# CONCEPTS & SYNTHESIS

## EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

# From competition to facilitation and mutualism: a general theory of the niche

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*Abstract.* Niche Theory is a central framework in ecology based on the recognition that most interactions between organisms are indirect, mediated by the biotic and abiotic dynamical environment these organisms live in. Despite its potential generality, the theory still mostly focuses on how resource–consumer dynamics mediate competition in ecological communities. However, it is being increasingly recognized that positive interactions between organisms also play an important role in driving the structure and functioning of ecological communities, from plants to microbes. In this paper, we present a unified theory of the niche that applies to both positive and negative interactions between organisms, mediated by one or two environmental factors. We show that classical concepts such as niche differences and fundamental and realized niches can naturally be expanded to facilitative and mutualistic interactions. In addition, we introduce and formalize new general niche concepts that appear exclusively in the presence of positive interactions: (1) the Allee niche, a region of environmental conditions for which a species can persist but not invade from low densities and (2) niche facilitation, when the presence of a species expands the set of environmental conditions under which a second species can invade and/or persist. To show the broad applicability of this theory, we illustrate these concepts using a diverse set of theoretical examples, from bacteria feeding on an inhibiting substrate, to nitrogen-fixing plants and the indirect mutualism between a plant and a carnivore species. In sum, our work shows how Niche Theory provides a natural framework for positive interactions in ecology, bringing a unified perspective and new conceptual tools to study ecological systems where these positive interactions occur.

*Key words: Allee effect; coexistence; competition; facilitation; Lotka-Volterra dynamics; mutualism; niche difference; Niche Theory; zero net growth isocline.*

## Introduction

Ecologists seek to parse out the enormous complexity of the natural world, to better be able to control and predict the stability and functioning of communities and ecosystems in an ever-changing world. Ecological theories organize our understanding of the mechanisms that structure these complex systems to help achieve that goal. These theories are particularly useful when they provide a unifying framework and associated concepts that transcend system specificity, a major challenge in ecology stemming from the incredible diversity of organisms and their interactions.

Modern Coexistence Theory (Adler et al. 2007, Mayfield and Levine 2010, Barabás et al. 2018, Chesson 2018) is one example of such a unifying framework, whose goal is to identify the general mechanisms through which species coexist in ecological communities. Rooted in the early models of species competition by Lotka (1925) and Volterra (1926), MacArthur and Levins's (1967) definition of niche overlap refined by Pianka (1974), and the recognition that a temporally fluctuating environment can maintain coexistence (Chesson 1994), it eventually emerged as a general theoretical framework built around Chesson's work (Chesson 2000,

2018). Modern Coexistence Theory provides a way to organize and quantify disparate coexistence mechanisms across diverse types of communities and scales. The apparent simplicity with which these mechanisms can be measured in practice has enticed ecologists to quantify the strength of coexistence in empirical systems (Adler et al. 2006, Angert et al. 2009, Adler et al. 2012, Narwani et al. 2013). Despite promising recent extensions to priority effects (Ke and Letten 2018, Grainger et al. 2019), recent work has, however, also pointed out some of the potential limitations of the theory (Saavedra et al. 2017, Barabás et al. 2018, Song et al. 2019). Even though progress has been made in this regard, the definition of niche overlap in an general multispecies context is still under debate (Song et al. 2019), with the structural stability approach emerging as a promising way forward (Petraitis 1989, Meszéna et al. 2006, Saavedra et al. 2017).

Contemporary Niche Theory, as coined by Chase and Leibold (2003), provides an alternative theoretical framework, which finds its roots in resource competition theory (MacArthur 1969, León and Tumpson 1975, Tilman 1980, 1982). In contrast to Modern Coexistence Theory, Niche Theory more explicitly acknowledges the central role played by the environment, through the core idea that interactions between organisms are indirectly mediated by the diverse biophysicochemical aspects of their shared environment (Chase and Leibold 2003, Meszéna et al. 2006). These reciprocal interactions create a feedback between organisms and their environment that works both ways: the environment selects which organisms can thrive in a particular location through these organisms' *requirements*, represented geometrically by the niche "hypervolumes" (Hutchinson 1957, Maguire 1973), and the resulting growing populations in turn affect their environment through their *impacts*, eventually causing population regulation. When applied to competing species, this dichotomy sheds light on the mechanisms that make coexistence possible, such as resource partitioning in resource competition theory (Tilman 1982). Since its early developments, Niche Theory has connected ecologically diverse situations under a few unifying principles, such as the general idea of environmental factors, also known as limiting or regulating factors, that encompasses resources, toxins and predators, and the competitive exclusion principle, which states that the number of species that coexist at equilibrium cannot exceed the number of regulating environmental factors (Levin 1970, Chase and Leibold 2003, Meszéna et al. 2006, Parvinen et al. 2020). One striking example of this conceptual unity is the realization that prey sharing predators interact as if they were competing, a phenomenon termed "apparent competition" by Holt (1977). The explicit connection between the niche concept and species' environment also offers broad applications. For example, biogeographers operationalize specie' requirements on large spatial scales when they correlate the spatial distribution of a species with climatic variables to reconstruct the climatic niche of a species, understand their distribution and predict range shifts caused by global change (Wake et al. 2009, Peterson et al. 2011). A finer focus on population demography has led to a refinement of the niche concept into its demographic components, such as the establishment and persistence niches (Holt 2009a), or the fecundity, growth, survival and recruitment niches (Pironon et al. 2018). At the more local scales, Niche Theory has been used by community ecologists in parallel with Modern Coexistence Theory to elucidate the competitive mechanisms leading to species coexistence, with recent theoretical work solidifying the connection (Kleinhesselink and Adler 2015, Letten et al. 2017, Advani et al. 2018).

Notably, both Modern Coexistence Theory and Contemporary Niche Theory have almost exclusively focused on competition and negative interactions, which represent only a subset of types of interactions that occur in nature. In fact, ecologists are increasingly recognizing the role played by positive interactions in natural communities, such as facilitation (Callaway 1995, Brooker et al. 2008, Filazzola and Lortie 2014) and mutualism (Bronstein 1994). It has been shown that these positive interactions have consequences for the distribution of plant species (Afkhami et al. 2014, Filazzola et al. 2017) and intra- and interspecific cooperation between microorganisms (Nadell et al. 2016, Estrela et al. 2018, Frost et al. 2018, Seto and Iwasa 2019, Zuñiga et al. 2019). Novel frameworks specifically tailored for these positive interactions have emerged, such as ecosystem engineering (Jones et al. 1994, Cuddington et al. 2009) and niche construction (Odling-Smee et al. 1996, 2003). Modeling work exploring the effect of including these positive interactions alongside negative ones on communities are diverse (Gross 2008, Kéfi et al. 2008, Jones et al. 2012, Bimler et al. 2018, Butler and O'Dwyer 2018, Goldford et al. 2018), with a few of them drawing explicit connections with Niche Theory in the context of niche construction (Kylafis and Loreau 2008, 2011), mutualism and cross-feeding (de Mazancourt and Schwartz 2010, Johnson and Bronstein 2019, Sun et al. 2019).

Yet, the full integration of positive interactions alongside competition in these general ecological theories is still lacking. On one hand, accommodating positive interactions in the current form of Modern Coexistence Theory has proven challenging, as the classical metric of niche overlap is not defined in that situation (Spaak and De Laender 2020). On the other hand, conceptual embedding of facilitation into Niche Theory has led to influential ideas such as the Stress Gradient Hypothesis (Bertness and Callaway 1994), the idea that positive interactions dominates in stressful environments, and "niche facilitation," the expansion of a species' niche by another through facilitation (Bruno et al. 2003, Bulleri et al. 2016). However, these theoretical developments have been mostly verbal. Using graphical intuition in the niche space, Holt (2009a) also proposed that positive interactions between conspecifics can lead to a mismatch

between the establishment niche, the environmental conditions under which a species can establish from low densities, and the persistence niche, the environmental conditions under which a species can persist at high densities. However, the general mechanisms underlying these different concepts and their interpretations in terms of organism–environment feedback have been insufficiently explored and formalized (Holt 2009*b*). This is an important shortcoming for a theory, because non-formalized, verbal concepts are more prone to ambiguity and semantic confusion, as exemplified by a recent debate on whether positive interactions can expand the fundamental niche (Rodriguez-Cabal et al. 2012, Stachowicz 2012).

In this paper, we overcome these deficiencies by introducing a general framework for Niche Theory with one and two environmental factors that goes beyond competition, spanning the full range of ecological interactions between organisms from negative to positive. When applied to the fundamental niche, our framework shows how positive feedbacks emerge mechanistically, naturally leading to Allee effects through a mismatch between the establishment and persistence niches. Extended to two interacting species, we show how and when positive interactions within and between species lead to facilitation of the realized niche, defined as one species expanding either the establishment or the persistence niche of the other species. Finally, we introduce a pair of metrics of niche difference, the impact niche difference and the sensitivity niche difference, to characterize the nature of pairwise interactions and quantify their strength. We then tie these metrics to classic characteristics of coexistence such as stability and equilibrium densities, and explicitly link them to other metrics such as Chesson's (2000) and Saavedra et al.'s (2017) niche differences. By making explicit the link between our pair of metrics and Lotka-Volterra models, we also show how the full set of possible Lotka-Volterra dynamics can be arranged along these two axis of niche difference. To show the generality of this framework, we illustrate it throughout the text with a broad range of theoretical examples, from a bacterial population feeding on an inhibiting substrate, to the competition for soil nutrients between nitrogen-fixing and non-fixing plant species and the "inter-trophic" interactions between plants and carnivores mediated through herbivores. As a whole, the framework presented here expands the generality of niche concepts, from intra- to interspecific interactions, form negative to positive interactions, and from within to across trophic levels.

## Niche Theory Framework

A central tenet of Niche Theory is that interactions between organisms happen indirectly through their shared environment (Chase and Leibold 2003, Meszéna et al. 2006). Before we can generalize Niche Theory to account for facilitation and mutualism between species, a natural first step consists in laying the theoretical foundations of how species interact with their environment by introducing the concepts of species requirements and impacts (also see Glossary in Box 1).

### General model

We decompose the environment into multiple components, hereafter called environmental factors. Traditionally these refer to abiotic resources, but can also include the abundance other species, such as predators (Holt 1977). In Niche Theory, the interactions between a species and its environment are conceptually decomposed into a two-way process: (1) the environment affects the growth rate of the species through the species' *requirements* and (2) the resulting change in density of the species affects the environment through the species' *impacts*. Following previous work (Meszéna et al. 2006, Barabás et al. 2014, Koffel et al. 2016, Lion 2018), a species–environment system composed of $j = 1, ..., n$ focal species with densities denoted $N_j$, interact through a dynamical environment $\mathbf{E} = (E_1, E_2, ..., E_p)$, whose $p$ components are the environmental factors $E_i$. Assuming that all interactions between and within species are mediated by the environment, and that the effect a species has on an environmental factor is proportional to its density, we can formulate a general model described by the equations

$$\frac{dN_j}{dt} = g_j(\mathbf{E})N_j \qquad (1a)$$

$$\frac{dE_i}{dt} = f_i(\mathbf{E}) + \sum_{j=1}^{n} e_{ij}(\mathbf{E})N_j. \qquad (1b)$$

Here $g_j(\mathbf{E})$ is the per capita growth rate of species $j$ and $e_{ij}(\mathbf{E})$ translates the per capita effect of species $j$ on the dynamics of environmental factor $i$; both are functions of the state of the environment $\mathbf{E}$.

The function $f_i(\mathbf{E})$ represents the intrinsic dynamics of the environmental factor $E_i$ in the absence of the $n$ focal species. For simplicity, we will assume from now that $f_i$ takes the form of $f_i(\mathbf{E}) = \Phi_i - \lambda_i E_i$, with $\Phi_i$ and $\lambda_i$ the input flux and the per unit output rate, respectively, at which each environmental factor $E_i$ moves in and out of the system (but see Appendix S1 for how to work with other classes of environmental factors). Such dynamics are sometimes called "chemostat dynamics" in the literature by analogy with the experimental device, but we use it here to encompass a broad class of ecological situations. For example, when the $N_j$'s are plant species and the $E_i$'s different limiting nutrients, e.g., soil nitrogen and phosphorus, $\Phi_i$ would be the inputs through atmospheric deposition or bedrock dissolution and $\lambda_i$ the leaching rate through the soil; in pelagic systems, $\Phi_i$ would represent nutrient input from land and the hypolimnion and $\lambda_i$ would represent outflow and mixing with the hypolimnion. Alternatively, when the $E_i$'s are the densities of various natural enemies, $\Phi_i$ would be their immigration rate

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### Box 1. Glossary

**Requirements** describe the environmental conditions, i.e. the values taken by the environmental factors (resource levels, predator abundances), necessary for a focal species to grow, encoded in the functional form of this species' growth rate. The sensitivities and establishment niche (see below) of a species are different manifestations of these requirements.

**Sensitivities** describe how a focal species' growth rate changes in response to a change in each environmental factor. Together, they form the sensitivity vector. In general, sensitivities are environment dependent, meaning that they are a function of the environmental state.

**Impacts** are the collection of a focal species' per capita effects on the environmental factors, rescaled by the intrinsic turnover rate of that factor. Together, they form the impact vector, and in general are environment dependent.

**Positive (negative) feedback loops** are indirect pathways through which an increase in species density increases (decreases) its per capita growth rate. In Niche Theory, they are mediated by the environmental factors and typically occur when sensitivities and impacts have equal (opposite) signs.

**Environmental state** is the collection of all environmental conditions. Its dynamics is driven by the interplay between the environment's internal dynamics and the impacts of the focal species.

**Zero Net Growth Isocline (ZNGI)** is the curve made of the set of environmental states for which the growth of a focal species is zero. When represented in the space of supply points, it is also the boundary of the establishment niche.

**Supply point** describes the externally controlled characteristics of the environment (e.g., substrate richness, macroclimate, regional herbivore abundances). In the absence of focal species, the environmental state equilibrates at the supply point.

**Establishment niche** is the set of supply points for which the focal species can invade, i.e., grow from low density.

**Persistence niche** is the set of supply points for which the system has at least one equilibrium where the focal species has a positive density.

**Traditional niche** is the set of supply points that belong in both the establishment and persistence niche.

**Allee niche** is the set of supply points that belong in the persistence niche but are not in the traditional niche.

**Fundamental niche(s)** are the niche(s) of a focal species in the absence of any other focal species.

**Realized niche(s)** are the niche(s) of a focal species in the presence of other focal species. Usually, a realized niche is strictly contained in the fundamental niche, but the opposite can be true in the presence of positive interactions between species.

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into the local community and $\lambda_i$ their mortality and/or emigration rates. In the absence of any of the focal species ($N_j = 0$ for all $j$), each environmental factor $E_i$ equilibrates to its "supply" level $\tilde{E}_i \equiv \Phi_i / \lambda_i$, which together form the *supply point* $\tilde{\mathbf{E}}$. This supply point, by definition, describes the externally controlled characteristics of the environment, such as the macroclimate or the chemical composition of the bedrock. The environmental state $\mathbf{E}$, on the other hand, describes the actual environment directly under the influence of the focal species $N_j$, such as the available nutrient concentration.

Eq. 1 is a formal way to regroup a general class of ecological models that fall under the scope of Niche Theory (Levin 1970, Chase and Leibold 2003, Meszéna et al. 2006, Koffel et al. 2016), encompassing resource competition (Tilman 1980, 1982, Grover 1997) and apparent-competition models (Holt 1977, Holt et al. 1994, Leibold 1996, Chesson and Kuang 2008). The examples below explore a variety of other ecological situations that can also be described by Eq. 1, including chemical warfare (allelopathy, inhibition), detoxification, inter-guild

interactions, and niche construction. As we will see, the possibility of positive interactions and feedback loops emerges naturally in this framework.

### Requirements and impacts

As stated earlier, a central tenet of Niche Theory is the decomposition of species–environment interactions into species requirements and impacts (Chase and Leibold 2003). This is usually represented by Zero Net Growth Isoclines (ZNGIs) and impact vectors using the graphical approach to Niche Theory (see Box 2 and Appendix S2; Tilman 1982, 1988, Chase and Leibold 2003, Koffel et al. 2016). Following this work, we define the impact of species $j$ on environmental factor $E_i$ as $I_{ij} \equiv e_{ij}(\mathbf{E})/\lambda_i$, i.e., the per capita impact of this species rescaled by the intrinsic turnover of that environmental factor (note that this choice differs from the definition of impacts by Meszéna et al. [2006], but this has no bearing on our results here; see calculations in Appendix S3 and Online Material 9.3 of Pásztor et al. 2016). The sign of the

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**Box 2. Graphical Approach to Niche Theory**

In this Box, we briefly introduce the basics of the graphical approach to Niche Theory, with a focus on geometrical intuition. For a more in-depth presentation, we refer the reader to the classic literature on the subject (MacArthur 1969, León and Tumpson 1975, Tilman 1980, 1982, Leibold 1996, Grover 1997, Chase and Leibold 2003), recent work by us that includes a review of the topic (Koffel et al. 2016) and the step-by-step guide in Appendix S2.

The goal of the graphical approach to Niche Theory is to illustrate graphically the equilibrium community of an ecological system represented by Eq. 1 and represent how it varies along environmental gradients. This relies on decomposing the feedbacks between each species and the environment into their requirement and impact components.

