Geometrical envelopes: extending graphical contemporary niche theory to communities and eco-evolutionary dynamics

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Abstract

Contemporary niche theory is a powerful structuring framework in theoretical ecology. First developed in the context of resource competition, it has been extended to encompass other types of regulating factors such as shared predators, parasites or inhibitors. A central component of contemporary niche theory is a graphical approach popularized by Tilman that illustrates the different outcomes of competition along environmental gradients, like coexistence and competitive exclusion. These food web modules have been used to address species sorting in community ecology, as well as adaptation and coexistence on eco-evolutionary time scales in adaptive dynamics. Yet, the associated graphical approach has been underused so far in the evolutionary context. In this paper, we provide a rigorous approach to extend this graphical method to a continuum of interacting strategies, using the geometrical concept of the envelope. Not only does this approach provide community and eco-evolutionary bifurcation diagrams along environmental gradients, it also sheds light on the similarities and differences

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between those two perspectives. Adaptive dynamics naturally merges with this ecological framework, with a close correspondence between the classification of singular strategies and the geometrical properties of the envelope. Finally, this approach provides an integrative tool to study adaptation between levels of organization, from the individual to the ecosystem.

Keywords: Coexistence, competition, zero net growth isocline, community ecology, species sorting, adaptive dynamics, evolutionary branching

1. Introduction

Competition is a ubiquitous interaction among living organisms, and thus a major driver of community structure and evolution by natural selection. As such, it was at the core of the very first mathematical models of population
5 dynamics and theoretical ecology (Lotka, 1925, Volterra, 1926, Gause, 1934). However, the explicit inclusion of resources for which species compete only came several decades later with the pioneering works of MacArthur and colleagues (MacArthur and Levins, 1964, MacArthur and Wilson, 1967, MacArthur, 1970). Mechanistic competition models, or modules, allow a useful graphical representation introduced by MacArthur and Levins (1964), developed by León and
10 Tumpson (1975) and largely popularized by Tilman (1980, 1982), which summarizes graphically the different outcomes of competition along environmental gradients, delimiting the coexistence regions from competitive exclusion or founder control. This method relies on the combination of three key graphical
15 ingredients: Zero Net Growth Isoclines (ZNGIs), consumption/impact vectors and supply points. These respectively represent a species' minimal requirements, its consumptive impacts, and the externally-driven resource availability in the absence of any consumer. Supported empirically (Miller et al., 2005), the theory also brings strong conceptual results on the conditions for coexistence

20 consistent with the competitive exclusion principle (Levin, 1970).

The concept of resource competition can be generalized to encompass any kind of regulating factors that mediate interspecific interactions. This was done by Chase and Leibold (2003) under the unifying umbrella of “contemporary
25 niche theory”, further formalized by recent developments (Mészéna et al., 2006, Barabás et al., 2014b). For example, two prey sharing one predator formally behave as if they were competing for a single resource, a situation referred to as apparent competition by Holt (1977). This allows the use of the graphical representation in this generalized framework, as was done with apparent com-
30 petition plus resource competition by Holt et al. (1994), Grover (1995), Leibold (1996) and Chase and Leibold (2003). Interference competition through explicit inhibitory product emission also fits in this framework, with the inhibitor playing the role of a regulating factor (Gerla et al., 2009). Recently, several authors further extended this graphical approach to take into account several phenom-
35 ena: nutrient cycling (Daufresne and Hedin, 2005), cooperation (de Mazancourt and Schwartz, 2010), niche construction (Kylafis and Loreau, 2011) and population structure, either spatial (Ryabov and Blasius, 2011, Haegeman and Loreau, 2015) or demographic (Loreau and Ebenhöh, 1994, Schellekens et al., 2010).

40 Popularized in the context of a couple of interacting species, these niche theoretic models can be scaled up to investigate community assembly, based on the idea that local environmental conditions are the drivers of species sorting from a large or potentially infinite number of species along a trade-off curve (Leibold et al., 2004). This approach relies on the key assumption that ‘everything is
45 everywhere’, namely that there is no dispersal limitation to a species’ presence (Baas Becking, 1934, De Wit and Bouvier, 2006). The associated generalized

graphical methods uses the concept of geometrical envelopes, the boundary of a family of curves, providing a natural way to look graphically at species sorting along an environmental gradient (Armstrong, 1979, Tilman, 1980, 1982, Leibold, 1996, Chase and Leibold, 2003, Schade et al., 2005, Danger et al., 2008). Community composition and levels of regulating factors along the gradient can thus be investigated. These mechanistic models naturally fit into trait-based approaches, which have garnered recent interest in ecology (Lavorel and Garnier, 2002, McGill et al., 2006, Westoby and Wright, 2006, Litchman and Klausmeier, 2008). Traits hold the key to linking trade-offs from the organism level to ecosystem functions and services, in both aquatic and terrestrial ecosystems (Litchman et al., 2007, Lavorel and Grigulis, 2012). Trait-based approaches also are a natural framework to study community responses to climate change (Adler et al., 2012, Thomas et al., 2012, Barabás et al., 2014b).

Simultaneously, it has long been recognized that organisms are the product of their evolutionary history (Dobzhansky, 1973) and there is growing evidence of the interplay between ecology and evolution (Thompson, 1998, Yoshida et al., 2003, Hairston et al., 2005, Grant and Grant, 2006, Stuart et al., 2014). However, the influence of this past or present evolution on food web modules remains understudied. Theoretically, those questions have been addressed during the last decades using Adaptive Dynamics (Hofbauer and Sigmund, 1990, Geritz et al., 1997, 1998, Dieckmann and Law, 1996). This powerful framework allows one to address evolution in arbitrarily complex ecological models. As an evolutionary game theory approach, this is done by including the density- and frequency-dependent selection arising from the feedback loop between the evolving population and its environment (Dieckmann and Metz, 2006). It clarifies the conditions under which evolution acts as an optimizing process (Dieckmann

and Ferrière, 2004, Metz et al., 2008) and leads to the concept of evolutionary
75 branching, a potential prelude to diversification (Geritz et al., 1997, 1998, Metz
et al., 1996, Dieckmann and Doebeli, 1999). Unlike species sorting, adaptive
dynamics considers local invasibility only. Evolution can thus get stuck on local
but not global fitness maxima. When applied to food web modules, this enables
one to investigate the evolutionary stability of coexistence in various ecological
80 situations (Schreiber and Tobiason, 2003, Shores et al., 2008, Klausmeier et al.,
2007, Zu et al., 2015). Yet the conditions that allow evolutionarily stable coex-
istence remain unclear, as ecological coexistence often vanishes on evolutionary
time scales through convergent selection. Importantly, the graphical represen-
tation is still helpful in those adaptive competition modules to perform invasion
85 analysis when combined with ZNGI geometrical envelopes (Mészéna and Metz,
1999).

The concept of the envelope has a long history in mathematical optimiza-
tion and its applications. It has for example its own theorem in economics,
90 the Envelope Theorem (Samuelson, 1947), and is related to the Pareto frontier
(Pareto, 1906), a multi-objective optimization concept first introduced in eco-
nomics and now commonly used in engineer and environmental sciences (Mar-
ler and Arora, 2004, Seppelt et al., 2013, Lester et al., 2013). Envelopes of
environment-dependent growth rate functions have been used in ecology to
95 identify the optimal species corresponding to given environmental conditions
(Eppley, 1972, Norberg, 2013). In resource competition theory, the idea of tak-
ing the ZNGI envelope of a continuum of competing strategies can be traced
back to Tilman (1982), who applied it heuristically to species sorting from a re-
gional pool or adaptive foraging at the individual scale. It has been used more
100 recently in the context of communities under the names ‘community ZNGI’

(Danger et al., 2008, Schade et al., 2005) or ‘overall ZNGI’ (Chase and Leibold, 2003). Meszna and Metz (1999) introduced the ZNGI envelope in the eco-evolutionary context and called it ‘the boundary’. They showed how evolution through the trait substitution process of adaptive dynamics can be pictured by
105 ZNGIs rolling along their envelope, and how this helps identify evolutionary singularities and deduce their properties, both graphically.

The aim of the paper is to unite the theoretical approaches to community assembly processes and eco-evolutionary dynamics under the common umbrella
110 of a graphical theory of interaction, using geometrical envelopes. This provides a promising tool to investigate adaptation, diversification and functioning along environmental gradients. We first review step-by-step how to apply the graphical method to competition modules with a few species, combining the concepts of invasion analysis and impact map. Then, we show through a rigorous mathe-
115 matical framework how those ideas can be naturally extended to a continuum of competitors using geometrical envelopes. Building on the intuitions of Meszna and Metz (1999), we demonstrate for general non-linear ZNGIs how their envelope geometry relates to local invasibility. Moreover, the use of the impact ray map allows us to identify and characterize geometrically the eco-evolutionary
120 singularities associated with a given supply point. This provides both community and eco-evolutionary bifurcation diagrams, predicting a vast range of possible adaptive behaviors along the environmental gradients. Conditions leading to robust coexistence, evolutionary priority effects and branching points can be easily identified, as they present unambiguous graphical signatures. Conceptu-
125 ally, this graphical approach shows how adaptive dynamics naturally combines with mechanistic competition theory. It also emphasizes the similarities and differences between species sorting from a regional pool and evolution through

small step mutations, a global versus local picture. The envelope approach provides a unified tool to navigate between scales through adaptation, from the individual to the ecosystem level. Finally, we illustrate the method through the example of a versatile model of competition on two resources (Schreiber and Tobiason, 2003), shedding new light on the conditions leading to the evolution of resource specialization.

2. Modeling framework and analysis

2.1. Standard graphical construction for n competitors

Let us first introduce the general class of mathematical models treated in this paper. We consider a community of n species, the abundances of which are denoted $\mathbf{N} = (N_1, N_2, \dots, N_n)$, which interact through p regulating factors $\mathbf{R} = (R_1, R_2, \dots, R_p)$. The dynamics of N_j and R_i obey the following equations:

$$\frac{dN_j}{dt} = w_j(R_1, R_2, \dots, R_p) N_j \quad (1a)$$

$$\frac{dR_i}{dt} = l_i(S_i - R_i) + \sum_{j=1}^n I_{ij}(R_1, R_2, \dots, R_p) N_j \quad (1b)$$

where w_j is the net growth rate of population j and I_{ij} its per capita impact on the regulating factor i . No assumptions are made about their expression, except that they both only depend on the regulating factors $\mathbf{R}$. We thus follow Meszéna et al. (2006) by considering that interactions between individuals are indirect, only mediated by the regulating factors. As a particular case of Meszéna et al. (2006), eq. (1b) assumes that the total impact of a population on a regulating factor is simply proportional to its density. Note that we have chosen the convention that resource consumption corresponds to negative impact I_{ij} but also allowed positive I_{ij} , for example with shared predators. Finally, the supply point $\mathbf{S} = (S_1, S_2, \dots, S_p)$ and the leaching or mortality rates l_i parametrize the semi-chemostat intrinsic dynamics of the regulating factors, which interact only indirectly, through the species $\mathbf{N}$. Particularly suited for experimental

setups (Novick and Szilard, 1950, Monod, 1950), this framework is classically
 used to describe abiotic resource dynamics in a wide range of systems (Tilman,
 1982, Grover, 1997, Loreau, 1998a). For biotic resources, a well chosen change
 155 of variables can be made to map logistic growth into the chemostat dynamics
 of eq. (1b) (see Appendix A). Examples of models following the particular
 form of eq. (1) include resource-consumer modules (Tilman, 1980, Wolkowicz
 and Lu, 1992, Schreiber and Tobiason, 2003), food webs with keystone preda-
 tion (Holt et al., 1994, Leibold, 1996), material-cycle models (Loreau, 1998b,
 160 Daufresne and Hedin, 2005) and interference competition through inhibitory
 product emissions (Gerla et al., 2009).

