

The Minimum Environmental Perturbation Principle: A New Perspective on Niche Theory

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ABSTRACT: Fifty years ago, Robert MacArthur showed that stable equilibria optimize quadratic functions of the population sizes in several important ecological models. Here, we generalize this finding to a broader class of systems within the framework of contemporary niche theory and precisely state the conditions under which an optimization principle (not necessarily quadratic) can be obtained. We show that conducting the optimization in the space of environmental states instead of population sizes leads to a universal and transparent physical interpretation of the objective function. Specifically, the equilibrium state minimizes the perturbation of the environment induced by the presence of the competing species, subject to the constraint that no species has a positive net growth rate. We use this “minimum environmental perturbation principle” to make new predictions for evolution and community assembly, where the minimum perturbation increases monotonically under invasion by new species. We also describe a simple experimental setting where the conditions of validity for this optimization principle have been empirically tested.

Keywords: niche theory, community ecology, invasions.

Introduction

The past century of research in theoretical ecology has revealed how simple mathematical models can have surprisingly rich behavior, with results that are often difficult to predict without running a numerical simulation. This is particularly the case when the number of simultaneously interacting species becomes large and an exhaustive exploration of the parameter space is no longer possible. But deriving ecological insight from these models requires abstracting from an individual simulation run, to find qualitative features of the dynamics that generically follow from the basic modeling assumptions.

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Fifty years ago, Robert MacArthur found hints of a general principle of this kind, concerning the properties of stable equilibrium states (MacArthur 1969, 1970). In a model of competition for substitutable resources, now known by his name, he showed that the equilibrium states optimize a certain quadratic function of the population sizes. Under some additional assumptions, this function had a natural interpretation in terms of the difference between available resource production and the harvesting abilities of the consumers. He obtained similar optimization principles for several other models, including one with direct interaction between resources and another representing competition to avoid predators, suggesting that this result might extend significantly beyond the specific context in which it was originally found. But he was unable to find an ecological interpretation of the objective function in these other cases, and no broader framework had yet been developed for systematically generalizing the principle.

In this article, we complete MacArthur’s work by situating it in the context of contemporary niche theory (for a thorough introduction, see Chase and Leibold 2003). This mathematical and conceptual framework effectively generalizes the original consumer resource model to allow for arbitrary environmentally mediated interactions, including saturating growth kinetics, competition for essential resources (e.g., as described by Liebig’s law of the minimum), and microbial systems with rampant by-product secretion. This framework first of all allows us to state the general conditions under which an optimization principle exists. But it also provides another benefit, by focusing our attention on the environmental state. Contemporary niche theory naturally lends itself to a graphical analysis in the space of environmental factors, where coexistence conditions can be geometrically determined (for a recent review, see Koffel et al. 2016). It turns out that conducting the optimization in this environmental space—instead of in the space of population sizes—leads to a generalizable ecological interpretation of the objective function.

In the following sections, we first review MacArthur’s original result and describe how his model is generalized

by the niche theory framework. Then we describe the conditions for the existence of an optimization principle in a niche model and show how the principle can be interpreted as a constrained minimization of the environmental perturbation induced by the competing species. We illustrate the scope of the result with seven examples: the three considered by MacArthur and four scenarios that depart from his assumptions in significant ways. One of these examples is taken from a classic experimental article on resource competition in rotifer populations (Rothhaupt 1988), where the model was shown to provide an excellent description of the experiments. We review how the conditions for an optimization principle can be directly verified in this case. Finally, we discuss an important corollary of our result, that the environmental perturbation monotonically increases during community assembly or evolution.

Background

MacArthur's Minimization Principle

MacArthur originally considered a model of competition among S consumer species for M substitutable resources (MacArthur 1970). The resources, with population densities R_α ($\alpha = 1, 2, \dots, M$), do not interact with each other directly, and each resource type is independently self-limiting with carrying capacity K_α . The dynamics of the consumer population densities N_i ($i = 1, 2, \dots, S$) and the resource abundances are described by the following set of differential equations:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right], \quad (1)$$

$$\frac{dR_\alpha}{dt} = \frac{r_\alpha}{K_\alpha} R_\alpha (K_\alpha - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha, \quad (2)$$

where $c_{i\alpha}$ is the successful encounter rate of species i searching for resource α , m_i is the “maintenance cost” or threshold consumption level for growth, w_α is the per capita “weight” or nutritional value of each resource, e_i is the quantity of nutritional value required for reproduction of a given species, and r_α is the low-density resource growth rate. A central feature of interest in any such model is the location of the stable equilibrium state $\bar{\mathbf{N}}, \bar{\mathbf{R}}$. MacArthur showed that this state can be identified by eliminating the R_α s and minimizing a quadratic function of the N_i s.

To eliminate the R_α s, MacArthur assumed that the resources relax quickly to the equilibrium state corresponding to the current consumer population sizes. Solving for R_α as a function of N_i in the equilibrium equations $dR_\alpha/dt = 0$, one obtains a closed set of dynamics for the consumer population sizes:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_{\alpha \in \mathbf{M}^*} r_\alpha^{-1} K_\alpha w_\alpha c_{i\alpha} \left(r_\alpha - \sum_j N_j c_{j\alpha} \right) - m_i \right]. \quad (3)$$

Here, the set \mathbf{M}^* is composed of resources with feasible abundances $\bar{R}_\alpha = r_\alpha - \sum_j N_j c_{j\alpha} \geq 0$. Any resources not satisfying this constraint are driven to extinction under the full dynamics. MacArthur noticed that these differential equations can be written in terms of the gradient of a quadratic function of the N_i s:

$$\frac{dN_i}{dt} = -e_i N_i \frac{\partial Q}{\partial N_i} \quad (4)$$

with

$$Q(\mathbf{N}) = \frac{1}{2} \sum_{\alpha \in \mathbf{M}^*} r_\alpha^{-1} K_\alpha w_\alpha \left(r_\alpha - \sum_j c_{j\alpha} N_j \right)^2 + \sum_j m_j N_j, \quad (5)$$

as is easily verified by performing the partial derivative and comparing with the original equation. Equation (4) implies that $\partial Q/\partial N_i = 0$ in equilibrium for all nonextinct populations i . The negative sign guarantees that this stationary point is a local minimum rather than a maximum. For the extinct populations, stability against reinvasion requires $\partial Q/\partial N_i > 0$. This means that setting $N_i = 0$ also minimizes Q along these directions, subject to the feasibility constraint $N_i \geq 0$ (Gatto 1982, 1990). We have plotted $Q(\mathbf{N})$ for a community with two consumer species in figure 1a, along with the equilibrium state eventually reached in a numerical simulation of equations (1) and (2).

This result was an important step forward in understanding the nature of equilibrium states in this model. It shows, for example, that there is only one stable equilibrium state, since Q is a convex function with a single local minimum. But this theorem as it stands is subject to several significant limitations. First of all, the restriction of the sum to the subset \mathbf{M}^* of resources with $r_\alpha - \sum_j c_{j\alpha} N_j \geq 0$ makes the objective function more complicated than it initially seems, since it is actually a piecewise function consisting of sectors that are linear along some axes and quadratic along others. This seems not to have been noticed by MacArthur, who took the sum over all M resources, or in subsequent discussion of his work (MacArthur 1970; Case 1980; Gatto 1982, 1990). In fact, the restriction of the sum problematizes the ecological interpretation MacArthur achieved for one special case of the model, as discussed in appendix A (apps. A–D are available online). Second, it remains unclear what assumptions are actually required to obtain a minimization principle. MacArthur took some steps in that direction by extending his result to the case of interacting resources and of competition to avoid predators. He noted