Graphically, the requirements of a species can be represented by the set of environmental factors for which that species has a positive growth rate. The boundary of this region, where the growth rate of that species is zero, is given by its Zero Net Growth Isocline (ZNGI), which is of particular importance. If that species is present in the community, the environment at equilibrium is necessarily located on that species' ZNGI, i.e., at the boundary of its niche (Fig. 1A). Note that the sensitivity vectors are locally perpendicular to the ZNGI. The impacts of a species, on the other hand, can be represented with a few of its impact vectors drawn along the ZNGI. Because impacts generally depend on the state of the environment (see *Requirements and impacts*), the direction of these vectors changes as we move along the ZNGI. Finally, the externally controlled, intrinsic characteristics of the environment are given by the supply points, which generate environmental gradients as they vary. Because supply points have the same dimensions as environmental factors, they can be represented alongside the ZNGI and the impact vectors in the space of environmental factors.

Equilibrium solutions of a species in monoculture are obtained by combining its ZNGI, impact vectors and the supply point. For a given supply point, one just has to identify which impact vector(s) goes through that point when extended backward; the point on the ZNGI where this impact vector originates then directly gives the environmental factors at equilibrium, while the distance between that point and the supply point is proportional to that species density. This means that all the supply points aligned behind an impact vector are associated with the same environmental conditions at equilibrium but with different species densities. If no impact vector goes through a supply point, this means that the species cannot persist under these conditions and goes extinct. The supply points for which a species can grow when rare and persist at equilibrium by itself can be represented in the space of environmental supplies directly, together forming the fundamental niche of that species (Fig. 1B).

The graphical approach is even more useful when considering several species in interaction. Then, the procedure described in the previous paragraph can be applied to each species independently, with the ZNGI of each species giving all potential one-species equilibria. However, the one-species equilibria of a given species whose environment states fall within the positive growth region of another species are unstable because this other species can invade, and must be discarded (dashed portions of ZNGIs in Fig. 1C). In practice, only portions of ZNGIs that are located outside the ZNGIs of other species are stable and thus kept, a procedure called invasion analysis (Fig. 1C). Finally, coexistence between two species can only happen for environmental factors located at "coexistence points," the intersection of their ZNGIs (black dot in Fig. 1C). The supply points located within the cone delimited by the impact vectors of the two species originating from that coexistence point correspond to coexistence equilibria. In general, coexistence is stable if these supplies are not associated with any stable one-species equilibria, as it is the case on Fig. 1C. From there, the realized niche of a species is simply the combination of the region of supplies where that species is present alone with the supplies where it coexists with other species.

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impacts $I_{ij}$ indicates the relationship between a species $j$ and the environmental factor $i$: in our convention, a population has a negative impact on a resource it consumes ($I_{ij} < 0$), and a positive impact on a natural enemy it feeds ($I_{ij} > 0$). We omit the dependence of $I_{ij}$ on the environment $\mathbf{E}$ to simplify the notation, but it is important to keep in mind that this dependence makes the impacts context dependent; a consequence of this dependency is that the impact $I_{ij}$ could switch from being positive to negative along an environmental gradient.

Conversely, the requirements of a species $j$ are given by how its growth rate depends on the state of the environment through the functional form of $g_j(\mathbf{E})$, and boils down to two aspects. (1) The ZNGI gives the set of most extreme environmental conditions under which a species experiences non-negative growth, mathematically given by $g_j(\mathbf{E}) = 0$; the ZNGI materializes the boundary of a species' niche (Box 2). (2) The *sensitivity* to the environmental factor $E_i$ (sensu Meszéna et al. 2006), denoted $S_{ij}$, quantifies how the growth of species $j$ changes in

A) Elements of the graphical approach



B) Fundamental niche



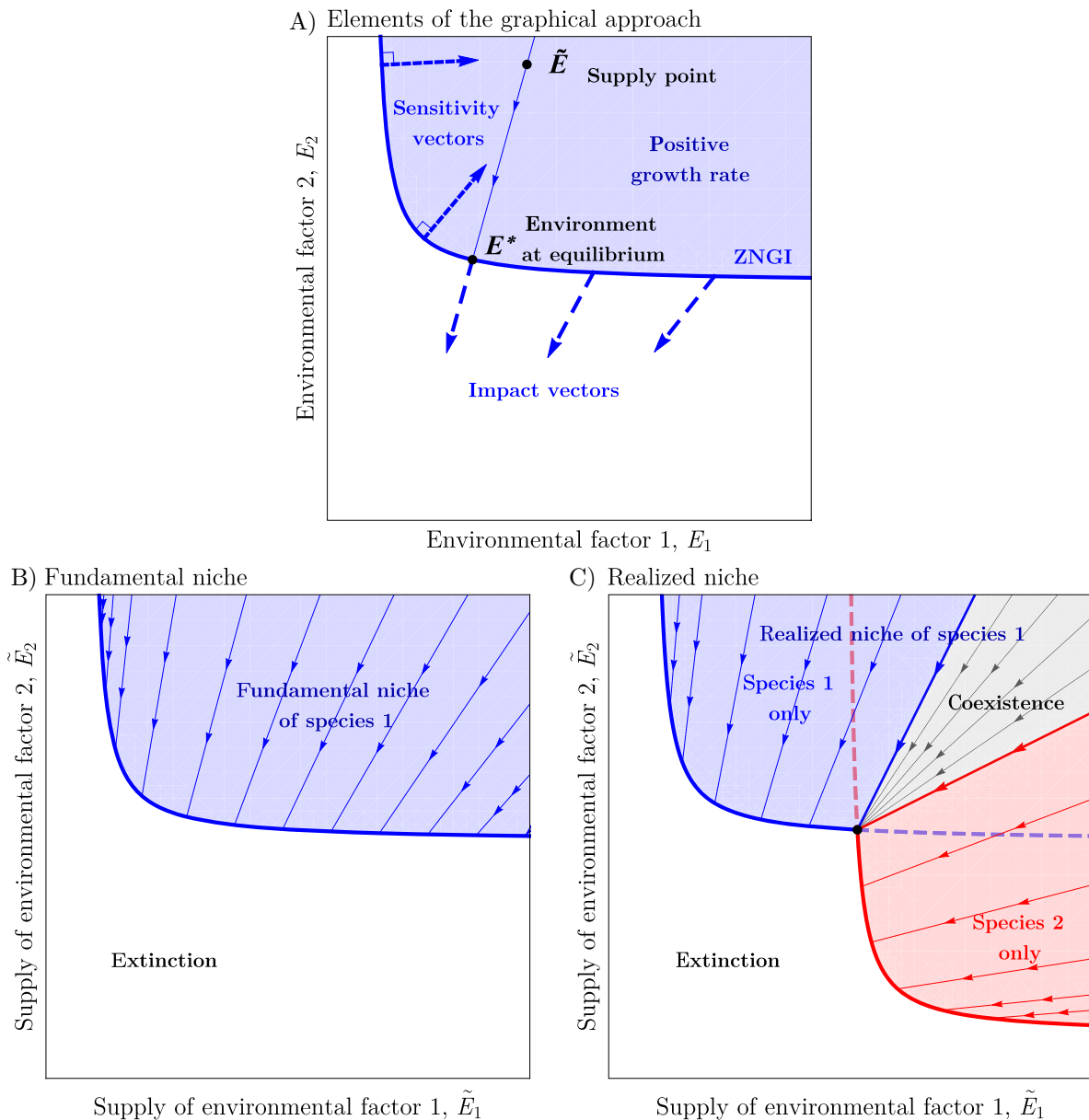C) Realized niche



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Fig. 1.   Graphical approach to Niche Theory. (A) The Zero Net Growth Isocline (ZNGI), which corresponds to the boundary of the region of positive growth rate, is combined graphically with the impact vectors and the supply point to determine the environment at equilibrium. Note that the sensitivity vectors are perpendicular to the ZNGI. (B) The supply points for which a species by itself can grow when rare and persist at equilibrium can be located in the space of environmental supplies, together forming the fundamental niche of that species. Impact vectors are superimposed to materialize how they help determine the environment at equilibrium. (C) The ZNGIs of two competing species can be combined to partition the space into four regions representing all the possible outcomes of community assembly along environmental gradients. Here, the realized niche of a species $i$ is obtained by combining the "species $i$ only" and "coexistence" regions. When species compete, as is the case here, their realized niche is smaller than their fundamental niche; this is not the case with positive interactions (see *Positive Interactions Between Species: Niche Expansion and the Realized Niche(s)*).

response to a change in environmental factor $i$, given by the partial derivative of the per capita growth rate $g_j(\mathbf{E})$ with respect to the environmental factor $E_i$

$$S_{ij} \equiv \frac{\partial g_j}{\partial E_i}. \qquad (2)$$

Taken together, the sensitivities of species $j$ form the sensitivity vector $\mathbf{S}_j$, which points in a direction perpendicular to that species' ZNGI (Box 2). Similar to species' impacts, the sign of the sensitivity $S_{ij}$ summarizes the relationship between a species and the components of its environment: a species has positive sensitivity to its

limiting resources ($S_{ij} > 0$) and negative sensitivity to its natural enemies ($S_{ij} < 0$). Additionally, when a consumer is solely limited by one essential resource, its sensitivity to other resources is zero. Like impacts, sensitivities implicitly depend on the environment **E** and can thus change sign along environmental gradients, as we will see in the coming examples.

NEGATIVE AND POSITIVE FEEDBACKS BETWEEN A SINGLE SPECIES AND ITS ENVIRONMENT: THE FUNDAMENTAL NICHE

Sensitivities and impacts can each be positive or negative. Estrela et al. (2018) combined these cases into a general classification of species–environment relationships with four ecological scenarios (Fig. 2). For example, the classic resource–consumer dynamics, where a focal population consumes a beneficial resource, corresponds to the "Deplete" scenario (MacArthur 1970, Tilman 1982, Grover 1995, Chase and Leibold 2003). Following Levins's (1974) ideas from loop analysis, positive sensitivities "times" negative impacts results in an overall negative feedback loop of that population on itself, classically called bottom-up control, negative density dependence or population regulation in the ecological literature, and the resource that mediates it is called a regulating factor (Levin 1970, Chase and Leibold 2003, Meszéna et al. 2006, Pásztor et al. 2016). Similarly, the traditional predator–prey configuration where a focal population sustains a detrimental natural enemy

illustrates the "Pollute" scenario (Fig. 2), leading to an overall negative density dependence of the focal population on itself, coined top-down regulation.

Consuming a resource and sustaining a natural enemy both lead to species regulation, but they represent only half of the possible scenarios (Fig. 2). What happens when a detrimental environmental factor is impacted negatively, or a beneficial environmental factor is impacted positively? In these two scenarios, the environmental factor can no longer be called a "regulating" factor, as it induces a positive feedback loop (Levins 1974, DeAngelis et al. 1986, Bianchi et al. 1989, Pásztor et al. 2016). These two situations emerge naturally in this classification and both are biologically relevant. For example, it is well known that some resources can inhibit growth or increase mortality when their concentration is too high. This has been documented with plankton photoinhibition (Gerla et al. 2011) or high-concentration substrate toxicity for microorganisms (Haldane 1930, Andrews 1968, Harmand et al. 2017), a situation that we will explore in our first example. Similarly, a plant with a high concentration of secondary metabolites can be detrimental to a maladapted herbivore that consumes it. In both situations, the focal population negatively impacts an environmental factor that negatively affects it ("Detoxify" scenario of Fig. 2). Conversely, an organism can positively impact an environmental factor that positively affects it, corresponding to the "Enrich" scenario of Fig. 2. This is the focus of positive niche construction
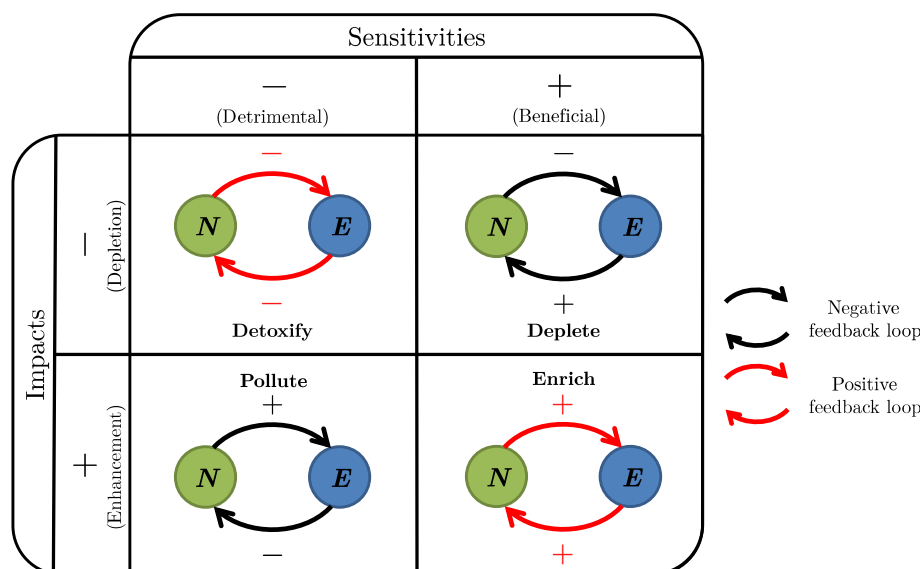


FIG. 2. The four qualitative possible combinations of impacts and sensitivities between a species and an environmental factor, leading to four generic ecological scenarios. Two of these scenarios correspond to the two traditional mechanisms of population regulation: in "Deplete," focal organisms are bottom-up controlled as they consume (− impact) a resource needed for growth (+ sensitivity) and, in "Pollute," they are top-down controlled as they feed (+ impact) an enemy that hurts them (− sensitivity). The two other scenarios lead to positive feedback loops, i.e., unregulated growth (red): in "Enrich," organisms produce (+ impact) a resource they need to grow (+ sensitivity) and in "Detoxify," organisms deplete (− impact) a resource that inhibits their growth (− sensitivity). The terminology has been borrowed and adapted from Estrela et al. (2018).

(Odling-Smee et al. 1996, Rietkerk and van de Koppel 1997, Kylafis and Loreau 2011, Matthews et al. 2014, Picot et al. 2018). As we will see in our second example, nitrogen-fixing plants that also consume soil nitrogen are an example of this scenario (Koffel et al. 2018*a*).

We again emphasize the fact that both sensitivities $S_{ij}$ and impacts $I_{ij}$ are functions of the environment **E**. This implies that the sign of the sensitivities, impacts, and feedback loop are also generally environment dependent, which can be of crucial importance as we will illustrate in two of our examples. Such environment dependence of the sign of interactions is not possible in traditional Lotka-Volterra systems, where interactions are of fixed sign, leading to unstable blowups in strong positive interactions regimes (May 1976, Vandermeer and Boucher 1978).

On a final note, the way we parametrized the Niche Theory model in Eq. 1 gives rise to impacts and sensitivities that appear to be completely independent, which allowed us to fully explore the four sign combinations. In some situations, however, ecological processes and physical constraints such as mass balance can lead to a dependency between impact and sensitivities. As we will see throughout our three examples, the emergence of positive feedbacks is still possible in the presence of this dependency.

