The shape of density dependence and the relationship between population growth, intraspecific competition and equilibrium population density

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Abstract

Many ecologists and evolutionary biologists use the logistic growth model to capture density dependence. However, assumptions and limitations of this popular model are not well appreciated. Here, we derive population growth models from underlying consumer-resource dynamics and show that the logistic is likely not applicable to many biological systems.

We first validate that filter feeders (type I functional response) using abiotic resources generally follow a convex density-regulation function, fully described by the continuous-time Beverton-Holt model. Furthermore, we show that saturating consumers (type II functional response) exhibit density-regulation functions that can switch from concave to convex. We derive a density-regulation function for saturating feeders on abiotic resources and show that more complex consumer dynamics can be well approximated with a continuous-time Maynard Smith-Slatkin model.

Importantly, we show how population level parameters, such as intrinsic rates of increase and equilibrium population densities are not independent, but are functions of the same underlying parameters. Our work highlights that the commonly assumed positive relationship between equilibrium population density and competitive ability is typically invalid. Alternatively, we propose simple and general relationships between intrinsic rates of increase and equilibrium population densities that capture the essence of different consumer-resource systems. Finally, we expand our considerations to include multiple consumer and resource species.

Relating population level models to underlying mechanisms allows us to discuss applications to evolutionary outcomes and how these models depend on environmental conditions, like temperature via metabolic scaling. Finally, we use time-series from microbial food chains to fit population growth models and validate theoretical predictions.

Density-regulation functions need to be chosen carefully as their shapes will depend on the study system's biology. Importantly, we provide a mechanistic understanding of correlations between model parameters, which has implications for theory and for formulating biologically sound and empirically testable predictions.

Introduction

Population regulation and density dependence of population growth are at the core of fundamental but also controversial research in ecology (see e.g., Turchin, 1999; Henle et al., 2004; Sibly et al., 2005; Herrando-Prez et al., 2012; Krebs, 2015; Saether et al., 2016). Density dependence of population growth is often captured by the logistic growth model (Verhulst, 1838) and its more complex extensions, such as the θ-logistic model (Gilpin and Ayala, 1973). Despite its widespread use, it is important to recall that the logistic model is an abstract description of population dynamics (Herrando-Prez et al., 2012). This level of abstraction makes the interpretation of parameters challenging and may lead to paradoxical behaviours (Mallet, 2012; Gabriel et al., 2005). These issues are especially apparent in the often used $r-K$ formulation with r_0 being the intrinsic rate of increase, K the carrying capacity and N the population density:

$$\frac{dN}{dt} = r_0 \left(1 - \frac{N}{K}\right) N. \tag{1}$$

Additional challenges have to be dealt with when these parameters, especially the carrying capacity K, are interpreted in an evolutionary context (e.g., "K-selection" MacArthur, 1962). For instance, Luckinbill (1979) set out to test $r-K$ selection theory using selection experiments in protist microcosms. Contrary to the expectation, he reported that r-selection actually led to higher carrying capacities, compared to the expected decrease in equilibrium population densities. Similar empirical evidence in the context of range expansions was reported recently by Fronhofer and Altermatt (2015) who showed that the interpretation of K as a parameter under selection and positively linked to competitive ability may be misleading. Although these and related issues have been discussed in detail by Matessi and Gatto (1984), Mallet (2012), Reznick et al. (2002) and Rueffler et al. (2006), to name but a few, current theory often continues using "K" as an evolving trait (e.g., Lande et al., 2009; Burton et al., 2010).

In order to resolve some of the issues associated with the logistic growth model as described by Eq. 1, Mallet (2012), for instance, has recently promoted the use of Verhulst's original $r-\alpha$ formulation of logistic growth (Verhulst, 1838). In comparison to the popular $r-K$ formulation (Eq. 1), Verhulst's model uses biologically interpretable parameters (Joshi et al., 2001; Ross, 2009; Mallet, 2012). Namely, it includes r_0 as the intrinsic rate of increase and α as the intraspecific competition coefficient:

$$\frac{dN}{dt} = (r_0 - \alpha N)N. \tag{2}$$

From Eq. 2 it follows that the population density at equilibrium is $\widehat{N} = r_0\alpha^{-1}$. Similarly to Eq. 1, density dependence is assumed to act linearly, with r_0 being the intercept (that is, the population growth rate when population density (N) is vanishingly small) and α representing the slope of population growth

rate over population density.

Other authors have acknowledged the dynamic relationship between populations and their resources that causes density dependence by resorting to using more mechanistic consumer-resource models. For instance Matessi and Gatto (1984) show how, in order to understand density-dependent selection, resource dynamics and especially consumer traits have to be taken into account (see also Fronhofer and Altermatt, 2015). Such consumer-resource models provide a framework that can be used in an eco-evolutionary context (for a detailed discussion see McPeek, 2017) because model parameters linked to resource use (search efficiency, handling time) are related to real, individual-level traits that can be subject to evolutionary change (Rueffler et al., 2006; Govaert et al., 2019). Importantly, bottom up population regulation due to renewing, depletable resources, as assumed in such consumer-resource models, is the most likely case according to Begon et al. (2006).

The disadvantage of these more mechanistic consumer-resource models is an increased complexity and number of parameters. Importantly, the quality and quantity of available data is often not sufficient for confronting such models to data. In an attempt to simplify, some studies have explored under what conditions population level growth models (e.g., the logistic Eq. 1 or 2) can be used to describe the underlying consumer-resource dynamics. For instance, the consumer-resource dynamics underlying the logistic growth model have already been described by MacArthur (1970). A few years later, deriving the $r - K$ logistic from the underlying resource dynamics, Schoener (1973) noticed that r and K share numerous parameters, implying that growth rates and resulting equilibrium densities may be linked through resource use traits (but see Getz, 1993). Similarly, Matessi and Gatto (1984) showed that selection for increased competitive ability ("K-selection") does in fact not maximize equilibrium densities, but rather minimizes death rates and maximizes foraging rates and assimilation efficiencies. More recently, Abrams (2009) compared the θ-logistic model (Gilpin and Ayala, 1973), an extension of the logistic model that allows for non-linear density dependence, to underlying dynamics in order to find plausible θ values. He showed that density dependence is non-linear if one assumes a Holling type II functional response for the consumer (see also Abrams, 2002), but that this non-linearity is different from the θ logistic model. He finally extended his works to type III functional response and non-linear numeric responses. Reynolds and Brassil (2013) discussed, extended and reinterpreted these findings. Similar work deriving discrete-time population growth models has been conducted, for example, by Geritz and Kisdi (2004) and Brännström and Sumpter (2005). In parallel to this line of research on intra-specific density dependence, Lotka-Volterra models of inter-specific competition and specifically the inter-specific competition coefficients ($\alpha_{i,j}$), have been linked to resource utilization through the concept of limiting similarity for example by MacArthur and Levins (1967), Schoener (1974) and Abrams (1975).

Here, we expand on this work and use consumer-resource models to derive different forms of population

growth models and to gain a better understanding of their parameters, that is, how these parameters may be interpreted in biological terms and how they are inter-related. We focus on consumers in food chains that are bottom-up regulated, as described previously. Importantly, our considerations are more mechanistic than most previous work (e.g. Abrams, 2009; Reynolds and Brassil, 2013), as we derive consumer density-dependent population growth without assuming that the resources grow logistically in the first place to avoid circularity in the argument (see the Supplementary Material S1 for a discussion of Lakin and Van Den Driessche, 1977). We furthermore investigate correlations between parameters that may constrain evolutionary trajectories. We use these derivations to show how intrinsic rates of increase, competitive abilities and equilibrium population densities are non-independent and provide correlation structures between those parameters. In addition, we demonstrate the potential of deriving climate driven population growth models by extending our results to include temperature dependence based on the metabolic theory of ecology (Brown et al., 2004) and multiple interacting species. Finally, we confront our theoretically derived growth models and trait correlation structures with time series data from microbial model populations using Bayesian inference.

Modelling populations using consumer-resource models

In order to derive population growth models and the density-regulation function capturing how consumer population growth rates (r) change depending on population density (N), we will use the following general consumer-resource model in which R is the resource and N is the consumer population density:

$$\frac{dR}{dt} = f(R) - g(R)N \tag{3a}$$

$$\frac{dN}{dt} = eg(R)N - dN. \tag{3b}$$

In this consumer-resource model, the function $f(R)$ captures the growth of the resources and the function $g(R)$ captures the functional response of the consumer (Holling, 1959), that is, how much resources are harvested by consumers depending on resource density. Furthermore, the constant e is the assimilation coefficient which translates consumed resources into consumer offspring and the constant d is the consumer's death rate.