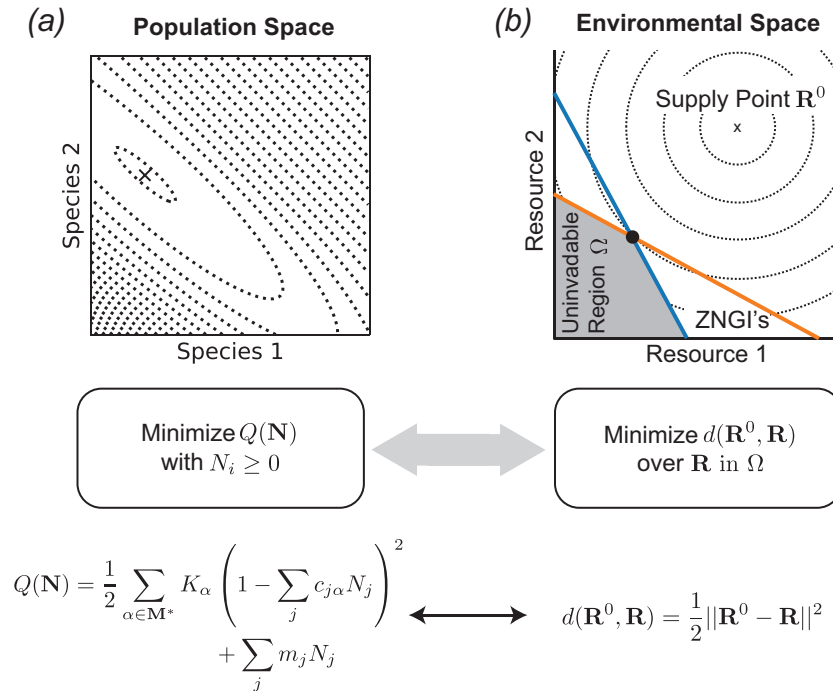


Figure 1: Reinterpreting MacArthur’s minimization principle. *a*, Contour lines of MacArthur’s objective function $Q(\mathbf{N})$ in the space of population sizes, as defined in full in equation (5). The cross (\times) marks the equilibrium eventually attained in direct numerical simulation of equations (1) and (2) with the same parameters ($r_{\alpha} = m_i = w_{\alpha} = 1$ for $\alpha = 1, 2, i = 1, 2; K_1 = 4.8, K_2 = 2.85, c_{1\alpha} = (0.5, 0.3), c_{2\alpha} = (0.4, 0.6)$). The direct simulation ends up at the point where Q is minimized, as predicted by MacArthur. Also shown for illustration is a simplified expression for Q with the r_{α} and w_{α} set to 1. *b*, Contour lines in the environmental space of resource abundances representing the dissimilarity measure $d(\mathbf{R}^0, \mathbf{R})$ with respect to the supply point \mathbf{R}^0 . The uninvadable equilibrium state, indicated by the black circle, minimizes d under the uninvadability constraint $g_i(\mathbf{R}) \leq 0$, which constrains the environmental state to lie within the shaded region Ω bounded by the zero-net-growth isoclines (ZNGI’s; colored lines). For MacArthur’s model of competition for noninteracting resources with $r_{\alpha} = w_{\alpha} = 1$ as in the previous panel, d is simply the Euclidean distance.

that for all of these cases, the key feature required was the symmetry of the interaction matrix in an effective Lotka-Volterra description of the scenario. But his approach cannot be straightforwardly applied to other important scenarios, such as when abiotic nutrients are supplied by a chemostat or when the growth kinetics saturate at high resource abundance.

The minimization principle has recently been extended to larger classes of population dynamics that allow for chemostat models of resource supply, suggesting that an optimization approach applies much more broadly than previously supposed (Tikhonov and Monasson 2017; Mehta et al. 2019b). But the assumptions under which these new results were obtained do not admit an obvious ecological interpretation, and so the precise extent of the approach remains unclear.

Contemporary Niche Theory

In the present work, we draw on the theoretical framework of contemporary niche theory, as consolidated by Chase

and Leibold (2003), and define the complete class of models within this framework that are subject to an optimization principle. Our results generalize MacArthur’s insight about the symmetry of the environmentally mediated interactions, revealing a minimization principle valid for all niche models that are symmetric in the relevant sense defined precisely below. We also show how the optimization perspective can provide an efficient way of identifying equilibrium states even for systems outside this class, where the principle does not strictly apply.

Table 1 lists the key elements of the theory, which aims to extract the essential features of MacArthur’s consumer resource model (MCRM; eqq. [1], [2]). The first of these features is the explicit consideration of the environment, with the abundances R_{α} of the M resources appearing alongside the population densities N_i of the S consumer species. Niche theory follows this basic scheme but with a broader notion of “resource” that includes any environmental factor that affects an organism’s growth rate (see Levin 1970; Tilman 1982). In microbial ecology, for example, concentrations of quorum-sensing molecules and antibiotics can

Table 1: Key quantities of niche theory

Symbol	Description	MCRM
N_i	Species abundance	Consumer population density ([individuals][length] ^{-D})
R_α	Environmental factor	Resource population density ([individuals][length] ^{-D})
g_i	Growth rate	$e_i[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i]$ ([time] ⁻¹)
$q_{i\alpha}$	Impact vector	$-c_{i\alpha} R_\alpha$ ([length] ^D [time] ⁻¹)
h_α	Supply vector	$\frac{r_\alpha}{K_\alpha}(K_\alpha - R_\alpha)$ ([individuals][length] ^{-D} [time] ⁻¹)
R_α^0	Supply point	K_α ([individuals][length] ^{-D})

Note: The final column lists how each quantity appears in MacArthur's consumer resource model (MCRM; eqq. [1], [2]), along with its units. D is the spatial dimension of the ecosystem (2 for terrestrial, 3 for aquatic).

act as resources in this extended sense (Momeni et al. 2017).

The second feature of the MCRM is that the reproductive rates of the consumers depend only on the state of the environment, as specified by the resource abundances. Niche theory preserves this assumption but allows this dependence to be described by an arbitrary set of functions $g_i(\mathbf{R})$. The consumers in the MCRM also affect the environment by depleting resources, with the per capita depletion rate depending only on the resource abundances. In niche theory, this assumption is encoded by representing the impact of the organisms on their environment by a set of per capita “impact vectors,” with the impact of species i on resource α described by a function $q_{i\alpha}(\mathbf{R})$ (Tilman 1982; Leibold 1995). In the MCRM, the impacts are closely related to the growth rates, since resources contribute to the growth rate only insofar as they are removed from the environment. But generalized resources can affect the growth rate in other ways (e.g., production of antibiotics specifically inhibiting growth of other species), so the niche theory framework allows the impact vectors to be defined by an independent set of arbitrary functions.

Finally, the resources in the MCRM have their own intrinsic dynamics, described by a set of independent logistic growth laws. Niche theory places no constraints on the form of the intrinsic resource dynamics, which are described by a “supply vector” with elements $h_\alpha(\mathbf{R})$ (Tilman 1982; Chase and Leibold 2003). Generally, however, it is assumed that these dynamics have some stable equilibrium \mathbf{R}_α^0 , which is known as the “supply point.”

These definitions lead to the following set of differential equations describing the population and environmental dynamics in a general niche model:

$$\frac{dN_i}{dt} = N_i g_i(\mathbf{R}), \quad (6)$$

$$\frac{dR_\alpha}{dt} = h_\alpha(\mathbf{R}) + \sum_i N_i q_{i\alpha}(\mathbf{R}). \quad (7)$$

Graphical Analysis with Zero-Net-Growth Isoclines

The central assumption of niche theory is that all interactions between species are mediated by environmental factors, such that $g_i(\mathbf{R})$ and $q_{i\alpha}(\mathbf{R})$ are functions of the environmental state \mathbf{R} alone and are independent of the population sizes N_i . This assumption makes it possible to graphically analyze the equilibrium states of these models in resource space (Tilman 1982). Central to the graphical approach is the hypersurface where $g_i(\mathbf{R}) = 0$, called the zero-net-growth isocline (ZNGI), depicted in a two-resource example in figure 1*b* (Tilman 1982; Leibold 1995). Environmental states along the ZNGI support reproduction rates that exactly balance death rates, leading to constant population sizes. The ZNGIs play an essential role in the formulation of our new optimization principle.