We will restrict our analysis of this system to its equilibria. Setting aside un-
 realistic fine-tuning between the demographic parameters, this implies that the
 165 maximal number of coexisting populations can not be greater than the number
 p of regulating factors, a classical result known as the Competitive Exclusion
 Principle (CEP) or Dimension-Diversity Theorem (Levin, 1970, Gyllenberg and
 Meszéna, 2005, Meszéna et al., 2006). Because of the non-linear feedback loops
 between the regulating factors and the population densities, it is generally not
 170 possible to find analytical expressions for the equilibria of eq. (1), except for
 some particular systems. However, it is possible to visualize those solutions
 graphically for up to three regulating factors, following a long tradition in the-
 oretical ecology (León and Tumpson, 1975, Tilman, 1980, 1982, Leibold, 1996,
 Grover, 1997, Chase and Leibold, 2003). The aim here is to review this graph-
 175 ical construction in the case of the general model of eq (1). Doing so, we will
 introduce the associated basic concepts and notations needed for our general-
 ization of this approach to the community and evolutionary frameworks in the
 next sections.

Table 1: Notation

Notation		Definition
		Regulating factor
i		index
p		total number
R_i		density
S_i		external supply
l_i		intrinsic per capita loss rate
Finite case	Continuous case	Interacting population
j	x	index/trait value
n	$\mathcal{X}$	total number/trait space
N_j	$N(x)$	abundance
w_j	$w(x)$	per capita net growth rate
I_{ij}	$I_i(x)$	impact on regulating factor i
$\tilde{I}_{ij}$	$\tilde{I}_i(x)$	renormalized impact on regulating factor i
	$H(x)$	second derivative of the invasion fitness
	$J(x)$	derivative of the fitness gradient
		Schreiber and Tobiason's model
α		resource interaction shape parameter
m		per capita mortality rate
g_i	$g(x)$	per capita gross growth rate
		Acronyms
ZNGI		Zero Net Growth Isocline
CEP		Competitive Exclusion Principle
ESS		Evolutionarily Stable Strategy
CSS		Convergence Stable Strategy
PIP		Pairwise Invasibility Plot

180 The method consists of two steps: invasion analysis and impact map. This decomposes the environmental feedback loop into its sensitivity and impact components following the terminology of Meszna and colleagues (Meszna and Metz, 1999, Meszna et al., 2006), which shares strong similarities with Chase and Leibold’s (2003) concepts of requirement and impact niches. To help visu-
185 alize our method, we will illustrate it by presenting the case of n populations $N_1, N_2, \dots, N_n$ interacting through two regulating factors R_1 and R_2 . While described in general terms in the main text, we will use a flexible resource competition model introduced by Schreiber and Tobiason (2003) as a concrete example (see Box 1 and Figures). The graphical construction of the ecological bifurca-
190 tion diagram follows two distinct steps, that will naturally be extended later in the eco-evolutionary case.

Invasion analysis. Let us first focus our attention on the population equations, eq. (1a). At equilibrium, they imply for every population that either $N_i = 0$ (the population is absent) or $w_i = 0$ (its net growth rate is zero). There are thus
195 three possible kind of equilibria: ‘empty’ or washout state with no population, one non-zero population only, or coexistence of two distinct populations with extinction of the other $n - 2$ populations. Coexistence of three or more different populations on two regulating factors is not possible due to the CEP. From equation (1a), the presence of a population i in the system restricts R_1 and
200 R_2 to $w_i(R_1, R_2) = 0$. Graphically, this defines the so-called Zero Net Growth Isocline of population i or ZNGI_i (Tilman, 1980). For each competitor i , this curve delimits in the (R_1, R_2) plane the regions where net growth is positive ($w_i > 0$) from the ones where net growth is negative ($w_i < 0$) (see Fig. 1). A direct implication is that coexistence between populations at equilibrium is
205 only possible for (R_1, R_2) where their two ZNGIs intersect. On the contrary, the

‘empty’ equilibrium with no population exists for any set of regulating factors, as none of the populations is imposing its zero net growth constraint on the regulating factors.

210 More importantly, the ZNGIs also allow one to investigate the stability against invasion of those equilibria through invasion analysis. A necessary condition for any equilibrium involving either 0, 1 or 2 populations to be stable is for the point (R_1, R_2) to be located outside the positive growth regions of all the other potential invaders (Tilman, 1982, Leibold, 1996). Thus, the potentially
 215 stable ‘empty’ equilibria are the ones for which (R_1, R_2) are simultaneously located outside (in the direction of lowered growth rate) the whole set of ZNGIs (shaded regions in Fig. 1). Population i stable equilibria can only be located on the portion of ZNGI_i that is outside all the other ZNGIs, and the same rule extends to stable coexistence points between two populations. The set of
 220 points (R_1, R_2) corresponding to non-empty potentially stable equilibria form what we can call the outer envelope of the ZNGIs (thicker border in Fig. 1). To conclude, a ZNGI directly represents both the minimum requirements and the competitive ability of its corresponding population.

225 *Supply point mapping.* We have so far identified the candidate (R_1, R_2) values associated with the different kinds of possible equilibria using eq. (1a) only. Yet the solutions (R_1, R_2) also have to satisfy the limiting factor equations eq. (1b) set equal to zero. When solved together, this obviously makes them functions of the parameters of the system, including the supply point. To draw a
 230 bifurcation diagram, we would like to know for every supply point which are the corresponding (R_1, R_2) at equilibrium and thus deduce its associated characteristics (‘empty’, one population or coexistence). In practice, the map is

Figure 1: Invasion analysis for a set of 4 competing populations consuming two resources R_1 and R_2 . Competitors are labeled with i from 1 to 4 (respectively blue, purple, yellow, and green). They follow Schreiber and Tobiasson (2003) model described in Box 1 with $x_i = 0.2i$ and $m = 1$. Resources are either A) interactive essential ($\alpha = -5$) or B) antagonistic ($\alpha = 2$). Invasion analysis consists in drawing the set of ZNGIs (thin), selecting its outer envelope corresponding to non-invadable single population equilibria (thick) and potential coexistence points (black dots); the stable ‘empty’ equilibria are located under the envelope (light blue). In the essential case, each strategy has a range of non-invadable equilibria and can potentially coexist with the neighboring populations. In the antagonistic case, the extreme strategies ($x_1 = 0.2$ and $x_4 = 0.8$) exclude all the other ones but can potentially coexist together.

performed using the supplementary constraints emerging from equations (1b) taken at equilibrium. First, note that this map is trivial for the regulating factors associated with the ‘empty’ equilibrium. Indeed, having all the N_i equal to 0 leads to $\mathbf{S} = \mathbf{R}$. This means that if we now draw the ZNGI envelope in the supply plane, all the supply points situated outside of it will map to the ‘empty’ equilibrium (White region, Fig. 2).

Where are the supply points leading to non-zero populations located? Let us first put aside the coexistence case, and focus on a single population equilibrium with $N_i \neq 0$ and $N_j = 0$ for $i \neq j$. Setting eq. (1b) equal to zero leads to

$$\mathbf{S} = \mathbf{R} + N_i \tilde{\mathbf{I}}_i(\mathbf{R}) \quad (2)$$

where $\tilde{\mathbf{I}}_i = (I_{1i}/l_1, I_{2i}/l_2)$ is the impact vector renormalized to account for different loss rates, N_i is a positive density and $\mathbf{R}$ belongs to ZNGI_{*i*} stable portion of the envelope. Eq. (2) means that for a given regulating factor point on ZNGI_{*i*}, the corresponding supply points $\mathbf{S}$ are located along the ray that starts from the point (R_1, R_2) when $N_i = 0$ and moves away from it following the direction vector $\tilde{\mathbf{I}}_i$ as N_i increases. This means that all the supply points along a given ray will map to the same regulating factor at equilibrium, but with different densities. Those ‘impact rays’, as we suggest to call them, thus allow us to deduce graphically the supply points regions associated with a given single population equilibrium by moving (R_1, R_2) along its corresponding ZNGI portion along the envelope (Fig. 2). Let us note the difference between working with the limiting factors $\mathbf{R}$ versus their supply $\mathbf{S}$. While the invasion analysis takes place in a density-independent framework as we compare the growth rates of the different competitors for given $\mathbf{R}$ (Fig. 1), including the supply point map and thus the environmental feedback loop for given $\mathbf{S}$ fully captures the density and frequency dependence of the model (Fig. 2).

In the coexistence case, the method is slightly different. Equations (1b) now leads to $\mathbf{S} = \mathbf{R} + N_i \tilde{\mathbf{I}}_i(\mathbf{R}) + N_j \tilde{\mathbf{I}}_j(\mathbf{R})$ with $\mathbf{R}$ at the two ZNGIs’ intersection. Thus, all the supply points situated in the cone originating at $\mathbf{R}$ and delineated by vectors $\tilde{\mathbf{I}}_i$ and $\tilde{\mathbf{I}}_j$ map to this coexistence equilibrium when both densities are positive (Fig. 2B). The impact vectors have to be different for this region not to be degenerate. However, this coexistence point is dynamically stable only if (see Appendix B):

$$(I_{1i}I_{2j} - I_{1j}I_{2i}) \left(\frac{\partial w_i}{\partial R_1} \frac{\partial w_j}{\partial R_2} - \frac{\partial w_i}{\partial R_2} \frac{\partial w_j}{\partial R_1} \right) > 0 \quad (3)$$

This is known as the mutual invasibility criterion and can be interpreted graph-

ically in terms of relative position between ZNGIs and impact rays (León and
Tumpson, 1975, Tilman, 1982, Leibold, 1996). Here, we simply note that it
graphically translates for this region as not being an overlap between the two
adjacent non-invadable single population regions (Fig. 2B). When those two
regions do overlap, coexistence is unstable and replaced by a priority effect be-
tween the two single-population equilibria (Fig. 2A).

Figure 2: Supply point map for a set of 4 competing populations consuming two resources R_1 and R_2 following the model of Box 1. Same configuration and parameters as Fig. 1. The stable ZNGI portions identified in Fig. 1 have been directly transposed into the supply point space. Starting from each non-invadable envelope portion (thick, plain), drawing a subset of the corresponding impact rays (thin, arrowed) helps visualizing the map that associates to every supply point its corresponding regulating factors at equilibrium. The boundaries of each portion map (thick, arrowed) combined with its corresponding ZNGI portion delimit zones of similar equilibria of the bifurcation diagram. A: there are four single-population zones (green, yellow, purple and blue) plus an empty one (white). Note that some of the former overlap, accounting for priority effects. B: there are two single-population zones (blue, green) plus an empty one (white) and a coexistence one (gray). Note that all the impact rays map to the same point in the latter case.

To summarize, an ecological bifurcation diagram as a function of the supply
points (S_1, S_2) can be obtained by combining ZNGIs and impact rays through
the following steps: (1) Draw the ZNGIs of the different populations and iden-
tify their outer envelope. (2) Locate the regulating factor points corresponding
to the ‘empty’ solutions (outside the envelope), population i only solutions (on

ZNGI_i portions of the envelope) and the coexistence solutions (where the latter portions intersect, typically making a ‘kink’ in the envelope). (3) Identify the regions of the supply point plane scanned by each population impact rays when
 285 its origin moves along its corresponding ZNGI portion (a subset of impact rays can also be represented). (4) Identify potentially stable coexistence ‘cones’ from the kinks of the envelope.

There are two major advantages of this graphical approach. First, it delimits
 290 its regions along the supply gradients for which a given species assemblage is present in the system. Historically, this allowed one to identify conditions for coexistence of two consumers (Tilman, 1982) and describe species succession along a nutrient gradient (Tilman, 1982, Leibold, 1996). Secondly, drawing the impact rays also allows one to deduce the equilibrium regulating factor levels
 295 and sometimes also population densities directly on the diagram. For consumers growing on essential resources, this is a way to identify which factor will be limiting for a given supply (Tilman, 1982). The direction of the impact vectors also enables one to assess the relative impact of a population on the regulating factors. But using impact rays has other advantages, which have been under-
 300 used so far. Sometimes, a given supply point can be reached by several impact rays, which means that it maps to several distinct equilibria. In this case, the system presents alternative stable states, which is the basis of the ‘founder effect’. There is an interesting diversity of situations that can be encountered depending on the states involved in this bistability. The most well-known case
 305 is one single population versus another one (Fig. 2A). But it is also possible to have alternative stable states inside a single population as it is often the case for structured populations (Schreiber and Rudolf, 2008, Guill, 2009, Schellekens et al., 2010), or between a community and an ‘empty’ state as it is common in

the presence of a positive feedback loop or an ecosystem engineer (Scheffer et al.,
 310 2001, Rietkerk et al., 2004, Kéfi et al., 2010). The graphical method presented
 here allows one to identify alternative stable states regions in the bifurcation
 diagram without ambiguity.