Using a time-scale separation argument, that is, assuming that resources quickly equilibrate ($\frac{dR}{dt} = 0$) and solving Eq. 3a for R we obtain the resource equilibrium density $\widehat{R}$ (piecewise defined, that is $\widehat{R} = 0$ if there is no positive equilibrium). The per capita consumer dynamics (density-regulation function) then become:

$$\frac{1}{N}\frac{dN}{dt} = eg(\widehat{R}) - d. \tag{4}$$

In order to understand how the form of the density-regulation function (Eq. 4) depends on different consumer and resource characteristics (e.g., filter feeders, saturating feeders, respectively, abiotic or biotic resources) we explore multiple realizations of $f(R)$ and $g(R)$, including a chemostat model for resource growth ($f(R)$) as well as type I (linear) and type II (saturating) functional responses for the consumer ($g(R)$). We start by exploring density-regulation functions that are appropriate for basal biotic consumers feeding on abiotic resources. Then, we use these density-regulation functions to describe biotic resources fed upon by higher tropic level consumers and derive density-regulation functions describing the dynamics of the latter consumers.

A simple case: filter feeders

Abiotic resources

For simplicity, we first assume that resources are abiotic, that is, resource population growth ($f(R)$) does not depend on resource population density, but rather on a fixed rate:

$$\frac{dR}{dt} = \omega R_0 - \omega R - aNR. \tag{5}$$

This resource model is often termed "chemostat model" with ω as the flow rate into and out of the system, and R_0 as the resource concentration flowing into the system. The corresponding consumer dynamics are:

$$\frac{dN}{dt} = eaRN - dN. \tag{6}$$

The amount of resources present at equilibrium can be obtained by setting Eq. 5 to zero, hence $\widehat{R} = \frac{\omega R_0}{\omega + aN}$. We can now substitute $\widehat{R}$ into Eq. 6 to obtain the per capita growth rate of the consumer:

$$\frac{1}{N}\frac{dN}{dt} = \frac{eaR_0}{1 + \frac{a}{\omega}N} - d. \tag{7}$$

As Thieme (2003) notes, this result parallels the continuous-time version of the population growth model proposed by Beverton and Holt (1957) and derived by Schoener (1978) and Ruggieri and Schreiber (2005):

$$\frac{dN}{dt} = \left(\frac{r_0 + d}{1 + \beta N} - d\right) N \tag{8}$$

where the intrinsic rate of increase of the consumer is

$$r_0 = eaR_0 - d \tag{9}$$

and the equilibrium density is obtained as

$$\widehat{N} = \frac{\omega(eaR_0 - d)}{ad} = \frac{r_0}{\beta d}. \tag{10}$$

In contrast to the logistic growth model (Eqs. 1 and 2) the density-regulation function described by Eq. 8 is not linear (see, e.g. Pástor et al., 2016). Rather, it is convex, implying a decreasing strength of density regulation with increasing population density (Fig. 1). Importantly, this implies that already for very simple consumer-resource systems the logistic growth model does not hold (but see Lakin and Van Den Driessche, 1977, and Supplementary Material S1 for a detailed discussion).

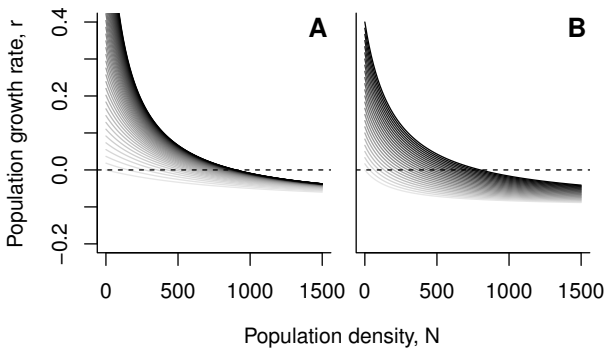

Figure 1: Density dependence for a filter feeding consumer (chemostat model for the resource and linear functional response for the consumer; Eq. 7). (A) Effect of changing the foraging rate (a) while keeping the assimilation efficiency constant ($e = 0.1$). (B) Effect of changing the assimilation efficiency parameter (e) while keeping the foraging rate constant ($a = 0.0005$). In both panels, darker shades of grey indicate higher parameter values. Parameter examples: $R_0 = 10000$, $\omega = 0.1$, $e \in [0.02, 0.1]$, $a \in [0.0001, 0.001]$, $d = 0.1$.

This derivation shows that filter feeding consumer populations feeding on abiotic resources will generally have a convex per capita growth rate function (Eq. 7, Fig. 1) that is best described by a Beverton and Holt (1957) model (Eq. 8) and not by the logistic growth model given in Eq. 2. Following Jeschke et al. (2004), filter feeders that exhibit a type I functional response include branchiopods, some insect larvae, bryozoans, ascidians and molluscs, for example. Of course, the relevance of our derivation for any specific system depends on whether it fulfils relevant assumptions such that density is indeed regulated by food resources which may not be the case if densities are defined by spatial resources, for example.

Importantly, intrinsic rates of increase (r_0; Eq. 9), competitive abilities ($\beta = \frac{a}{\omega}$; Eq. 8) and equilibrium population densities ($\widehat{N}$; Eq. 10) depend on the same set of underlying parameters and are therefore not independent. Competitive ability (β; Eq. 8) and intrinsic rates of increase (Eq. 9) are both linear functions of foraging rate (a). Note that the intrinsic rate of increase can nevertheless be independent of competitive ability, if the differences are driven by the assimilation efficiency (e). For populations of consumers best

characterized by this model, equilibrium densities ($\widehat{N}$) will always increase with increasing intrinsic rates of increase, regardless of whether this is due to an increase in foraging rate (a) or assimilation efficiency (e). However, the increase will be linear for e and concave for a. If density independent mortality (d) is vanishingly small, the equilibrium population density ($\widehat{N}$) is only a function of the assimilation efficiency (e) because the foraging rate (a) cancels out.

Biotic resources

Since the population dynamics of filter feeding consumers of a first trophic level can be described by the Beverton-Holt model (Eq. 8), we can investigate population dynamics of the next tropic level. We start by considering a filter feeding resource where $f(R)$ can be described by Eq. 8 and a filter feeding consumer where $g(R)$ is linear, that is, a type I functional response. Without repeating the previously described derivation, we can use the principle of the inheritance of the curvature described by Abrams (2009), stating that the curvature of the density-regulation function of a consumer with a linear functional response is identical to the curvature of the density-regulation function of its resource. Hence, the population dynamics of any filter feeding consumers in a food chain with a basal abiotic resource will follow the Beverton-Holt model (Eq. 8).

A more complex case: saturating feeders

Abiotic resources

Up to now we have assumed a type I, that is linear, functional response for $g(R)$ which has been shown to be likely only applicable to some filter feeding organisms (Jeschke et al., 2004). While keeping resources abiotic ($f(R)$ as a chemostat model; Eq. 5), we next explore the form of the density-regulation function, as well as how intrinsic rates of increase, competitive abilities and equilibrium population densities are linked, if the consumer follows a saturating (type II) functional response ($g(R) = \frac{aR}{h+R}$, where h is the half-saturation constant).

Assuming resource equilibrium, we have to solve a quadratic equation (see Supplementary Material S2 for details). Substituting the resource equilibrium into the consumer equation results in a density-regulation function that is only slightly more complex than the Beverton-Holt model (Eq. 8; Fig. 1):

$$\frac{dN}{dt} = \left(\frac{2(r_0 + d)}{1 + \beta N + \sqrt{1 + \beta N(\beta N - \delta)}} - d \right) N. \tag{11}$$

with $\delta = \frac{2(R_0 - h)}{R_0 + h}$, $\beta = \frac{a}{\omega(R_0 + h)}$ as the competitive ability, $r_0 = \frac{eaR_0}{R_0 + h} - d$ as the intrinsic rate of increase

and

$$\widehat{N} = \frac{4r_0(r_0 + d)}{\beta d(4r_0 + 2d + \delta d)} \tag{12}$$

as the equilibrium density.

While the density-regulation function may now exhibit both concave and convex sections (Fig. 2, Eq. 11 and see Supplementary Material S3) it only depends on 4 parameters. The most relevant parameter driving the extent of the concave portion of the density-regulation function is the parameter δ and therefore the half-saturation constant (h in Eq. S15 and δ in Eq. 11; Fig. 2C). The density-regulation function is concave at low densities only if $\delta > 0$ (which is equivalent to $R_0 > h$; see Supplementary Material S3). The smaller the half-saturation constant, the more the concave part of the density-regulation function will approach a threshold-like shape. Ultimately the foraging rate becomes independent of consumer population density ($\delta \to 2$) which leads to exponential growth. By contrast, the larger the half-saturation constant is, the more the type II functional response will approach a type I, that is, a linear shape ($\delta \to -2$). The latter case approaches the Beverton-Holt model (Eq. 8; see Supplementary Material S2 for details).