### Example 1: Inhibiting substrate

To illustrate the concepts of sensitivities, impacts, and positive environmental feedback loops, let us consider the classic example of a population of consumers growing on a substrate that acts as a resource at low concentrations but turns detrimental at high concentrations. Biological examples are widespread, and include microorganisms and their substrates, such as inhibition of *Nitrosomas* by ammonia (Andrews 1968, Harmand et al. 2017) and photoinhibition of phytoplankton (Gerla et al. 2011), the toxicity of highly concentrated nitrogen for terrestrial plants (Britto and Kronzucker 2002), and the inhibition under high concentrations of most limiting nutrients for animals (Boersma and Elser 2006). Growth inhibition under high resource concentrations is usually modeled using a hump-shaped uptake function ρ, such as the Haldane function (Haldane 1930), also known as a Type IV functional response (Andrews 1968; Fig. 3A) described by

$$\rho(R) = \mu \frac{\alpha R}{\mu + \alpha R + \beta R^2}. \tag{3}$$

Here $R$ is the concentration of the substrate, $\alpha$ the affinity of the consumer for the substrate, $\mu$ the maximal growth rate of the consumer in the absence of inhibition ($\beta = 0$), and $\beta$ a parameter that characterizes the strength of inhibition. After a rapid initial increase with $R$, the uptake rate of the consumer hits a maximum and then slowly decreases with $R$ as substrate concentrations further increase (Fig. 3A). When this uptake function is embedded into a classic resource–consumer situation, we get
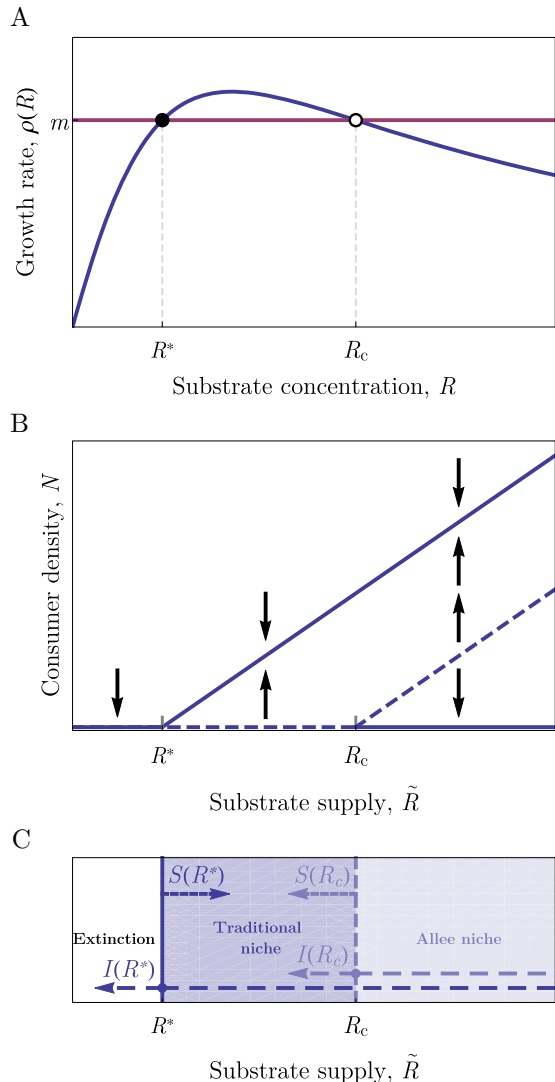
Fig. 3. Example of a single species consuming a single inhibiting substrate. (A) Consumer growth rate (blue) and mortality ($m$, purple) as a function of substrate concentration is hump-shaped, leading to two possible concentrations at equilibrium where net growth is zero. The second equilibrium with concentration $R_c$ is unstable (white dot), as its negative sensitivity combined with negative impact result in a positive feedback loop. (B) Bifurcation diagram of consumer density at equilibrium as a function of substrate supply. Under high supplies, there is a bistable regime between persistence and extinction, which signals presence of an Allee effect for the consumer. (C) Niche of the consumer along a gradient of substrate supply. For intermediate supplies, $R^* < \tilde{R} < R_c$, the consumer species has a traditional niche and, for high supplies $R_c < \tilde{R}$, the species has an Allee niche, see *Establishment and persistence niches* for details.

$$\frac{dN}{dt} = [\rho(R) - m]N \tag{4}$$

$$\frac{dR}{dt} = \Phi_R - \lambda_R R - q\rho(R)N \tag{5}$$

where $N$ is the population density of the consumer, $m$ its per capita mortality rate, $q$ a coefficient that converts the substrate into consumer biomass, and $\Phi_R$ and $\lambda_R$ the input flux and leaching rate of the substrate, respectively, leading to the substrate supply point $\tilde{R} \equiv \Phi_R/\lambda_R$. This is a simple instance of Eq. 1 with a single population $N_1 \equiv N$, a single environmental factor $E_1 \equiv R$, and net per capita growth rate $g_1 \equiv \rho(R) - m$. Following our previous definitions, sensitivity $S$ and impact $I$ of the consumer on the substrate are given by

$$S(R) \equiv \frac{\partial \rho}{\partial R} = \frac{\mu\alpha(\mu - \beta R^2)}{\mu + \alpha R + \beta R^2} \quad (6)$$

$$I(R) = -q\rho(R)/\lambda_R. \quad (7)$$

It is clear that the sign of $S$ is environment dependent, as the slope of the growth function $\rho$ switches from positive to negative as it hits its maximal value (Fig. 3A), which, as Eq. 6 tells us, happens for $R = \sqrt{\mu/\beta}$ (see Appendix S4 for a more thorough analysis). On the other hand, the impact $I$ is always negative: the population always consumes the substrate since $\rho(R) > 0$. Therefore, increasing substrate concentrations leads to a switch from a negative feedback loop to a positive one. This provides a concrete illustration of how a situation can switch from the Deplete scenario to the Detoxify scenario (Fig. 2).

What are the consequences of this positive feedback loop on the dynamics of the system? Let us look at the equilibria of the system. In the presence of the consumer, the substrate concentration at equilibrium where net growth $\rho - m$ is zero can be seen in Fig. 3A; it happens when the growth rate $\rho(R)$ intersects the mortality rate $m$ (see the mathematical derivation in Appendix S4 or elsewhere in the literature, e.g., Ranjan and Bagchi 2016, Harmand et al. 2017, Rapaport 2018). In contrast to standard monotonic growth functions in consumer–resource systems, such as linear or Monod, the humped shape of $\rho$ leads not to one, but two zero net growth concentrations, denoted $R^*$ and $R_c$ here, with $R^* < R_c$. The associated consumer density at equilibrium is then deduced setting the right side of Eq. 5 to zero.

Looking at the environment-dependent sign of the feedback loop, we can quantitatively assess the stability of these two equilibria. Impacts are negative at both equilibria, as follows from their definition in Eq. 7. Furthermore, we see graphically (Fig. 3A, C) that the sensitivity of the consumer is positive when $R = R^*$ and negative when $R = R_c$. This means that the consumer is regulated at $R^*$ through a classic consumer–resource-like negative feedback loop, while $R_c$ is associated with a positive feedback loop. Local stability analysis confirms that equilibrium $R^*$ is stable while equilibrium $R_c$ is unstable (Appendix S4). As we will see in the next subsection, the instability of equilibrium $R_c$ signals an Allee effect, where a high abundance of the consumer can hold resource availability below $R_c$ under high supplies and persist, whereas it is unable to withstand such supplies when starting from low abundance, and thus goes extinct.

*Establishment and persistence niches*

Let us now look at the consequences of positive feedback loops between a species and its environment for its niche by introducing the concepts of the establishment and persistence niches (Holt 2009a). Following Holt's (2009a) terminology, we first define the *establishment niche* of a species as the set of environmental conditions for which this species has a positive growth rate when rare. Such environmental conditions correspond to characteristics of the environment **E** that exist independently of the focal species, such as baseline soil fertility or background herbivore density when the focal species is a plant. In Niche Theory, the supplies $\tilde{E}_i$ are usually chosen to represent these extrinsic characteristics of the environment, as they give the value of the environmental factors $E_i$ at equilibrium when all the focal species are absent. Varying these supplies makes it possible to generate environmental gradients along which we can delimit the niche of the focal species. Formally, the establishment niche of species $j$ is given by the set of supply points $\tilde{\mathbf{E}} = (\tilde{E}_1, \dots \tilde{E}_i, \dots \tilde{E}_p)$ for which $g_j(\tilde{\mathbf{E}}) > 0$, where $g_j(\tilde{\mathbf{E}})$ is the growth rate of an invading population of species $j$, often called the *invasion growth rate* in short.

Second, we define the *persistence niche* of a species as the environmental conditions under which that species can persist at a locally stable equilibrium or other attractor (Holt 2009a). Formally, the persistence niche is given by the set of supplies $\tilde{\mathbf{E}}$ for which there exists a locally stable attractor associated with a non-zero equilibrium population $\widehat{N}_j$. As illustrated below, the establishment and persistence niches do not necessarily coincide. Such mismatches between establishment and persistence niches have well-known analogs in the Allee effect literature, where positive density dependence at low density can lead to extinction if population density goes below a certain threshold, which is equivalent to saying that a population cannot invade or establish starting from a very low density (Courchamp et al. 1999, Cuddington et al. 2009, Holt 2009a). For this reason, we call the environmental conditions $\tilde{\mathbf{E}}$ where a species can persist but not invade its *Allee niche*. Life in the Allee niche is precarious: a strong perturbation can push the species' density under the minimal threshold for recovery, leading to extinction. Conversely, we can think of the region of supply points that belongs to both the persistence and establishment niches as the *traditional niche*. Finally, note that a last possibility could be the existence of environmental conditions under which a species can invade but not persist, called *niche destruction* by Holt (2009a). However, such an outcome does not occur when the environmental factors have a unique attractor as in the chemostat dynamics assumed so we ignore it hereafter.

Let us illustrate these niche concepts with the previous example of a population consuming an inhibiting substrate. Fig. 3B shows the locally stable (solid) and locally unstable (dashed) equilibrium consumer density $\widehat{N}$ as a function of substrate supply. We see that for supplies $\tilde{R}$ that are either below the minimal resource concentration $R^*$ or above the critical concentration $R_c$, the equilibrium where the consumer is absent ($\widehat{N} = 0$) is stable, which means that the establishment niche is limited to the supplies located between $R^*$ and $R_c$ (Fig. 3C). This is consistent with Fig. 3A, where we have seen that below $R^*$, there is not enough substrate to for the consumer population to grow, while above $R_c$, the substrate reaches toxic concentrations that prevent the consumer from establishing from low densities.

Conversely, the persistence niche comprises all the supply points greater than $R^*$, as they all admit a locally stable equilibrium with positive density (Fig. 3B). Thus, the establishment and persistence niches do not coincide, leading to an Allee niche for supplies located above $R_c$. How to explain this? Starting from a high enough density, a consumer population can strongly impact the substrate by consuming it so that its concentration decreases below the toxic threshold given by $R_c$. When this happens, population growth rate turns positive, decreasing substrate concentrations even more, until $R^*$ is reached and the consumer population is stabilized. Such a positive feedback loop leads the consumers to collectively detoxify their environment (Estrela et al. 2018), where they would have failed to establish when starting in low numbers. The consumer population uses the positive feedback loop to expand its persistence niche outside of the region where invasion is possible, a phenomenon that can be called "ecological niche construction" (Kylafis and Loreau 2008). Note that the context-dependency of consumer sensitivity $S$ to substrate concentration (positive when substrate concentrations are low, negative when high) is key here for the system to eventually reach a stable equilibrium: the positive feedback loop that emerges at high substrate concentration vanishes as these concentration decrease, leading to a purely consumptive system where the limiting substrate regulates the consumer population. As we will see with the next example, the Allee niche is not limited to the inhibiting substrate example, but can emerge from a wide variety of species–environment interactions.

### Example 2: Nitrogen-fixing plants

In the previous example, we saw how a mismatch between the establishment and the persistence niche can arise from an environment-dependent positive feedback loop, even with a single environmental factor. We now introduce a second, slightly more complex example that involves two environmental factors. Let us consider a plant–soil system composed of nitrogen-fixing and non-fixing plant species that consume two nutrients, soil nitrogen N and phosphorus P (Fig. 4A; Menge et al.

2009, Koffel et al. 2018a). N and P are modeled as essential nutrients using Liebig's law of the minimum (Tilman 1982), which means that plant growth is limited by only one nutrient at a time, the nutrient the plant needs the most under given conditions. As both nutrients positively influence plant growth, this means that the sensitivities $S_{Nj}$ and $S_{Pj}$ of a nitrogen-fixing species $j$ are always either positive (for the limiting nutrient) or zero (for the non-limiting nutrient). Other details of the general mathematical approach can be found in Koffel et al. (2018a). In this example, we consider three distinct plant strategies: a *non-fixer* that only consumes soil nutrients, a *facultative N fixer* that can partially compensate for soil N depletion through fixation, and an *obligate N fixer* that can grow even in the total absence of soil N due to fixation but is unable to down-regulate fixation at high N availability. Following empirical evidence of the costliness of N fixation, we also assume that efficiency of N-fixation trades off against P acquisition (Koffel et al. 2018a), so that the non-fixer is the most effective at acquiring P, the facultative N fixer shows an intermediate performance, and the obligate N fixer is the least effective at acquiring P.

Fig. 4B–D illustrates the fundamental niches of these three species along phosphorus and nitrogen supplies using the graphical approach to Niche Theory (see Box 2 for details of the approach). For the non-fixing plant (Fig. 4B), the establishment and persistence niches are identical, so there is no Allee niche, and we recover the traditional niche of a plant limited by two nutrients (Tilman 1982). The boundary of this niche (defined by the ZNGI) is L-shaped, as expected for essential resources: the non-fixer is only found in environments where both phosphorus and nitrogen meet its minimal demands, with the vertical segment of the ZNGI corresponding to phosphorus-limited equilibria and the horizontal segment corresponding to nitrogen-limited equilibria. The net impact of the non-fixer is always consumptive (downward-pointing arrows in Fig. 4B), which prevents the emergence of a positive feedback loop and ensures that both N-limited and P-limited equilibria are stable.

The niche of the facultative N fixer presents some similarities with the non-fixer (compare Fig. 4C to B). First, the establishment niche is again located inside an L-shaped boundary that represents the minimal levels of nutrients necessary for the facultative N fixer to establish. This region is shifted relative to the niche of the non-fixer, as facultative N fixers can establish under lower N supplies due to their reduced dependence on soil N through fixation, but they pay a cost in phosphorus acquisition that translates into higher minimal P requirements. Interestingly, the N-limited equilibria of the facultative N fixer are unstable (horizontal boundary of the traditional niche, dashed). This is a consequence of the enriching effect of fixation and recycling on soil N overcoming the negative impact of uptake, leading to a positive feedback loop of the fixer under low soil N concentrations. This is materialized by the impact vectors
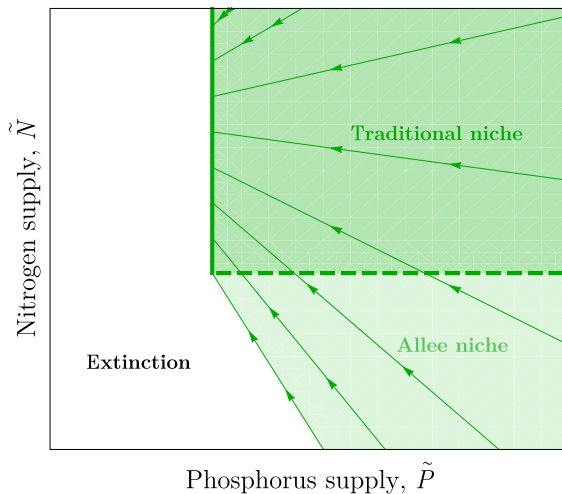
A) Schematic of ecosystem
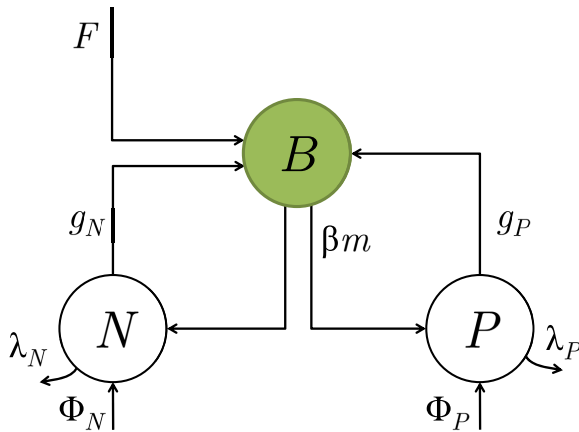
B) Non-fixer's fundamental niche
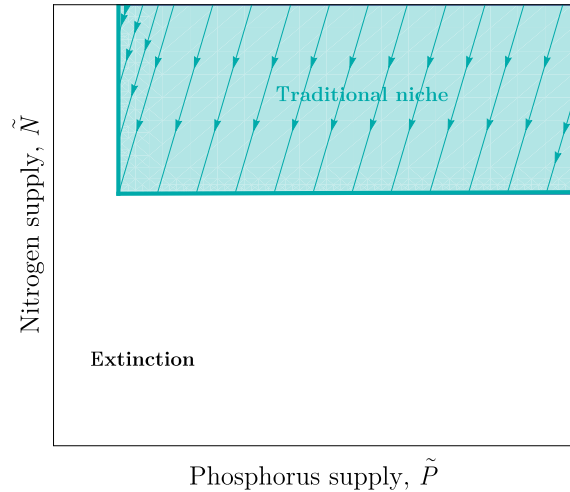
C) Facultative N fixer's fundamental niche

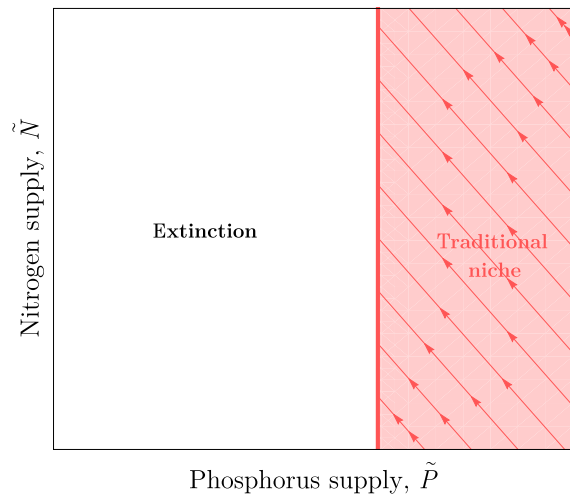D) Obligate N fixer's fundamental niche

FIG. 4. Fundamental niches of N-fixing and non-fixing plant species consuming two nutrients. (A) Schematic of the ecosystem made of a plant species ($B$) interacting with soil nitrogen (N) and phosphorus (P) pools (Koffel et al. 2018$a$). Both nutrients enter and exit the system at constant input rates ($\Phi_N$, $\Phi_P$) and per capita output rates ($\lambda_N$, $\lambda_P$). The two nutrients are essential, which means that plants consume them jointly as they grow ($g_N$, $g_P$). N fixers use N fixation up to a rate $F$ to supplement their needs, with $F$ trading off against the efficiency of P acquisition ($g_P$). Finally, dead plant material is generated at mortality rate $m$ and returned to the nutrient pools with a recycling efficiency β. We represented the fundamental niches of three species that differ in their fixing abilities: a non-fixer (teal, B), a facultative N fixer (green, C) and an obligate N fixer (red, D). Superimposed impact vectors help visualizing how the plants affect soil nutrient levels. (B) The niche of the non-fixer shows this species' low P and high N requirements. The non-fixer always consumes both N and P (downward-pointing arrows). (C) The facultative N fixer has intermediate requirements for invasion, but also displays an Allee niche where it can persist but not invade under very low N supplies. This is a consequence of the recycling-mediated positive feedbacks associated with positive net effect on soil N (upward-pointing arrows). (D) The obligate N fixer can invade and persist under any N availability if P supply is high-enough. Note that it always has a positive net effect on soil N as it cannot down-regulate fixation.

pointing up under low N concentrations (net enrichment in N), in contrast with the non-fixer case. In our classification of feedback loops, this illustrates the Enrich scenario of Fig. 2 where both sensitivities and impacts are positive. The positive feedback loop leads to a mismatch between the establishment niche and the persistence niche, as can be seen in Fig. 4C: the positive feedback loop extends the persistence niche well below

the minimal N requirements for invasion. This means that a population of N-fixing plants can persist in very N-depleted soils (low or even zero $\tilde{N}$) due to fixation and recycling, where establishment from a small population is impossible, leading to an Allee niche under low N availability.