For a given collection of species, the ZNGIs fix the boundaries of the “uninvadable” region Ω illustrated in figure 1*b*, defined as the set of environmental states \mathbf{R} satisfying $g_i(\mathbf{R}) \leq 0$ for all species i . All stable equilibrium states lie within this region, for any choice of supply vector and impact vector. The interior of the region does not support growth of any species in the collection, so any interior point can trivially be made into an “empty” stable equilibrium state by simply placing the supply point there and driving all of the consumer species extinct. All nonempty equilibrium points lie on the boundary of Ω , which is the outer envelope of the ZNGIs of all of the species in the pool (see Koffel et al. 2016). Points that lie on a ZNGI but are outside Ω can be valid equilibrium states, but they are unstable against invasion by species within the focal collection.

Results

General Criteria for Existence of Optimization Principle

Our first main result is that MacArthur's observation on the conditions for the existence of an optimization principle can be extended to all models within the niche theory framework: equilibrium states of a niche theory model

optimize an objective function whenever the environmentally mediated interactions among species are symmetric.

Interaction symmetry is usually treated within the context of a generalized Lotka-Volterra model, which represents the interactions with a matrix of constant coefficients. But it can be defined more generally within niche theory by considering a small externally imposed perturbation in the abundance of a given species from some reference state. This perturbation will slightly shift the equilibrium resource abundances, which will in turn affect the growth rates of the other species. These environmentally mediated interactions are symmetric if the effect on the growth rate of species j of a change in the abundance of species i is the same as the effect on species i of the same change in species j .

When all species are very similar to each other, this condition is straightforward to evaluate. But when species significantly differ in body size or other important characteristics, the quantification of abundance becomes ambiguous. In the case of body size differences, measuring the population in terms of total biomass gives a very different result than counting the number of individuals. This makes it unclear whether “the same” change in abundance is the same additional number of individuals or the same increase in total biomass. Whether the interactions are symmetric will depend on the choice of unit of measurement.

To resolve this ambiguity, we define the interactions to be symmetric whenever there is at least one way of quantifying abundance under which symmetry is achieved. Mathematically, this can be expressed as the requirement that $dg_i/d(a_jN_j) = dg_j/d(a_iN_i)$ for some choice of positive scaling factors a_i . This flexibility in the relevant notion of symmetry was already noted by Gatto (1982) in the context of MacArthur’s original work and is here generalized to arbitrary models within the niche theory framework. It is actually slightly more general even than Gatto realized, because the scaling factors need not be constant but can depend on the current state of the ecosystem. This flexibility makes a wide variety of resource competition models symmetric in the relevant sense.

Since the effect of a change in population size on the environment is determined the impact vector while the effect of the change in environment on other species is determined by their growth rates, symmetry clearly requires the growth rates and impact vectors to be related in a special way. In appendix B, we show that the required relationship takes the following form:

$$q_{i\alpha}(\mathbf{R}) = -a_i(\mathbf{R})b_\alpha(\mathbf{R})\frac{\partial g_i}{\partial R_\alpha}, \quad (8)$$

where a_i is the scaling factor introduced above and b_α are functions of \mathbf{R} that are the same for all species but can vary from resource to resource. Since the scaling factors a_i have

already been defined to be positive, the new functions b_α should also be positive so that each species acts on the resource in a way that limits its own growth (see Tilman 1982). This proof of equation (8) as the condition for symmetry is somewhat technical, but once it is established, we can substitute this expression into equations (6) and (7) to obtain the following set of conditions for a stable equilibrium:

$$\text{Steady populations } 0 = a_iN_i g_i(\mathbf{R}), \quad (9)$$

$$\text{Steady environment } 0 = \frac{h_\alpha(\mathbf{R})}{b_\alpha(\mathbf{R})} - \sum_i a_i N_i \frac{\partial g_i}{\partial R_\alpha}, \quad (10)$$

$$\text{Noninvasibility } 0 \geq g_i(\mathbf{R}), \quad (11)$$

$$\text{Feasible populations } 0 \leq a_i N_i. \quad (12)$$

These are almost identical to the well-known Karush-Kuhn-Tucker (KKT) conditions for constrained optimization under the constraints $g_i \leq 0$, with the scaled population sizes $a_i N_i$ playing the role of the generalized Lagrange multipliers (also called KKT multipliers) and with $h_\alpha(\mathbf{R})/b_\alpha(\mathbf{R})$ taking the place of the negative gradient of the optimized function (Bertsekas 1999; Boyd and Vandenberghe 2004). These conditions generalize the theory of Lagrange multipliers to the case of inequality constraints, with the first equation setting the Lagrange multipliers $a_i N_i$ to zero for points below the constraint surface ($g_i < 0$), where the constraint has no effect. The KKT conditions were also employed by Gatto in his analysis of MacArthur’s minimization principle, and they also appear in a different context within optimal foraging theory (Gatto 1982; Tilman 1982).

It turns out, as shown in appendix B, that interaction symmetry also requires that $h_\alpha(\mathbf{R})/b_\alpha(\mathbf{R})$ can be written as the gradient of a function, which we will call $d(\mathbf{R})$:

$$\frac{\partial d}{\partial R_\alpha} = -\frac{h_\alpha(\mathbf{R})}{b_\alpha(\mathbf{R})}. \quad (13)$$

The equilibrium conditions listed above thus guarantee that $d(\mathbf{R})$ is locally extremized over the uninhabitable region Ω bounded by the outer envelope of the ZNGIs. Since the intrinsic dynamics of the environment push the state \mathbf{R} along the direction of the supply vector \mathbf{h} , equation (13) implies that this extremum is in fact a minimum.

This result generalizes MacArthur’s minimization principle to all niche models with symmetric environmentally mediated interactions. Stable equilibria of such models can be determined in four basic steps: (1) find b_α and a_i by comparing the impact vectors with the derivative of the growth rates using equation (8); (2) compute d from b_α and the

supply vector using equation (13); (3) impose constraints $g_i \leq 0$, requiring that the environment lie in the uninhabitable region; and (4) minimize $d(\mathbf{R})$ under these constraints. The minimizing value is the equilibrium state $\bar{\mathbf{R}}$ of the environment, and the Lagrange multipliers that enforce the constraints are equal to $a_i \bar{N}_i$.

Objective Function Measures Environmental Perturbation from Surviving Species

Our second result is that the quantity $d(\mathbf{R})$ has a natural and universal ecological interpretation. From equation (13), we see that the unconstrained minimum of d lies at the supply point \mathbf{R}^0 where $\mathbf{h}(\mathbf{R}^0) = 0$. Since this equation only defines the minimized function $d(\mathbf{R})$ up to a constant offset, we are free to set its minimum value to be zero: $d(\mathbf{R}^0) = 0$. We now have a quantity that is always positive and equals zero only when the environment is in its unperturbed equilibrium state. This makes $d(\mathbf{R})$ a natural way of quantifying the “distance” to the supply point. To indicate the fact that the function measures the size of the change from \mathbf{R}^0 to \mathbf{R} , from now on we will put both of these vectors as arguments and write $d(\mathbf{R}^0, \mathbf{R})$.

In light of this interpretation of the objective function, we can state the minimum environmental perturbation principle (MEPP), valid for all symmetric niche models: uninhabitable equilibrium states minimize the perturbation of the environment away from the supply point, subject to the constraint that no species in the regional pool has a positive growth rate.

Extension to Asymmetric Models

Our third result is an extension of MEPP to models without symmetry. Any impact vector $q_{i\alpha}$ can be decomposed into a sum of two terms $q_{i\alpha} = q_{i\alpha}^S + q_{i\alpha}^A$, where $q_{i\alpha}^S$ satisfies equation (8) and $q_{i\alpha}^A$ accounts for the rest of the impact. If the model has a stable equilibrium point, the minimization principle can be recovered by simply fixing the “excess” impact $N_i q_{i\alpha}^A$ of each species to its equilibrium value and treating it as part of the supply vector h_α . This extra supply leads to a shift in the supply point from \mathbf{R}^0 to a new value $\tilde{\mathbf{R}}^0$, defined as the point where the effective supply vector $\tilde{h}_\alpha = h_\alpha + \sum_i \bar{N}_i q_{i\alpha}^A(\mathbf{R})$ vanishes. We can thus formulate an extended statement of MEPP, valid under these broader conditions: uninhabitable equilibrium states minimize the perturbation of the environment away from the effective supply point $\tilde{\mathbf{R}}^0$, subject to the constraint that no species in the regional pool has a positive growth rate.