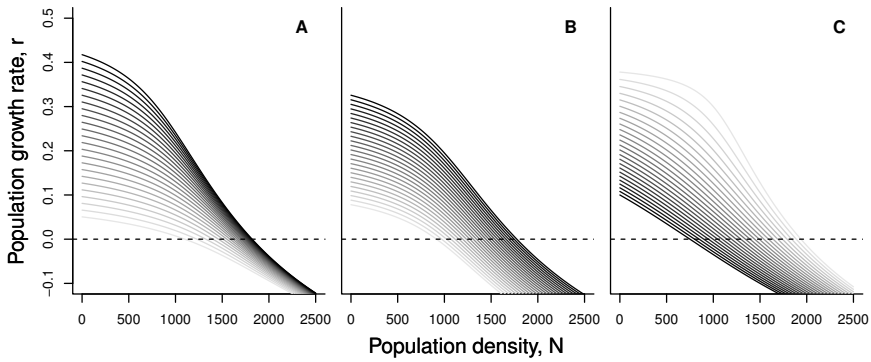

Figure 2: Density dependence for a consumer with a saturating, that is, type II, functional response (Eq. S15) while resource remain abiotic. (A) Effect of changing the foraging rate (a) while keeping the assimilation efficiency ($e = 0.1$) and the half-saturation constant ($h = 9000$) fixed. (B) Effect of changing the assimilation efficiency parameter (e) while keeping foraging rate ($a = 9$) and half-saturation constant ($h = 9000$) fixed. (C) Effect of changing the half-saturation constant (h) while keeping foraging rate ($a = 9$) and assimilation efficiency ($e = 0.1$) fixed. In all panels darker shades of grey indicate higher parameter values. Parameter examples: $R_0 = 100000$, $\omega = 0.1$, $e \in [0.07, 0.1]$, $a \in [6, 10]$, $h \in [2500, 50000]$, $d = 0.5$.

Once more, intrinsic rates of increase (r_0; Eq. S13), competitive abilities (β; Eq. S16) and equilibrium population densities ($\widehat{N}$; Eq. 12) depend on the same set of underlying parameters and are therefore not independent. All three parameters increase with the maximal foraging rate (a) and decrease with the half-saturation constant (h). While competitive ability does not depend on the assimilation efficiency (e), equilibrium population densities and population growth rates increase with increasing assimilation

efficiency.

Biotic resources

Consumers can of course also exhibit saturating functional responses ($g(R)$), while feeding on biotic resources. In this case Eqs. S4a and S4b have to be adjusted as shown in the Supplementary Material S5 (Eqs. S26a–S26b) which yields an even more complex density-regulation function (Fig. 3).

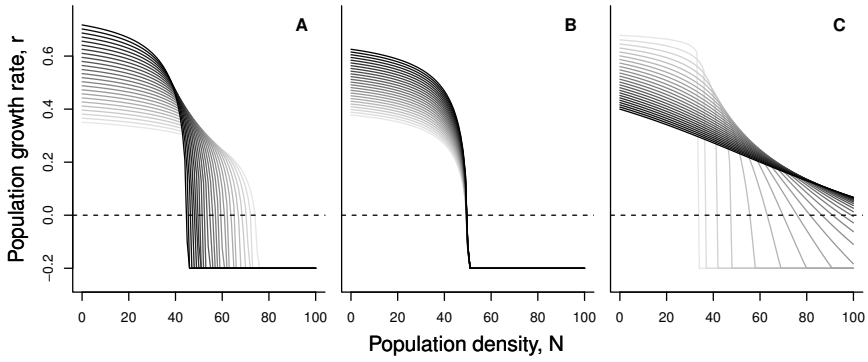

Figure 3: Density dependence for a consumer in a consumer-resource system with biotic resources (following the Beverton-Holt model; Eq. 8) and a saturating, that is, type II, functional response. (A) Effect of changing the foraging rate (a) while keeping assimilation efficiency ($e = 0.1$) and the half-saturation constant ($h = 900$) fixed. (B) Effect of changing the assimilation efficiency parameter (e) while keeping foraging rate ($a = 9$) and half-saturation constant ($h = 900$) fixed. (C) Effect of changing the half-saturation constant (h) while keeping foraging rate ($a = 9$) and assimilation efficiency ($e = 0.1$) fixed. In all three panels, darker shades of grey indicate higher parameter values. Parameter examples: $r_{0,R} = 0.5$, $\beta_R = 0.001$, $d_R = 0.05$, $e \in [0.07, 0.1]$, $a \in [6, 10]$, $h \in [250, 5000]$, $d = 0.2$.

While some simplifications are possible, the resulting density-regulation function remains unwieldy with its 7 parameters (see Eq. S34). Interestingly, Eq. S34 is a density-regulation function that, at least in part, behaves similarly to the well known, continuous-time version of the Maynard Smith and Slatkin (1973) model (see Supplementary Material S6 and Fig. S4):

$$\frac{dN}{dt} = \left(\frac{r_0 + d}{1 + (\beta N)^\gamma} - d \right) N. \tag{13}$$

In this model, the equilibrium density is $\widehat{N} = \frac{1}{\beta} \left(\frac{r_0}{d} \right)^{\frac{1}{\gamma}}$. The Maynard Smith-Slatkin model with $\gamma > 1$ is a good approximation of the dynamics described by Eq. S34 and by Eq. 11 (see Supplementary Material S4). Specifically, it is flexible enough (Bellows, 1981) to reproduce both the convex and concave parts of the density-regulation function (see Fig. S4) which are driven by the shape exponent γ (see Eq. 13).

Fitting the Maynard Smith-Slatkin model to a wide range of parameter combinations highlights that correlations between intrinsic rates of increase (r_0) and competition coefficients do not change qualitatively, while correlations with the equilibrium density do. Up to here, for abiotic or biotic resources

and filter feeding consumers, the equilibrium density was always a monotonically increasing function of foraging rates. We here find that this relationship is unimodal or monotonically decreasing for biotic resources and saturating consumers (Fig. 4). The complexity of the shape of the density-regulation function is well captured by high values of the shape parameter ($\gamma \gg 1$) of the Maynard Smith-Slatkin model.