With this graphical construction, we have provided only some necessary con-
 315 ditions for the local stability of the different equilibria through invasion analysis,
 but those are not always sufficient. For example, a single population may have
 alternative stable states through an Allee effect. These stable states are gener-
 ally separated by unstable states that would not be identified explicitly as such
 by the scheme presented above. However, a careful study of the envelope of
 320 the impact rays moving along the ZNGI for a single-population equilibrium can
 supplement this by further restricting an impact ray to its stable portion (see
 Appendix B). This idea will be used again in the eco-evolutionary case to iden-
 tify branching points (see supply point mapping in section 2.3). Limit cycles
 and other nonequilibrium attractors are also a possibility, even when criterion
 325 (3) is satisfied, as the other stability criteria can not always be satisfied. Again,
 this would not be detectable on the graphical analysis. However, these two sit-
 uations do not happen for simple systems like the standard two consumers on
 two resources (Tilman, 1982, Chase and Leibold, 2003, Schreiber and Tobiason,
 2003), although they can for three or more resources (Huisman and Weissing,
 330 1999).

2.2. Extension to a continuum of competitors: the ZNGI envelope

We now extend the previous framework from a discrete set of populations to a
 continuous set of strategies. The evolution of quantitative traits and phenotypic
 plasticity can be considered as occurring among a continuous set of strategies, as
 335 can community assembly (Tilman, 1982, 1988, Chase and Leibold, 2003). Our

motivation here is twofold. First, we aim at providing a rigorous framework to address the question of species sorting in communities and integrate this effect at the ecosystem scale. Second, this introduces the basic tools necessary to perform the eco-evolutionary analysis of the next section. This will highlight the similarities and differences between the species sorting and the adaptive dynamics approaches.

Formally, the generalization to a continuum of competitors is straightforward with the results of the previous section in mind. Omitting time-dependencies to lighten the notation, the dynamics of the system now reads:

$$\frac{\partial N(\mathbf{x})}{\partial t} = w(\mathbf{R}, \mathbf{x}) N(\mathbf{x}) \quad (4a)$$

$$\frac{dR_i}{dt} = l_i(S_i - R_i) + \int_{\mathbf{x} \in \mathcal{X}} I_i(\mathbf{R}, \mathbf{x}) N(\mathbf{x}) \quad (4b)$$

where the subscript j is now replaced by its continuous analog, the trait vector $\mathbf{x}$, which contains the functional traits that fully describe the strategy of the population with density $N(\mathbf{x})$. The global impact of the competitors on regulating factor i is now obtained by integrating the impact $I_i(\mathbf{R}, \mathbf{x})$ of every strategy $\mathbf{x}$ over the whole trait space $\mathcal{X}$. This trait space has to be seen as the collection of all the variable trait combinations that could possibly be present in the system. We assume in practice that $\mathcal{X}$ is a connected subset of a real vector space. Usually, this trait space is constrained by trade-offs inequalities which account for correlations between the traits. This usually excludes ‘Hutchinsonian demons’ that outcompete all other species (Kneitel and Chase, 2004). In practice, those trade-offs are often taken to be saturated, *i.e.* as equalities instead of inequalities, in order to reduce the dimensionality of the trait space. When not, they simply add boundaries to the trait space. Note that we work at equilibrium, so the CEP still applies, which means that the $N(\mathbf{x})$ can only

360 be a sum of delta functions with a number of peaks lesser or equal to the number of regulating factors p . From now, we will assume the trait space $\mathcal{X}$ to be unidimensional, *i.e.* an interval, to simplify the analysis and denote the trait as x (but see Appendix C and Discussion).

Global invasion analysis. Let us extend the ideas presented in the previous section to a continuum of competitors using geometrical envelopes of ZNGIs. 365 This corresponds to species sorting, as all the strategies from the trait space are considered as potential invaders. Our aim here is to unify the different approaches and terminologies present in the literature (Meszena and Metz, 1999, Chase and Leibold, 2003, Danger et al., 2008), provide some analytical and 370 geometrical properties of envelopes, and combine them with impact rays to construct community/eco-evolutionary bifurcation diagrams.

The concept of the envelope is easy to understand graphically and allows an extension of the invasion analysis to a continuum of competitors. Let us 375 superimpose a large number of ZNGIs sampled from the trait space $\mathcal{X}$ and identify their discrete outer envelope in the sense of the previous section. When the number of ZNGI sampled tends toward infinity, this discrete envelope tends toward a (generally) smooth curve called the outer geometrical envelope of the ZNGI family (Fig. 3A). Note that to every point of this envelope, there is a 380 tangent ZNGI. Mathematically, this condition of tangency formally defines the geometrical envelope. Indeed, the points $\mathbf{R}$ belonging to the envelope of a set of ZNGI_x from $\mathcal{X}$ locally satisfy:

$$w(\mathbf{R}, x) = 0 \quad (5a)$$

$$\partial_x w(\mathbf{R}, x) = 0 \quad (5b)$$

where equation (5a) accounts for the fact that $\mathbf{R}$ has to belong to one of the

Figure 3: Graphical representation of a continuous set of populations consuming two resources R_1 and R_2 following the model of Box 1 in the interactive essential case ($\alpha = -5$). A: the local envelope (thick, green) of the continuum of strategies $0 \leq x \leq 1$ has been displayed. A discrete subsample of strategies had their ZNGIs represented (thin, gray) and the corresponding trait value displayed at the point of contact with the envelope (thick, black). This local envelope appears to be global, as all the ZNGIs are situated above it. B: supply point mapping through the impact rays (arrowed lined). Ecologically, there is a single strategy outcompeting all the other ones when there is enough resources (supply points above the envelope). The optimal strategy tends to be specialized on R_1 as it becomes scarcer compared to R_2 , and vice-versa. Contrary to the discrete case (Fig. 2A), there is no priority effect zones between neighbor strategies. PIPs (black = resident can't exist, gray = +, white = -) have been displayed for comparison with adaptive dynamics framework (see section 2.3 and Fig. 5).

ZNGIs and equation (5b) imposes the supplementary condition of tangency.

385 Note that $\mathbf{R}$ is a priori considered independently of x in the invasion analysis and thus not targeted by the partial derivative. In practice, an explicit equation of the envelope linking R_2 to R_1 can be obtained by eliminating x from equations (5) or implicitly through a parametric equation.

390 Before moving on, let us emphasize the fact that eq. (5b) is a first order, that is, local criterion. As such, this does not insure that the envelope obtained with eq. (5b) has the global outer envelope behavior we are looking for. This situation can be understood by analogy with the problem of finding the global maximum of a differentiable function on a closed set. Setting its derivative equal
395 to zero only locates the function's local extrema, which can be either maxima

Figure 4: A: Local envelope (thick, green) for a continuum of strategies $0 \leq x \leq 1$ in the antagonistic case ($\alpha = 2$). A discrete subsample of strategies has been picked with their ZNGIs represented (thin, gray) and the corresponding trait value displayed at the point of tangency with the envelope (thick, black). The local envelope is an inner one and thus not part of the global one (thick), instead made of two portions of the boundary ZNGIs corresponding to the R_1 and R_2 specialists (resp. blue and red). B: supply point mapping *via* the impact rays (arrowed lined). There is room for coexistence in the ‘cone’ (gray) originating from the kink (black dot). Those results are very similar to the ones obtained in the discrete case (Fig. 2B).

or minima. The same happens with the local envelope obtained through eq. (5b). It can coincide with the global outer envelope we are looking for (Fig. 3A) and thus have its points $\mathbf{R}$ situated outside the whole ZNGI set as they satisfy $w(\mathbf{R}, x) \leq 0$ for any x . However, some portions of this envelope could also be local but not global while others could be inner envelopes, *i.e.* situated inside the whole ZNGI set with $w(\mathbf{R}, x) \geq 0$ for any x (green segments in Fig. 4A). Those inner envelope portions have to be discarded in the global analysis as they are highly unstable, with every strategy able to invade. There is one last situation to consider. Back to our analogy of maximizing a function, the global maximum could also be situated on the boundaries of its domain and thus not be detected by setting its derivative equal to zero. In our case, it means that the global outer envelope could also be made of ZNGIs whose traits are located on the boundaries of $\mathcal{X}$ (red and blue segments in Fig. 4A). To conclude, the

global invasion analysis is performed in the continuous case by putting together
410 the local envelope defined by eq. (5) and the boundary ZNGIs, and keeping
their global outer envelope only (see Fig. 3, 4).

When solving eq (5), a singular trait $x^*(\mathbf{R})$ is associated with every point $\mathbf{R}$
of the envelope (see Box 1 and Fig. 3,4). This trait corresponds to the ZNGI_x
415 that contributes to the envelope at that point $\mathbf{R}$. In the case of a global outer
envelope, it means that this strategy x is optimal for those specific regulating
factor values $\mathbf{R}$, by outcompeting all the other strategies. Note that the global
outer envelope can contain kinks where there is a discontinuity of $x^*(\mathbf{R})$ as $\mathbf{R}$
moves along the envelope. This means that two distinct ZNGIs are tangent to
420 the envelope at that specific point. As an important consequence, those are
the only values of the regulating factors where globally stable coexistence is
possible. Although kinks are generally plentiful in the discrete case between
neighboring strategies (Fig. 1), the majority of those kinks usually vanish when
the continuous limit is taken (Fig. 3). When globally stable coexistence of two
425 different strategies from a continuum does occur, the associated kinks in the
global envelope emerge at the self-intersections of the local envelope to which
has been added its boundary ZNGIs when needed (Fig. 4). This is one of the
major difference with the previous discrete approaches (Leibold, 1996, Chase
and Leibold, 2003) which we will discuss later. These kinks make globally sta-
430 ble coexistence particularly easy to find and characterize graphically.

Supply point mapping. There is virtually no difference with the discrete strategy
case. We only have to remember that there is a unique non-invadable strategy
 $x^*(\mathbf{R})$ associated with every point of the global envelope that is not a kink.
435 Plugging this relationship between the traits and the regulating factors into

the renormalized impact vector $\tilde{\mathbf{I}}(\mathbf{R}, x) = \mathbf{I}(\mathbf{R}, x)/l_i$ allows us to draw the impact rays originating on the envelope points, thus performing the mapping from the ZNGI envelope to the supply point. The envelope thus behaves like a community-wide ZNGI, with its associated impact rays. The functioning of
440 the whole community can indeed be understood as a single entity that behaves like a single population. At a kink, the coexistence cone is obtained by plotting the impact rays associated with the two coexisting strategies, and the stability criterion (3) is checked as before.

445 To summarize, the outcome of species sorting among a continuum of strategies can be seen from the community bifurcation diagram as a function of the supply points (S_1, S_2) . It is obtained by combining the envelope and impact rays through the following steps: (1) From the local envelope of the ZNGI continuum and its boundary ZNGIs, keep the global outer envelope. (2) For every
450 point of this envelope, identify the corresponding ‘optimal’ strategy. (3) Locate the regulating factor points corresponding to the ‘empty’ solutions (outside the envelope) and the potential coexistence solutions (the kinks). (4) Represent the supply point map by drawing impact rays from the envelope. (5) Identify the potentially globally stable coexistence ‘cones’ from the kinks.