It is not immediately obvious how to use this result to find an unknown equilibrium state, however, because $\tilde{\mathbf{R}}^0$ depends on the equilibrium values of N_i and R_α . In appendix B, we describe how the minimization problem can

be solved without prior knowledge of \bar{N}_i and \bar{R}_α using an approach inspired by related problems in machine learning. In brief, the algorithm iteratively solves the minimization problem using the current estimate of these equilibrium values and then updates the estimate with the results of the minimization. In the section on asymmetric examples below, we show numerically that this algorithm can successfully converge to the true equilibrium state for two important kinds of asymmetry. In both of these cases, the modified supply vector also has a clear ecological interpretation in terms of the specific mechanisms that break the symmetry of the interactions.

Examples and Discussion

To illustrate our general results, the following sections report the minimized function d for seven commonly used ecological models that can be cast in the language of contemporary niche theory. Of the infinite variety of possible ways of quantifying environmental changes, we will see that this function holds a privileged status, since it naturally reflects the importance of a given change for the ecological dynamics of the community. Full derivations of all results can be found in appendix C, where we also report explicit expressions for the matrix of effective pairwise interactions.

Symmetric Examples

We begin with the three models considered by MacArthur in his original article on the minimization principle (MacArthur 1970): the model of competition for noninteracting resources discussed above and two generalizations. The first of these allows for interaction between different resource types (e.g., plants competing for space or water), and the second includes competition among consumers to avoid shared predators. MacArthur obtained minimization principles in the space of population sizes for all of these models, under the condition that the environmentally mediated interactions among consumer species remain symmetric. By performing the minimization in resource space, we obtain a unified physical interpretation in terms of the environmental perturbation, with the different models giving rise to different perturbation measures d , which reflect the ways in which environmental changes impact the community. This reinterpretation also allows us to readily generalize the minimization principle to a scenario not considered by MacArthur, one where nutrients are supplied externally via a chemostat.

Figure 2 graphically depicts the optimization problem of each of these four scenarios and also compares the results of constrained optimization of d with direct numerical integration of the dynamical equations for two of them.

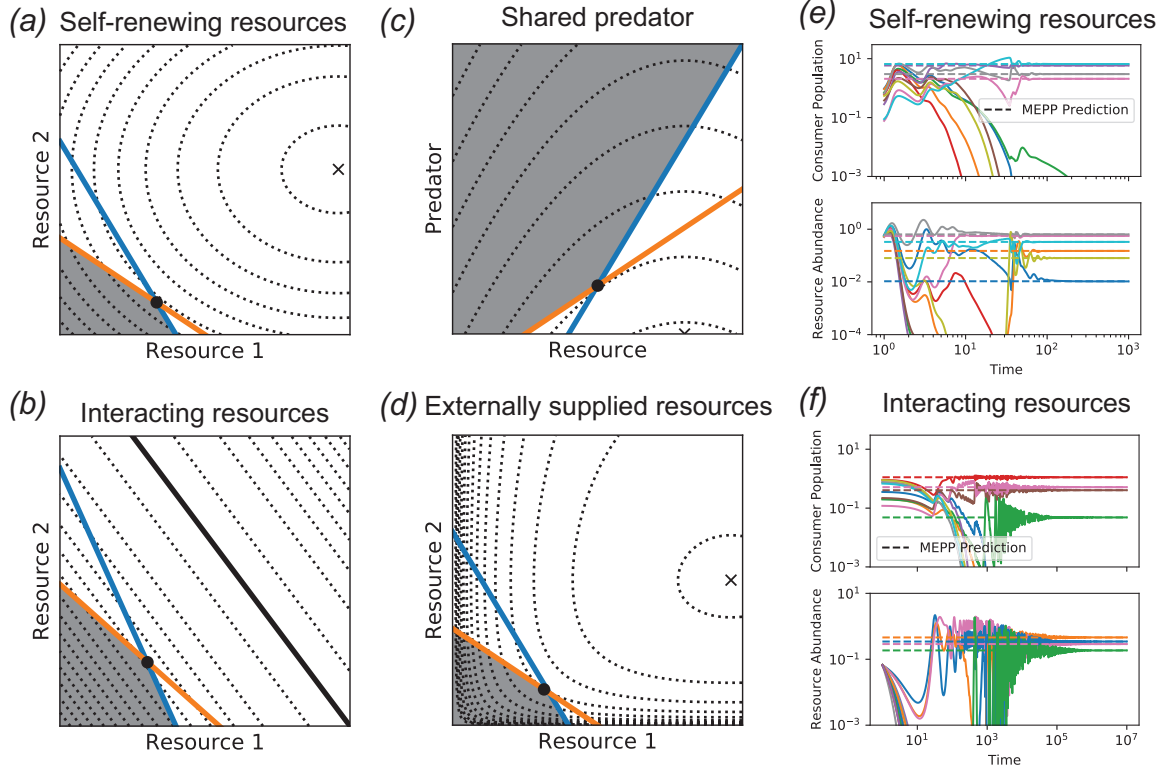


Figure 2: Examples with symmetric interactions. *a–d*, Zero-net-growth isoclines, uninvadable region Ω , and contours of perturbation measure $d(\mathbf{R}^0, \mathbf{R})$ for the four examples discussed in the text where the environmentally mediated interactions are symmetric and the minimum environmental perturbation principle (MEPP) straightforwardly applies. The black circle indicates the final state of a numerical simulation of the corresponding differential equations. *e, f*, Simulations of two of the models with larger numbers of species and resources, compared with the predictions of MEPP for the uninvadable equilibrium state. Consumer abundances are obtained from the Lagrange multipliers that enforce the constraints during optimization. See appendix D for all simulation parameters.

See figure C1 (available online) for simulations of the other two examples.

Noninteracting Resources. We begin with MacArthur’s primary model, presented in equations (1) and (2). This is a model of competition for noninteracting self-renewing resources, whose intrinsic population dynamics in the absence of consumers are described by independent logistic growth laws. The objective function in this case is simply the weighted Euclidean distance of the resource abundance vector from the supply point:

$$d(\mathbf{R}^0, \mathbf{R}) = \frac{1}{2} \sum_{\alpha} w_{\alpha} r_{\alpha} K_{\alpha}^{-1} (R_{\alpha} - R_{\alpha}^0)^2, \quad (14)$$

where the supply point $R_{\alpha}^0 = K_{\alpha}$ is here simply equal to the vector of resource carrying capacities. The contribution of each resource to this distance is weighted by the ecological significance of changes in its abundance. This weight has three components. The first factor, w_{α} , measures the nutritional value of the resources. Resources with low values of

w_{α} contribute less to the growth for consumer populations, and changes in their abundance are therefore less important. The second factor, r_{α} , controls the rate of resource renewal. Abundances of resources with high rates of self-renewal are more difficult to perturb than those of resources that grow back slowly, and so a given shift in abundance is more significant for the former than for the latter. Finally, the factor of K_{α}^{-1} reflects the fact that a perturbation of the same absolute size is less significant if the carrying capacity is larger.

As discussed in appendix C, an important feature of the optimization perspective in all of MacArthur’s examples is that the resource feasibility constraint $R_{\alpha} \geq 0$ must be enforced explicitly. This causes difficulties for the interpretation of MacArthur’s original principle in the space of population sizes, but it fits easily into the resource space picture. For any niche model, the minimization is always subject to the constraint that the environment must lie in the uninvadable region Ω , and the feasibility condition simply means that the lower boundary of this region must also be included in the optimization protocol.