The obligate N fixer always leads to a positive feedback loop because it never down-regulates fixation

(Fig. 4D). Yet, there is no mismatch between its establishment and persistence niches: fixation is so strong that the obligate fixer can grow even in the complete absence of soil N supply, enabling it to invade any conditions that satisfy its P requirements. This example shows that positive feedback loops do not systematically lead to an Allee niche (Kéfi et al. 2016); here, the obligate fixer is never really limited by soil N in the first place, making the positive feedback loop superfluous from the obligate fixer's perspective. Still, as we will see in the next section, the positive impact of the obligate N fixer on soil N can benefit other co-occurring species.

### POSITIVE INTERACTIONS BETWEEN SPECIES: NICHE EXPANSION AND THE REALIZED NICHE(S)

In the previous section, we explored how positive feedback loops between a species and its environment (associated with both the Detoxify and Enrich scenarios of Fig. 2) give rise to positive interactions between conspecifics, in turn leading to a mismatch between the establishment and persistence niches that we called the Allee niche. As we considered only a single species, the niche concepts explored so far pertained to that species' *fundamental niche*. We now explore the effect of positive interactions on the niches of two species in interaction, thus investigating their *realized niches* (Chase and Leibold 2003). We know that pairwise interactions can take a variety of forms, ranging from competition and predator–prey interaction to commensalism, facilitation, and mutualism. However, only recently has the spectrum of pairwise interactions been fully enumerated graphically in the context of two-dimensional environmental feedbacks (Estrela et al. 2018). Using the niche framework introduced here, we can go further by formalizing mathematically all these environmentally mediated two-species interactions, and explore species dynamics, coexistence and niches for each of these cases. While this full exploration will be presented in the next section, we first focus in this section on two ecological scenarios that involve the plant species from the previous section. Using the graphical approach to Niche Theory presented in Box 2, we illustrate two ways in which positive interactions between these plant species can expand species' niches, leading to realized niches that differ notably from their fundamental niches (Fig. 4).

In our first scenario, one species facilitates another by expanding the second's traditional niche (Bruno et al. 2003, Stachowicz 2012, Filazzola et al. 2017). This is what happens when the non-fixing plant interacts with the obligate N-fixing plant (Fig. 5A–C). The positive effect of the obligate N fixer on soil N levels enables the non-fixer to persist under N supplies where it could not have persisted on its own. This leads to an expansion of the establishment and persistence niches of the non-fixer (compare Fig. 5A with Fig. 4B). How does this work in

practice? Let us consider an environment characterized by a supply point located in the expansion of the non-fixer niche that also belongs to the traditional niche of the obligate N fixer (black dot in Fig. 5A). Looking at the invasion dynamics of the two species (Fig. 5B), only the obligate N fixer can establish at first. As it establishes and reaches its carrying capacity, soil N levels in the system increase above the minimal N requirements of the non-fixer (Fig. 5C), enabling the non-fixer to grow and establish in the ecosystem. Ultimately, both species coexist in this environment, as the obligate N fixer is limited by P and the non-fixer by N (Tilman 1982, Agawin et al. 2007). Interestingly, niche expansion is completely one sided here, as the obligate N fixer does not benefit from the presence of the non-fixer. In fact, the non-fixer reduces the niche of the N fixer, as the former outcompetes the latter in the high N and low P supply region, so that the overall interaction between the two species effectively resembles a predator–prey or host–parasite interaction.

In the second scenario, one species can facilitate another by expanding only that species' establishment niche. This happens when the facultative N-fixing plant interacts with the obligate N fixer (Fig. 5D–F). The mechanism, described theoretically in a variety of ecological systems (Gerla et al. 2011, Harmand et al. 2017, Koffel et al. 2018a, Rapaport 2018), is the following: by definition, the facultative N fixer cannot invade in its Allee niche as soil N levels are too low. However, if P levels are high enough, the obligate N fixer can invade there. As this happens, the obligate N fixer establishes and increases soil N levels through recycling of fixed N (Fig. 5E, F). Soil N then reaches a point where invasion of the facultative fixer becomes possible. As both species grow, competition for P becomes stronger. Because the facultative N fixer is a better competitor for P, it ends up excluding the obligate fixer, reaching its persistence equilibrium alone. The obligate N fixer played a transitory but crucial role; it acted as a pioneer species that enabled the facultative N fixer to overcome its Allee threshold, expanding the traditional niche of the facultative N fixer. When such facilitation-driven species replacement happens between a large number of species, it can generate realistic succession dynamics associated with ecosystem development (Koffel et al. 2018a).

### POSITIVE INTERACTIONS AND NICHE DIFFERENCE

In the previous sections, we revisited the fundamental and realized niche concepts in light of intra- and interspecific positive interactions. We now introduce a pair of metrics of niche difference that can be generalized to positive interactions. Chesson's metric of niche overlap in a two-species Lotka-Volterra model has recently gathered a lot of interest (Letten et al. 2017), but does not lend itself to positive interactions due to sign issues (Spaak and De Laender 2020). Structural approaches
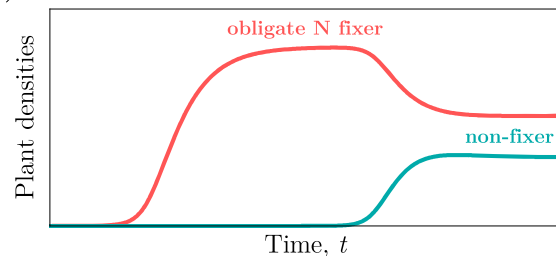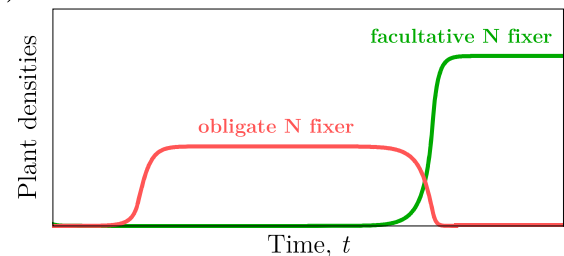
**A)**  Non-fixer's realized niche
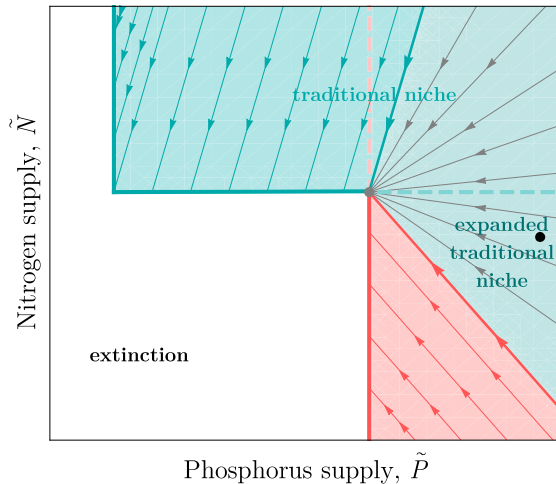
**D)**  Facultative N-fixer's realized niche
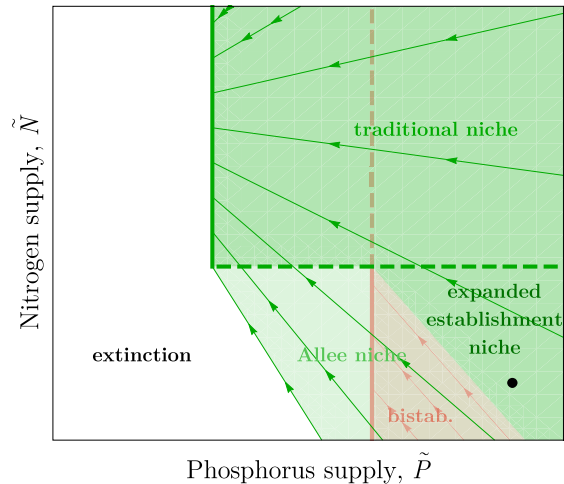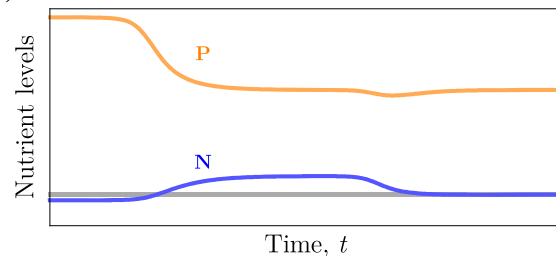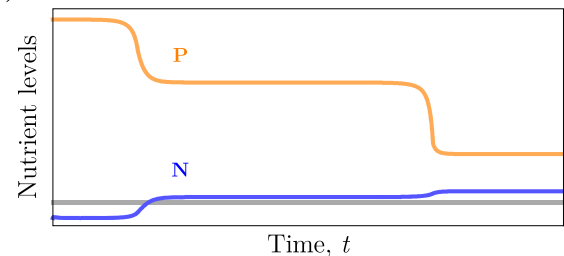


FIG. 5.    Realized niches and ecosystem trajectories of the non-fixer and facultative N fixer in the presence of the obligate N fixer. The ecosystem trajectories show the establishment of the plant community (B, E) and associated changes in soil nutrients (C, F) through time under relatively N-limited supplies (black dots in A, D). (A–C) The facilitating presence of the obligate fixer (red) expands the traditional niche of the non-fixer (teal) where they coexist (gray region, A). At low N supplies (black dot, A), the non-fixer can only invade after the obligate N fixer has established (B) because it needs the latter to enrich N levels (blue, C) above its minimal N requirements (gray line, C). Note that the realized niche of the obligate fixer is smaller than its fundamental niche due to competition with the non-fixer (compare A with Fig. 4D). (D–F) The facilitating presence of the obligate fixer (red) expands the traditional niche of the facultative N fixer (green) by expanding its establishment niche only. At low N supplies (black dot, D), the non-fixer can only invade after the obligate N fixer has established (E) because it needs the latter to enrich N levels above its minimal N requirements (gray line, F). However, they do not end up coexisting as the obligate N fixer eventually gets excluded as the facultative N fixer further depletes P (orange, F). Note that a bistability region between the facultative and obligate fixers ("bistab.") exists within the facultative fixer's Allee niche where the facultative fixer could persist on its own but facilitation is not strong enough for it to invade (red region, D).

(Petraitis 1989, Meszéna et al. 2006, Saavedra et al. 2017), on the other hand, provide natural geometrical definitions for niche difference and overlap, and are not subject to such caveats, so we will use these latter approaches as a starting point here. Our aim is two-fold. First, we introduce a pair of metrics of niche difference that accommodates positive interactions, and show how this pair of metrics can be used to classify the qualitative dynamics of all possible pairwise interactions, starting with a symmetrical situation. Second, we relate these metrics to three quantitative properties of species coexistence: dynamical stability, structural stability (the

stability of an equilibrium to parameter change) and equilibrium densities.

We focus hereafter on the two-species–two-environmental-factor case. Even though some of the ideas presented below can be expanded to the *n*-species–*p*-environmental factor case (Meszéna et al. 2006, Saavedra et al. 2017), fully understanding multispecies coexistence remains an outstanding challenge and our approach is no exception to that rule. Yet, we believe that our results on the two-dimensional case provide a robust perspective on how to include positive interactions in a general theory of the niche. We rely mostly on graphical intuition in the main text, with some mathematical details found in Appendix S5. Until stated otherwise, we for now consider the two species to satisfy the generic dynamics of Eq. 1, which means in particular that our approach applies to ZNGIs of any shape. Still, we use straight lines to represent the ZNGIs in all the figures of this section for simplicity. The only assumption we make in the first part of this section is that the ZNGIs of the two species intersect at a point that we denote $\mathbf{E}^*$ and call the "coexistence point." As the impact and sensitivity vectors of the two species at the coexistence point will prove central to coexistence, we will abuse notation and from now designate these as $\mathbf{S}_i \equiv \mathbf{S}_i(\mathbf{E}^*)$ and $\mathbf{I}_i \equiv \mathbf{I}_i(\mathbf{E}^*)$. Note that if the two ZNGIs were to intersect more than once (a situation that can naturally occur when at least one of them is nonlinear), one simply needs to treat these different coexistence points separately.

### *A pair of niche difference metrics*

Building on work by Petraitis (1989), Meszéna et al. (2006), and Saavedra et al. (2017), we introduce a pair of metrics of niche differences (also see Letten et al. 2017). The *sensitivity niche difference* $\Omega_S$ is given by the oriented angle (i.e., potentially negative) between the sensitivity vectors $\mathbf{S}_1$ and $\mathbf{S}_2$, or, equivalently, the angle between the two ZNGIs. The *impact niche difference* $\Omega_I$ between species 1 and 2 is given by the oriented angle between the impact vectors $\mathbf{I}_1$ and $\mathbf{I}_2$ (Fig. 6). These metrics can be applied equally to situations involving negative and/or positive interaction, a situation that has not yet been explored in the literature cited above (note that it is also possible to define an associated pair of algebraic metrics for niche overlap, the *sensitivity niche overlap* $\rho_S$ and *impact niche overlap* $\rho_I$ [Meszéna et al. 2006], defined by $\rho_S \equiv \mathbf{S}_1^{\mathrm{T}} \mathbf{S}_2 = \|\mathbf{S}_1\| \cdot \|\mathbf{S}_2\| \cdot \cos\Omega_S$ and $\rho_I \equiv \mathbf{I}_1^{\mathrm{T}} \mathbf{I}_2 = \|\mathbf{I}_1\| \cdot \|\mathbf{I}_2\| \cdot \cos\Omega_I$ respectively, where "$\|\cdot\|$" designates the norm [the "length"] of a vector). As we will see, this pair of metrics provides a useful way of quantifying the magnitude of (1) positive interactions between a pair of species, (2) structural and dynamical stability, (3) equilibrium densities of coexistence, and (4) niche expansion through facilitation and mutualism. We first illustrate our approach and results in symmetrical models where the sensitivities and impacts of one species are mirror images of the niches of the other (Fig. 6), then treat the asymmetrical situation in the next section.
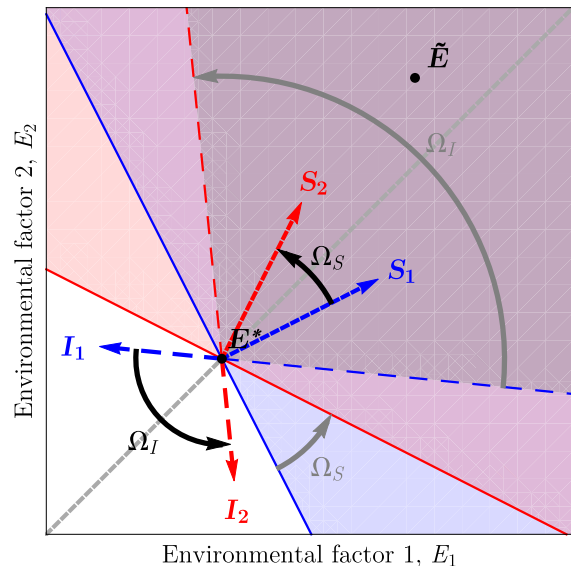


Fig. 6. General situation for two species (1, blue; 2, red) interacting through two environmental factors $E_1$ and $E_2$. The sensitivity niche difference $\Omega_S$ is defined as the oriented angle between the sensitivity vectors of the two species, and the impact niche difference $\Omega_I$ is defined as the oriented angle between the impact vectors of the two species. Sensitivity vectors are, by definition, perpendicular to their corresponding ZNGI (solid). The two ZNGIs intersect at the equilibrium point $\mathbf{E}^*$. When the supply point $\tilde{E}$ falls in the gray region between the two impact vectors (dashed), there is a feasible coexistence equilibrium. We show in *Quantifying coexistence* that for this particular configuration, this equilibrium is also stable.