455 2.3. *Eco-evolutionary extension: link with adaptive dynamics*

The global invasion analysis presented above considered that all the possible strategies from the trait space can invade the system and compete together. This explains why we have focused on determining the global envelope and discarded local but not global envelope portions. By doing so, we adopted an
460 ‘everything is everywhere’ approach (Baas Becking, 1934, De Wit and Bouvier, 2006). At the opposite, the strategy space could be explored by evolving a single population through small mutation steps. In the previous section, we have

presented a natural way to extend the graphical invasion analysis to a continuum of strategies by introducing the ZNGI envelope concept. As was shown
465 by Meszéna and Metz (1999), this framework naturally allows us to address eco-evolutionary equilibria of adaptive dynamics (Hofbauer and Sigmund, 1990, Geritz et al., 1997, 1998). In fact, the idea of addressing evolution with a graphical mutant invasion analysis can be traced back as far as the early developments of resource competition theory (MacArthur and Levins, 1964, MacArthur and
470 Wilson, 1967). Some methods based on graphical arguments in the trait space have already been developed to analyse evolutionary outcomes (Levins, 1962) and recently extended to fit in the density- and frequency-dependent context of adaptive dynamics (Rueffler et al., 2004, de Mazancourt and Dieckmann, 2004).

475 Here, we propose to further explore and describe the relationship between the ZNGI envelope and its geometrical properties and the evolutionary singular points and their classification. We will first provide some analytical results to support the intuition of Meszéna and Metz (1999). We will show how those results can be combined with the supply point mapping to provide a complete
480 graphical characterization of the singular points. This approach makes it possible to draw eco-evolutionary bifurcation diagrams along the supply gradients. The whole approach relies on the observation that the growth function $w(\mathbf{R}, x)$, represented by ZNGI_x , is actually the invasion fitness of a mutant x in a resident-dominated environment $\mathbf{R}(y)$. This means that the local envelope equations (5)
485 coupled with the supply point map given by the impact rays directly give the singular points of adaptive dynamics where the fitness gradient is zero. In the particular case of a one-dimensional trait x , we will show how the singular point classification is directly linked with the geometrical properties of the envelopes (but see Appendix C and discussion for the multidimensional case).

Local invasion analysis. The local evolutionary stability (in the sense of non-invasibility) of a singular point can be characterized using the second derivative of the invasion fitness (Geritz et al., 1998):

$$H(x) = \left[\frac{\partial^2 w(\mathbf{R}(y), x)}{\partial x^2} \right]_{y=x} \equiv \frac{\partial^2 w}{\partial x^2}. \quad (6)$$

495 Following adaptive dynamics terminology, a singular point for which H is negative is said to be a (local) Evolutionarily Stable Strategy (ESS), uninvadable by nearby strategies. This quantity is related to the geometrical properties of the envelope through the following relationship (see Appendix C for demonstration in the multidimensional trait case):

$$500 \quad H(x) = \frac{\partial w}{\partial R_2} \cdot \left(\frac{\partial^2 R_2}{\partial R_1^2} \Big|_E - \frac{\partial^2 R_2}{\partial R_1^2} \Big|_Z \right) \Big/ \left(\frac{dx}{dR_1} \right)^2 \quad (7)$$

where $\partial^2 R_2 / \partial R_1^2|_E$ and $\partial^2 R_2 / \partial R_1^2|_Z$ are the second derivatives of respectively the envelope and the tangent ZNGI, and thus quantify their curvature. The difference between the two latter terms describes the relative curvature and thus position between the envelope and the tangent ZNGI: when negative, the envelope is located under the ZNGI set. Conversely, when this difference is positive, the envelope is located above the ZNGI set. The sign of $\partial w / \partial R_2$ translates this relative position along the y axis in terms of relative fitness: when positive (as it is the case within our example, since R_2 is a resource), ‘under’ means ‘outer envelope’ ($w(\mathbf{R}, x) \leq 0$ for any nearby x) and ‘above’ means ‘inner envelope’ ($w(\mathbf{R}, x) \geq 0$ for any nearby x); conversely, when $\partial w / \partial R_2 < 0$, ‘under’ means ‘inner’ and ‘above’ means ‘outer’. Eq. (7) makes the formal link with adaptive dynamics: outer envelope portions always correspond to ESS while the inner ones, which were discarded during the global invasion analysis, are associated with non-ESS. Inner envelope portions play an important role in the

eco-evolutionary case as they can be associated with branching points (see below). Eq. (7) proves and generalizes the results of Meszena and Metz (1999) to the case of non-linear ZNGIs, as the curvature of the ZNGI comes into play. As demonstrated for ecological coexistence, evolutionarily stable coexistence can be found at the self-intersections of the local envelope. We showed that its evolutionary stability is directly linked to the ones of its two constituting strategies: coexistence is evolutionarily stable if and only if situated at the intersection of two outer ZNGI envelope portions (see Appendix C for demonstration). In any case, ESS characterization of singular points only depends on ZNGIs.

Figure 5: Eco-evolutionary bifurcation diagram along the supply gradients for the antagonistic case ($\alpha = 2$). A: full envelope composed of a non-ESS local portion (green) and two boundary ZNGIs (blue, red). The impact ray map (arrows, thin) helps visualizing the number and the properties of the singular points associated with a given supply point of the diagram. For example, every supply point inside the zone delimited by the impact ray envelope (black, thin) gives two boundary CSS, two repellers and one branching point. B: we only kept the global envelope and the skeleton of the impact ray map. Each zone delimited that way shares common properties that can be illustrated with PIPs (gray = +, white = -) being displayed at the exact location of their corresponding supply point (black dot, A). Invasion fitness is not defined for resident traits that do not allow the resident to exist (black).

Supply point mapping. It is in fact possible to further characterize the singular
 525 points graphically. Let us introduce the Jacobian of the fitness gradient

$$\begin{aligned} J(x) &= \frac{d}{dx} \left[\frac{\partial w(\mathbf{R}(y), x)}{\partial x} \right]_{y=x} \\ &\equiv \left(\frac{\partial}{\partial x} + \frac{\partial \mathbf{R}}{\partial x} \cdot \frac{\partial}{\partial \mathbf{R}} \right) \frac{\partial w}{\partial x} = H(x) + \frac{\partial \mathbf{R}}{\partial x} \cdot \frac{\partial}{\partial \mathbf{R}} \frac{\partial w}{\partial x} \end{aligned} \quad (8)$$

According to the adaptive dynamics classification of singular points, this Jacobian gives information about the singular point's convergence stability, telling if it is an attractor or a repeller for the 1D adaptive dynamics (Eshel, 1983, Geritz et al., 1998). More precisely, the singular point is said to be convergence
 530 stable if J is negative. Note that this differs from the previous criterion based on the second derivative H : for example, a singular point can be convergent stable but not evolutionarily stable, which is known as a branching point and can lead a single strategy to diversify into evolutionarily stable coexistence of two different strategies (Eshel, 1983, Metz et al., 1996, Geritz et al., 1997, 1998).
 535 It is possible to show the following relationship between J and H (see Appendix C for demonstration in the multidimensional trait case):

$$J = \left(\frac{\partial R_1}{\partial S_1} \Big|_Z \Big/ \frac{\partial R_1}{\partial S_1} \Big|_E \right) H \quad (9)$$

where $\partial R_1 / \partial S_1|_Z$ and $\partial R_1 / \partial S_1|_E$ describe how R_1 responds to its variation in supply, when R_1 moves along respectively the tangent ZNGI (ecological case,
 540 fixed strategy) and the envelope (eco-evolutionary case, adaptive strategy). The same relationship can be obtained for R_2 simply by replacing 1 by 2 from Eq. (9). First, note that $\partial R_1 / \partial S_1|_Z$ is non-negative for the usual consumer-resource or predator-prey interactions (but see Appendix B and C). This implies that J and H share the same signs when $\partial R_1 / \partial S_1|_E > 0$: an ESS is a CSS and a non-
 545 ESS is a repeller. Conversely, J and H have opposite signs when $\partial R_1 / \partial S_1|_E < 0$: an ESS is then non-convergent (Garden of Eden strategy) and a non-ESS is a

branching point (Geritz et al., 1998). This last situation can be understood as follows: the eco-evolutionary feedback is so strong that the sign of the limiting factor response to supply variation, materialized by $\partial R_1/\partial S_1|_E$, is completely
550 reversed compared to the purely ecological situation.

How can the sign of $\partial R_1/\partial S_1|_E$ be read graphically? To see this, we need to introduce the notion of envelope of impact rays, following the same definition of envelope introduced earlier in the case of ZNGIs. Indeed, the set of impact
555 rays generated by moving the regulating factor point along the ZNGI envelope usually itself possesses an envelope (black curve, Fig. 5 and movie S1 in the Supplementary Material). A given impact ray will touch and be tangent to this envelope at a unique contact point. The line portion of the impact ray situated between its origin and this point corresponds to supply points satisfying
560 $\partial R_1/\partial s_1|_E > 0$ while the other part corresponds to $\partial R_1/\partial s_1|_E < 0$. In general, crossing this envelope in the supply point space corresponds to the appearance or the disappearance of a pair of impact rays, i.e. singular points (see Fig. 5-6). This whole scheme can be understood as a way to use the supply point mapping to explicitly construct how the eco-evolutionary system responds to a local trait
565 perturbation, following the ideas presented by Meszéna and Metz (1999).

We can understand how this works in practice by looking at our example (see also movies S2 and S3 in the Supplementary Material) . In the interactive essential resource case, there is no impact ray envelope (see Fig. 3). According to
570 the previous section, this means that $\partial R_1/\partial s_1|_E > 0$ and thus all ESS are CSS. The absence of an impact ray envelope also implies that impact rays never cross each other, which explains why there is never more than one singular point per supply point. In the antagonistic resource case, there is always an impact ray

Figure 6: Details of the supply point map and its associated Pairwise Invasibility Plot (PIP) in the antagonistic case ($\alpha = 2$) for high but imbalanced (A,B) and balanced (C,D) resource supply, *i.e.* respectively $\mathbf{S} = (1.8, 2.8)$ and $\mathbf{S} = (2.8, 2.8)$. A: the impact rays map this supply point to three different eco-evolutionary equilibria on the envelope. The associated singular trait values are also displayed. B: PIP depicting the sign (gray = +, white = -) of the invasion fitness of a mutant with trait x' in a resident population with trait x . For a given resident strategy x , the success of the different invaders can be read along the corresponding vertical line. The limiting curves between the white and the gray regions correspond to invasion fitness equal to zero. Among them, the one-to-one line reminds us that the resident is at equilibrium. The eco-evolutionary fixed points are located at the intersection of this one-to-one line with the other contour or the boundary (colored dots). There are three of them here: one repelling singular point (green) and two boundary CSS $x = 0$ (red) and $x = 1$ (blue). The two latter strategies are locally non-invadable but not globally, as strategies different enough from them can invade. C,D: Contrary to the imbalanced case, this supply points gets mapped to three different points on the non-ESS envelope portion (green). Note that the middle impact ray corresponding to $x = 0.5$ goes through its tangency point on the impact ray envelope (black, thin) before hitting the ZNGI envelope (C). As explained in the main text, this is the signature of this singular point being a branching point, as can be visualized on the PIP (D).

envelope (see Fig. 5-6). Underneath the impact ray envelope, the same reason-
575 ing goes as for the interacting resource case. There is thus never more than one
non-ESS repeller in that region (Fig. 6A,B). In contrast, above the impact ray
envelope the impact ray map folds over on itself, leading to three singular points
per supply point (Fig. 6C,D). Among them, the impact ray in the middle goes
through its envelope tangency point before hitting the ZNGI envelope, which
580 means that $\partial R_1/\partial s_1|_E < 0$ and it thus corresponds to a branching point (Fig.
6D). The two other singular points are non-ESS repellers. In our example, the
impact ray envelope thus delimits the region where non-boundary impact rays
intersect. The emergence of alternative stable states as we cross the impact ray
envelope is a well-known phenomenon in bifurcation theory, where it is referred
585 to as a ‘cusp catastrophe’ (Strogatz, 2015).

As in the previous sections, evolutionary stable coexistence is only possible
for supply points located between the two impact rays originating from a kink
of the ZNGI envelope. Mutual invasibility, obtained by satisfying equation (3),
590 is also needed to ensure that this coexistence is ecologically stable. Moreover,
when polymorphism is saturated (as many distinct strategies as regulating fac-
tors) we have $J = H$ for each of the two coexisting strategies (see Appendix C).
Thus, evolutionarily stable coexistence is automatically convergence stable co-
existence and further evolutionary branching is impossible, in accordance with
595 the CEP (Mészéna and Metz, 1999). This last result is consistent with a recent
study of saturated polymorphism (Kisdi and Geritz, 2016).