Interacting Self-Regulation. In reality, self-renewing resources like plants or algae usually compete directly with each other for space, water, light, and nutrients. MacArthur therefore generalized his model to allow for this kind of interaction. For concreteness, we focus on the case where the resources are plants competing for space, with each individual of species α occupying an area a_α . In this two-dimensional example, N_i and R_α are both naturally measured in units of individuals per land area. The fraction of the land that is available for new plant growth is then given by $1 - \sum_\alpha a_\alpha R_\alpha$. This results in the following set of equations, with the per capita growth rate of the plants equal to a bare rate r_α times the free space fraction:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right], \quad (15)$$

$$\frac{dR_\alpha}{dt} = r_\alpha R_\alpha \left(1 - \sum_\beta a_\beta R_\beta \right) - \sum_i c_{i\alpha} N_i R_\alpha. \quad (16)$$

As MacArthur points out, the model with interacting resources requires additional assumptions to guarantee symmetry (MacArthur 1970). In appendix C, we show that a sufficient assumption is to make the growth rates r_α the same for all resources ($r_\alpha = r$) and the nutritional value of each plant species proportional to its size ($w_\alpha = wa_\alpha$). In this case, the objective function is

$$d(\mathbf{R}) = \frac{wr}{2} \left(1 - \sum_\alpha a_\alpha R_\alpha \right)^2. \quad (17)$$

We have dropped the \mathbf{R}^0 from the argument of d for this example because in the absence of consumers there is a multiplicity of equivalent unperturbed equilibrium states. In fact, every combination of plants that fills all of the available space is a possible equilibrium. The objective function straightforwardly measures the perturbation away from this set of states and is simply proportional to the square of the free area fraction.

Competition to Avoid Predators. MacArthur’s final example adds another trophic level, allowing the consumer species to compete to avoid predators in addition to the competition for resources. The predators contribute an extra mortality term to the dynamics for the consumer population densities, which depends on the predator densities P_a ($a = 1, 2, 3, \dots, M_p$). If we assume the same mass-action model for predation as for primary resource consumption, we obtain the following model:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] - \sum_a p_{ia} P_a N_i, \quad (18)$$

$$\frac{dR_\alpha}{dt} = \frac{r_\alpha}{K_\alpha} R_\alpha (K_\alpha - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha, \quad (19)$$

$$\frac{dP_a}{dt} = \sum_i \eta_i p_{ia} N_i P_a - u_a P_a, \quad (20)$$

where p_{ia} is the rate of predation of predator a on species i , u_a is the intrinsic mortality rate for predator species a , and η_i is the nutritional value for predators of consumer (prey) species i .

MacArthur claims that this model generically produces symmetric interactions, probably because he was not considering the role of the consumer nutritional content η_i (MacArthur 1970). For arbitrary η_i and e_i this turns out to be false, but we show in appendix C that symmetry is restored if we assume that the biomass conversion efficiencies of the consumers are proportional to the inverse of their nutritional values ($e_i = e_0/\eta_i$). This assumption is in fact well motivated on physical grounds, since e_i^{-1} measures the amount of excess consumption required to produce a new individual of species i . If more consumption is required to produce an individual of a given species, then that individual should also hold more nutritional value for its predators.

In this symmetric case, we can obtain a minimization principle by treating the predators as components of the environment. The objective function is

$$d(\mathbf{R}^0, \mathbf{P}^0, \mathbf{R}, \mathbf{P}) = \frac{1}{2} \sum_\alpha \frac{r_\alpha}{K_\alpha} w_\alpha (R_\alpha - R_\alpha^0)^2 + \frac{1}{e_0} \sum_a u_a P_a, \quad (21)$$

with supply point $R_\alpha^0 = K_\alpha$, $P_a^0 = 0$. This is the same as for the original consumer resource model, with the addition of the predator-dependent term $\sum_a u_a P_a$. The new term is minimized when all of the predators are extinct, which is the “unperturbed state” for predators that cannot survive in the absence of prey. Each predator is weighted by its mortality rate, reflecting the same logic as the presence of r_α in weights of the resource perturbations. Finally, the balance between the importance of the resource and predator terms is set by e_0 , which controls the efficiency of energy transfer between trophic levels. Perfect efficiency corresponds to $e_0 = 1$. Larger values of e_0 correspond to lower efficiency, which makes the contributions of the predators less important.

Externally Supplied Resources. In the three preceding examples, resources are self-renewing with exponential growth at low densities. Microscopic ecosystems, however, are commonly maintained in the laboratory using serial dilutions, whereby a fraction f of the sample volume is periodically transferred to fresh media with resource abundances R_α^0

at time interval T , with the rest discarded or frozen for later analysis. This creates a new timescale $\tau = T/(1-f)$ over which the resource concentrations relax toward R_α^0 in the absence of reproduction or consumption, leading to the following set of dynamical equations:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] - \tau^{-1} N_i, \quad (22)$$

$$\frac{dR_\alpha}{dt} = \tau^{-1} (R_\alpha^0 - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha. \quad (23)$$

Note that we have also added an extra term, $\tau^{-1}N_i$, to the dynamics of the consumers, to account for the dilution of the consumer populations caused by this protocol. Adding this term is equivalent to modifying the maintenance cost m_i , but writing it explicitly allows us to preserve the physiological meaning of m_i as an intrinsic property of the consumer species.

This model produces symmetric interactions between consumer species regardless of the choice of parameter values. The objective function is no longer quadratic, however, but is given by a weighted Kullback-Leibler divergence:

$$d(\mathbf{R}^0, \mathbf{R}) = \tau^{-1} \sum_\alpha w_\alpha \left[R_\alpha^0 \ln \frac{R_\alpha^0}{R_\alpha} - (R_\alpha^0 - R_\alpha) \right]. \quad (24)$$

This is a natural way of quantifying the difference between two vectors with all positive components, such as probabilities or chemical concentrations (Rao and Esposito 2016). As in the original MacArthur model, the contribution of each resource is weighted by its nutritional value w_α . But now the feasibility constraint $R_\alpha \geq 0$ need not be enforced explicitly because $d(\mathbf{R}^0, \mathbf{R})$ diverges as $R_\alpha \rightarrow 0$, guaranteeing that the constrained optimum will always lie in the feasible region.

Asymmetric Examples

We now turn to two important scenarios where interactions are unavoidably asymmetric: a recently introduced microbial consumer resource model (MiCRM) where consumers generically produce metabolic by-products, and competition for essential resources described by Liebig's law of the minimum. The fundamental asymmetry of these models results from the fact that organisms can affect the environment in ways that are unrelated to their own growth rate, whether by producing novel by-products or by consuming resource types that do not limit their growth. In this section, we describe how this "extra" supply or consump-

tion is accounted for by a shift in the effective supply point $\tilde{\mathbf{R}}^0$, as illustrated in figure 3.

Microbial Consumer Resource Model. The MiCRM describes microbial consumers that generically produce metabolic by-products, as illustrated in figure 3a (Goldford et al. 2018; Marsland et al. 2019, 2020). A fraction l_α of the growth value resulting from uptake of resource α is released back into the environment, after being transformed into a variety of other resource types through internal metabolic reactions. A matrix $D_{\beta\alpha}$ specifies the fraction of by-product from consumption of resource α that is released as resource β . This results in the following dynamical equations:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha (1 - l_\alpha) w_\alpha c_{i\alpha} R_\alpha - m_i \right], \quad (25)$$

$$\frac{dR_\alpha}{dt} = \tau^{-1} (R_\alpha^0 - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha + \sum_{i\beta} N_i D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} R_\beta. \quad (26)$$

The addition of by-product secretion breaks the symmetry of the effective interactions in the original consumer resource model. When species A produces a by-product that benefits species B, species B may not produce any by-product accessible to species A. Even in cases where the exchange is mutual, there is no reason why the size of the benefit would be identical in both directions. In appendix C, we analyze a different cross-feeding model introduced by Butler and O'Dwyer (2018), where by-products are produced at a constant rate, and show that the effective interactions remain asymmetric even when the secretion matrix is symmetric. This is due to the fact that the actual benefit accrued to each species still depends on the current standing resource abundances and is not fully determined by the intrinsic properties of the species.