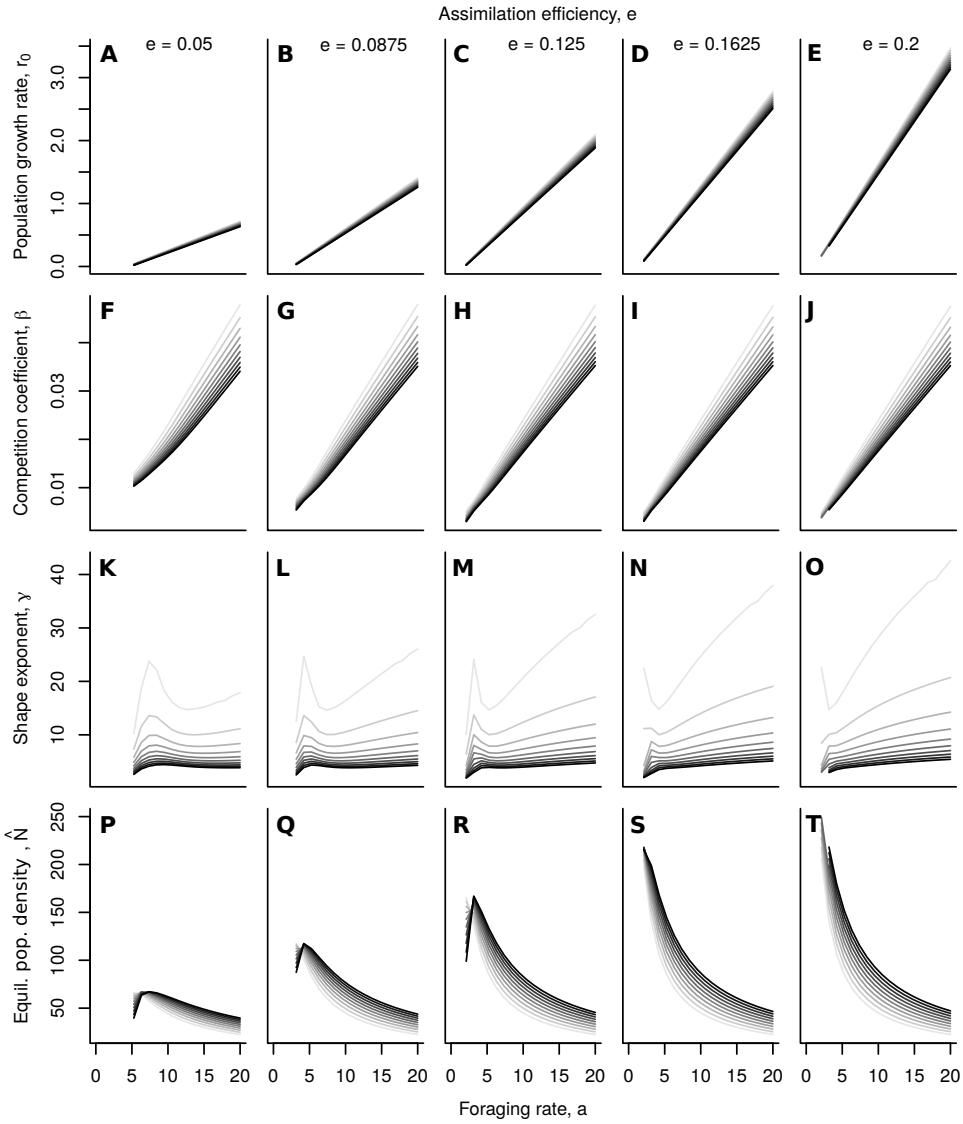

Figure 4: Correlations between consumer-resource parameters and the parameters of the Maynard Smith-Slatkin model for a saturating consumer (type II functional response) feeding on biotic resources (following the Beverton-Holt model). The Maynard Smith-Slatkin model was fitted using a least-squares approach to the respective realisation of Eq. S34. Darker shades of grey indicate higher parameter values of the half-saturation constant ($h \in [900, 2000]$). The assimilation efficiency ($e \in [0.05, 0.2]$) increases from left to right. Parameter examples: $a \in [0, 20]$, $d = 0.2$, $r_{0,R} = 0.5$, $\beta_R = 0.001$, $d_R = 0.05$.

Confronting population growth models with data

Fitting population growth models to data: a Bayesian approach

Our theoretical considerations show non-linear density-regulation functions for consumers that are bottom-up regulated and experience continuous-time dynamics (Figs. 1, 2 and 3). In the simplest case of filter feeders and abiotic resources the dynamics of the consumer follow exactly the Beverton-Holt model (Eq. 8). For more complex cases involving saturating feeders (non-linear functional responses) or biotic resources Eq. 11 holds or the Maynard Smith-Slatkin model (Eq. 13) can be used as a good approximation.

To test these predictions in a real biological system, we used populations of the freshwater ciliate model organism *Tetrahymena thermophila* as a consumer that feeds on the bacterium *Serratia marcescens*. Starting at low population densities, we recorded population growth trajectories over the course of two weeks for 7 different genotypes, each replicated 6 times. We fit the logistic, the Beverton-Holt model, Eq. 11 and the Maynard Smith-Slatkin model to these dynamics using a Bayesian approach (see Supplementary Material S7 and Rosenbaum et al. (2018) for details) to avoid the pitfalls of likelihood ridges (Clark et al., 2010; Delean et al., 2012) and compared fits using WAIC as an information criterion (McElreath, 2016).

Given our theoretical considerations, as well as the fact that the bacterial resources were replenished regularly in the microcosms (effectively mimicking abiotic resource flows), we expect either the Beverton-Holt model (BH) or Eq. 11 to fit best to the dynamics. Indeed, over the 42 growth curves the logistic model had, on average, the worst fit (mean WAIC = 5.68), followed by the Beverton-Holt model (mean WAIC = 0.64) and the Maynard Smith-Slatkin model (mean WAIC = 0.22) while Eq. 11 performed best on average (mean WAIC = -0.16; see Fig. 5 for an example and Fig. S5 for all fits). In only 3 out of the 42 dynamics the logistic was found to fit best (Fig. S5). The remaining growth curves were found to follow most often Eq. 11 (26 out of 42), the Beverton-Holt model (7 out of 42) or the Maynard Smith-Slatkin model (6 out of 42). This finding is in good accordance with work showing that *Tetrahymena* may follow a type II functional response (Fronhofer and Altermatt, 2015).

Implications and extensions

Our derivations and the empirical support for Eq. 11 and the Beverton-Holt and Maynard Smith-Slatkin models received clearly show the value of considering alternatives to the logistic growth model. Even more importantly, our work highlights the underlying consumer-resource parameters being responsible for changes of and correlations between population level growth parameters. In the following section we discuss evolutionary consequences of our findings, and showcase extensions of our models to include temperature-dependence or multiple resource and consumer species.

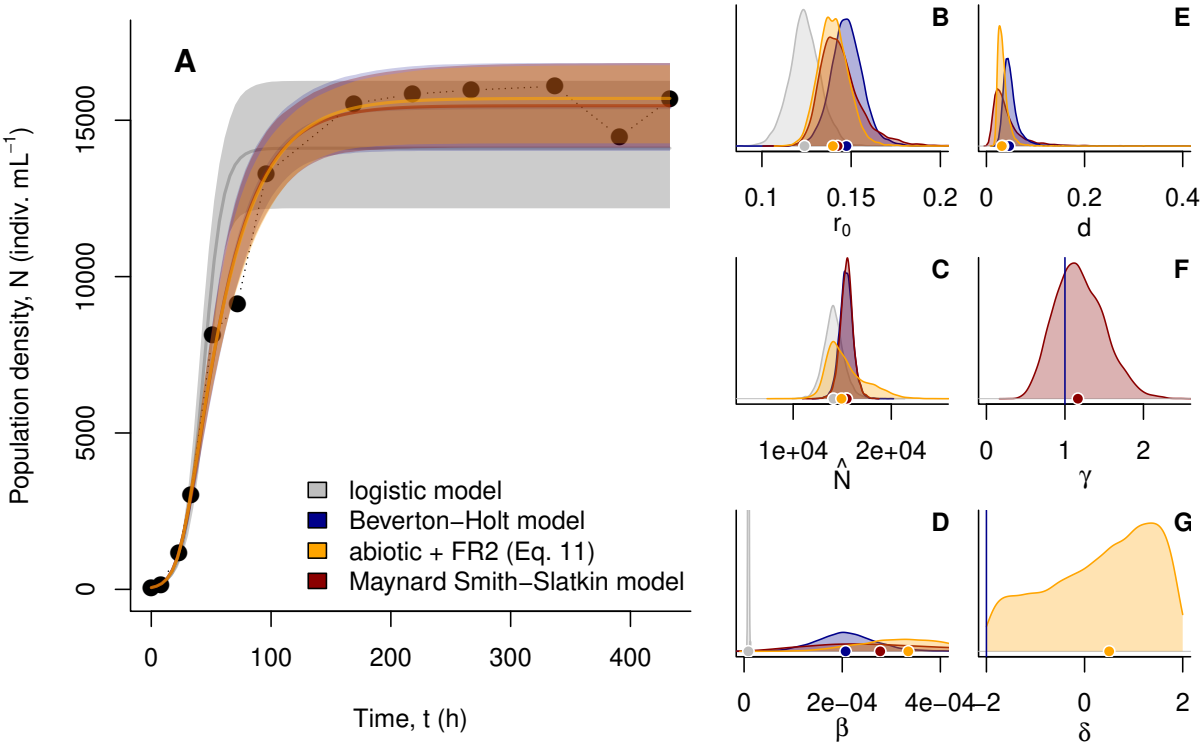

Figure 5: Fitting population growth models to *Tetrahymena thermophila* dynamics using Bayesian inference (see Supplementary Material S7 and Rosenbaum et al. (2018) for details). We fitted the logistic (black; Eq. 1), the Beverton-Holt model (blue; Eq. 8), Eq. 11 (orange), as well as the Maynard Smith-Slatkin model (red; Eq. 13) and compared fits using WAIC. Eq. 11 fitted best (WAIC = -19.50), but was very similar to both the Maynard Smith-Slatkin model (WAIC = -17.87) and to the Beverton-Holt model (WAIC = -16.77) while the logistic model clearly performed worst (WAIC = -241). As becomes clear in panel (A) the logistic model was not able to capture the asymmetry of the empirical growth curve well. We report medians and the 95th percentile of the posterior predictive distribution. Panels (B-G) show the posterior distributions of the parameters of the four models. Because resource dynamics were very strictly controlled, we predicted that this system follows abiotic resource dynamics, which is in good accordance with the fit of Eq. 11 and the low estimate of γ (see F and Fig. S3). As a consequence, *Tetrahymena thermophila* likely exhibits a type II functional response which is in good accordance with work by Fronhofer and Altermatt (2015).