To summarize, an eco-evolutionary bifurcation diagram along the regulating
factors supply can be obtained in the unidimensional trait case through the
600 following steps: (1) Draw the ZNGI envelope. (2) Identify the ESS and non-

Figure 7: Correspondance between the classification of singular strategies and their graphical characterization in the standard consumer-resource or predator-prey case where $I_2 \cdot \partial w / \partial R_2 > 0$, e.g. Schreiber and Tobiason's (2003) or Leibold's (1996). The classification has been adapted and simplified from Geritz et al. (1997). 'tangent IR' and 'non-tangent IR' stand for 'impact ray tangent to its envelope' and 'impact ray not tangent to its envelope', while 'cv.' stands for 'convergence'. The case where $I_2 \cdot \partial w / \partial R_2 < 0$ (e.g. nitrogen fixing) is obtained by permuting 'tangent IR' and 'non-tangent IR' from the figure.

ESS portions (given by the envelope's relative position with ZNGIs) and add boundary ZNGIs if necessary. (3) Draw the impact ray envelope and a subset of impact rays to represent the supply point map. (4) If there is an evolutionarily stable self-intersection of the ZNGI envelope, draw the coexistence cone. (5)

605 Identify the different regions delimited and the properties of the associated singular points (Fig. 7). Note that superimposing a Pairwise Invasibility Plot (PIP) (Geritz et al., 1997) for every region of the diagram helps in visualizing the eco-evolutionary characteristics of the system, like the number and properties of the singular points and mutual invasibility associated with singular dimorphism

610 (Fig. 3-6). Indeed, those conserved singular point characteristics make PIPs qualitatively similar inside a given region of the diagram.

Box 1: Schreiber and Tobiason consumer-resource model

Schreiber and Tobiason (2003) studied the evolutionary ecology of n consumer populations feeding on two resources with densities R_1 and R_2 . Their model is a particular case of model (1) from the main text,

with:

$$w_i(R_1, R_2) = g_i(R_1, R_2) - m \quad (10)$$

$$g_i(R_1, R_2) = [(x_i R_1)^\alpha + ((1 - x_i) R_2)^\alpha]^{\frac{1}{\alpha}} \quad (11)$$

where x_i and $1 - x_i$ account for investment in acquisition of respectively resource 1 and 2 (note this implies a linear trade-off), m is the constant per capita mortality rate and α controls the shape of the interaction between resources. Following Tilman's (1980, 1982) classification of resources relations, $\alpha < 0$ represents interactive essential resources (both necessary and slightly better in balanced proportions), $0 < \alpha < 1$ represents complementary resources (substitutable but better in balanced proportions), $\alpha = 1$ represents perfectly substitutable resources, and $\alpha > 1$ represents antagonistic resources (substitutable but worse in balanced proportions). The limiting cases $\alpha \rightarrow -\infty$ and $\alpha \rightarrow +\infty$ lead to respectively essential and switching resources (growth is limited by respectively the most limiting and the most abundant resource). The growth rate (11) is thus an elegant mathematical way to control the nutritional interaction between the resources. The intrinsic resource dynamics follows chemostat dynamics as in eq. (1b) with $l_1 = l_2$. Finally, population N_i influences the resources dynamics in model (1) through its impact vector. For $\alpha < 1$, we retain the mass action law used by Schreiber and Tobiason (2003):

$$(I_{i1}, I_{i2}) = -[x_i R_1, (1 - x_i) R_2] \quad (12)$$

This describes purely random encounters and removal of both resources, proportionally to their densities through acquisition rates. This con-

sumption process does not satisfy conservation of mass in general, as $I_{i1} + I_{i2} \neq g_i$ for $\alpha \neq 1$. Thus, removal of a certain resource density does not translate into an equivalent consumer growth. In the case of antagonistic resources, this situation would describe nutritional antagonism during the assimilation process, like synergistic effects of toxic compounds (Tilman, 1980). For this reason, we rather used the following impacts in the $\alpha \geq 1$ case:

$$(I_{i1}, I_{i2}) = -g_i^{1-\alpha}[(x_i R_1)^\alpha, ((1-x_i)R_2)^\alpha] \quad (13)$$

Conservation of mass is here satisfied, and antagonism comes from the foraging strategy of the consumer itself. It describes the behavioral switching of a predator, focusing disproportionately on its most abundant prey (Murdoch, 1969). This situation can emerge when resources are spatially distributed (Murdoch et al., 1975) or through the formation of a search image (Pietrewicz and Kamil, 1979, Dukas and Kamil, 2001).

As explained in the main text, the ZNGI of a given population i is obtained by setting $g_i(R_1, R_2) - m = 0$. Its concavity is controlled by the sign of $\alpha - 1$, as can be visualized in Fig. 1: the antagonistic case ($\alpha > 1$) give concave ZNGIs while complementary and interactive essential ($\alpha < 1$) gives convex ones. Moreover, computing the equation of the ZNGIs envelope through eq. (5) gives the eco-evolutionary singular points of the system. Solving them in this particular case leads to the following implicit envelope equation:

$$\left(R_1^{\frac{\alpha}{1-\alpha}} + R_2^{\frac{\alpha}{1-\alpha}}\right)^{\frac{1-\alpha}{\alpha}} - m = 0 \quad (14)$$

This also gives the expression of the singular trait as a function of the resource level:

$$x(R_1) = \left(\frac{R_1}{m} \right)^{\frac{\alpha}{1-\alpha}} \quad (15)$$

When substituted into the impact vector expression, this gives the impact map linking supply points to the corresponding singular points. The resulting ZNGI envelopes and associated impact maps are represented in Fig. 3-5. In the antagonistic case, the envelope had to be supplemented with the boundary ZNGIs. Those are the horizontal and vertical lines going through the point $(1, 1)$, and correspond to the two specialist strategies $x = 0$ and $x = 1$.

615

3. Discussion

In this paper, we show how the graphical approach of contemporary niche theory can be extended to a continuum of strategies to give insights into community assembly processes and eco-evolutionary dynamics along environmental
620 gradients. In section 2.1, we reviewed the graphical approach by providing a general step-by-step recipe to create ecological bifurcation diagrams along environmental gradients. In section 2.2, we adapted this recipe to the situation of a continuum of competitors using geometrical envelopes, enabling us to study community assembly from a large species pool. Finally, in section 2.3 we
625 demonstrated that combining this extension of the graphical approach with the adaptive dynamics framework leads to eco-evolutionary bifurcation diagrams summarizing the various possible evolutionary outcomes of the system.

3.1. Extension to structured populations

In this paper, we have restricted our attention to unstructured populations,
630 demographically and spatially. This was done for the sake of simplicity, as

there is no further complication to apply this graphical method to the case of linearly structured populations, that are defined by their dynamics satisfying $d\mathbf{N}_i/dt = \mathbf{w}_i(R_1, R_2, \dots, R_p)\mathbf{N}_i$, where the $\mathbf{N}_i$ are vectors of abundances at the different states (ages, sizes, or patches, for example) and $\mathbf{w}_i$ the net growth matrix (Leslie, 1948, Caswell, 2001). In this case, the ZNGI equation is obtained by setting the largest eigenvalue of the net growth matrix equal to zero (Loreau and Ebenhöf, 1994, Schellekens et al., 2010, Haegeman and Loreau, 2015). The corresponding eigenvector determines the population structure at equilibrium, thus reducing the impact on the regulating factors to a one-dimensional problem similar to the unstructured case. Conversely, there is no such general rule in the case of non-linear population structure, e.g. two-sex models (but see Szilágyi and Meszéna 2009, Barabás et al. 2014a). However, it may still be possible to define a ZNGI, as is the case for the Droop model after a quasi steady state approximation (Klausmeier et al., 2004). Therefore, it is generally possible to apply the envelope method to study the eco-evolution of structured populations.

3.2. Extension to higher trait space dimensions

In this paper, we restricted the presentation of the eco-evolutionary graphical method to the case of a unidimensional trait space. However, it is still possible to define a local envelope in the general case of a trait space with dimension k by replacing the trait derivative of eq. (5) by a k -dimensional trait gradient. This k -dimensional trait envelope can be seen as the outcome of a recursive scheme consisting of taking successively k times the envelope along every trait vector component, starting from the ZNGI multidimensional set. In any case, the ZNGI envelope keeps the property of being a unidimensional curve. This has important ecological consequences, as was pointed out by a more general result of Meszéna and Metz (1999): the singular strategies are necessarily contained in a $p - 1$ sub-manifold of the trait space, where p is the number of regulating

factors. This means that there is only a specific set of trait combinations that can be evolutionarily stable strategies, all the other ones being automatically
660 discarded whatever the supply point. This introduces correlations between the traits of organisms that could ever be observed. This process can be thought as a pure ‘competitive filtering’ as it only relies on the invasion analysis. It is thus completely independent of the details of the embedding environment and as such, a very general result. Note that Tilman’s (1982) R^* rule is a special
665 case of this result, where a single limiting factor usually leads to a unique singular strategy, or at least a countable number, whatever the supply point. Can a singular point still be characterized locally from the geometry of the envelope in the multidimensional case? Even if the relationships (7) and (9) can be extended to the k -dimensional case (see Appendix C), they do not give enough
670 information to perform this full characterization.

To conclude, a ZNGI envelope can be obtained for any dimension of the trait space. It selects from the full trait space the strategies that are singular and represents graphically their competitive ability. Their local characteristics
675 can not be deduced from simple graphical properties, but global evolutionary stability remains easy to identify.

3.3. From local to global invasibility

The two perspectives presented in sections 2.2 and 2.3 can be seen as two opposite but complementary pictures. The first, sometimes called the ‘everything
680 is everywhere’ picture, assumes that all the imaginable strategies from the trait space have a chance to invade the system. The details of the creation and maintenance of this diversity of invaders is simply assumed (Sauterey et al., 2015). This can be seen as the existence of a hyperdiverse regional species pool - the system being embedded in an heterogenous and connected landscape - or with

685 mutations of arbitrary size. By contrast, the second approach focuses on the
 invasion of a local neighborhood of strategies around the resident, as mutations
 are small. In this approach, evolution can be ‘trapped’ at a local-only ESS, and
 diversification from a monomorphic population only emerges from a branching
 point. The two approaches can lead to similar bifurcation diagrams, as it is
 690 the case for interactive essential resources in the example (Fig. 3) where all the
 local singular points are global CSS. However, the presence of locally non-ESS
 envelope portions lead to significant differences between the two pictures. In
 the case of antagonistic resources from our example, the local analysis identifies
 regions of priority effect between two locally stable specialists and a branch-
 695 ing point (Fig. 5B, 6D). Those details do not matter in the global analysis,
 replaced by evolutionarily stable coexistence of the two specialists (Fig. 4B).
 The link between the two frameworks can be seen from the PIPs in the sec-
 ond picture, as shown in Fig. 5B: evolution under small mutations can be read
 on the diagonal neighborhood, but information about invasion of any strategy
 700 is also available away from it. Another remark clear in the previous example
 is that there is no reason for the evolutionarily stable coexistence region and
 the branching region to coincide. Evolutionarily and convergence stable dimor-
 phism are indeed possible in the absence of branching, thus emerging through
 invasion or ‘macro-mutation’ (Geritz et al., 1999) (Fig. 5B). An example of this
 705 situation was discussed by Wolf et al. (2007), Massol and Crochet (2008), Wolf
 et al. (2008). Conversely, branching can happen in a region where evolutionary
 stable coexistence is not possible: one of the two morphs would inevitably expe-
 rience evolutionary suicide along its eco-evolutionary trajectory (Matsuda and
 Abrams, 1994, Rankin and López-Sepulcre, 2005, Parvinen, 2005). Local and
 710 global approaches are the two extremes of a general invasion analysis picture
 that can be visualized by combining local and global bifurcation diagrams and

associating them with PIPs.