Being able to quantify the niche differences $\Omega_S$ and $\Omega_I$ makes it possible to classify the qualitative nature of the net interaction between two species. Let us first look at the impact and sensitivity niche differences separately, starting with impacts. In the absence of impact niche difference ($\Omega_I = 0$) the two impact vectors completely overlap, which means that the two species have the exact same impacts on the environment (Fig. 7B). As we will see in *Quantifying coexistence*, this situation is structurally unstable, as the range of parameters compatible with coexistence is unlikely to be obtained without fine tuning. Now, let us increase $\Omega_I$ between the two species in one direction or the other. Since we can always switch the roles played by species 1 and 2, without loss of generality we consider the case where $\Omega_I > 0$. When $0° < \Omega_I < 90°$, we say that the two species have partially overlapping impacts, a situation classically encountered when the two species compete for resources (Fig. 7A, C; also see Appendix S5: Figs. S2, S3). When $\Omega_I = 90°$, the overlap between the two impacts is zero and the impact vectors are orthogonal, a situation that arises when the two species specialize on different resources (Fig. 7D). When $90° < \Omega_I < 180°$, the overlap between the two impact vectors becomes negative, and we say that the two species have complementary impacts (Fig. 7E, G).
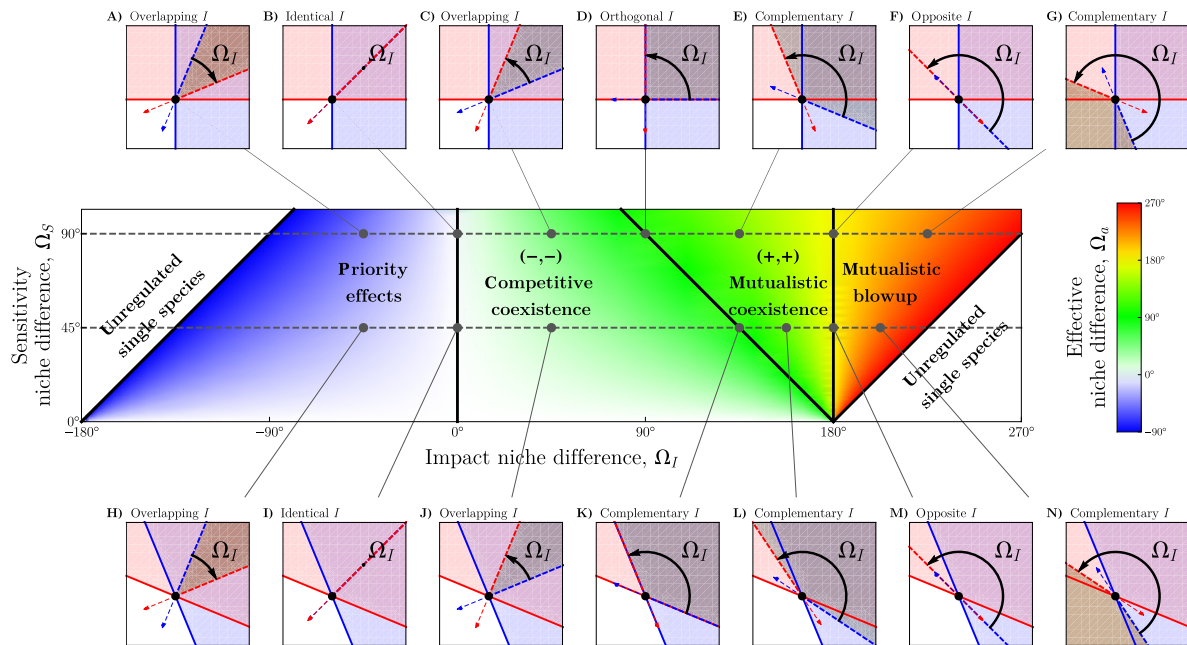
FIG. 7. All possible two-species dynamical regimes along varying sensitivity and impact niches differences $\Omega_S$ and $\Omega_I$ in the symmetric case. The insets illustrate these regimes in the niche space, with ZNGIs (solid), impact vectors (dashed), and the two-species feasibility region, either stable (gray) or unstable (brown), along varying impact niche differences $\Omega_I$ while the sensitivity niche difference $\Omega_S$ is kept constant. We show two situations for $\Omega_S$: orthogonal sensitivities ($\Omega_S = 90°$, like essential resources; A–G) and overlapping sensitivities ($\Omega_S = 45°$, an example of substitutable resources; H–N). (A–G) Starting from priority effects when $\Omega_I$ is negative (A), increasing $\Omega_I$ leads to competitive exclusion as it crosses $0°$ (B) and coexistence when smaller than $90°$ (C) when sensitivities are orthogonal. When $\Omega_I$ is increased, it leads to independent coexistence (D) as it crosses $180° - \Omega_S$ ($90°$ in this example) and then mutualistic coexistence (E). Mutualistic coexistence eventually turns into mutualistic blowup (G) as $\Omega_I$ crosses the $180°$ threshold (G). (H–N) The transition from priority effects to coexistence in the overlapping sensitivities case mimics the orthogonal sensitivities case (H, I, and J). However, the transition to mutualistic coexistence now happens only for impacts complementary enough to compensate for these overlapping sensitivities (K). We also represented the effective niche difference $\Omega_a$ as a heat map in the background of the main figure, except in the two regions of the figure where single species are unregulated (white). In the "priority effect" region, impact and sensitivity niche differences take opposite signs, leading to an overall negative $\Omega_a$. As $\Omega_I$ turns positive, $\Omega_a$ turns positive and coexistence is stable ("competitive coexistence"). When the sum of the niche differences $\Omega_I + \Omega_S$ becomes larger than $180°$, $\Omega_a$ turns larger than $90°$ signaling true mutualism between the two species ("mutualistic coexistence"). Finally, as $\Omega_I$ increases further across $180°$, mutualism between the two species becomes too strong, $\Omega_a$ becomes larger than $180°$ and coexistence turns unstable ("mutualistic blowup").

As we will see in our third example, this situation can arise in a situation of "apparent mutualism" between plants and carnivores mediated through herbivores, or with cross-feeding bacteria (Sun et al. 2019). When $\Omega_I = 180°$, niche overlap is maximally negative and the two species have exactly opposite impacts, meaning that their impacts are perfectly complementary (Fig. 7F). As we will see in *Quantifying coexistence*, this situation comes with a complete loss of dynamical stability. The same classification can be performed on the sensitivities. Sensitivity vectors can be identical ($\Omega_S = 0°$), partially overlapping ($0° < \Omega_S < 90°$, e.g., Fig. 7H–N), orthogonal ($\Omega_S = 90°$, Fig. 7A–G; classic situation when two species coexist on essential resources), complementary ($90° < \Omega_S < 180°$) or opposite ($\Omega_S = 180°$).

### Quantifying coexistence

To be useful, these metrics of sensitivity and impact niche differences must relate to measurable characteristics of coexistence between the two species. This requires the two metrics to be looked at jointly. We will specifically consider three aspects of coexistence: dynamical stability, structural stability, and effects on species densities. In the general framework of Niche Theory given by Eq. 1, some of these aspects can be complex to quantify, due to the non-linearity and environment dependence of species requirements and impacts, which manifest themselves in the curvature of the ZNGIs and impact vectors. To move forward, we will thus assume that these non-linearities are negligible, which means in practice that both $S_i$ and $I_i$ do not depend on the environment, leading to linear ZNGIs and parallel impact vectors. Similar assumptions are made in Box 3 in order to establish the correspondence between the niche and Lotka-Volterra models and their parameters. Under these assumptions, each species's growth rate is a linear function of the environmental factors, taking the general form $g_i(\mathbf{E}) = g_{0,i} + S_{1i}E_1 + S_{2i}E_2$. The basal growth rate $g_{0,i}$ controls the intercept, simply giving the growth rate

**Box 3. Correspondence Between Niche Theory and Lotka-Volterra Models**

In this Box, we present how to transform the general Niche Theory model of Eq. 1 into a Lotka-Volterra model (see also MacArthur 1970, Meszéna et al. 2006, Barabás et al. 2014). This correspondence solidifies the connection between the central parameters of Niche Theory (sensitivities, impacts and supplies) and the parameters of Lotka-Volterra models (intrinsic growth rates and community matrix). We then derive the expressions for dynamical stability, structural stability, and species densities of the equilibrium of the Lotka-Volterra model. The equivalence between the two approaches makes it possible to apply some of the results from this Box in the main text to connect these characterizations of coexistence to the sensitivity and impact niche differences.

To be rigorous, this transformation relies on two assumptions: (1) the linearization of the growth rate of the coexisting species around the coexistence point, leading in practice to linear ZNGIs as assumed later in the main text and (2) the impact vectors being assumed constant or approximately so, the latter happening when the supply point is close to the coexistence point, which translates into the densities of the coexisting species being kept small. This second assumption is not completely essential to perform the transformation, but greatly facilitates the interpretation of the resulting competition coefficients in terms of sensitivities and impacts (we refer the interested reader to the *General case* section of Appendix S3 where this assumption is relaxed). As the Lotka-Volterra model only tracks the dynamics of the $n$ species, this transformation is performed by reducing the dynamics of the $p$ environmental factors, which is done through a Quasi-Steady-State Approximation (Appendix S3). This leads to the following Lotka-Volterra dynamics for $n$ species:

$$\frac{dN_i}{dt} = \left( r_i - \sum_{j=1}^{n} a_{ij} N_j \right) N_i \tag{8}$$

where $r_i$ is the intrinsic growth rate of species $i$ and $a_{ij}$ the competition coefficient of species $j$ on species $i$. Importantly, these coefficients are functions of the parameters of the Niche Theory model. The competition coefficients are simply given by $a_{ij} \equiv -\mathbf{S}_i^{\mathrm{T}} \mathbf{I}_j$, which is the matrix notation for the scalar product between the impact vector of species $j$ and the sensitivity vector of species $i$, where the minus sign stems from Lotka-Volterra models using a different sign convention than ours, i.e., that positive $a_{ij}$ mean competitive interactions. Introducing the *sensitivity matrix* $\mathscr{S}$, whose columns are the sensitivity vectors $\mathbf{S}_i$, and the *impact matrix* $\mathscr{I}$, whose columns are the impact vectors $\mathbf{I}_i$, we can gather the $a_{ij}$ into the community matrix $\mathbf{a} \equiv -\mathscr{S}^{\mathrm{T}} \mathscr{I}$. The intrinsic growth rate are given by $r_i \equiv \mathbf{S}_i^{\mathrm{T}} (\tilde{\mathbf{E}} - \mathbf{E}^*)$, the matrix notation for the scalar product between the sensitivity vector of species $i$ and the vector of environmental surpluses $\tilde{\mathbf{E}} - \mathbf{E}^*$.

Under the assumptions presented above, these two representations, Lotka-Volterra and Niche Theory, are completely equivalent, and highly complementary for developing a general theory of positive interactions. Interestingly, our underlying mechanistic model from Niche Theory gives a structure from where the Lotka-Volterra parameters emerge, as competition coefficients can be decomposed as the product of the impact and sensitivity matrices (MacArthur 1970, Meszéna et al. 2006, Barabás et al. 2014). As part of the generic framework of this manuscript, we will consider generic signs for the $a_{ij}$, except for the $a_{ii}$ that we will assume to be all positive (see Appendix S6 for an exploration of the regimes where this is not true). This basically ensures that the two species are each self-regulated in the neighborhood of coexistence when taken in isolation, discarding here the possibility of single-species positive feedback loops, which was the focus of *Negative and Positive Feedbacks Between a Single Species and Its Environment: The Fundamental Niche*. The intrinsic growth rate $r_i$ also has a natural ecological interpretation: it is given by the vector product of the environmental surpluses $\tilde{\mathbf{E}} - \mathbf{E}^*$ with this species' sensitivity to them. Geometrically, $r_i$ measures the shortest distance between the supply point and the ZNGI, as the latter is assumed to be linear here. When the environmental surplus vector is orthogonal to the sensitivity vector, this means that the supply point is located on the ZNGI, and growth is zero.

For a direct comparison with the results presented in the main text, we now focus on the two-species–two-environmental-factor case and derive the mathematical criteria for dynamical stability, structural stability and species densities at equilibrium.

### Dynamical stability (Pásztor et al. 2016)

Applying standard local stability analysis, the coexistence equilibrium of Eq. 8 is stable if and only if the Jacobian $\mathbf{J}$ has a negative trace ($\mathrm{tr}\,\mathbf{J} = a_{11}\widehat{N}_1 + a_{22}\widehat{N}_2 > 0$) and a positive determinant ($\det\mathbf{J} = \widehat{N}_1\widehat{N}_2\det\mathbf{a} > 0$). The condition on the trace is always satisfied given that we assumed each species to be self-regulated ($a_{ii} > 0$). The second condition has a classic interpretation in two-species competitive systems, expressed as "intraspecific competition

has to be stronger than interspecific competition for the two species to coexist" (Chesson 2000). This condition is equivalent to the condition on dynamical stability presented in the main text after noticing that $\det\mathbf{a} = (-1)^2 \cdot \det\mathscr{S}^T\mathscr{I} = \det\mathscr{S} \cdot \det\mathscr{I}$.

### Structural stability ( Meszéna et al. 2006, Saavedra et al. 2017 )

At equilibrium, the densities of the coexisting species are given by

$$\hat{N}_i = \sum_{j=1}^{2} a_{ij}^{-1} r_j. \tag{9}$$

Following Saavedra et al. (2017), the structural stability of coexistence to changes in intrinsic growth rate $r_i$ is given by the angle $\Omega_a$ between the two columns of $\mathbf{a}$, formally satisfying $\mathbf{a}_1{}^T\mathbf{a}_2 = \|\mathbf{a}_1\| \cdot \|\mathbf{a}_2\| \cdot \cos\Omega_a$. To distinguish $\Omega_a$ from the other geometrical metrics presented in the main text, we call it the "effective niche difference." It can be written more explicitly as (where we used arccosine instead of arcsine to more naturally account for niche differences larger than 90°)

$$\Omega_a = \arccos\left[ \pm\sqrt{1 - \left(\frac{\det\mathbf{a}}{\|\mathbf{a}_1\| \cdot \|\mathbf{a}_2\|}\right)^2} \right] \tag{10}$$

where the "±" sign has to be alternatively taken equal to "+" or "−" to ensure that $\Omega_a$ is differentiable. This expression of $\Omega_a$ can further be related to the two measures of niche difference $\Omega_S$ and $\Omega_I$ (see *Quantifying coexistence*).

### Effects on species densities

Let us compare species densities $\hat{N}_1$ and $\hat{N}_2$ when they coexist to the densities these species would achieve if they were present only by themselves, the densities in monoculture $K_1$ and $K_2$. By definition, $K_i = r_i/a_{ii}$ when $r_i > 0$ (we are still assuming self-regulation, i.e., $a_{ii} > 0$), or zero otherwise. Focusing on species 1, the sign of the difference between $\hat{N}_1$ and $K_1$ indicates if species 1 competes with or is facilitated by species 2. First, if species 1 goes extinct in isolation ($K_1 = 0$) but the two species coexist when present, this obviously means that species 2 facilitates species 1. Otherwise ($K_1 \neq 0$), we have the following relationship:

$$\hat{N}_1 - K_1 = -\frac{a_{12}}{a_{11}} \cdot \hat{N}_2 \tag{11}$$

which states that species 1 has a higher biomass in the presence of species 2 ($\hat{N}_1 > K_1$), when $a_{12} < 0$. This comes to no surprise for those familiar with the Lotka-Volterra competition model, but has an insightful graphical interpretation of facilitation in the framework of Niche Theory (see *Quantifying coexistence*).

of species $i$ when environmental factors are zero. Note that $g_{0,i}$ can be negative, as when the $E_i$ are resources ($S_{ji} \geq 0$). Then, $-g_{0,i}$ can be interpreted as the basal mortality rate of species $i$. Note that the coordinates of the coexistence point $\mathbf{E}^*$ can be computed easily in this linear situation by inverting the linear system $g_1(\mathbf{E}^*) = 0$ and $g_2(\mathbf{E}^*) = 0$.

*Dynamical stability (Pásztor et al. 2016).*—Applying standard local stability analysis, we get the necessary condition that coexistence is stable only if the Jacobian matrix $\mathbf{J}$ evaluated at the coexistence point has a positive determinant, i.e., $\det\mathbf{J} = \hat{N}_1 \cdot \hat{N}_2 \cdot \det\mathscr{S} \cdot \det\mathscr{I} > 0$ (Koffel et al. 2016; the full list of necessary and sufficient conditions

is given by the Routh-Hurwitz stability criteria; Edelstein-Keshet 1988). Note that this is only a necessary condition, but we will assume that the other conditions for stability are satisfied as long as each species is independently self-regulated, the only case of interest in the main text (see Box 3 for a similar condition on the transformed Lotka-Volterra system). Using the identity, $\det\mathscr{S} \cdot \det\mathscr{I} = \|\mathbf{S}_1\|\|\mathbf{S}_2\|\|\mathbf{I}_1\|\|\mathbf{I}_2\| \cdot \sin\Omega_S \cdot \sin\Omega_I$ the condition on the determinant can be simply rewritten as $\sin\Omega_S \cdot \sin\Omega_I > 0$, making the connection between stability and the sensitivity and impact niche differences explicit (Meszéna et al. 2006). In the well-known purely competitive situation, i.e., with partial niche overlaps ($-90° < \Omega_S, \Omega_I < 90°$), this criterion states that "each species impacts the most the

environmental factor that limits its growth the most" (Tilman 1982, Leibold 1996). Note that this criterion is actually general, as it does not depend on our two assumptions of linear ZNGIs and constant impact vectors, and thus applies to any situation with non-linear growth rates and environment-dependent impacts as framed by Eq. 1 and studied graphically in the previous sections (Koffel et al. 2016). This criterion has a straightforward geometrical interpretation: the relative order between the two impact vectors has to be the same as the relative order between the two sensitivity vectors (e.g., both arranged clockwise as in Fig. 6), or, equivalently, $\Omega_S$ and $\Omega_I$ have to have the same sign. Hence, the two metrics of niche difference have to be considered jointly to inform on the dynamics of the two species.