Evolutionary consequences

Besides being crucial to ecology, density dependence and resulting density-dependent selection represent a central link between ecology and evolution (Travis et al., 2013), and is essential for the occurrence of eco-evolutionary feedbacks (Govaert et al., 2019). From an evolutionary point of view, Matessi and Gatto (1984) show that density-dependent selection ("K-selection") should minimize equilibrium resource availability and consequently $\frac{d}{ea}$, rather than maximizing $\widehat{N}$ (note parallels to R^* theory, Tilman 1980 and MacArthur's minimum principle, MacArthur 1969, Gatto 1990 and Ghedini et al. 2018). Therefore, density-dependent selection can be predicted to increase r_0 and β, either leading to an increase or a decrease in equilibrium densities, depending on resource and consumer behaviour. Most importantly, a

negative correlation does not result from a trade-off between population growth rates and competitive ability, as both parameters are always positively correlated. The decrease in equilibrium densities is rather a consequence of increased competition. This is an important distinction to classical $r - K$ selection assumptions.

Interestingly, Getz (1993) derives $r - K$ models from underlying consumer-resource models and shows that r_0 and K may be independent if one considers a parameter capturing the maximal growth rate. This parameter only acts on r_0 and may lead to a difference between r and K selected populations. Some parallels can be found in our work: for both filter and saturating feeders, we find that for vanishingly small density independent mortalities ($d \to 0$), the equilibrium population density ($\widehat{N}$) is independent of the assimilation coefficient (e). By contrast, if we assume abiotic resources and vanishingly small density independent mortalities, the equilibrium population density becomes independent of the maximal foraging rate (a). Only in these cases evolution in the respective parameters (a or e) can lead to an change in growth rate (r_0) without affecting the equilibrium population density ($\widehat{N}$).

In a classical $r - K$ selection study, Luckinbill (1979) investigated the consequences of adaptation to a low density environment. Using protists as model organisms, he showed that, in contrast to $r-K$ selection theory, r-selection did not only lead to an increase in r_0 but simultaneously to an increase in equilibrium densities ($\widehat{N}$). This result can be explained by our work if the protists exhibit a type I functional response (Fig. 7A–C) or feed on abiotic resources (chemostat; Fig. 7D–F). Adaptation to high-density environments may be mainly driven by changes in foraging rates (a) as has been prominently investigated in *Drosophila* (Mueller et al., 1991). In line with the prediction of Matessi and Gatto (1984) that selection in high-density environments should minimize $\frac{d}{ea}$, Joshi and Mueller (1988) and Mueller (1990) report that selection in high-density environments increases feeding rate (bite size). Furthermore, Joshi and Mueller (1996) find a trade-off between foraging rate (a) and assimilation efficiency (e) in *Drosophila*. Similarly, Palkovacs et al. (2011) report that Trinidadian guppies from low-predation environments which have experienced high population densities show adaptations towards increased resource consumption rates.

Finally, on a larger geographical scale, a widely held assumption is that organisms should be most abundant and exhibit the highest densities in their range core (Burton et al., 2010). However, the generality of this pattern has recently come under scrutiny: in an experimental evolution study, Fronhofer and Altermatt (2015) showed the evolution of lower equilibrium densities in range core populations (see also Fronhofer et al., 2017). More generally, Dallas et al. (2017) could not find increased densities in range cores across 1400 species, including vertebrates and trees. Our current work provides a potential explanation for the lack of this pattern, and even for an inverse pattern: if species feed on biotic resources, exhibit non-linear functional responses, and evolution maximizes foraging rate (a) rather than assimilation efficiency (e), low equilibrium densities will be the result (Fig. 4).

Temperature scaling of equilibrium densities

Besides having evolutionary consequences, our work has implications for instance in the context of global change research. Linking consumer-resource parameters and population level entities explicitly is at the centre of efforts to understand how populations behave under changing climatic conditions, specifically changing temperatures (Uszko et al., 2017). Equilibrium density relates population dynamics to community and ecosystem processes, because it provides a mechanistic link between individual performance, intraspecific interactions, and the total biomass and productivity of a species. Yet, as Gilbert et al. (2014) state, understanding the temperature-dependence of the equilibrium density has long remained a knowledge gap. Important progress has been made recently by Uszko et al. (2017) who for the first time include a mechanistic formulation of prey equilibrium density as a function of temperature in a predator-prey model.

In order to analyse how the equilibrium densities change with temperature, we used metabolic theory of ecology (Brown et al., 2004) that states that a given biological rate I will depend on temperature as follows:

$$I = I_0 e^{-\frac{E_a}{kT}} \tag{14}$$

with E_a as the activation energy, k the Boltzmann constant and T as the absolute temperature. While this relationship has been directly applied to population growth rates and competition coefficients, the effect of temperature on the equilibrium density has been less straight-forward to infer and justify theoretically (Gilbert et al., 2014; Bernhardt et al., 2018). Similarly to Uszko et al. (2017), our work provides a mechanistic way forward, at least in the case of abiotic resources. For filter feeders, we can take the expression for equilibrium density in Eq. 10 and substitute Eq. 14 for all biological rates, that is, the feeding rate a and the death rate d, except for the efficiency e, which has been shown to be temperature independent (Del Giorgio and Cole, 1998; López-Urrutia and Morán, 2007). For simplicity, we assume the parameters of the abiotic resource to be temperature-independent and that all activation energies E_a are identical. Then

$$\widehat{N}(T) = \frac{\omega(e_0 a_0 R_0 - d_0)}{a_0 d_0} e^{\frac{E_a}{kT}}. \tag{15}$$

This result implies that, as temperature increases, equilibrium density decreases as shown in Fig. 6B for filter feeding consumers feeding on abiotic resources (for details of the derivation see the Supplementary Material S8).

We can apply the same thoughts to the entire density-regulation function which then behaves as depicted in Fig. 6A. The simultaneous increase of population growth rate and competition coefficient with temperature decreases the equilibrium density and makes the density-regulation function steeper

around the equilibrium density.

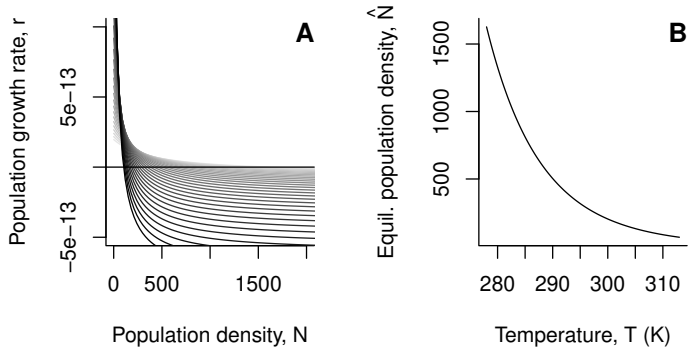

Figure 6: (A) Temperature scaling of the density-regulation function for filter feeding consumers feeding on abiotic resources. With increasing temperature (darker grey) the density-regulation function becomes steeper because r_0 and the competition coefficient β increase. (B) Temperature scaling of equilibrium population density. See the Supplementary Material S8 for a detailed derivation.

The negative scaling of equilibrium density with temperature holds more generally, for all cases of abiotic and biotic resources and shapes of functional responses investigated here (see Supplementary Material S8). Clearly, changing the temperature scaling law captured by Eq. 14 along the lines suggested by Uszko et al. (2017), that is, to be unimodal, because some rates may decline beyond certain critical temperature values, would change these results. While an in-depth analysis is beyond the scope of our current work, this extension highlights the potential of our framework. Of course, our derivations can be used to investigate the effects of other scaling laws, such as body size scaling, which we will not analyse any further here.

Multi-species models

While all our considerations have up to now been focused on one consumer species, natural systems rather consist of communities of multiple consumers and resources. Based on our derivations, we can expand our work to multiple species. Considering our simplest case, abiotic resources and a filter feeding consumer, we can add n consumer species to the system (see Ruggieri and Schreiber, 2005, for an example with two consumers). After solving for resource equilibrium equilibrium, substitution and some reparametrization (see Supplementary Material S9), we obtain the consumer dynamics for species i:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_{0,i} + d_i}{1 + \sum_{j=1}^{n} \beta_j N_j} - d_i. \tag{16}$$

Based on Eq. 16, coexistence is only possible if growth and death rates are identical, because all consumers feed on one resource and do not interact in any other way. In analogy to Matessi and Gatto (1984) the

species that minimizes $\frac{d_i}{r_{0,i}+d}$ excludes the others (see also Hofbauer and Sigmund, 1989).