The equilibrium state of the MiCRM minimizes the same objective function as the chemostat model discussed above in equation (24) but with a modified supply point:

$$\tilde{R}_\alpha^0 = R_\alpha^0 + \tau \sum_{i\beta} \bar{N}_i D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} \bar{R}_\beta. \quad (27)$$

The second term is equal to the total quantity of resource α produced by all consumer species over the chemostat turnover time τ . This modification thus accounts in an intuitive way for the extra supply due to by-product secretion. Figure 3 shows the location of the true supply point \mathbf{R}^0 and the effective supply point $\tilde{\mathbf{R}}^0$ for an example with two species

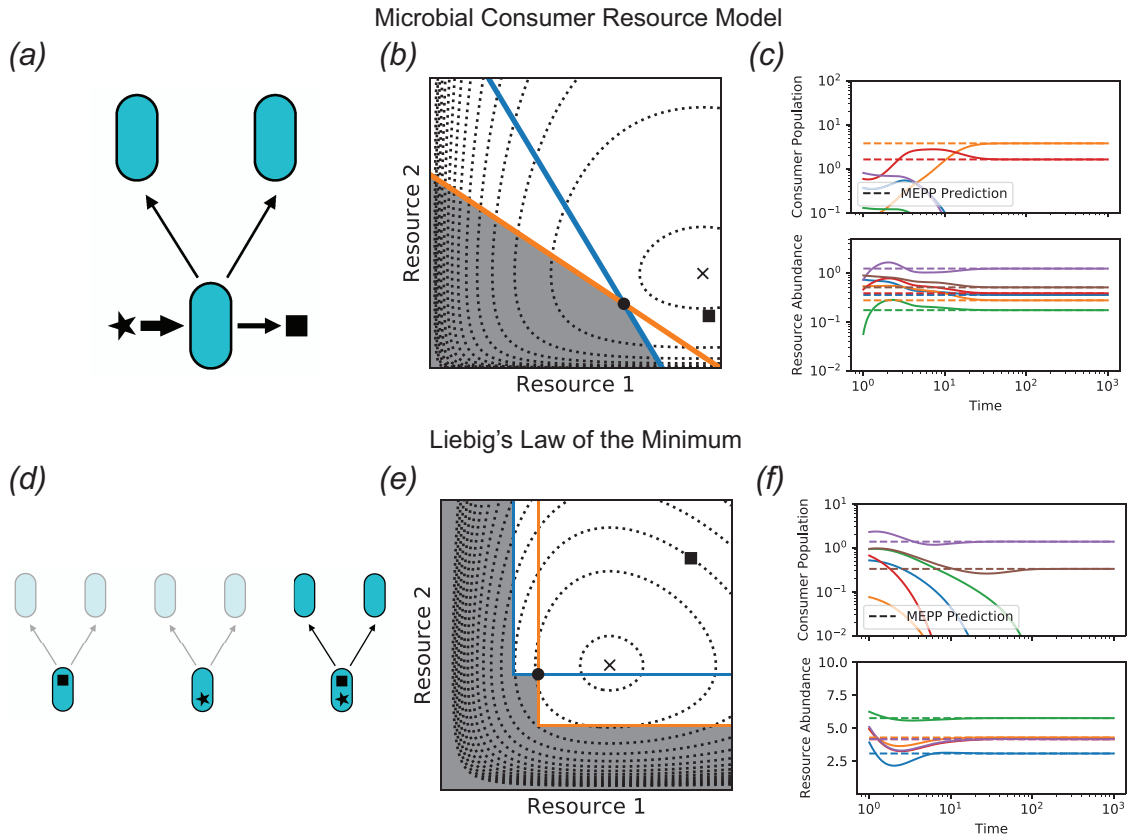


Figure 3: Examples with asymmetric interactions. *a*, Microbial consumer resource model (eqq. [25], [26]). The model describes microbial ecosystems where by-products of resource metabolism can be used as growth substrates for other organisms. *b*, Zero-net-growth isoclines (ZNGIs; colored lines) and the uninvadable region (shaded) for a pair of microbial species in the presence of two interconvertible resources. Contour lines represent the function $d(\tilde{\mathbf{R}}^0, \mathbf{R})$ that is minimized in the uninvadable equilibrium state. The square is true supply point \mathbf{R}^0 and the cross (\times) is effective supply point $\tilde{\mathbf{R}}^0$, accounting for the by-products generated in one chemostat turnover time τ . The black circle is the equilibrium state reached by a direct numerical simulation. *c*, Simulation of 10 microbial species and five resource types, along with extended minimum environmental perturbation principle (MEPP) predictions obtained using the iterative algorithm described in appendix B. *d*, Liebig's law of the minimum (eqq. [28], [29]). The law describes the dependence of an organism's growth rate on several essential nutrients (square and star), which must all be present in sufficient abundance in order for the organism to reproduce. *e*, ZNGIs, uninvadable region, objective function, and supply points. *f*, Simulation of 10 species competing for three essential resources, along with extended MEPP predictions. See appendix D for parameters.

and two resource types. Although the environment is directly supplied with very low levels of resource 2, the by-product secretion moves the supply point up higher in that direction, allowing both species to coexist.

As noted above, the correction to the supply point depends on the equilibrium population sizes \bar{N}_i and resource abundances \bar{R}_β , and it can therefore be calculated exactly only when the problem is already solved. But figure 3c shows that a simple iterative algorithm (described in app. B) successfully finds a self-consistent solution that agrees with direct numerical simulation.

Liebig's Law of the Minimum. In all of the examples presented above, resources were perfectly substitutable. But

there are many ecological scenarios where different resource types serve different biological needs, and all of them must be simultaneously present at sufficient abundance in order to sustain growth, as illustrated in figure 3d. One typical example is competition of plants for nitrogen, phosphorous, and water, which are all required for the production of biomass. Such growth kinetics are commonly described by Liebig's law of the minimum, where the growth rate is determined by the availability of the most limiting resource. The standard choice of impact vector for this model assigns each species i a constant stoichiometry $\nu_{\alpha i}$, which specifies the fraction of total consumption allocated to each resource type (Tilman 1982; Letten et al. 2017). Using Michaelis-Menten growth kinetics for each

resource with maximum velocities $\mu_{i\alpha}$ and Michaelis constants $k_{i\alpha}$, we have

$$\frac{dN_i}{dt} = N_i \left[\min_{\beta} \left(\left\{ \frac{\mu_{i\beta} R_{\beta}}{k_{i\beta} + R_{\beta}} \right\} \right) - m_i \right], \quad (28)$$

$$\frac{dR_{\alpha}}{dt} = \tau^{-1}(R_{\alpha}^0 - R_{\alpha}) - \sum_i N_i \nu_{\alpha i} \min_{\beta} \left(\left\{ \frac{\mu_{i\beta} R_{\beta}}{k_{i\beta} + R_{\beta}} \right\} \right). \quad (29)$$

If each species were to deplete only its limiting resource, the effective interactions in this model would remain symmetric and the equilibrium state would minimize the perturbation away from the true supply point, as measured by equation (24). But this is biologically unreasonable, since the whole point of “essential” resources is that all of them must be taken up together in order to generate growth. The consumption of nonlimiting resources shifts the effective supply point \tilde{R}_{α}^0 by subtracting the amount of each resource α consumed over the chemostat turnover time τ by organisms that are not limited by this resource. Figure 3e shows this drop in the supply point for an example with two resources and two consumers.

In figure 3f, we apply the same iterative scheme mentioned above to self-consistently obtain the equilibrium state

and effective supply point and compare the results with direct numerical simulation. This model generically exhibits multiple alternative stable states, and so care must be taken to ensure that both methods end up in the same one. In the simulations shown here, we simply initialized the direct simulation close to the MEPP prediction.

Application to Zooplankton Competition Experiments

In the 1980s, Karl Rothhaupt performed a set of detailed experiments on resource competition in zooplankton to test Tilman’s recent graphical formulation of niche theory (Rothhaupt 1988). This study provides a convenient setting for illustrating how the key assumption of symmetric interactions can be confirmed or rejected and how the perturbation $d(\mathbf{R}^0, \mathbf{R})$ can be measured.

Figure 4 shows growth rates for the zooplankton *Brachionus rubens* and *Brachionus calyciflorus* fed with different concentrations of the algae *Chlamydomonas sphaeroides* and *Monoraphidium minutum*. These plots show that the growth rates saturate at high levels of resource concentration, and it turns out that the relevant concentrations for the competition experiments lie well outside the initial linear regime. This means we must consider a model that goes beyond any of the examples discussed above and explicitly incorporates the saturation.