Let us further explore this criterion by varying the impact niche difference $\Omega_I$ while keeping $\Omega_S$ fixed ($\Omega_S = 90°$ and $\Omega_S = 45°$ in the two rows of examples of Fig. 7). Starting from the competitive coexistence case ($0 < \Omega_I < 90°$), there are two ways for det$\mathbf{J}$ to become negative, which happens when $\sin\Omega_I$ goes through zero. First, as we just discussed, stability can be lost when $\Omega_I = 0$, the well-known transition from coexistence to priority effects (C to B to A, and J to I to H on Fig. 7). The second situation, less often considered, happens when positive interactions become too strong, i.e., when reaching perfect niche complementary, where the impact vectors of the two species are opposite and each species provides exactly what the other one consumes ($\Omega_I = 180°$, leading to $\sin\Omega_I = 0$; E to F to G, and L to M to N on Fig. 7). Crossing this threshold signals a flip in the overall structure of population regulation, with the net two-species impact now pointing in the same direction as net requirements, resulting in a two-species positive feedback loop ("mutualistic blowup"). Under our linear approximation, this instability of the coexistence equilibrium has two possible outcomes: either both species go extinct or both species blowup as their densities diverge to infinity. This is the two-species analog of the situation we presented in the one-species case, leading here to a two-species Allee niche. Note that this is a purely pairwise effect, as both species are well regulated when present only by themselves. Since unbounded growth is impossible in practice, the possibility of divergence signals that an important aspect of the environment has been omitted. This could be remedied by introducing a third, purely regulating, environmental factor (Sun et al. 2019).

*Structural stability (Meszéna et al. 2006, Saavedra et al. 2017).*—The structural stability of coexistence can be quantified by the range of parameters compatible with coexistence. Following Saavedra et al. (2017), we will focus on the conditions under which the coexistence equilibrium is feasible, i.e., both species have positive densities. At the coexistence equilibrium, it is easy to show when the growth rates $g_i$ are linear as assumed above that these densities are given by

$\widehat{\mathbf{N}} = \left(-\mathscr{S}^T \mathscr{I}\right)^{-1} \mathbf{g}_0 - \mathscr{I}^{-1} \tilde{\mathbf{E}}$, with $\mathbf{g}_0$ the vector of basal growth rates. Because our approach explicitly includes the supply $\tilde{\mathbf{E}}$, this expression differs slightly from previous work by Meszéna et al. (2006), with consequences for how to define structural stability. The next step to quantify structural stability is to chose which parameters we want to look at, with two natural options.

First, we can look at structural stability to changes in environmental supplies $\tilde{\mathbf{E}}$, which quantifies how sensitive coexistence is to changes in external environmental conditions. We see from the expression of $\widehat{\mathbf{N}}$ above that the connection between the densities and the supplies only involves the impacts. This makes sense, as we know geometrically that coexistence is feasible when the environmental surplus vector $\tilde{\mathbf{E}} - \mathbf{E}^*$ is located between the two impact vectors $\mathbf{I}_1$ and $\mathbf{I}_2$ (Tilman 1982, Chase and Leibold 2003, Koffel et al. 2016). The more similar the impact vectors are, the smaller that region of supply is, which means that coexistence is less structurally stable (Fig. 6). Conveniently, and in line with Saavedra et al. (2017), our angular metric of impact niche difference $\Omega_I$ directly quantifies the extend of that region and thus plays the role of *structural niche difference* to changes in supplies.

Second, we can look at structural stability to changes in $\mathbf{g}_0$, which now quantifies how sensitive coexistence is to changes in basal growth/mortality. Because $\mathbf{g}_0$ controls the intercept of the growth rate, a change in basal growth rates while keeping other parameters fixed translates geometrically into moving the ZNGIs while keeping their directions fixed, which in turn changes the location of the equilibrium point $\mathbf{E}^*$ at their intersection (Meszéna et al. 2006). We see from the expression of $\widehat{\mathbf{N}}$ above that structural stability of coexistence to changes in basal growth involves both sensitivities and impacts through the inverse of the matrix $\mathscr{S}^T \mathscr{I}$. Using the correspondence with Lotka-Volterra models presented in Box 3, we can directly transpose the results of Saavedra et al. (2017) who applied the same logic as presented above to obtain an angular measure of structural niche difference to changes in growth rate. We call this metric the effective niche difference $\Omega_a$, which is equal to

$$\Omega_a = \arccos\left[\pm\sqrt{1 - \left(\frac{\det\mathscr{S} \cdot \det\mathscr{I}}{\|\mathscr{S}^T\mathbf{I}_1\|\|\mathscr{S}^T\mathbf{I}_2\|}\right)^2}\right] \qquad (12)$$

where the "$\pm$" sign has to be alternatively taken equal to "+" or "−" to ensure that $\Omega_a$ is differentiable. This analytical expression could be further expanded in terms of $\Omega_I$ and $\Omega_S$ but is complex and not particularly insightful (Appendix S5), suggesting that there is no straightforward mathematical link between Saavedra et al. (2017)'s definition of the niche difference in a Lotka-Volterra system and Meszéna et al. (2006)'s sensitivity and impact niche differences.

Still, this relationship can be visualized graphically. Fig. 7 shows the outcome of interaction as a function of

$\Omega_I$ and $\Omega_S$ in our symmetrical example. In this figure, we restricted the value of the sensitivity niche differences to $0° < \Omega_S < 90°$, which spans classic competition cases from totally overlapping substitutable resources ($\Omega_S = 0°$) to essential resources ($\Omega_S = 90°$), and let the impact vectors vary between $-180° < \Omega_I < 270°$. This range of values is sufficient to show all the qualitatively different outcomes. Note that our convention defines niche differences *up to two turns*, i.e., *modulo* 720°, to keep track of the absolute location of the two vectors, so that we can differentiate mutualistic blowup ($\Omega_I > 180°$, Fig. 7G and onward) from priority effects ($\Omega_I < 0°$, Fig. 7A and backward) when these situation would otherwise present the same relative angle between the two vectors (see Appendix S5 for an extended version of Fig. 7). Many of these configuration of niche differences are excluded from the current analysis because they correspond to unstable regimes where each species is unregulated even when taken in isolation (Boucher 1985; Appendix S6). Fig. 7 shows that $\Omega_a$ increases from $-90°$ to $270°$ with increasing $\Omega_I$. In fact, we can combine the analysis of the "dynamical stability" section with the values attained by $\Omega_a$ to split Fig. 7 into four different regimes: priority effects ($-90° < \Omega_a < 0°$), competitive coexistence ($0° < \Omega_a < 90°$), mutualistic coexistence ($90° < \Omega_a < 180°$) and mutualistic blowup ($180° < \Omega_a < 270°$). As we have seen in the "dynamical stability" paragraph, only the competitive coexistence and mutualistic coexistence regimes are stable. Both the priority effects and mutualistic blowup regimes are unstable, and can be separated from each other by the value taken by their effective niche difference.

*Effects on species densities.*—Finally, let us look at how niche differences affect the densities of the two species when they coexist, particularly in the competitive and mutualistic cases described above. More precisely, let us compare the equilibrium densities $\widehat{N}_1$ and $\widehat{N}_2$ when coexisting to the equilibrium densities these species would achieve if they were present only by themselves, denoted $K_1$ and $K_2$. In general, the relationship between densities in polyculture and monoculture is complex in Niche Theory models, so we again rely on the assumption that impacts and sensitivities are constant. Because the correspondence between the niche and Lotka-Volterra parameters derived in Box 3 was based on the same assumption, we can directly apply the monoculture densities $K_i$ obtained there and use the correspondence to get $K_i = \mathbf{S}_i^T(\tilde{\mathbf{E}} - \mathbf{E}^*)/(-\mathbf{S}_i^T\mathbf{I}_i)$ when $\mathbf{S}_i^T(\tilde{\mathbf{E}} - \mathbf{E}^*) > 0$ (we are still assuming self-regulation, i.e., $\mathbf{S}_i^T\mathbf{I}_i < 0$), or is equal to zero otherwise. Note that the condition $\mathbf{S}_i^T(\tilde{\mathbf{E}} - \mathbf{E}^*) > 0$ means graphically that the supply point $\tilde{\mathbf{E}}$ is located "above" the ZNGI, where "above" means on the side of the ZNGI where net growth is positive. Now, focusing on species 1, the sign of the difference between $\widehat{N}_1$ and $K_1$ indicates if species 1 competes with or is facilitated by species 2. First, if species 1 goes extinct in isolation ($K_1 = 0$) but the two species coexist when present, this obviously means that species 2 facilitated species 1.

Otherwise ($K_1 \neq 0$), we have the following relationship (see Box 3):

$$\widehat{N}_1 - K_1 = -\frac{\mathbf{S}_1^T\mathbf{I}_2}{\mathbf{S}_1^T\mathbf{I}_1} \cdot \widehat{N}_2 \qquad (13)$$

which states that species 1 has a higher biomass in the presence of species 2 ($\widehat{N}_1 > K_1$), when $\mathbf{S}_1^T\mathbf{I}_2 > 0$. Remembering that $\mathbf{S}_1^T\mathbf{I}_2$ is the dot product between $\mathbf{S}_1$ and $\mathbf{I}_1$, this has an insightful graphical interpretation of facilitation in the framework of Niche Theory: saying that species $i$ is facilitated by species $j$ is equivalent to saying that the impact vector $\mathbf{I}_j$ of species $j$ is located "above" the ZNGI of species $i$, graphically translating $\mathbf{S}_i^T\mathbf{I}_j > 0$ (Fig. 7E–G). Conversely, $\mathbf{S}_i^T\mathbf{I}_j < 0$ means that species $i$ is harmed by species $j$, leading to a lower density of species $i$ in coexistence. Note that because there is no obvious relationship between $\mathbf{S}_1^T\mathbf{I}_2$ and $\mathbf{S}_2^T\mathbf{I}_1$, there is no reason that facilitation of species 1 by species 2 implies that the opposite is true, so that species 1 could facilitate species 2 while species 2 competes with species 1 (as we will see in the non-symmetric example of the next section). This happens in the example of coexistence between the N-fixing and non-fixing plants. As can now directly be read on Fig. 5D, the N fixer indeed facilitates the non-fixer while the non-fixer harms (competes with) the N fixer.

Mutualism, on the other hand, happens when both $\mathbf{S}_1^T\mathbf{I}_2 > 0$ and $\mathbf{S}_2^T\mathbf{I}_1 > 0$. This is the case in the symmetrical example we are focusing on here. When this happens, both species reach higher densities in coexistence than in monoculture, leading to synergism. This regime happens when the central inequality $\Omega_S + \Omega_I > 180°$ is satisfied, which coincides with the region where $\Omega_a > 90°$ identified earlier as the "mutualism" region from the dynamical stability perspective (Fig. 7). An interesting consequence is that a non-zero sensitivity overlap between two species (e.g., $\Omega_S = 45°$) can be "compensated" by a highly complementary impact overlap (say $\Omega_I > 135°$), in sum leading to mutualism (Fig. 7L). Similarly, mutualism can occur even when impacts overlap as long as the requirements are complementary enough. Looking at Fig. 7F, L, we also see that the condition $\Omega_S + \Omega_I > 180°$ for mutualism to occur in the symmetrical example also signals that each species expands the realized niche of the other as they coexist. This can be seen graphically as the backwards extensions of the impact vectors of one species being located under the ZNGI of the other, something that was also visible in the N-fixing example that we used to introduce the concept of niche expansion (Fig. 5A). Formally, a structural measure of niche mutualism could be given by the angle $\Phi = \Omega_I + \Omega_S - 180°$. Niche mutualism happens when $\Phi$ is positive, and its magnitude quantifies the extent of supply points for which facilitation happens. Finally, as was noted before, increasing $\Omega_I$ above 180° eventually destabilizes mutualism because the net direction of the impacts vectors flips. This is interesting because two self-regulated species can together escape
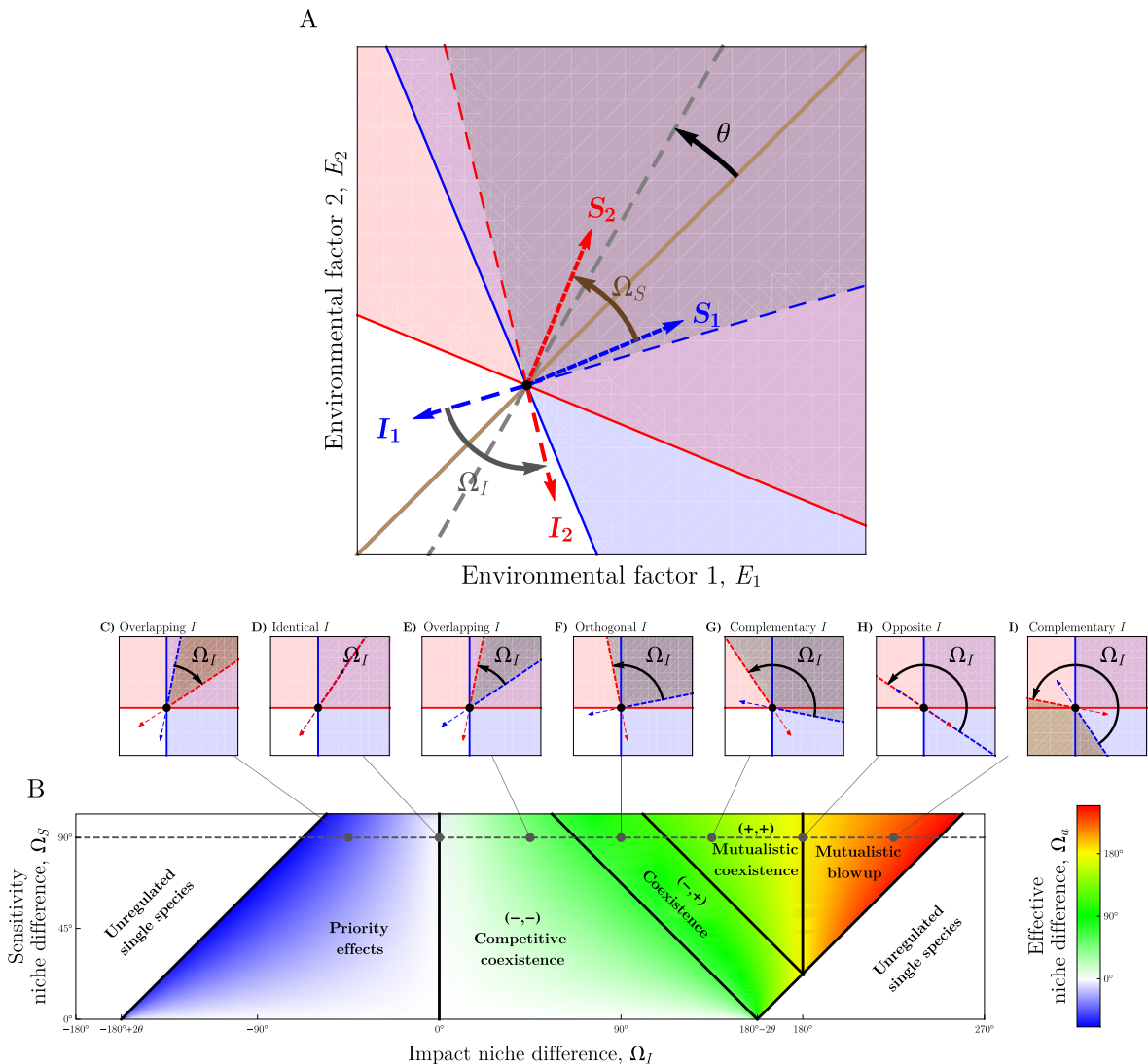
FIG. 8.   Two-species dynamics in the asymmetrical case. (A) Setup more general than the symmetrical case of Fig. 6, as the centroid of the coexistence region (gray, dashed) is tilted relatively to the centroid of the sensitivity vectors (solid, brown) by an angle θ. As a consequence, interactions between the two species are overall less detrimental/more beneficial to one of the two species (on this particular example, species 2 is favored over 1). (B) As a consequence of this asymmetry, intermediate sensitivity and impact niche differences lead to a new regime of "(−, +) coexistence" where species 1 facilitates species 2 while species 2 competes with species 1 (θ = 11.25° in this particular example).

regulation by creating a pairwise positive feedback loop. Even though looking thoroughly at the consequence of such two-species positive feedback loops is out of the scope of this paper, it is natural to expect alternative stable states between stable coexistence equilibrium for the pair, and a state where at least one of the species has gone extinct (Sun et al. 2019).

### Asymmetric interactions

For simplicity, the results of the previous section were illustrated with symmetrical examples, where the centroids, i.e., the average directions, of the sensitivity and impact vectors were aligned. In this situation, when positive interactions happen, they are necessarily reciprocal, leading to mutualism. Yet, as was explored earlier with the case of N-fixing and non-fixing plants, facilitation is sometimes unrequited. How to expand the previous example to account for this situation? Our symmetrical example can be slightly complexified by "tilting" both impact vectors in one direction, for example clockwise. Let θ denote the angle between the centroid of the sensitivity vectors and the centroid of the impact vectors (Fig. 8A). Up to a global rotation, this

situation is the most general situation. A consequence of this asymmetry it that it tilts overall interactions in favor of one species over the other, here species 2 over species 1. We restrict ourselves in the main text to a quick graphical study of this situation; see Appendix S5 for a deeper exploration.

The main result is a slightly more complex bifurcation diagram and relationship between the niche differences $\Omega_S$ and $\Omega_I$ and the effective niche difference $\Omega_a$ (Fig. 8 B). We now see that a gap opens between the competitive coexistence and mutualistic coexistence regimes, filled up by a "$(-, +)$ coexistence" regime. There, species 2 benefits from facilitation by species 1, while species 1 suffers from competition with species 2 (Fig. 8F). Ecologically, this situation is formally similar to a classic situation of parasitism along the mutualism—parasitism continuum, and the dynamics, when mapped onto a Lotka-Volterra model, are formally similar to a predator–prey system (Appendix S5: Fig. S5C). Finally, let us also note that the overall region where each single species is regulated has shrunk; this can be explained by the tilt in favor of one species making it "easier" for one species to go unregulated as niche difference increases.

