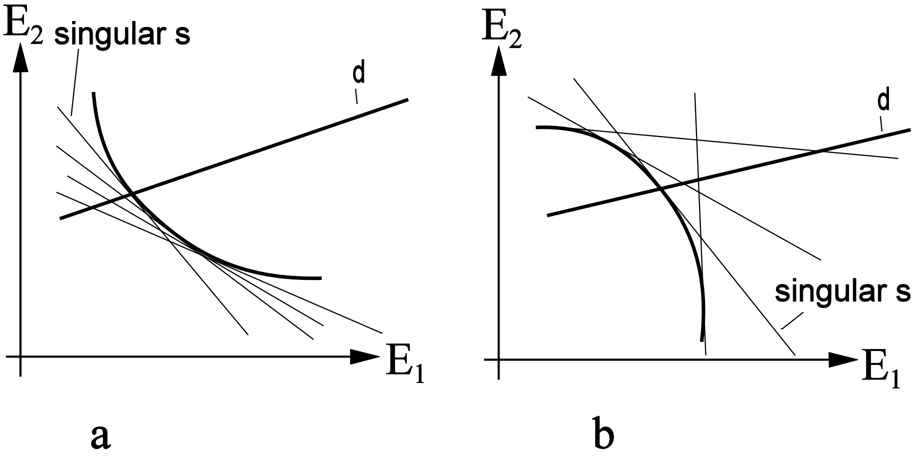

Figure 6: Evolution of strategy s in a two-dimensional environment in the presence of another strategy d. The thin lines represents the ZNGIs of the different versions of strategy s while the thick line is the ZNGI of strategy d.

than two environmental dimensions in order to discuss local adaptive dynamics in a one-dimensional trait space or considering more than one trait dimension if the environment is two-dimensional.

Appendix: The wedge product and its properties

First, as a review of notations, let us remind ourselves that the determinant of a $K \times K$ matrix a_{ij} is defined as

$$\det \boldsymbol{a} = \sum_{\sigma \in S^K} (-1)^\sigma a_{1\sigma(1)} \cdot a_{2\sigma(2)} \cdot \ldots \cdot a_{K\sigma(K)} = \sum_{\sigma \in S^K} (-1)^\sigma \prod_{l=1}^{K} a_{l\sigma(l)}$$

where S_K is the group of permutations of the index set $\{1, \ldots, K\}$ and $(-1)^\sigma$ is ± 1 if the permutation σ is even or odd.

Define the wedge product of vectors $\boldsymbol{u}$ and $\boldsymbol{v}$ (elements of an arbitrary vector space $\boldsymbol{V}$) as their anti-symmetrized tensor product:

$$\boldsymbol{u} \wedge \boldsymbol{v} = \frac{1}{\sqrt{2}} (\boldsymbol{u} \circ \boldsymbol{v} - \boldsymbol{v} \circ \boldsymbol{u}).$$

The same is true for K number of vectors $\boldsymbol{a}^i \in \boldsymbol{V}$ $(i = 1, \ldots, K)$:

$$\bigwedge_{i=1}^{K} \boldsymbol{a}^i = \frac{1}{\sqrt{K!}} \sum_{\sigma \in S^K} (-1)^\sigma \boldsymbol{a}^{\sigma(1)} \circ \boldsymbol{a}^{\sigma(2)} \circ \ldots \circ \boldsymbol{a}^{\sigma(K)}.$$

(The prefactor $1/\sqrt{K!}$ is a question of taste, of course.)

If you are not familiar with tensors, the simplest way to imagine them is as a matrix that is not necessarily two-dimensional: The number of indices can be any positive integer. In index notation, the tensor product of vectors $\boldsymbol{a}^1, \boldsymbol{a}^2, \ldots, \boldsymbol{a}^K$ *is:*

$$\left(\boldsymbol{a}^1 \circ \boldsymbol{a}^2 \circ \ldots \circ \boldsymbol{a}^K \right)_{j_1, j_2, \ldots, j_K} = \prod_{l=1}^{K} a^l_{j_l}$$

where a^i_j *denotes the* j*th component of the vector* $\boldsymbol{a}^i$*. (For* $K = 2$*, this is identical to the diadic product of vectors.)*