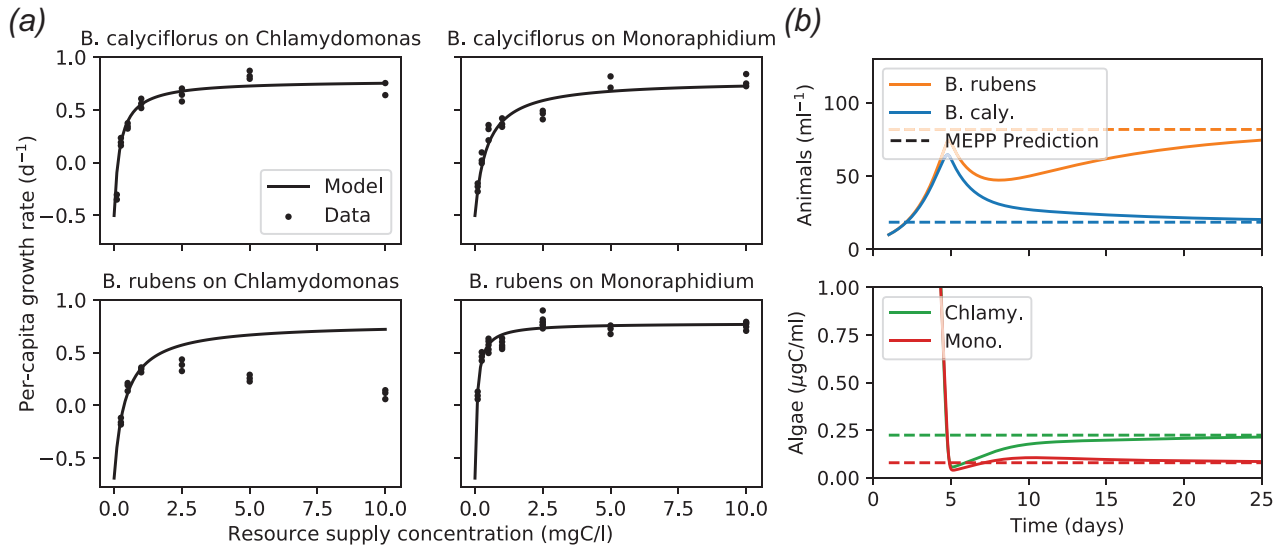


Figure 4: Applying the minimum environmental perturbation principle (MEPP) to laboratory experiments. *a*, Growth rate measurements reported in Rothhaupt (1988) for two species of zooplankton (*Brachionus rubens* and *Brachionus calyciflorus*) fed with different concentrations of two species of algae (*Chlamydomonas sphaeroides* and *Monoraphidium minutum*). Black lines are simultaneous fits to equation (30), with resource-independent maximal uptake rates $J_{i\alpha} = J_i$ and with the maximal clearance rates $c_{i\alpha}$ equal to the directly measured values listed in table 2. Inferred parameter values are also listed in the table. For *B. rubens* on *Chlamydomonas*, additional ecological mechanisms came into play at high food densities that are not captured by a type II growth model, and so only the three lowest densities were used for fitting. *b*, Simulations and MEPP predictions using the parameters in table 2, with supply point $w_c R_c^0 = 6$, $w_m R_m^0 = 4$ ($\mu\text{g C/mL}$), and $\tau = 5$ days.

Saturating Growth Kinetics. We model the saturation of the growth kinetics using Holling's type II functional response, combining the contributions of the two resources in the manner appropriate to a well-mixed environment (Holling 1959; Vincent et al. 1996). We can use the same parameters with the same definitions as in the MCRM but with the addition of a set of handling times $t_{i\alpha}$ for each consumer-resource pair:

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_{\alpha} w_{\alpha} \frac{c_{i\alpha} R_{\alpha}}{1 + \sum_{\beta} c_{i\beta} t_{i\beta} R_{\beta}} - m_i \right]. \quad (30)$$

In the experiments of interest, the intrinsic value w_{α} of each species of algae is taken to be proportional to its carbon content, accounting for the significant difference in size between the two species, and resource abundances are reported as carbon concentrations $w_{\alpha} R_{\alpha}$. It is therefore convenient to analyze the model in terms of the maximum carbon uptake rate defined by

$$J_{i\alpha} = \frac{w_{\alpha}}{t_{i\alpha}} \quad (31)$$

instead of using the handling time directly.

In the wild, we would expect the resource equation for this system to have the same logistic supply vector as MacArthur's original model (eq. [2]), with modified impact vectors to account for the saturation. But Rothhaupt's competition experiments follow the serial dilution protocol described above in the "Externally Supplied Resources" section, with algae supplied at a given concentration from an external source at fixed time intervals and with experiments performed in the dark to minimize algae growth. We therefore use the chemostat supply vector of equation (23) and obtain

$$\frac{dR_{\alpha}}{dt} = \tau^{-1} (R_{\alpha}^0 - R_{\alpha}) - \sum_i N_i \frac{c_{i\alpha} R_{\alpha}}{1 + \sum_{\beta} c_{i\beta} t_{i\beta} R_{\beta}}. \quad (32)$$

In general, this model gives rise to asymmetric interactions. But they become symmetric when the maximum carbon uptake rates $J_{i\alpha}$ for each species i are independent of the food source α . In this case, as shown in appendix C, MEPP applies and the equilibrium state minimizes the same objective function as the ordinary chemostat model given in equation (24). The only difference is in the formula for the boundaries of the uninhabitable region Ω , which are now given by equation (30). In terms of the weighted concentration $w_c R_c$ of *Chlamydomonas* and the concentration $w_m R_m$

of *Monoraphidium* with supplied concentrations $w_c R_c^0$ and $w_m R_m^0$, the perturbation measure is

$$d(\mathbf{R}^0, \mathbf{R}) = \tau^{-1} \left[w_c R_c^0 \ln \frac{w_c R_c}{w_c R_c^0} + w_m R_m^0 \ln \frac{w_m R_m}{w_m R_m^0} - (w R^0 - w R) \right], \quad (33)$$

where $w R = w_c R_c + w_m R_m$ and $w R^0 = w_c R_c^0 + w_m R_m^0$ are the total carbon concentrations in the ecosystem and in the supply, respectively. MEPP predicts that the equilibrium concentrations of *Chlamydomonas* and *Monoraphidium* minimize this function, subject to the constraint that the growth rates of both zooplankton species given by equation (30) are zero or negative.

Testing the Model. The key assumption about the maximum carbon uptake rates can be directly tested in principle by supplying the animals with large concentrations of each type of food and checking whether the growth rates are the same in both cases. Figure 4 confirms that the maximum growth rate of *B. calyciflorus* is indeed the same for both food sources, to within experimental uncertainty. The growth kinetics of *B. rubens* at large *Chlamydomonas* concentrations are nonmonotonic, however, which Rothhaupt attributes to mechanical disturbance of the feeding process that is not reflected in Holling's type II growth law (Rothhaupt 1988). Thus, we can only use the model in equations (30) and (32) for this case at low food concentrations, where this additional mechanism can be neglected. The resource independence of $w_{\alpha}/t_{i\alpha}$ can therefore only be tested indirectly for this organism, using the goodness of fit of the low-concentration data points to equation (32) when this condition is imposed.