### Example 3: Positive interactions between trophic levels

To show the wide applicability of our approach, let us look at a final example of positive interactions in a small food web, this time between two species that belong to two different trophic levels. With this example, we show that the approach and concepts of Niche Theory can be applied to plants and carnivores interacting *across* trophic levels, revisiting the trophic cascade, a classic of ecological theory, using the graphical approach to Niche Theory. More precisely, we show how we can use the framework presented here to quantify (1) the extent of niche facilitation of each species on the other and (2) their niche difference(s). The idea that we can use tools from Niche Theory to characterize coexistence between species across trophic levels paves the way toward a more general theory of the niche and species coexistence whose focus in not just on competitive interactions within a trophic level. This echoes a recent call by Godoy et al. (2018) to use feasibility and stability conditions to integrate niche and network theories into a single framework. Here, we provide a concrete example of how this can be done in practice using Niche Theory.

We consider a small food web module where a basal plant population $P$, is consumed by two herbivores $H_1$ and $H_2$, themselves preyed on by a top carnivore $C$ (Fig. 9A). The usual focus in this "diamond food web" module is the competitive interactions between the two species in the middle trophic level, $H_1$ and $H_2$ (Holt et al. 1994, Leibold 1996, Grover and Holt 1998, Koffel et al. 2018b), but here we focus on the indirect mutualistic interactions between the plant $P$ and the carnivore

$C$ across trophic levels, with the two herbivores $H_1$ and $H_2$ playing the role of the shared environmental factors that mediate these interactions. This perspective might seem unconventional at first, but nothing in Niche Theory prevents environmental factors from being biotic, a possibility at the heart of apparent competition (Holt 1977) and included in the general framing of the theory (Levin 1970, Chase and Leibold 2003, Meszéna et al. 2006).

Mathematically, the dynamics of the three-level food web module can be written (Fig. 9A)

$$\frac{dC}{dt} = (e_{C,1}a_{C,1}H_1 + e_{C,2}a_{C,2}H_2 - m_C)C \tag{14a}$$

$$\frac{dH_1}{dt} = \Phi_1 - \lambda_1 H_1 + a_{1,P}e_{1,P}H_1 P - a_{C,1}H_1 C \tag{14b}$$

$$\frac{dH_2}{dt} = \Phi_2 - \lambda_2 H_2 + a_{2,P}e_{2,P}H_2 P - a_{C,2}H_2 C \tag{14c}$$

$$\frac{dP}{dt} = (r_P - a_{1,P}H_1 - a_{2,P}H_2)P \tag{14d}$$

where $r_P$ is the intrinsic growth rate of the plant, $m_C$ the mortality rate of the carnivore, $\lambda_1$ and $\lambda_2$ the turnover rates of the herbivores, and $a_{i,j}$ and $e_{i,j}$ the per capita attack rate and conversion efficiency of species $i$ consuming species $j$. To fit the generic framework of Niche Theory in Eq. 1, we consider that the dynamics of our environmental factors, the herbivore populations, are controlled by both local processes (consumption of the focal plant and predation by the carnivore) and an external process (herbivore immigration into the local food web at rates $\Phi_1$ and $\Phi_2$). This means that the turnover rates $\lambda_1$ and $\lambda_2$ account for both local mortality and emigration from the local food web. Adding this external component to the dynamics of herbivores ensures that herbivores can persist locally even in the absence of the focal plant $P$; when the carnivore $C$ is also absent, the two herbivore populations equilibrate at their baseline densities, the "herbivore supplies" $\tilde{H}_1 = \Phi_1/\lambda_1$ and $\tilde{H}_2 = \Phi_2/\lambda_2$. This assumes that the food web of Eq. 14 is embedded in a larger-scale ecosystem herbivores can immigrate from, while the plant and carnivore populations are sedentary, with $\tilde{H}_1$ and $\tilde{H}_2$ quantifying the regional abundance of the two herbivores. An alternative ecological interpretation to the "herbivore supplies" $\tilde{H}_1$ and $\tilde{H}_2$ is to assume that the herbivores are generalists and can sustain themselves in the absence of the focal plant by consuming other plant species. In either case, varying these "herbivore supplies" generate environmental gradients in herbivore pressure and prey availabilities for the plant and the carnivore, along which we can study the structure and assembly of the small food web. Importantly, herbivore immigration is not necessary for this system to be meaningful, and the more classic situation without herbivore immigration is simply recovered
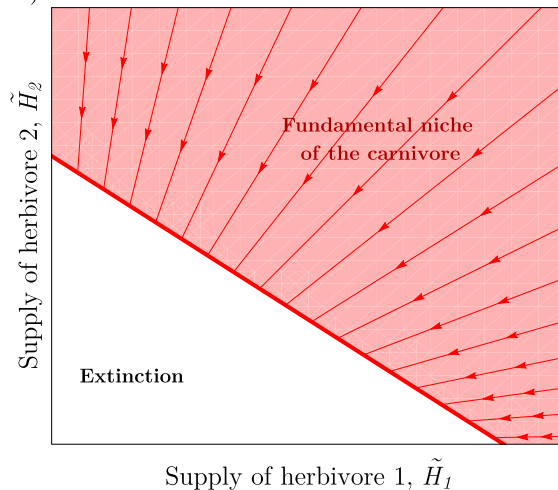
A) Schematic of ecosystem
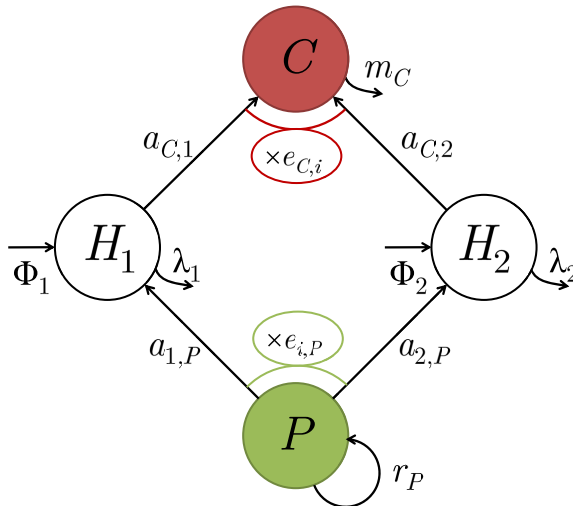
B) Plant's niche
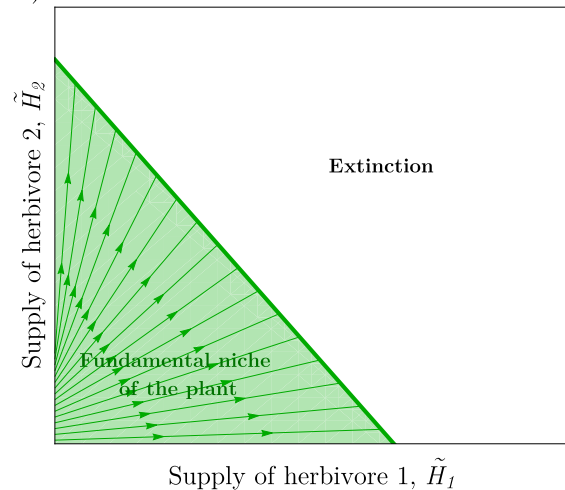
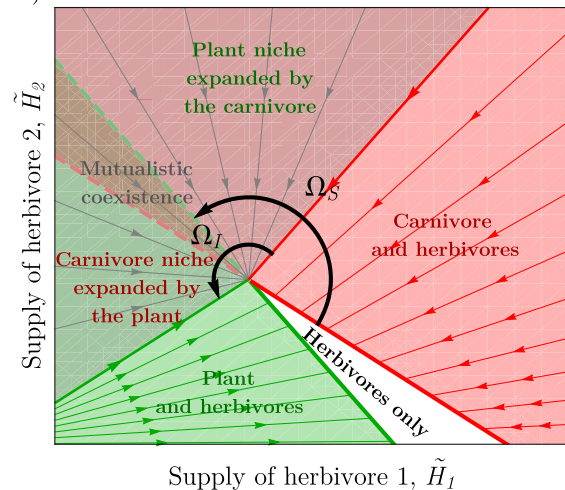C) Carnivore's niche

D) Realized niches

FIG. 9. Indirect mutualism between a plant and a carnivore species mediated by herbivores in a local ecosystem. (A) The plant ($P$, green) benefits the carnivore ($C$, red) by feeding the herbivores, and the carnivore benefits the plant by consuming the herbivores. Local herbivore density does not rely solely on the focal plant, as it is partially controlled by immigration from the surrounding landscape, through the rates $\Phi_1$ and $\Phi_2$. Herbivores differ in their relative "quality": herbivore 1 strongly grazes the focal plant and does not feed the carnivore well, while herbivore 2 damages the plant less and feeds the carnivore better. (B) Fundamental niche of the plant along gradients of herbivore immigration. The plant can only persist below a certain level of total herbivore immigration, materialized by its linear ZNGI (green, thick line). (C) Fundamental niche of the carnivore. The carnivore can only persist above a certain level of total herbivore immigration, materialized by its linear ZNGI (red, thick line). (D) Realized niches of the plant and the carnivore in interaction. Under low herbivore immigration, the plant can persist as the carnivore is excluded (green region). Similarly, high herbivore immigration enables the carnivore to persist in the absence of the plant (red region). Under intermediate immigration regimes that favor the relative abundance of herbivore 1, both the plant and the carnivore go locally extinct because herbivores are too abundant from the plant perspective, but not abundant enough from the carnivore perspective (white region). Conversely, under immigration that favors the relative abundance of herbivore 2, the plant and carnivore coexist together alongside the herbivores (gray region), strongly facilitating each other by expanding their niches. There, plant and carnivore biomass reach high levels, as indicated by an impact niche difference close to 180° on this example.

when $\tilde{H}_1 = \tilde{H}_2 = 0$, which graphically corresponds to focusing on the supply point located at the origin of the niche space.

Because this model fits within the Niche Theory framework of Eq. 1, we can directly apply the approach presented in this paper to represent the plant and the carnivore niches along gradients in herbivore densities. As our two focal species, the plant and the carnivore, belong to different trophic levels, their niches differ in a qualitative way (compare Fig. 9B and C). Supporting mathematical calculations can be found in Appendix S7. Because neither of these two species displays an Allee

niche, we will here refer to their traditional niche simply as "the niche". The plant's fundamental niche represents the conditions under which it persists when the carnivore is absent (Fig. 9B); the niche is delimited by a linear ZNGI, with herbivore levels for which plant persistence is possible located under the ZNGI. The impact vectors show how the presence of the plant impacts both herbivore populations; quite logically, plants feed the herbivores, so that these vectors are pointing upward and herbivore densities end up being larger in the plant's presence than what they would be in a pure immigration–emigration balance. Interestingly, in the example depicted here, we can also see that herbivore 1 excludes herbivore 2 from the food web module in the absence of immigration of herbivore 2 (green impact vector along the $x$-axis), even in the total absence of immigration of herbivore 1 (origin of Fig. 9B). This is a consequence of competition between the two herbivores for the plant, and signals that herbivore 1 is a better competitor than herbivore 2, with a lower break-even concentration $R^*$ for the plant $P$. Second, let us look at the fundamental niche of the carnivore, i.e., the conditions for which the carnivore persists in the absence of the plant (red region in Fig. 9C). The ZNGI of the carnivore is also linear, indicating that the two herbivores are substitutable prey for the carnivore. As opposed to the plant, the fundamental niche of the carnivore is located above its ZNGI, as the carnivore needs sufficient food to persist. Its impact vectors roughly point toward the origin, because predation reduces herbivore densities.

The plant and carnivore ZNGIs cross in Fig. 9D, meaning that there are herbivore densities for which both the plant and the carnivore can coexist at equilibrium alongside the two herbivores, leading to the full food web (the two other cases where the ZNGIs do not cross are presented in Appendix S7: Fig. S1). This happens for all herbivore supplies located in the coexistence region (gray region in Fig. 9D). Applying our metrics of niche difference, is it straightforward that niche differences always satisfy $\Omega_I > 90°$ and $\Omega_S > 90°$, which is not a surprise as the plant and the carnivore have complementary requirements for, and impacts on, the herbivores. Moreover, it is also straightforward that the carnivore indirectly benefits the plant ($\mathbf{S}_P \cdot \mathbf{I}_C > 0$) and the plant indirectly benefits the carnivore ($\mathbf{S}_C \cdot \mathbf{I}_P > 0$), so that the plant–carnivore interaction is effectively mutualistic. This happens because the plant increases herbivore densities by feeding them, helping the carnivore. Equivalently, the carnivores decrease herbivore densities by consuming them, helping the plant. This latter, indirect positive impact of the carnivore on the plant is the core idea behind trophic cascade (Hairston et al. 1960, Oksanen et al. 1981). Classical ecological examples include sea otters benefiting kelp forest by consuming urchins off of North America's Pacific Coast (Watson and Estes 2011), and wolves benefiting trembling aspen as they modify the foraging behavior of elks seeking to lower predation risks in Yellowstone (Fortin et al. 2005).

Yet, the fact that the plant also benefits the carnivore by feeding herbivores, effectively leading to plant–carnivore "apparent mutualism", and the consequences in terms of niche do not seem to have been systematically explored in this literature. As we have seen in the previous section, the strength of this mutualism determines if coexistence is stable or not. In the situation depicted in Fig. 9D, $\Omega_I$ is less than 180°, which signals stable mutualistic coexistence (gray region). As a consequence, both species see their realized niche greatly extended through niche facilitation, to regions of supplies where neither the plant or the carnivore could subsist on their own ("carnivore niche expanded by the plant" and "plant niche expanded by the carnivore" in Fig. 9D). In the region where both the plant and the carnivore could subsist on their own (brown overlap region), mutualism still leads both the plant and the carnivore population to reach higher densities when coexisting together as described in the previous section. Conversely, $\Omega_I$ greater than 180° would lead to mutualistic blowup (Figs. 7, 8B), an unstable regime that emerges when mutualism is so strong that the mutualistic pair escapes regulation (see Appendix S7: Fig. S2). Interestingly, this situation can emerge under realistic regimes of trophic transfers ($e_{i,j} < 1$) and in the complete absence of herbivore supplies, showing a non-trivial way in which plant and carnivore can jointly overcome top-down and bottom-up control, respectively. Mirroring the study of single-species positive feedback loops explored in the first section of this manuscript, such mutualistic blowup is in practice bound to eventually hit another limitation not accounted for in the current model (Sun et al. 2019). As a result, we can think of this mutualistic blowup regime as resulting in a traditional niche plus an extended region of Allee niche from the perspective of the mutualistic pair (see Appendix S7: Fig. S2). In this Allee niche region, the mutualists can persist together at high densities, but are unable to invade if one of them starts at low densities and at least one of the mutualists goes extinct as a consequence. This means that there is a bistable regime between mutualistic coexistence and a form of "dissassembled mutualism" (plant only, carnivore only, or neither of them).

## DISCUSSION

### Implication of the theory for niche modeling

By expanding Niche Theory to include positive interactions, we provide a rigorous framework for implementing the mechanisms of niche and range expansion through facilitation and mutualism in niche modeling approaches (e.g., Afkhami et al. 2014, Bulleri et al. 2016, Filazzola et al. 2017; see Appendices S2, S8 for summary guides for theoreticians and empiricists on how to apply our framework). The strength of the Niche Theory presented here is that it accounts for the feedback from organisms to their local environment, which is not often

accounted for in the niche modeling literature, despite its close conceptual proximity to Niche Theory. Our approach recognizes the dual nature of the environment, i.e., differentiates between the large-scale environmental conditions that covary with physical space (e.g., climatic and geological gradients, formalized here by the supply point), and the very local environmental conditions that are under the direct influence of organisms, for example through niche-construction and -destruction activities (e.g., micro-climate or nutrient availability, formalized here by the environmental factors; also see Soberón [2007]). This dual nature of the environment also leads to a plural definition of the niche, as one can conceptualize the niche as "living" either in the abstract space of required environmental conditions or in the physical space along the large scale environmental conditions (Stachowicz 2012). This ambiguous definition of the niche was pointed out by Stachowicz (2012) as a response to an objection by Rodriguez-Cabal et al. (2012) that positive interactions cannot expand the fundamental niche. Our framework here concurs with Stachowicz (2012) as our result clearly shows how environmentally mediated positive interactions between conspecifics can expand the fundamental niche of a species in both the supply space and the physical space through the Allee niche (Figs. 3C, 4C).

It would be interesting to apply our formalization of Holt's (2009a) establishment and persistence niches to physically locate the regions exhibiting an Allee niche within a species range, where that species only persists due to strong positive feedbacks. This could be particularly helpful in conservation, as populations located in the Allee niche are at particular risk of local extinction due to environmental perturbations, and could also inform restoration strategies by providing a minimal population size or density necessary for a successful re-establishment. For example, coast redwoods (*Sequoia sempervirens*) in California are known to critically depend on fog capture to meet their water requirements, with the efficiency of fog capture being larger for a tree within a redwood grove than in isolation (Dawson 1998). This positive feedback loop might be the only thing enabling some (if not all) redwood forests to persist in locations where they could not establish starting with a few trees today (Cuddington et al. 2009). A similar situation involves semiarid ecosystems, where plant communities collectively favor water infiltration and nutrient retention, in turn enabling their persistence (Rietkerk and van de Koppel 1997). The conservation challenges associated with these positive feedbacks in semi-arid vegetation are already known, but our approach coupled with niche modeling could provide additional tools to delimit physically the regions where this ecosystem is the most at risk. Interestingly, it has been shown theoretically that semi-arid vegetation located in its Allee niche may self-organize in spatial patterns (Klausmeier 1999, Kéfi et al. 2010), which suggests that such patterns could serve as a spatial signature to locate the Allee niche.