If there is any interspecific interaction that is not resource mediated, an additional interaction term may be added in analogy to a death term as follows:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_{0,i}+d}{1+\sum_j \beta_j N_j} - \sum_j \alpha_{ij} N_j - d_i. \tag{17}$$

This additional density-dependent mortality term allows for coexistence of more than one species (McPeek, 2012). Possible mechanisms behind the additional interaction term include cannibalism at the intraspecific level and chemical compounds (that is, allelopathy) at both the intra- and interspecific levels.

Finally, for more than one (abiotic) resource and more than one (filter feeding) consumer we obtain for species i after simplification:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_r \frac{b_{i,r}}{1+\sum_j \beta_{j,r} N_j} - d_i \tag{18}$$

where $b_{i,r} = e_{i,r} a_{i,r} R_{0,r}$ is the resource specific birth term of species i and $\beta_{j,r} = \frac{a_{j,r}}{\omega_r}$ is the competition coefficient.

Further extensions to include more complex trophic interactions via Eq. 11 and non-trophic interactions via additional mortality terms can be included as described above. Of course, if such complexities are relevant to a biological system, it may be useful to model these interactions explicitly using an appropriate foodweb model instead of attempting a simplification by focusing on the consumer level.

Discussion and conclusion

Our results, based on deriving density-regulation functions from underlying consumer-resource models, show that the parameters of population level growth models (e.g., r_0 and β) and equilibrium population densities ($\widehat{N}$) are not independent, but are all functions of consumer traits such as foraging rate and assimilation efficiency (Fig. 7). This holds true regardless of the underlying consumer-resource dynamics. In contrast to previous work, we derive a priori expectations about the relationship between growth rates, competitive abilities and equilibrium densities that capture the essence of three different consumer-resource systems: filter feeders, saturating feeders and consumers feeding on abiotic resources (Fig. 7). Contrary to the widely held belief that growth rates and equilibrium densities are negatively correlated, we show that various relationships must be expected, depending on the underlying consumer-resource dynamics (Fig. 7). In accordance with previous work (e.g., Thieme, 2003; Johst et al., 2008; Abrams, 2009; Reynolds and Brassil, 2013) we show that (i) the logistic model (Eqs. 1 and 2) assuming linear density de-

pendence may only be appropriate under very specific conditions, such as competition for spatial resources like nesting sites or territories (see Supplementary Material S1), and that (ii) most ecological systems will rather follow concave or convex density-regulation functions (Fig. 7), because most systems are bottom-up regulated (Begon et al., 2006). As discussed in Abrams (2009), the curvature of these density-regulation functions is different from what the θ-logistic model (Gilpin and Ayala, 1973) can achieve. We here show that filter feeders, and generally organisms with linear functional responses (Jeschke et al., 2004), follow a convex density-regulation function that is exactly described by a continuous-time version of the Beverton-Holt model (Eq. 8; see also Thieme 2003 and Pástor et al. 2016, for example). For consumers feeding on abiotic resource and following a saturating functional response, we provide a mechanistically derived density-regulation function (Eq. 11). More complex consumer-resource systems can be approximately described by a continuous-time version of the Maynard Smith-Slatkin model (Eq. 13).

Based on our theoretical work, we predict filter feeders to generally exhibit a positive correlation between growth rates, competitive abilities and equilibrium population densities (Fig. 7A–C). The form of this relationship will depend on whether higher growth rates are achieved by increasing foraging rates or by increasing assimilation efficiencies (Fig. 7C). For foraging strategies that are characterized by a type II, that is, saturating functional response (Fig. 7B) while keeping the resources abiotic, we show that the appropriate density-regulation function can be both concave and convex (Fig. 2 and 7E). Increasing foraging rates and assimilation coefficients will still increase both growth rates and equilibrium densities (7F and Fig. S3), while the effect of the half-saturation constant is the opposite. The relationship between growth rates and equilibrium densities may be different for more complex systems characterized by both biotic resources and non-linear functional responses (7G–I and Fig. 4). Specifically, changing foraging rates and half-saturation constants may lead to non-monotonic relationships between growth rates and equilibrium densities. These considerations highlight that population growth and competitive ability are correlated, usually positively, and that equilibrium densities are a result of underlying consumer-resource dynamics that may correlate positively or negatively with population growth and competitive ability. This has important implications for evolutionary considerations as discussed above.

Previous work has investigated the shape of density-regulation functions empirically, by using times-series data from growth experiments and natural population dynamics. For example, Borlestean et al. (2015) investigated the curvature of density dependence in a *Chlamydomonas* chemostat. While the authors report to be surprised by the general convexity of the density-regulation function, these results are in perfect accordance with our predictions (Fig. 7B). In a comparative study, Sibly et al. (2005) used a large dataset to show that the relationship between growth rate and density is generally convex, that is, exhibits first a fast decrease and then slows down ($\theta < 1$ in the θ-logistic model). This result corresponds to our scenario for filter feeders and abiotic resources (Fig. 7B), which is rather surprising,

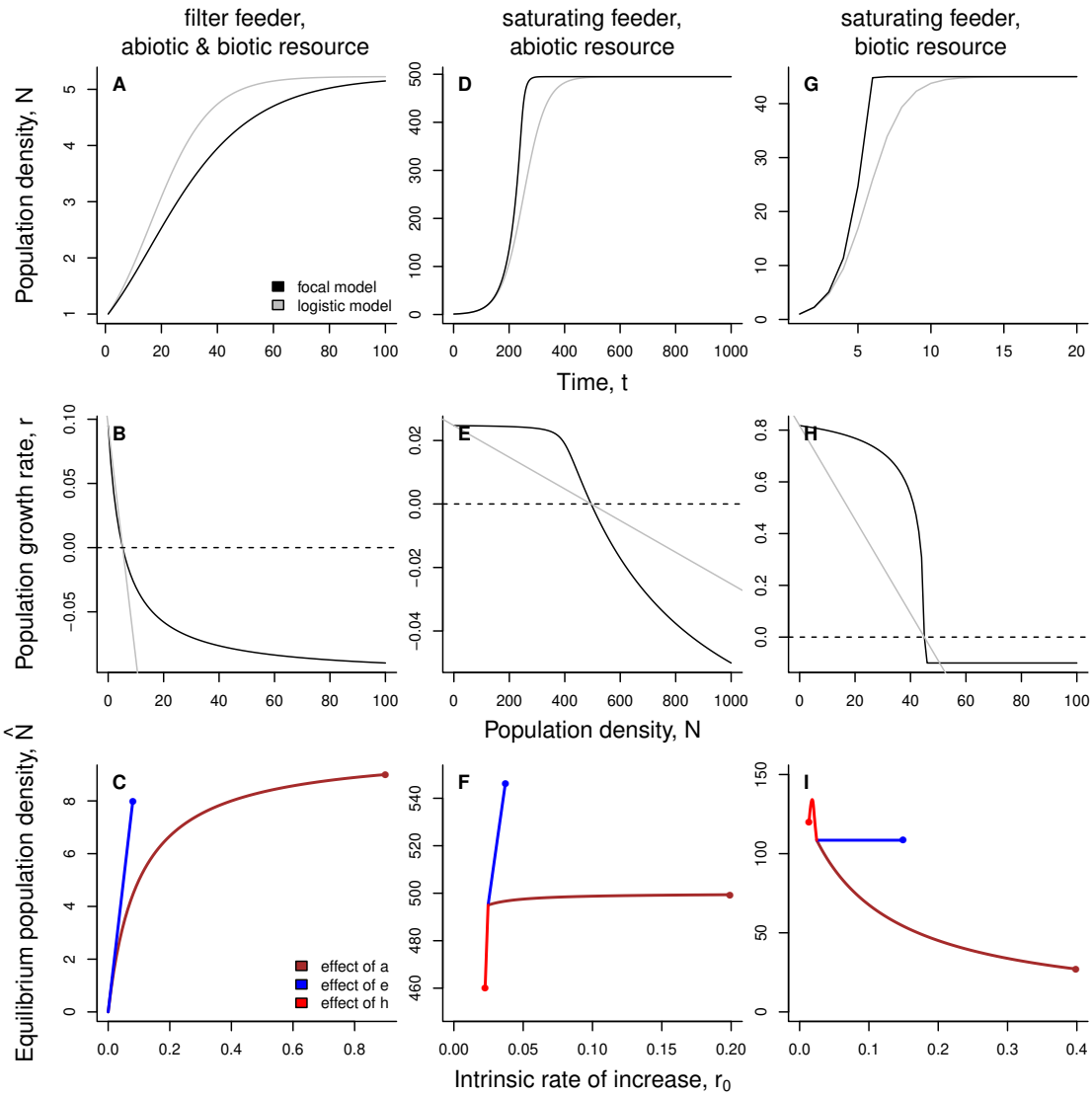

Figure 7: Summary of population growth models (upper row; grey is the logistic for reference), density-regulation functions (central row) and relationships between equilibrium population density ($\widehat{N}$) and intrinsic rate of increase (r_0; bottom row). The points in the latter plots visualize the largest a, e or h value.