There is also a second, hidden assumption, which was already made in MacArthur's original model with linear growth kinetics, concerning the dual role of the parameter $c_{i\alpha}$. This parameter has units of volume/time in an aquatic scenario and mechanistically represents a clearance rate, that is, the volume of water cleared of food organisms by an individual consumer per unit time. In the saturating model the actual clearance rate is a function of food density, but $c_{i\alpha}$ still represents the maximal clearance rate, when food is scarce and handling time is not the limiting factor. This parameter can thus be directly measured by simply counting the number of food organisms ingested by an individual consumer over a short period of time over which the food density is approximately constant. Rothhaupt carried out such measurements using radiolabeled algae and reported the maximum clearance rates for all four consumer-resource pairs. The mean values over at least

Table 2: Parameter values for zooplankton competition experiments

Symbol	Description	Value
<i>Brachionus calyciflorus:</i>		
e_c	Individuals produced per unit carbon uptake	13.8 individuals/ μg carbon
J_c	Maximal carbon uptake rate	.0927 μg carbon/day
m_c	Minimum viable carbon uptake rate	.0363 μg carbon/day
c_{cc}	Maximal <i>Chlamydomonas</i> clearance rate	.427 mL/day
c_{cm}	Maximal <i>Monoraphidium</i> clearance rate	.211 mL/day
<i>Brachionus rubens:</i>		
e_r	Individuals produced per unit carbon uptake	72.8 individuals/ μg carbon
J_r	Maximal carbon uptake rate	.0202 μg carbon/day
m_r	Minimum viable carbon uptake rate	.00947 μg carbon/day
c_{rc}	Maximal <i>Chlamydomonas</i> clearance rate	.0490 mL/day
c_{rm}	Maximal <i>Monoraphidium</i> clearance rate	.252 mL/day

Note: Maximal clearance rates are reproduced from a table of measurements using radiolabeled algae reported in Rothhaupt (1988), converted to a consistent set of units. The other parameters come from fitting equation (30) to an independent set of growth rate measurements reported in the same study, as shown in figure 4.

10 independent measurements are reproduced in table 2 (for complete methods, number of replicates, and uncertainties, see Rothhaupt 1988).

The assumption made in both the MCRM and in equations (30) and (32) is that the same parameters $c_{ic\alpha}$ also determine the relative effects of different resource types on the consumer growth rate. To test this assumption, we performed a simultaneous nonlinear regression of equation (30) for each species to sets of growth rate measurements on

both food sources, as shown in figure 4. The clearance rates $c_{ic\alpha}$ were held fixed at their directly measured values, and the maximum carbon uptake rates were assumed to be independent of food source, leaving three free parameters: e_i , J_i , and m_i . The best-fit values are tabulated along with the clearance rates in table 2. These three parameters are sufficient to provide an excellent fit to both growth curves, with the exception of the high *Chlamydomonas* concentrations with *B. rubens* mentioned above.

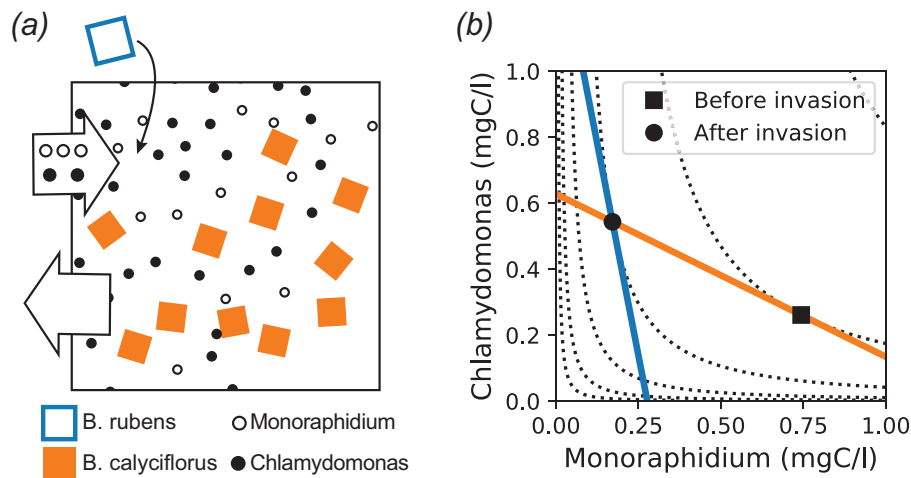


Figure 5: Consequences for community assembly. *a*, Schematic of a hypothetical community assembly experiment, taking place in a chemostat supplied with a constant influx of *Monoraphidium* and *Chlamydomonas* as food. The system is first allowed to relax to equilibrium with *Brachionus calyciflorus* as the only consumer species, and then *Brachionus rubens* is added to the chamber. *b*, Zero-net-growth isoclines (solid colored lines) and contour lines of d (dotted) using the experimentally determined parameters in table 2, at dilution rate $\tau^{-1} = 0.45/\text{day}$ and supply levels $w_c R_c^0 = 6$ and $w_m R_m^0 = 4$ ($\mu\text{g C}/\text{mL}$). The initial equilibrium of the assembly experiment is indicated by the black square, where d is minimized subject only to the constraint that *B. calyciflorus* has a vanishing growth rate. The final equilibrium is represented by the black circle and lies on a higher contour line of d .

*Consequences for Community Assembly
and Eco-Evolution*

In addition to providing a clear interpretation of MacArthur's principle and facilitating generalization, MEPP makes new predictions for scenarios where new species are added to an existing community. Specifically, MEPP implies that the perturbation measure $d(\mathbf{R}^0, \mathbf{R})$ is a monotonically increasing function under successive invasions for any monostable niche model with symmetric environmentally mediated interactions.

To illustrate this result, we consider the hypothetical community assembly experiment depicted in figure 5. We take the setup of Rothhaupt described above and start with both resources present but with *B. calyciflorus* as the only consumer. Serial dilutions are performed according to the same protocol until species and resource abundances reach equilibrium, and then *B. rubens* is added to the system. MEPP implies that the initial equilibrium minimizes $d(\mathbf{R}^0, \mathbf{R})$ of equation (33) under the single constraint that the net growth rate of *B. calyciflorus* vanishes. When *B. rubens* is introduced, a second constraint is added, leading to a new constrained optimum $\bar{\mathbf{R}}$. Since the new optimization is subject to more constraints, the new minimum is necessarily further from zero than the original, as is clear from figure 5b.

The fact that d increases monotonically under all successful invasions has a number of significant consequences for monostable ecosystems with symmetric interactions. First of all, it implies that community assembly and evolution are unidirectional processes under these conditions and that limit cycles or chaos in the space of community compositions do not occur (for examples of such complex evolutionary dynamics in models that violate these assumptions, see Doebeli et al. 2017). In fact, given two snapshots of an evolving system, one can determine which came earlier and which came later by measuring the resource abundances and computing d . Without knowing anything about the consumer species, one can say that the snapshot with the higher value of d must have come later. This also makes it possible to rule out possible trajectories for community assembly. If one observes two systems with the same resource supply in different equilibrium states, one can determine whether one of them can be assembled from the other by invading with the missing species. If community A has a larger value of d than community B, then changing the composition of A to match B requires directly killing off some species and cannot be accomplished through any set of successive invasions.

Conclusions

MEPP provides a new perspective on niche theory, which opens up a number of interesting avenues for further in-

vestigation. First of all, measuring the environmental perturbation d could shed light on the robust empirical correlation between diversity and productivity (Tilman et al. 2014). Since each species places an independent constraint on the domain of optimization, as noted above, d will be positively correlated with species richness whenever MEPP applies. Larger d means that the equilibrium resource abundances are further from the supply point for more diverse communities, which typically implies that more of the available resources are being converted to biomass. In cases where increased diversity fails to improve biomass yields, part of the explanation may lie in a significant asymmetry in the interactions that causes a major shift in the effective supply point.

MEPP also has important implications for evolution. It was recently shown that the graphical methods of niche theory can be applied to evolution through consideration of a continuum of ZNGIs, representing all possible phenotypes (Koffel et al. 2016). Any evolutionarily stable phenotype (or collection of coexisting phenotypes) must lie on the outer envelope formed by all of these ZNGIs. Since MEPP is valid for any number of species, it also applies to this continuum limit as long as the essential condition of interaction symmetry holds.

The fact that d is strictly nondecreasing under sequential invasions also suggests a connection to recent work on evolutionary optimization in the presence of environmental feedbacks (Metz et al. 2008). By computing the minimum value of d for every possible combination of coexisting phenotypes, one can construct a community-level fitness landscape on which all evolutionary trajectories always travel monotonically uphill. These connections have yet to be fully explored and remain an important area for future study.

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Statement of Authorship

R.M., W.C., and P.M. conceptualized the problem and carried out the mathematical analysis. R.M. wrote the manuscript, and P.M. critically revised it.

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