For a finite dimensional $\boldsymbol{V}$, one can spell the wedge product out in index notation:

$$\left(\bigwedge_{i=1}^{K} \boldsymbol{a}^i \right)_{j_1, j_2, \ldots, j_K} = \frac{1}{\sqrt{K!}} \sum_{\sigma \in S^K} (-1)^\sigma \prod_{l=1}^{K} a^{\sigma(l)}_{j_l}.$$

In this K dimensional matrix, the only elements that can be non-zero are those where $j_1, j_2, \ldots, j_K$ are all different values. Consequently, the wedge product vanishes for $K > \dim \boldsymbol{V}$. For $K = \dim \boldsymbol{V}$, all non-zero element equals to $\pm \det \boldsymbol{a} / \sqrt{K!}$, where matrix $\boldsymbol{a}$ is built from the vectors $\boldsymbol{a}^i$. As we have $K!$ number of such non-zero elements, the (Euclidean) norm of the wedge product is

$$\left| \bigwedge_{i=1}^{K} \boldsymbol{a}^i \right| = |\det \boldsymbol{a}|$$

for $K = \dim \boldsymbol{V}$. As it is well-known, $|\det \boldsymbol{a}|$, which is the wedge product of the $\boldsymbol{a}^i$s, is the K dimensional volume of the paralellepiped spanned by the vectors $\boldsymbol{a}^i$. For $K < \dim \boldsymbol{V}$ (including the case $\dim \boldsymbol{V} = \infty$), one can still say that the wedge product is the K dimensional volume in the subspace generated by our vectors. The K dimensional volume vanishes for $K > \dim \boldsymbol{V}$, as predicted by the wedge product.

If we have a scalar product defined in our vector space, we can introduce a scalar product for tensors component-wise and denote it by $*$. For instance,

$$\left(\boldsymbol{e}^1 \circ \boldsymbol{e}^2 \circ \ldots \circ \boldsymbol{e}^K\right) * \left(\boldsymbol{f}^1 \circ \boldsymbol{f}^2 \circ \ldots \circ \boldsymbol{f}^K\right) = \prod_{l=1}^{K} \left(\boldsymbol{e}^l \boldsymbol{f}^l\right).$$

Direct calculation shows the validity of Eq. (13):

$$\left(\bigwedge_{i=1}^{K} \boldsymbol{e}^i\right) * \left(\bigwedge_{j=1}^{K} \boldsymbol{f}^i\right) =$$

$$\left(\frac{1}{\sqrt{K!}} \sum_{\sigma \in S^K} (-1)^\sigma \boldsymbol{e}^{\sigma(1)} \circ \ldots \circ \boldsymbol{e}^{\sigma(K)}\right) \cdot \left(\frac{1}{\sqrt{K!}} \sum_{\sigma' \in S^K} (-1)^{\sigma'} \boldsymbol{f}^{\sigma'(1)} \circ \ldots \circ \boldsymbol{f}^{\sigma'(K)}\right) =$$

$$\frac{1}{K!} \sum_{\sigma \in S^K} \sum_{\sigma' \in S^K} (-1)^{\sigma\sigma'} \prod_j \left(\boldsymbol{e}^{\sigma(j)} \cdot \boldsymbol{f}^{\sigma'(j)}\right) = \sum_{\sigma \in S^K} (-1)^\sigma \prod_l \left(\boldsymbol{e}^l \cdot \boldsymbol{f}^{\sigma(l)}\right) =$$

$$= \det \left(\boldsymbol{e}^i \cdot \boldsymbol{f}^j\right).$$

The last thing we need is the relation

$$(\boldsymbol{u} \wedge \boldsymbol{v})^2 + (\boldsymbol{u} \cdot \boldsymbol{v})^2 = \boldsymbol{u}^2 \cdot \boldsymbol{v}^2,$$

which is the basis of Eqs. (14) and (15). We leave this for the reader as an exercise.

Scalar, tensor, and wedge products can be defined in infinite dimensional spaces, including function spaces, without problems. If u and v are two functions, their scalar product is:

$$\int_{-\infty}^{+\infty} f(x) g(x) dx;$$

their tensor product is:

$$(f \circ g)(x, y) = f(x) \cdot g(y);$$

and their wedge product is:

$$(f \wedge g)(x, y) = \frac{1}{\sqrt{2}} \left[f(x) g(y) - f(y) g(x)\right].$$

All of the formulas above remain valid for functions. This is the basis of the application of our framework for resource utilization functions (Box 9).

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