3.4. Up- and downscaling with ZNGI envelopes

We have explained in section 2.2 how the envelope approach allows one
715 to scale up from the population to the community level to sort out the best
competitor from a continuum of strategies. It is also possible to scale down
from the population to the individual level in the context of phenotypic plasticity
(Tilman, 1982). Indeed, dynamical allocation in response to environmental cues
could allow an individual to explore the trait space in search of the optimal
720 strategy, in the sense of competition. The envelope approach gives a practical
tool to do so: from all the accessible behaviors represented by the continuous set
of ZNGIs, the optimization procedure only retains their envelope, which can be
seen as the new integrated ZNGI of the plastic individuals. Adding the family
of adaptive impact rays, a direct parallel can be drawn between populations
725 of plastic and non-plastic individuals (Tilman, 1982, Schade et al., 2005). The
only difference is that the traits of the former are optimized, thus depending
on the limiting factor values. A corollary is that a variety of adaptive ZNGI
shapes can arise from simple non-plastic ones. As such, the envelope method
provides a practical procedure to navigate through levels of organization by
730 taking into account adaptation and flexibility, from individuals to communities
(Smith et al., 2011, Norberg, 2013).

3.5. Coevolution from distinct functional groups and discontinuous mutations

The envelope approach is easy to apply to the evolution of n independent
guilds, for example from different functional groups. Those guilds must share
735 some regulating factors to be able to interact, but can belong to completely
different trait spaces, or be bound by completely distinct trade-offs. Each
guild would lead to its own eco-evolutionary envelope, that can then be com-
pared as if they were ZNGIs in the standard discrete invasion analysis (section

2.1), as emphasized in the previous subsection. Examples could include plants
740 and decomposers along a material cycle (Loreau, 1998a), nitrogen-fixing and
non-nitrogen-fixing phytoplankton (Boushaba and Pascual, 2005, Agawin et al.,
2007) or pairs of cooperators (de Mazancourt and Schwartz, 2010). This picture
could also allow one to study the global eco-evolutionary outcomes of a strategy
composed of a combination of continuous and discrete traits. From the previous
745 point of view, this means allowing a jump from one functional group to another
through discontinuous mutations. With a unidimensional bounded continuous
trait, invasion analysis could still be accurately depicted coupling several PIPs
together into a ‘meta-PIP’.

3.6. *From discrete to continuous set of strategies*

750 The continuous approach presented in section 2.2 clarifies some results iden-
tified in the finite number of strategies context. Indeed, the study of species
sorting along environmental gradients has usually been addressed using a large
but finite number of competitors. This led some authors to conclude that “coex-
istence was more likely among the most similar form” (Leibold, 1996). Fig. 1A
755 from the interactive essential case contains the signature of this phenomena, as
neighboring ZNGIs cross at potential coexistence points. This does not lead to
coexistence here because of our choice of impact vectors but the idea is the same.
However, we argue that this pattern of coexistence of similar forms is degenerate
and corresponds to some kind of nearly ‘neutral coexistence’, i.e. not ecologi-
760 cally robust sensu Meszéna et al. (2006). This can be seen when looking at
the continuous limit in Fig. 3. The coexistence points identified earlier have
vanished, as neighboring ZNGIs are now infinitely close. In eco-evolutionary
terms, this coexistence is not evolutionarily robust as evolution tends to destroy
it. Yet, this does not mean that evolutionarily stable coexistence can not hap-
765 pen in the continuous limit, as we have seen in the antagonistic case (Fig. 4). It

is, however, far less common as it relies on self-intersection of the local envelope, but more robust. Note that those differences depends heavily on the topology of the strategy space: disconnected in the finite case versus connected after the continuous limit. This is in practice related to the question of the existence of
770 infinitely many intermediate forms between different strategies.

If this pattern of coexistence vanishes at the continuous limit, it still leaves a signature on the invasion dynamics. More precisely, whether the potential coexistence points lead to stable coexistence or priority effect influences the
775 shape of the PIPs around the singular points. This can be seen in the interactive essential resource example. For high resource supplies, priority effect between neighboring strategies (Fig. 1A) translates into CSS strategies that cannot directly invade their neighborhood and are only attained monotonically through ever-decreasing evolutionary steps (see PIPs on Fig. 3B). This is one of the
780 eight singular strategy types identified by the adaptive dynamics classification (Geritz et al., 1997). On the contrary, we predict that coexistence between neighboring strategies in the finite strategy case would lead to CSS strategies able to invade their neighborhood. Giving a mathematical proof of this is out the scope of this paper. However, those results are intuitive, as priority effects
785 between neighboring strategies indicate that they are protected from invasion by the other strategies. To conclude, while neighboring coexistence or priority effect vanish when the continuous limit is taken, they leave their signature on the eco-evolutionary characteristics of the singular points.

3.7. Importance of the regulating factor space

790 For a given strategy, the corresponding ZNGI summarizes its competitive ability. This is measured in the regulating factor space, where the competitiveness of different strategies can be compared. In the case of a single regulating

factor, the ZNGI reduces to one number, so all the strategies can be ordered and compared without ambiguity. This result is known as Tilman’s R^* rule (Hsu
795 et al., 1977, Tilman, 1982, Grover, 1997, Chase and Leibold, 2003) and leads to a pessimization principle in the eco-evolutionary case (Metz et al., 2008). This strict ordering is in general impossible with more regulating factors: invasion analysis with the envelope is the closest equivalent to that rule. Optimization is now multi-objective, so a Pareto front is needed to find the optimal strategies, and this role is played by the envelope. This is why the regulating factor space
800 is so central: it controls species sorting and adaptation through this multi-objective optimization. However, the map between a strategy from the trait space and its ZNGI in the regulating factor space is non-trivial. For example, constraints on organisms encoded by trade-offs are usually inferred at the trait
805 level. Yet, nothing ensures that they efficiently translate into a trade-off in competitive ability of the ZNGI set in the regulating factor space. Another effect of this map is to control the presence of evolutionarily stable coexistence. Indeed, it relates the geometrical characteristics of the ZNGI envelope to the ones of the trait space. For example, some trait space geometries lead to kinked global
810 envelopes and thus potentially to evolutionarily stable coexistence while other do not.

3.8. *Evolution of resource use*

Applying the envelope method to Schreiber and Tobiason’s (2003) resource competition model allowed us to confirm and visualize their results. More-
815 over, we could specify how the number of singular points and their properties depended on the resource supplies through bifurcation diagrams. For $\alpha < 1$, there is always a single generalist CSS, under the condition that there is a sufficient supply of resources (Fig. 3). The antagonistic case ($\alpha > 1$) was further characterized with the help of the impact ray map and its envelope (Fig. 5).

820 First, there is always a zone of supply points for which evolutionary branching
 is possible. This is true for both the choice of impact vector expressions used
 by Schreiber and Tobiason (2003) and the modification we proposed. However,
 this zone is pushed infinitely far away from the envelope for $\alpha \rightarrow \infty$ when using
 eq. (12) while it stays close to it when using eq. (13). The former is consis-
 825 tent with Schreiber and Tobiason’s (2003) observations. The latter states that
 branching is still possible on highly antagonistic resources if switching is more
 abrupt. Note that branching demands a sufficiently large and balanced supply
 of the two resources to take place. Moreover, this branching point, when it
 exists, is always unique and separated from the boundary attracting strategies
 830 by two repellers. Also note that it is possible not to have any singular point but
 still one or two attractive boundaries for low enough resources.

The consumer-resource model of the example also gives some insights in the
 case of strictly essential resources. This corresponds to the limit obtained when
 835 $\alpha \rightarrow -\infty$, leading to a growth rate (11) following Liebig’s Law of the Minimum
 and an associated L-shaped ZNGI (León and Tumpson, 1975, Tilman, 1982). It
 is actually in this context that the use of ZNGI envelopes first appeared (Tilman,
 1988) and later spread (Schade et al., 2005, Klausmeier et al., 2007, Danger et al.,
 2008). The standard approach consists in getting the envelope equation simply
 840 by tracking the position of the ZNGI corner. The first order criterion (5b) is
 not only unnecessary in this case, it actually fails to give the envelope equation
 when applied directly, as the L-shaped ZNGI is non-differentiable at its corner.
 However, this problem can be worked around by taking the limit when $\alpha \rightarrow -\infty$
 of the general envelope equation (14), leading to a consistent result. Contrary
 845 to the standard approach, our method is easy to generalize to a trait space of
 arbitrary dimension. It could thus be used to further investigate the evolution

of consumers feeding on essential resources (Klausmeier et al., 2004, Shores et al., 2008).

3.9. Conclusion and perspectives

850 In this paper, we presented a graphical approach based on geometrical envelopes that can be used to perform invasion analysis and supply point mapping with a continuum of interacting strategies. We showed how relevant this technology is to two biological pictures, namely species sorting and adaptive dynamics, paving the way for an ‘evolutionary theory of the niche’ (Holt, 2009). Because
855 of its generality, this approach could be applied to investigate a variety of ecological situations: the evolution in a diamond-shaped food web (Leibold, 1996), cooperation through trading (de Mazancourt and Schwartz, 2010), informed dispersal (Haegeman and Loreau, 2015), nitrogen fixing (Agawin et al., 2007) or niche construction (Kylafis and Loreau, 2011), for example.

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A. Transformation toward decoupled chemostat dynamics

1155 We provide here two examples of change of variables that enable one to map more general regulating factors dynamics to a chemostat dynamics form presented in equations (1b). This allows one to apply the graphical method presented in this paper to those extended situations after the change of variables.

A.1. Logistic growth

1160 First, let us consider that a regulating factor R follows a logistic resource dynamics:

$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K} \right) + \sum_{j=1}^n I_j(R) N_j \quad (\text{A.1})$$

Introducing the change of variables $\rho = 1/R$, it is straightforward that:

$$\frac{d\rho}{dt} = r(\kappa - \rho) + \sum_{j=1}^n \chi_j(\rho) N_j \quad (\text{A.2})$$

1165 with $\kappa = 1/K$ and $\chi_j(\rho) = -I_j(1/\rho)\rho^2$. Thus, this change of variable maps a logistic growth in R toward a chemostat dynamics in ρ . Note that the consumer-resource relationship with the N_j s is reversed by the change of variable: if a N_j was consuming R , it is now feeding ρ . This can be understood by looking at the dimensions of the new variable: if R is in individual per surface area, ρ is
 1170 in surface area per individual. Thus, decreasing prey density by consumption conversely increases available surface area per individual.

A.2. Linear coupling through diffusion

Our second example considers two diffusion-coupled chemostats, thus following the intrinsic dynamics:

$$\frac{dR_1}{dt} = l_1(S_1 - R_1) - d_{12}R_1 + d_{21}R_2 \quad (\text{A.3})$$

$$\frac{dR_2}{dt} = l_2(S_2 - R_2) + d_{12}R_1 - d_{21}R_2 \quad (\text{A.4})$$

1175 This system being linear, it can be rewritten under the general matrix form in the presence of interacting populations:

$$\frac{d\mathbf{R}}{dt} = \mathbf{T} - \mathbf{M}\mathbf{R} + \sum_{j=1}^n \mathbf{I}_j(\mathbf{R}) N_j \quad (\text{A.5})$$

with

$$\mathbf{T} = \begin{pmatrix} l_1 S_1 \\ l_2 S_2 \end{pmatrix} \quad \text{and} \quad \mathbf{M} = \begin{pmatrix} l_1 - d_{12} & d_{21} \\ d_{12} & l_1 - d_{21} \end{pmatrix} \quad (\text{A.6})$$

1180 Then, diagonalization gives $\mathbf{M} = \mathbf{P}\mathbf{D}\mathbf{P}^{-1}$ with $\mathbf{D} = \text{diag}(\lambda_1, \lambda_2)$ leading to:

$$\frac{d\boldsymbol{\rho}}{dt} = \mathbf{D}(\boldsymbol{\sigma} - \boldsymbol{\rho}) + \sum_{j=1}^n \boldsymbol{\chi}_j(\boldsymbol{\rho}) N_j \quad (\text{A.7})$$

with $\boldsymbol{\rho} = \boldsymbol{P}^{-1}\boldsymbol{R}$, $\boldsymbol{\sigma} = \boldsymbol{D}^{-1}\boldsymbol{P}^{-1}\boldsymbol{T}$ and $\chi_j(\boldsymbol{\rho}) = \boldsymbol{P}^{-1}\boldsymbol{I}_j(\boldsymbol{P}\boldsymbol{\rho})$. As $\boldsymbol{D}$ is a diagonal matrix, the regulating factor vector $\boldsymbol{\rho}$ nows follows decoupled chemostat dynamics.