Similarly, our exploration of apparent mutualism between plant and a carnivore shows that indirect positive interactions cascading through a food web ultimately have consequences on the niches of the two species involved. As discussed earlier, the cascading effects of predators on plant fitness have been studied before, but their consequences in terms of species niche have not been explored. As these interactions work both ways, the establishment of a very palatable plant species in an ecosystem could boost local herbivore populations, in turn enabling a predator to establish that could not subsist in the absence of that plant. Conversely, the loss of large carnivores and decreased hunting pressure in North America are known to have led to a sharp increase in ungulate herbivore population, notably of white-tailed deer (*Odocoileus virginianus*), which, in turn, has cascaded on local plant communities, leading to local extinctions of native species such as *Trillium* and other woodland herbaceous species (Russell et al. 2001). Using our framework, one can understand these local extinctions as a consequence of "niche contraction" from the realized to the fundamental niche caused by the extirpation of the carnivore. Conversely, localities where plants persisted after the loss of the carnivore could be understood as belonging to this plant's fundamental niche. When the positive feedback between the plant and the carnivore is strong enough, an Allee effect at the mutualistic-pair level can emerge. This means that a plant and a carnivore species could persist in an ecosystem, but reducing either the plant or the carnivore density could lead to an extinction cascade of both of them due to non-trivial indirect effects of reorganization of the herbivore community. This last example, although purely theoretical, shows how strong feedbacks that propagate through simple food webs can have important consequences for a species niche that go beyond the usual focus on the effects of that species' competitors.

### Signature of positive interactions

In this paper, we saw that the impact on species dynamics of positive interactions between individuals falls broadly into two categories. First, positive interactions can be relatively weak, not completely offsetting negative interactions, so that the overall regulating effect of net interactions is maintained. When this is the case, the effects of positive interactions remain mostly quantitative (Kylafis and Loreau 2011). In the two-species case, weak positive interactions lead to increased niche complementary without qualitatively changing the stability of coexistence, as long as the effective niche difference $\Omega_a$ remains smaller than 180° (equivalent in the example of Fig. 7 to an impact niche difference $\Omega_I$ smaller than 180°). Yet, we saw that positive interactions quantitatively increase structural stability, expand the niche of both species and increase their equilibrium densities. In the single species case, small positive interactions between conspecifics similarly alleviate competition,

decreasing the strength of population regulation and leading to an overall increase in population density (not shown).

Second, positive interactions can be strong enough that they completely counteract negative interactions, leading to a qualitative change in dynamics driven by positive feedback loops. In the two-species case, this happens when $\Omega_a$ is larger than 180°. The coexistence equilibrium becomes unstable, which signals a bistable regime between an equilibrium where at least one of the two species goes extinct, and a trajectory where the density of both species increases jointly (and would eventually settle on a stable coexistence equilibrium if a third regulating environmental factor was explicitly modeled). This mimics the one-species situation where impacts and sensitivities pointing in the same direction signal a destabilizing positive feedback loop around that equilibrium, located between the extinction and persistence equilibria. In both cases, strong positive interactions can only be transient because of their fundamentally unstable nature; at the final stable equilibrium, the signature of strong positive interactions will be lost.

This means that strong positive interactions will necessarily be overlooked if we focus on the properties of a community close to their equilibrium. We can think of several ways to overcome this issue. One could naturally change focus to try to detect and quantify these transient regimes of fast growth, but locating the unstable equilibrium point in the first place might prove to be challenging. Building on the niche-based approach presented here, another option is looking for alternative stable states along environmental gradients. Indeed, we have seen in *Negative and Positive Feedbacks Between a Single Species and Its Environment: The Fundamental Niche* that these alternative stable states are one of the unambiguous signature of strong positive interactions, and take the form of persistence without recovery from low density. There are classical examples of this situation in well-studied populations subject to Allee effects (Courchamp et al. 1999), and we also expect this to happen with obligate mutualists and cross-feeding (Sun et al. 2019). Yet, a more diffuse, apparent mutualism can emerge between two species through indirect interactions. Coupling invasion analysis from low density with persistence at high density, for focal species alone or in pairs, along varying environmental factors should make it possible to detect such strong positive interactions.

Note that this approach of also looking at persistence from high density differs quite significantly from the recent trend that focuses exclusively on species growth rate when rare to quantify niche overlap and eventually define species coexistence (Chesson 2000, Grainger et al. 2019). But, in the context of Allee effects and other alternative stable states, populations can persist on reasonably long time scales even though invasion from very low densities was prohibited. If strong interactions and feedback loops are more common in nature than

expected, crafting a theory of coexistence that deals satisfactorily with alternative stable states will be essential.

### Effects of positive interactions on the ecosystem and its functioning

One advantage of Niche Theory over other frameworks in community ecology is that the dynamics of the environment is explicitly represented. In addition to allowing for more mechanistic and context-dependent interactions, an explicit environment also means that the theory can naturally be used to investigate how positive interactions between organisms affect the environment itself and impact ecosystem functioning.

Using the examples of organisms consuming an inhibiting substrate and N-fixing plants, we showed how positive intraspecific interactions can give rise to Allee effects under some environmental conditions, where the focal species cannot grow from low densities but can persist at high densities. From a population perspective and in line with the Allee effect literature, this can be interpreted as the existence of alternative stable states between a species persisting and going extinct. Now these alternative stable states also have an environmental component, so from an ecosystem perspective the environment also presents alternative states, separated by what are classically called catastrophic shifts in the ecosystem ecology literature (Scheffer et al. 2001). Mirroring what happens on the population side, one of these alternative environmental states exhibit conditions unsuitable for a given species (e.g., low N availability, or toxic concentrations of the substrate) while the other has conditions favorable for persistence (e.g., higher N availability, or lowered substrate concentration). This idea that some organisms can actively affect their environment in a direction that is more favorable to their persistence is known in the literature as "ecosystem engineering" (Jones et al. 1994, Cuddington et al. 2009) or "positive niche construction" (Odling-Smee et al. 1996, Kylafis and Loreau 2008, 2011).

Such improvement by organisms of their local environment rarely benefits only them. Instead, it often "leaks out" more broadly, potentially benefiting other species in that ecosystem. This is what we saw in our second example, when the non-fixing species ended up coexisting with the N fixer under low N supplies. This means that positive environmental modifications by one species can have far-reaching consequences for the community and the ecosystem as a whole. In a recent paper (Koffel et al. 2018a), we used a similar model of facilitation by N fixers to show how successive establishment and replacement by a suite of N-fixing species that vary in their fixing abilities can lead to a progressive ecosystem development through N accumulation and increasing total biomass. This example suggests that environmentally mediated positive feedback loops can have major consequences for the development and functioning of ecosystems.

In this context, our theory provides a general framework to think about the interplay between environmentally mediated positive feedbacks and the regulation of biogeochemical cycles and other ecosystem functions. For example, several studies have suggested that the mechanisms through which N-fixation is regulated, from the physiological responses at the organism level to changes in relative abundance at the community level, could explain some major biogeochemical patterns such as the N:P ratio in the deep oceans (Lenton and Klausmeier 2007), or contrasting N limitation patterns between tropical and temperate terrestrial forest ecosystems (Menge et al. 2008, Hedin et al. 2009, Sheffer et al. 2015). Interestingly, we just discussed that these positive feedbacks can be associated with alternative stable states, which means that the resulting biogeochemical cycles can themselves present a fragility to catastrophic shifts (Koffel et al. 2018a). More generally, our approach reinforces the idea that some classic frameworks in ecosystem sciences such as ecosystem development (Odum 1969) and primary succession (Walker and del Moral 2003) would strongly benefit from getting more tightly integrated with frameworks that explicitly rely on the interactions between organisms and their environment, such as Niche Theory and resource competition (DeAngelis 1992, Levin 1998, Loreau 1998).

### A general theory of the niche

In this paper, we presented a general mechanistic theory of the niche based on impacts and sensitivities to environmental factors, and an associated graphical approach, allowing us to represent the outcome of community assembly along environmental gradients, with a broader range of applicability than is usually presented (see Appendix S2 for a step-by-step guide).

First, we hope we convinced the reader that most ecological situations involving indirect interactions can be formalized by Niche Theory: environmental factors can range from abiotic (e.g., nutrients, toxins, temperature) to biotic (e.g., bacteria, plants, herbivores, etc.), following a diverse array of dynamics (see Appendix S1 for extensions of the theory to non-chemostat dynamics), and their interactions with a focal species can span all four combinations of impacts and sensitivities, i.e., Estrela et al.'s (2018) scenarios of Detoxify, Deplete, Pollute and Enrich (Fig. 2). The theory has been presented here on unstructured populations for simplicity, but it is important to note that it can be applied to structured populations as well (Schellekens et al. 2010, Haegeman and Loreau 2015, Appendix S9 presents the general rational behind the extension to structured population). Importantly, the graphical approach to Niche Theory presented here applies well to highly non-linear species–environment interactions, as it naturally accounts for non-linear functional responses, curved ZNGIs and context-dependent impact vectors (see Fig. 1 and Koffel et al. 2016, 2018b; Wickman et al.

2019). This generality is a foundational aspect of Niche Theory (Tilman 1980, Chase and Leibold 2003), despite a tendency in the recent literature to focus exclusively on the essential and substitutable resource cases (Letten et al. 2017), potentially limiting the generality of results derived when based only on these two particular examples. When two focal species are considered together, we also showed how Niche Theory, classically applied to intraguild competitive situations, can equally be applied to "asymmetrical facilitation" (formally akin to predator–prey) and mutualism, within but also between trophic levels (such as between plants and carnivores).

Temporal and spatial variation provide another important aspect of species interactions that we have not addressed so far. While we are not aware of such a general framework within Niche Theory, several studies nevertheless provide promising directions. Levins (1979) was the first to suggest that the mean and variance of a single time-varying resource effectively behave like two separate environmental factors (known as "relative non-linearity" in Modern Coexistence Theory; Chesson 2000). In a similar vein, Miller and Klausmeier (2017) recently used a two-season model to show how the two seasonal averages of a single varying resource act as two separate environmental factors. On the spatial side, Haegeman and Loreau (2015) applied the same ideas to a two patch model, allowing them to use the graphical approach. However, it remains unclear how to extend these ideas to more complex situations, as they in general translate into a large, if not infinite, number of effective environmental factors, or lead to intricate temporal couplings between environmental factors and varying species density (the "storage effect" in Modern Coexistence Theory; Chesson 2000, Barabás et al. 2018). Thus, applying the niche framework presented in this manuscript to these general situations involving environmental variability remains an open question.

As the diverse set of ecological scenarios presented above is examined through the lens of Niche Theory, we see some relatively novel dynamics with connections to classical concepts, easy to explore and represent with the graphical approach. Intraspecific positive feedback loops, for example, can give rise to an Allee niche, a region of Allee effects when impact vectors extend beyond the establishment niche. More generally, the graphical approach efficiently detects and represents all possible kinds of alternative stable states (Koffel et al. 2016), which also includes the classic multispecies priority effects (between two or more species, but also between one species and a pair of coexisting ones) and within-species alternative stable states (as can commonly occurs with structured population, e.g., Schellekens et al. 2010). Positive interactions between two species naturally lead to "niche facilitation" when the backwards extension of the impact vector of the facilitator goes beyond the fundamental niche of the facilitated, formalizing a classic ecological concept (Bruno et al. 2003). Similarly, we have seen that when such pairwise positive

interactions are too strong, they lead to an Allee niche at the species-pair level. This could in turn be visualized using Niche Theory in three dimensions after including a third regulating factor (Sun et al. 2019).

We also provided a general recipe for translating locally any Niche Theory model into an effective Lotka-Volterra model to connect our general metrics of sensitivity and impact niche difference to an effective single metric of niche difference. To do so, we used a general approach based on a Quasi-Steady-State Approximation (QSSA) on the environmental factors dynamics (Chesson 1990, Meszéna et al. 2006, Barabás et al. 2014) and applied it to the particular dynamics of the environmental factors as modeled in Niche Theory through Eq. 1. The QSSA is a more rigorous and generalizable procedure than a somewhat ambiguous algebraic decomposition provided by Tilman (1982) in his Appendix and reused recently by Letten et al. (2017). As was advocated by Letten et al. (2017), we also believe these two approaches, Niche Theory and effective Lotka-Volterra model, are highly complementary. For example, we saw that the effective Lotka-Volterra models are in general only meaningful locally (a consequence of their linear nature), as exemplified by the propensity to unbounded growth in situations involving positive interactions. Conversely, Niche Theory models can capture the context-dependency of positive interactions, such that mutualistic growth eventually stops as other regulatory mechanisms come into play.

Note that unlike the graphical approach and geometrical metrics of niche differences, which can be applied to the general class of Niche Theory models, the transformation to a Lotka-Volterra model given in Box 3 relies on the underlying assumptions of constant sensitivities and impacts, which is only approximately true in the vicinity of coexistence points (see Appendix S3). This in turn means that our generic results on how the niche difference metrics inform structural stability to a change in basal growth rate (Eq. 12) and the effects on species densities (Eq. 13), derived from that Lotka-Volterra transformation, are also conditioned by such assumptions (while the results on dynamical stability and structural stability to changes in supply are general). In fact, there is no general analytical result that compares species densities in coexistence from their densities in monoculture in Niche Theory, which justifies why such assumptions are needed in the first place to obtain system-independent results. Still, such results might be obtainable for some specific systems, such as essential and substitutable resources, and deviation from these assumptions in the form of curved ZNGIs and non-parallel impact vectors offer interesting directions to be explored in future work.

Finally, the graphical approach to Niche Theory presented here could, Because of its generality, be applied to a broad class of ecological situations that involve facilitation or mutualism. In addition to classic mutualistic relationships such as plant–pollinator, plant–frugivore,

plant–mycorrhiza, and legume–rhizobia interactions, our approach also opens the door to quantifying more indirect mutualistic interactions within food webs, such as the interactions between plants and carnivores. Another example that could be addressed using the approach presented here involves interactions between plants and decomposers, which combines indirect mutualism through production of dead biomass by the plant and mineralization by the decomposer, with potential competition between the two guilds for the released inorganic nutrients (Daufresne and Loreau 2001). More generally, our approach is particularly suited to look at context-dependent interactions along environmental gradients. Theories like the "stress gradient hypothesis" and the "mutualism–parasitism continuum" would benefit from being looked at through the lens of Niche Theory. We also recently showed how the graphical approach to Niche Theory presented here can be adapted to evolutionary approaches in trait-based frameworks (Koffel et al. 2016), paving the way for an "evolutionary theory of the niche" (Holt 2009a). Combined with the present work, these tools should make it possible to investigate a broad spectrum of questions concerning the evolution of facilitation and mutualism, and their stability to cheating in the examples listed above.

### Toward a general theory of species interactions and coexistence?

In this paper, we also advocated for the development of a general theory of species interactions. More particularly, we used the framework of Niche Theory, specifically tailored to indirect interactions mediated by explicit environmental factors, to show how a concept like niche difference, usually used to quantify the strength of competition, can equally be applied to situations that involve positive interspecific interactions. Our approach suggests building on the connection between lower-level metrics of direct interactions between the focal species and their environment (the sensitivity and impact niche differences) and an effective, indirect metric of niche difference. With several possible options to pick from for the latter, we identified pros and cons for each metric, which suggests that there is no ideal metric to measure effective niche difference. On one hand, Chesson's (2000) metric of niche overlap in the two-species case (see Song et al. 2019 for the distinction with the multispecies metric) presents a relatively natural expression as a function of the sensitivity and impact niche differences (see Appendix S10) but cannot be extended to positive interactions and does not work beyond two species (Saavedra et al. 2017). On the other hand, Saavedra et al.'s (2017) structural metric has a less natural mathematical expression in terms of sensitivity and impact niche differences (Appendix S5), but encompasses the full range of possible ecological interactions, from competition to facilitation and mutualism. Moreover, all of these angular metrics can theoretically be naturally

extended to the multispecies case using solid angles (Saavedra et al. 2017), or, equivalently, the determinants of the impact and sensitivity matrices for saturated communities (Meszéna et al. 2006). However, it is unclear to us how this would work with our approach where angles need to be oriented to keep track of the relative position of impacts and sensitivities, and to which degree these low-dimensional metrics are informative of dynamical stability in these multispecies communities. More generally, this brings us back to the outstanding challenge of understanding multispecies coexistence, and the extent to which the graphical approach presented here in two-dimensional environmental spaces scales up to $n$-dimensional systems remains to be explored. Also note that our quantification of niche difference relied on looking at the local behavior of two species dynamics near a (potentially unstable) coexistence point; how to quantify niche overlap globally, in a non-local way, remains to our knowledge an open question. Finally, as coexistence theory moves away from an exclusive focus on direct, intraguild competition toward the inclusion of any indirect, network-mediated interaction (Godoy et al. 2018), it becomes unavoidable for the theory to be able to accommodate for potentially positive interactions, as exemplified by our study of trophic cascade.

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## Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1458/full