given that the dataset included mammals, birds, fish and insects. However, as Clark et al. (2010) laid out in detail, the dominance of $\theta < 1$ values may be due to technical difficulties in fitting the θ-logistic model. Nevertheless, this study, along with the findings of Eberhardt et al. (2008) who suggested that the θ-logistic usually outperforms the logistic in a number of vertebrate species, clearly highlight the general non-linearity of density-regulation functions. These examples show the value of our work, as it provides theoreticians and empiricists with theoretically grounded assumptions on the occurrence of specific shapes of density dependence and trait correlations. Besides the implications discussed above, the curvature of density dependence itself is highly relevant for a population's response to stressors. Hodgson et al. (2017)

demonstrated that when density dependence is concave the effect of stressors on focal populations is always amplified, while the response can be amplified or dampened for convex density dependencies.

Of course, it is important to keep in mind that our models are simplified representations of population dynamics and ignore, for instance, age or stage structure (Mueller, 1997). We do not include Allee effects (Allee, 1931; Courchamp et al., 2008), that is, reduced population growth at low densities. There are numerous mechanisms that can lead to Allee effects and we speculate that these may lead to different functional relationships between population growth and population density. At a descriptive level, demographic Allee effects can be included as shown in Kubisch et al. (2016) for discrete time systems, for example. Our considerations also do not include time-lags in density-dependence (Ratikainen et al., 2008) which are relevant in both theoretical and applied contexts, for example for population stability. For reasons of space we also do not discuss discrete time models. Note that Turchin (2003) and Thieme (2003) treated this topic in detail and mechanistic derivations of the Ricker model have for example been used by Melbourne and Hastings (2009).

Finally, we would like to reiterate the point made by Mallet (2012): we cover a long-discussed topic in ecology. Multiple authors have noted difficulties with the $r - K$ formulation of the logistic and potential non-linearities in density dependence. Advanced textbooks like Thieme (2003) and Pástor et al. (2016) have shown that for filter feeders and abiotic resources the continuous-time version of the Beverton-Holt model can be derived. Mallet (2012) discusses how using the $r - \alpha$ formulation of the logistic, where appropriate, alleviates some of the problems encountered with the $r - K$ formulation. While these considerations are highly relevant to both empiricists and theoreticians, they seem to remain largely ignored. We hope that the insights provided here, as well as our expansion of past work towards more complex consumer-resource interactions resulting in an understanding of functional relationships between population level parameters, will help to change how density regulation is treated in ecology and evolution.

Author contributions

E.A.F. conceived the study. E.A.F., L.G. and S.J.S. analysed the mathematical models. E.A.F. gathered the empirical data. E.A.F. performed the statistical analyses including fitting of population growth models. E.A.F. wrote the manuscript and all authors commented on the draft.

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Data availability

Data will be deposited in Dryad and R-code will be made available via GitHub and a Zenodo DOI.

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Supplementary Material

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The shape of density dependence and the relationship between population growth, intraspecific competition and equilibrium population density

S1 Derivation of the logistic model by Lakin and Van Den Driessche (1977)

Multiple authors have reported that one can derive the logistic growth model (Eqs. 1 or 2) for consumers from underlying consumer-resource dynamics (e.g. MacArthur, 1970; Thieme, 2003; Abrams, 2009; Reynolds and Brassil, 2013). Most of these derivations, however, assume that the underlying resource dynamics (Eq. 3a in the main text) follow a logistic growth model (Eqs. 1 or 2 in the main text) which, given the principle of inheritance of the curvature of density dependence reported by Abrams (2009), appears circular. Reynolds and Brassil (2013) justify their usage of the logistic for describing resource dynamics by referring to work by Lakin and Van Den Driessche (1977) who indeed derive the logistic from a chemostat model. In the Lakin and Van Den Driessche (1977) model resource dynamics (R) are described as follows:

$$\frac{dR}{dt} = \omega R_0 - \omega R - aN \tag{S1}$$

with ω being the flow rate into and out of the system, and R_0 the resource concentration flowing into the system. The consumer dynamics (N) are thought to follow

$$\frac{dN}{dt} = eaRN \tag{S2}$$

where e is the assimilation efficiency of the consumer (N) and a its foraging rate. As described in the main text (Eq. 4), one can assume that the resources are at equilibrium ($\frac{dR}{dt} = 0$) and solve Eq. S1 for

R to obtain the equilibrium resource population density $\widehat{R} = R_0 - \frac{aN}{\omega}$. Then the per capita consumer dynamics follow

$$\frac{1}{N}\frac{dN}{dt} = eaR_0 - \frac{ea^2}{\omega}N. \tag{S3}$$

This formulation is identical to the linear density-regulation function assumed in the Verhulst (1838) model (Eq. 2 in the main text) with setting $r_0 = eaR_0$ and $\alpha = \frac{ea^2}{\omega}$ (see also Fig. S1). While this result may seem satisfactory, it is worth noting that in Eq. S1 the consumer harvests a constant amount of resources (aN; type I functional response), regardless of resource availability. Biologically, this seems a rather unrealistic assumption.

Despite its artificiality, this model already hints at the non-independence of population growth rates (r_0) and competitive abilities (here α, the slope of the density-regulation function). As depicted in Fig. S1 population growth rates and competitive abilities will covary. The relationship is either linear or quadratic, depending on whether the assimilation efficiency (e; Fig. S1B) or the foraging rate (a; Fig. S1A) is the underlying driver (since $r_0 = eaR_0$ and $\alpha = \frac{ea^2}{\omega}$). It is also interesting to note that the equilibrium density, here defined as $\widehat{N} = \frac{r_0}{\alpha} = \frac{R_0\omega}{a}$ is not a function of the assimilation efficiency (e) and decreases with increasing foraging rate (a).

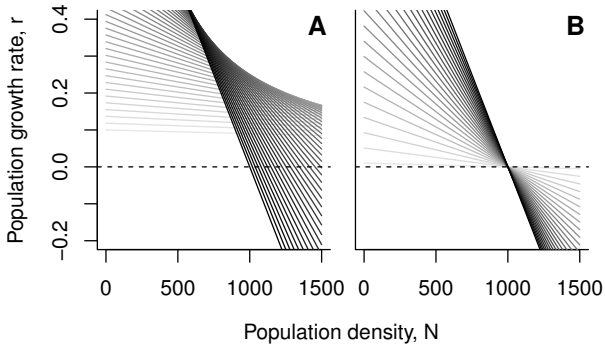

Figure S1: Density dependence for a consumer following the Lakin and Van Den Driessche (1977) model. (A) Effect of changing the foraging rate (a) while keeping the assimilation efficiency constant ($e = 0.01$). Darker shades of grey indicate higher parameter values. (B) effect of changing the assimilation efficiency parameter (e) while keeping the foraging rate constant ($a = 0.1$). Parameter examples: $R_0 = 1000$, $\omega = 0.1$, $e \in [0.0001, 0.01]$, $a \in [0.01, 0.1]$.