1185 **B. Analytical study of ecological equilibria for the two consumers on two resources system**

B.1. Model

In the case of two consumers competing for two resource in a chemostat, model (1) can be rewritten:

$$\frac{dN_i}{dt} = w_i(R_1, R_2)N_i \quad (\text{B.1})$$

$$\frac{dR_i}{dt} = l_i(S_i - R_i) + \sum_{j=1}^2 I_{ij}(R_1, R_2)N_j \quad (\text{B.2})$$

1190 Let us first classify the different equilibria of the system and characterize their local stability.

B.2. Equilibria

Those equations present different kinds of solutions at equilibrium:

Equilibrium (0). corresponds to the case where both populations are absent,

1195 *i.e.* $N_1 = N_2 = 0$. Then $R_1 = S_1$ and $R_2 = S_2$.

Equilibrium (1). corresponds to the case where only population 2 is absent, *i.e.*

$N_1 \neq 0$ and $N_2 = 0$. The system can be rewritten:

$$\begin{aligned} 0 &= w_1(R_1, R_2) \\ \tilde{I}_{12}(R_1, R_2)(S_1 - R_1) &= \tilde{I}_{11}(R_1, R_2)(S_2 - R_2) \\ N_1 &= \frac{(R_1 - S_1)}{\tilde{I}_{11}(R_1, R_2)} \end{aligned} \quad (\text{B.3})$$

where we have used the simplifying notation $\tilde{I}_{ij} = I_{ij}/l_i$. The regulating factor values at equilibrium (R_1, R_2) are obtained by solving the first two equations

1200 together. N_1 is then deduced from the result using the third equation.

Equilibrium (2). corresponds to the case where only population 1 is absent, *i.e.* $N_2 \neq 0$ and $N_1 = 0$. The equilibrium values can be deduced from the previous paragraph by switching subscripts.

Equilibrium (1+2). corresponds to the case where the two populations coexist, *i.e.* $N_2 \neq 0$ and $N_1 \neq 0$. Then (R_1, R_2) are given after solving:

$$0 = w_1(R_1, R_2)$$

$$0 = w_2(R_1, R_2)$$

The densities values at equilibrium follow with:

$$\mathbf{N} = \tilde{\mathbf{I}}^{-1}(\mathbf{S} - \mathbf{R}) \quad (\text{B.4})$$

where $\mathbf{N} = (N_1, N_2)^T$, $\mathbf{S} = (S_1, S_2)^T$, $\mathbf{R} = (R_1, R_2)^T$ and $\tilde{\mathbf{I}}$ is a 2 by 2 matrix with coefficients $\tilde{I}_{ij} = I_{ij}/l_i$. Note that $\tilde{\mathbf{I}}$ is invertible if and only if the renormalized impacts vectors of the two populations are not colinear, which is improbable in the absence of fine-tuning.

B.3. Stability

The stability of those different types of equilibria can be assessed introducing the Jacobian of the system:

$$\mathbf{J}(N_1, N_2, R_1, R_2) = \begin{pmatrix} w_1 & 0 & \partial_1 w_1 N_1 & \partial_2 w_1 N_1 \\ 0 & w_2 & \partial_1 w_2 N_2 & \partial_2 w_2 N_2 \\ I_{11} & I_{12} & -l_1 + \sum_{j=1}^2 \partial_1 I_{1j} N_j & \sum_{j=1}^2 \partial_2 I_{1j} N_j \\ I_{21} & I_{22} & \sum_{j=1}^2 \partial_1 I_{2j} N_j & -l_2 + \sum_{j=1}^2 \partial_2 I_{2j} N_j \end{pmatrix} \quad (\text{B.5})$$

where we have omitted the explicit dependencies in (R_1, R_2) and the notation ∂_i stands for $\partial/\partial R_i$. This Jacobian can be evaluated for the different kinds of

equilibria we have identified. It is not to be confused with the Jacobian of the fitness gradient J of eq. (8).

1220 *Equilibrium (0).* The Jacobian can be rewritten as:

$$\mathbf{J} = \begin{pmatrix} w_1 & 0 & 0 & 0 \\ 0 & w_2 & 0 & 0 \\ I_{11} & I_{12} & -l_1 & 0 \\ I_{21} & I_{22} & 0 & -l_2 \end{pmatrix} \quad (\text{B.6})$$

As $(R_1, R_2) = (S_1, S_2)$, the empty equilibrium is stable if both $w_1(S_1, S_2) < 0$ and $w_2(S_1, S_2) < 0$, which means that none of the two populations can invade. There is no other constraint as the chemostat dynamics are ‘intrinsically’ stable.

1225 *Equilibrium (1).* After permutation, the Jacobian can be rewritten as a block-diagonal matrix:

$$\mathbf{J} = \begin{pmatrix} w_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{K} \end{pmatrix} \quad (\text{B.7})$$

with

$$\mathbf{K} = \begin{pmatrix} 0 & \partial_1 w_1 N_1 & \partial_2 w_1 N_1 \\ I_{11} & -l_1 + \partial_1 I_{11} N_1 & \partial_2 I_{11} N_1 \\ I_{21} & \partial_1 I_{21} N_1 & -l_2 + \partial_2 I_{21} N_1 \end{pmatrix} \quad (\text{B.8})$$

1230 Thus, a first necessary condition is non-invasibility by population 2 through $w_2(R_1, R_2) < 0$. Routh-Hurwitz criteria applied on $\mathbf{K}$ gives a second necessary condition $\det \mathbf{K} < 0$. It is actually possible to show that:

$$\det \mathbf{K} = l_2 N_1 I_{11} \frac{\partial w_1}{\partial R_1} \bigg/ \frac{\partial R_2}{\partial S_2} \quad (\text{B.9})$$

The object $\partial R_2 / \partial S_2$ has an intuitive geometrical interpretation linked to the envelope of the impact rays. The scheme is similar to the one developed in the main text in the eco-evolutionary context (see supply point map in section 2.3).
1235 Indeed, the family of impact rays associated with a given ZNGI can possess an

envelope. When it is the case, a given impact ray is tangent to its envelope at a particular point. The line portion of the impact ray situated between its origin
1240 and this point corresponds to supply points satisfying $\partial R_1/\partial s_1|_Z > 0$ while the other part corresponds to $\partial R_1/\partial s_1|_Z < 0$. In the classical consumer-resource situation where $I_{11}\partial w_1/\partial R_1 < 0$, this means that only the supply points situated before the envelope on the impact ray map to stable equilibria, the other ones being unstable. This graphical criterion shares strong similarities with
1245 the eco-evolutionary case presented in the main text. Note that the condition $\det \mathbf{K} < 0$ is necessary but not sufficient to ensure stability.

Equilibrium (2). can be deduced from the previous paragraph by switching subscripts. Note that we get the necessary condition $\det \mathbf{K}' < 0$ for stability with :

$$1250 \quad \det \mathbf{K}' = l_1 N_2 I_{22} \frac{\partial w_2}{\partial R_2} \bigg/ \frac{\partial R_1}{\partial S_1} \quad (\text{B.10})$$

Equilibrium (1 + 2). The Jacobian can be rewritten as:

$$\mathbf{J} = \begin{pmatrix} 0 & 0 & \partial_1 w_1 N_1 & \partial_2 w_1 N_1 \\ 0 & 0 & \partial_1 w_2 N_2 & \partial_2 w_2 N_2 \\ I_{11} & I_{12} & -l_1 + \sum_{j=1}^2 \partial_1 I_{1j} N_j & \sum_{j=1}^2 \partial_2 I_{1j} N_j \\ I_{21} & I_{22} & \sum_{j=1}^2 \partial_1 I_{2j} N_j & -l_2 + \sum_{j=1}^2 \partial_2 I_{2j} N_j \end{pmatrix} \quad (\text{B.11})$$

The necessary condition for stability $\det \mathbf{J} > 0$ can be obtained where:

$$\det \mathbf{J} = (I_{11} I_{22} - I_{12} I_{21}) \left(\frac{\partial w_1}{\partial R_1} \frac{\partial w_2}{\partial R_2} - \frac{\partial w_1}{\partial R_2} \frac{\partial w_2}{\partial R_1} \right) N_1 N_2 \quad (\text{B.12})$$

1255 this is the mutual invasibility criterion of eq. (3) in the main text. We recognize in eq. (B.12) the general decomposition of $\det \mathbf{J}$ as the product of the impact and sensitivity map volumes (Meszéna et al., 2006).

C. Demonstration of the geometrical relationships in the k -dimensional traitspace case

1260 The aim of this section is to link the ZNGI and impact ray envelope properties to the eco-evolutionary properties of the corresponding singular points. We restrict our attention to the case of two regulating factors R_1 and R_2 , for a completely general k -dimensional trait $\mathbf{x}$.

C.1. Monomorphic singular point

1265 When there is only one singular population in the system, the eco-evolutionary invasion analysis of eq. (5) can be generalized to the k -dimensional case as:

$$w(\mathbf{R}, \mathbf{x}) = 0 \quad (\text{C.1})$$

$$\partial_{\mathbf{x}} w(\mathbf{R}, \mathbf{x}) = \mathbf{0} \quad (\text{C.2})$$

where we have used the simplifying notation for the fitness gradient:

$$\partial_{\mathbf{x}} w(\mathbf{R}, \mathbf{x}) \equiv \left[\frac{\partial w(\mathbf{R}(\mathbf{y}), \mathbf{x})}{\partial \mathbf{x}} \right]_{\mathbf{y}=\mathbf{x}} \quad (\text{C.3})$$

1270 the notation $\partial/\partial_{\mathbf{x}}$ standing for a nabla operator along $\mathbf{x}$. Graphically, we recognized in the main text that this set of equations parametrizes the ZNGI envelope. This particular expression of the fitness gradient as a partial derivative along its second coordinate is specific to the fact that mutant and resident only interact indirectly through the regulating factors. This has to be combined with the supply point map:

$$1275 \quad v(\mathbf{S}, \mathbf{R}, \mathbf{x}) = 0 \quad (\text{C.4})$$

with $v(\mathbf{S}, \mathbf{R}, \mathbf{x}) = (S_1 - R_1)\tilde{I}_2(\mathbf{R}, \mathbf{x}) - (S_2 - R_2)\tilde{I}_1(\mathbf{R}, \mathbf{x})$. Jointly solving this system gives the singular point trait values.

How can we link the tangent ZNGI and ZNGI envelope relative curvature
1280 to the properties of its corresponding singular points? As was done in the main

text in the unidimensional case, we need to introduce the Hessian matrix of the invasion fitness $\mathbf{H}$:

$$\mathbf{H}(\mathbf{x}) = \left[\frac{\partial}{\partial \mathbf{x}} \frac{\partial}{\partial \mathbf{x}^T} w(\mathbf{R}(\mathbf{y}), \mathbf{x}) \right]_{\mathbf{y}=\mathbf{x}} \equiv \partial_{\mathbf{x}} \partial_{\mathbf{x}}^T w \quad (\text{C.5})$$

The ZNGI and envelope curvatures at the singular point are both given by second derivatives. The ZNGI curvature can be obtained differentiating $w(R_1, R_2, \mathbf{x}) = 0$ twice with respect to R_1 , where $R_2 = f(R_1)$:

$$-\partial_{R_2} w \cdot \frac{\partial R_2}{\partial R_1} \Big|_Z = \partial_{R_1} w \quad (\text{C.6})$$

$$-\partial_{R_2} w \cdot \frac{\partial^2 R_2}{\partial R_1^2} \Big|_Z = \partial_{R_1}^2 w + 2 \frac{\partial R_2}{\partial R_1} \partial_{R_2} \partial_{R_1} w + \left(\frac{\partial R_2}{\partial R_1} \right)^2 \partial_{R_2}^2 w \quad (\text{C.7})$$

where $\mathbf{x}$ has been kept fixed for this calculation as we are interested by the properties of the tangent ZNGI. This is not the case for the ZNGI envelope.

The envelope curvature is obtained differentiating $w(R_1, R_2, \mathbf{x}) = 0$ twice with respect to R_1 and using $\partial_{\mathbf{x}} w(R_1, R_2, \mathbf{x}) = \mathbf{0}$, where $R_2 = g(R_1)$ and $\mathbf{x} = \mathbf{h}(R_1)$:

$$-\partial_{R_2} w \cdot \frac{\partial R_2}{\partial R_1} \Big|_E = \partial_{R_1} w \quad (\text{C.8})$$

$$\begin{aligned} -\partial_{R_2} w \cdot \frac{\partial^2 R_2}{\partial R_1^2} \Big|_E &= \partial_{R_1}^2 w + 2 \frac{\partial R_2}{\partial R_1} \partial_{R_2} \partial_{R_1} w + \left(\frac{\partial R_2}{\partial R_1} \right)^2 \partial_{R_2}^2 w \\ &\quad + \frac{\partial \mathbf{x}^T}{\partial R_1} \left(\partial_{R_1} \partial_{\mathbf{x}} w + \frac{\partial R_2}{\partial R_1} \partial_{R_2} \partial_{\mathbf{x}} w \right) \end{aligned} \quad (\text{C.9})$$

Note that the first order derivatives are the same for the ZNGI and the envelope, which is a result of their tangency and is known in economics as the "Envelope Theorem" (Samuelson, 1947). However, the second derivatives differ by a term that accounts for the fact that $\mathbf{x}$ also varies along the envelope. Differentiating $\partial_{\mathbf{x}} w(R_1, R_2, \mathbf{x}) = \mathbf{0}$ once with respect to R_1 shows how the last term of (C.9) is actually related to the Hessian:

$$\frac{\partial \mathbf{x}^T}{\partial R_1} \left(\partial_{R_1} \partial_{\mathbf{x}} w + \frac{\partial R_2}{\partial R_1} \partial_{R_2} \partial_{\mathbf{x}} w \right) = - \frac{\partial \mathbf{x}^T}{\partial R_1} \mathbf{H} \frac{\partial \mathbf{x}}{\partial R_1} \quad (\text{C.10})$$

In conclusion, combining all the previous results as the sum $-(C.9)+(C.7)-(C.10)$ and using the fact that $\partial R_2/\partial R_1$ coincides for both ZNGI and envelope leads to the final result:

$$\frac{\partial w}{\partial R_2} \left(\left. \frac{\partial^2 R_2}{\partial R_1^2} \right|_E - \left. \frac{\partial^2 R_2}{\partial R_1^2} \right|_Z \right) = \frac{d\mathbf{x}^T}{dR_1} \cdot \mathbf{H} \cdot \frac{d\mathbf{x}}{dR_1} \quad (C.11)$$

When $\mathbf{x}$ is a scalar, the latter expression directly rewrites as eq. (7), which concludes the proof.

The second result presented in the main text relates the convergence properties of a singular point to the impact ray envelope. Let us introduce the Jacobian of the fitness gradient $\mathbf{J}$:

$$\mathbf{J}(\mathbf{x}) = \frac{\partial}{\partial \mathbf{x}} \left[\frac{\partial}{\partial \mathbf{x}^T} w(\mathbf{R}(\mathbf{y}), \mathbf{x}) \right]_{y=\mathbf{x}} \quad (C.12)$$

$$\equiv \left(\partial_{\mathbf{x}} + \partial_{\mathbf{x}} \mathbf{R}^T \cdot \partial_{\mathbf{R}} \right) \partial_{\mathbf{x}}^T w \quad (C.13)$$

We thus have:

$$\mathbf{J}(\mathbf{x}) = \mathbf{H}(\mathbf{x}) + \partial_{\mathbf{x}} \mathbf{R}^T \cdot \partial_{\mathbf{R}} \partial_{\mathbf{x}}^T w \quad (C.14)$$

It is very important to understand that the dependency of $\mathbf{R}$ in $\mathbf{x}$ depicted by the term $\partial_{\mathbf{x}} \mathbf{R}^T$ comes from solving completely the ecological system by combining ZNGI and impact ray equations (C.1,C.4) for $\mathbf{S}$ fixed. This has to be done for any strategy, singular or not. Note that this object is not directly related to the expression $d\mathbf{x}/dR_1$ manipulated above, which tracks how a singular strategy varies along the envelope. Differentiating $w(\mathbf{R}, \mathbf{x}) = 0$ and $v(\mathbf{S}, \mathbf{R}, \mathbf{x}) = 0$ with respect to $\mathbf{x}$ and evaluating it at a singular point gives the following relation-

ships:

$$\partial_{\mathbf{x}} R_1 = -\partial_{\mathbf{x}} v \left/ \left(\partial_{R_1} v + \frac{\partial R_2}{\partial R_1} \partial_{R_2} v \right) \right. \quad (\text{C.15})$$

$$\partial_{\mathbf{x}} R_2 = \frac{\partial R_2}{\partial R_1} \partial_{\mathbf{x}} R_1 \quad (\text{C.16})$$

Let us first use eq. (C.16) only to rewrite:

$$\mathbf{J} - \mathbf{H} = \partial_{\mathbf{x}} R_1 \left(\partial_{R_1} \partial_{\mathbf{x}}^T w + \frac{\partial R_2}{\partial R_1} \partial_{R_2} \partial_{\mathbf{x}}^T w \right) \quad (\text{C.17})$$

after multiplying eq. (C.17) on the right by $d\mathbf{x}/dR_1$, the RHS reads as the
1320 transpose of the LHS of eq. (C.10). When also multiplied by $d\mathbf{x}^T/dR_1$ on the left, it leads to:

$$\frac{d\mathbf{x}^T}{dR_1} \mathbf{J} \frac{d\mathbf{x}}{dR_1} = \left(1 - \frac{d\mathbf{x}^T}{dR_1} \cdot \partial_{\mathbf{x}} R_1 \right) \frac{d\mathbf{x}^T}{dR_1} \mathbf{H} \frac{d\mathbf{x}}{dR_1} \quad (\text{C.18})$$

Finally, coming back to the expression of $\partial_{\mathbf{x}} R_1$ given by eq. (C.16):

$$1 - \frac{d\mathbf{x}^T}{dR_1} \cdot \partial_{\mathbf{x}} R_1 = \left(\partial_{R_1} v + \frac{\partial R_2}{\partial R_1} \partial_{R_2} v + \frac{d\mathbf{x}^T}{dR_1} \cdot \partial_{\mathbf{x}} v \right) \left/ \left(\partial_{R_1} v + \frac{\partial R_2}{\partial R_1} \partial_{R_2} v \right) \right. \quad (\text{C.19})$$

$$\equiv \left. \frac{dv}{dR_1} \right|_{\text{E}} \left/ \left. \frac{dv}{dR_1} \right|_{\text{Z}} \right. \quad (\text{C.20})$$

Now, there is a last step to make the link with the supply point map. Differenti-
1325 ating (C.4) once with respect to S_1 , along a ZNGI and the envelope respectively leads to:

$$\left. \frac{\partial R_1}{\partial S_1} \right|_{\text{Z}} = -\tilde{I}_2 \left/ \left. \frac{dv}{dR_1} \right|_{\text{Z}} \right. \quad (\text{C.21})$$

$$\left. \frac{\partial R_1}{\partial S_1} \right|_{\text{E}} = -\tilde{I}_2 \left/ \left. \frac{dv}{dR_1} \right|_{\text{E}} \right. \quad (\text{C.22})$$

Putting the pieces together, we finally get the result:

$$\left. \frac{\partial R_1}{\partial s_1} \right|_{\text{E}} \frac{d\mathbf{x}^T}{dR_1} \mathbf{J} \frac{d\mathbf{x}}{dR_1} = \left. \frac{\partial R_1}{\partial s_1} \right|_{\text{Z}} \frac{d\mathbf{x}^T}{dR_1} \mathbf{H} \frac{d\mathbf{x}}{dR_1} \quad (\text{C.23})$$

When $\mathbf{x}$ is a scalar and $dx/dR_1 \neq 0$, the latter expression directly rewrites as
 1330 eq. (9), which concludes the proof.

Using the ecological stability criteria (B.10) obtained in the previous section
 for a single-population, we have:

$$\left. \frac{\partial R_1}{\partial s_1} \right|_Z = -\beta \tilde{I}_2 \frac{\partial w}{\partial R_2} \quad (\text{C.24})$$

1335 where β is a positive function when the ecological equilibrium is stable and
 the two other terms of the RHS are related to the relationship between the
 population and the regulating factor R_2 . For the usual consumer-resource and
 predator-prey interactions, this thus leads to $\partial R_1 / \partial s_1 > 0$.

1340 Note that the two main relationships obtained here in the case of a general
 k -dimensional trait $\mathbf{x}$ only give information on the Hessian and Jacobian of the
 eco-evolutionary system along the envelope, i.e. the direction $d\mathbf{x}/dR_1$. In the
 one dimensional case, this is not a problem as soon as this direction exists (is
 non-zero): it leads to a squared term with thus no effect of its sign for the first
 1345 result or can be simplified in the second result. For dimensions greater than
 one, this projection leads to insufficient information on the multiple eigenvalues
 of both the Hessian and Jacobian matrices, not allowing to conclude on the
 ESS and convergent properties of the singular points based only on the relative
 position between the ZNGI and its envelope. Also note that contrary to the one
 1350 dimensional case, eco-evolutionary stability in the k -dimensional case may also
 depend on the specific shape of the mutation process (Leimar, 2009).

C.2. Dimorphic singular point

When there are two coexisting singular populations in the system with traits $\mathbf{x}_1 \neq \mathbf{x}_2$, the eco-evolutionary invasion analysis reads:

$$w(\mathbf{R}, \mathbf{x}_i) = 0 \quad (\text{C.25})$$

$$\partial_{\mathbf{x}} w(\mathbf{R}, \mathbf{x}_i) = \mathbf{0} \quad (\text{C.26})$$

1355 with $i = 1, 2$. As in the ecological case, this is enough to fully determine the regulating factors at the eco-evolutionary equilibrium, thus the supply point map is not needed here. According to the adaptive dynamics picture, the eco-evolutionary properties of this singular coalition directly emerges from those of its constituents. Thus, we still have:

$$1360 \quad \frac{\partial w}{\partial R_2} \left(\left. \frac{\partial^2 R_2}{\partial R_1^2} \right|_{\text{E}} - \left. \frac{\partial^2 R_2}{\partial R_1^2} \right|_{\text{Z}} \right) = \frac{d\mathbf{x}_i^T}{dR_1} \cdot \mathbf{H} \cdot \frac{d\mathbf{x}_i}{dR_1} \quad (\text{C.27})$$

and thus this coalition is evolutionarily stable if and only if both coexisting strategies satisfy the geometrical condition relatively to their local envelope. The situation is a bit different for the convergence characteristics as $\mathbf{R}$ is obtained without the supply point map (and is thus independent of it) in the dimorphic case. Differentiating $w(\mathbf{R}, \mathbf{x}_1) = 0$ and $w(\mathbf{R}, \mathbf{x}_2) = 0$ with respect to $\mathbf{x}_i$ and evaluating it at the singular point where $R_2 = g(\mathbf{x}_1, \mathbf{x}_2)$ gives the trivial result:

$$\partial_{\mathbf{x}_i} R_1 = \partial_{\mathbf{x}_i} R_2 = \mathbf{0} \quad (\text{C.28})$$

Thus, the regulating factors at equilibrium around a singular coalition are linearly independent from the traits of this coalition. As a result, $\mathbf{J} = \mathbf{H}$ for each 1370 of the two coexisting strategies, so the convergence properties are automatically linked to the invasion one. This means that ESS coalitions are automatically CSS ones and further branching is excluded. This result obtained here in the case of a saturated dimorphism (two populations on two regulating factors)

strongly echoes to the situation of a single population evolving on a single re-
1375 source, and can be generalized to any number of regulating factors (Kisdi and
Geritz, 2016).