S2 Consumer dynamics with a type II functional response and abiotic resources

For a consumer N with a type II functional response feeding on an abiotic resource (R; chemostat model) we assume the following dynamics:

$$\frac{dR}{dt} = \omega R_0 - \omega R - \frac{a}{h+R} NR \tag{S4a}$$

$$\frac{dN}{dt} = e\frac{a}{h+R} RN - dN \tag{S4b}$$

Assuming resource equilibrium, we have to solve the following equation:

$$\frac{dR}{dt} = 0 \Leftrightarrow \omega R_0 - \omega R - \frac{a}{h+R} NR = 0$$

Assuming that $h + R \neq 0$, we can multiply both sides with $h + R$. Rearranging terms results in the following quadratic equation:

$$-\omega R^2 + (\omega R_0 - aN - h\omega)R + h\omega R_0 = 0.$$

This quadratic equation has two solutions:

$$\widehat{R}_1 = \frac{(\omega R_0 - aN - h\omega) - \sqrt{D}}{2\omega} \tag{S5}$$

$$\widehat{R}_2 = \frac{(\omega R_0 - aN - h\omega) + \sqrt{D}}{2\omega}, \tag{S6}$$

with $D = (\omega R_0 - aN)^2 + 2h\omega(\omega R_0 + aN) + h^2\omega^2$. We only use the second solution in further calculations as the first solution is negative and thus not biologically meaningful. Substituting $\widehat{R}_2$ into Eq. S4b results in

$$\frac{1}{N}\frac{dN}{dt} = \frac{ea\left(\omega R_0 - aN - h\omega + \sqrt{D}\right)}{2\omega h + \omega R_0 - aN - h\omega + \sqrt{D}} - d. \tag{S7}$$

Calculating N at population equilibrium (i.e., $\widehat{N}$) is done by setting Eq. S7 equal to zero. Solutions thus are: $\widehat{N} = 0$ or solving the following equation to N:

$$\frac{ea\left(\omega R_0 - aN - h\omega + \sqrt{D}\right)}{2\omega h + \omega R_0 - aN - h\omega + \sqrt{D}} = d. \tag{S8}$$

Note that this equation is of the form

$$\frac{ea(X + \sqrt{D})}{2\omega h + X + \sqrt{D}},$$

with $X = \omega R_0 - aN - h\omega$. We can then use the binomial product $(a+b)(a-b) = a^2 - b^2$ to simplify equation (S8) by multiplying the numerator and denominator with $X - \sqrt{D}$. This results in:

$$\frac{ea(X+\sqrt{D})}{2\omega h + X + \sqrt{D}} = \frac{ea(X+\sqrt{D})}{2\omega h + X + \sqrt{D}} \cdot \frac{X-\sqrt{D}}{X-\sqrt{D}} = \frac{ea(X^2 - D)}{2\omega h(X-\sqrt{D}) + X^2 - D} \tag{S9}$$

where $(X+\sqrt{D})(X-\sqrt{D}) = X^2 - D$. Substituting $X = \omega R_0 - aN - h\omega$ and $D = (\omega R_0 - aN)^2 + 2h\omega(\omega R_0 + aN) + h^2\omega^2$ into $X^2 - D$ gives

$$\begin{aligned}
X^2 - D &= (\omega R_0 - aN - h\omega)^2 - (\omega R_0 - aN)^2 - 2h\omega(\omega R_0 + aN) - h^2\omega^2 \\
&= (\omega R_0 - aN)^2 - 2h\omega(\omega R_0 - aN) + h^2\omega^2 - (\omega R_0 - aN)^2 - 2h\omega(\omega R_0 + aN) - h^2\omega^2 \\
&= -2h\omega(\omega R_0 - aN) - 2h\omega(\omega R_0 + aN) \\
&= -2h\omega^2 R_0 + 2h\omega aN - 2h\omega^2 R_0 - 2h\omega aN \\
&= -4h\omega^2 R_0
\end{aligned}$$

For the denominator we get $(2\omega h + X + \sqrt{D})(X - \sqrt{D}) = 2\omega h(X - \sqrt{D}) + (X + \sqrt{D})(X - \sqrt{D})$. For the second term we already know that it equals to $-4h\omega^2 R_0$. Thus the denominator becomes:

$$2\omega h(X - \sqrt{D}) - 4h\omega^2 R_0 = -2\omega h(\omega R_0 + aN + h\omega + \sqrt{D}).$$

We thus simplify Eq. S8 to

$$\frac{2ea\omega R_0}{\omega R_0 + aN + h\omega + \sqrt{D}} = d, \tag{S10}$$

and we can rewrite Eq. S7 to:

$$\frac{1}{N}\frac{dN}{dt} = \frac{2ea\omega R_0}{\omega R_0 + aN + h\omega + \sqrt{D}} - d. \tag{S11}$$

Now we can solve this equation to find the density N at equilibrium ($\widehat{N}$). We first need to assume that $\omega R_0 + aN + h\omega + \sqrt{D} \neq 0$. Note that we can rewrite Eq. S10 to an expression of the form $Y + N = \sqrt{Z + N}$ by rearranging Eq. S10 to

$$\frac{\omega}{d}\Big(2eaR_0 - d(R_0 + h)\Big) - aN = \sqrt{D}$$

Now squaring both sides and solving to N results in:

$$\widehat{N} = \frac{e\omega}{d}\left(\frac{d(R_0 + h) - eaR_0}{d - ae}\right). \tag{S12}$$

From Eq. S11 we can calculate r_0 by assuming $N = 0$:

$$r_0 = \frac{eaR_0}{R_0 + h} - d \tag{S13}$$

From this we find that

$$eaR_0 = (r_0 + d)(R_0 + h), \tag{S14}$$

which we can substitute into Eq. S11. This then gives the density-regulation function for consumer dynamics with a type II functional response and abiotic resources:

$$\frac{1}{N}\frac{dN}{dt} = \frac{2\omega(r_0 + d)(R_0 + h)}{\omega(R_0 + h) + aN + \sqrt{\omega^2(R_0 + h)^2 - 2\omega(R_0 - h)aN + a^2N^2}} - d \tag{S15}$$

We can simplify this equation by defining the competitive ability β as in Eq. 8 as $\beta = \frac{a}{\omega(R_0+h)}$:

$$\frac{1}{N}\frac{dN}{dt} = \frac{2(r_0 + d)}{1 + \beta N + \sqrt{1 + \beta N(\beta N - \delta)}} - d. \tag{S16}$$

with $\delta = 2\frac{R_0-h}{R_0+h}$. If $\delta \to 2$, then the denominator of Eq. S16 simplifies to $1 + \beta N + \sqrt{(1 - \beta N)^2} = 1 + \beta N + |1 - \beta N|$. Hence, when $1 - \beta N \geq 0$, this simplifies Eq. S16 to

$$\frac{1}{N}\frac{dN}{dt} = r_0.$$

This implies exponential growth as a result of $h \to 0$, that is, foraging being resource independent. By contrast, if $\delta \to -2$, then the denominator of Eq. S16 simplifies to $1 + \beta N + \sqrt{(1 + \beta N)^2} = 2(1 + \beta N)$. This reduces Eq. S16 to

$$\frac{1}{N}\frac{dN}{dt} = \frac{r_0 + d}{1 + \beta N} - d$$

which results into the Beverton-Holt model (Eq. 8 in main text). This result is expected, because $\delta \to -2$ is a result of $h \to \infty$ which leads to a linear functional response.

Solving equation (S16) to equilibrium density ($\hat{N}$) then gives:

$$\widehat{N} = \frac{4r_0(r_0 + d)}{\beta d(4r_0 + 2d + \delta d)} \tag{S17}$$

S3 Curvature of the density-regulation function — type II functional response and abiotic resources

We will use the following general consumer-resource model

$$\frac{dR}{dt} = f(R) - g(R)N \tag{S18a}$$
$$\frac{dN}{dt} = eg(R)N - dN \tag{S18b}$$

where R is the resource and N the consumer population density. The function $f(R)$ captures the growth of the resources and the function $g(R)$ captures the functional response of the consumer. In order to have a general idea of the form of the per-capita growth function of the consumer ($r(N) = \frac{1}{N}\frac{dN}{dt}$), we can take the first and second derivative with respect to N of $r(N)$. This then equals:

$$\frac{dr}{dN} = e\frac{dg}{dN} \tag{S19a}$$
$$\frac{d^2r}{dN^2} = e\frac{d^2g}{dN^2}. \tag{S19b}$$

Hence, if we have information on the sign of $\frac{dg}{dN}$ and $\frac{d^2g}{dN^2}$, this will provide information on the sign of $\frac{dr}{dN}$ and $\frac{d^2r}{dN^2}$. But as g is a function of R and R is a function of N, the first and second derivative of g to N can be rewritten as:

$$\frac{dg}{dN} = \frac{dg}{dR}\frac{dR}{dN} \tag{S20a}$$
$$\frac{d^2g}{dN^2} = \frac{d^2g}{dR^2}\left(\frac{dR}{dN}\right) + \frac{dg}{dR}\frac{d^2R}{dN^2}. \tag{S20b}$$

So we need to find expressions for $\frac{dR}{dN}$ and $\frac{d^2R}{dN^2}$. To do so, note that at resource equilibrium ($\frac{dR}{dt} = 0$), we find that

$$N = \frac{f(R)}{g(R)} = v(R).$$

If we set this fraction to a function $v(R)$, and implicitly differentiate to N, this yields:

$$1 = \frac{dv}{dR}\frac{dR}{dN},$$

as R is a function of N. From which it follows that

$$\frac{dR}{dN} = \frac{1}{v'(R)}, \tag{S21}$$

where $v'(R) = \frac{dv}{dR}$. A second implicit differentiation yields:

$$0 = \frac{d^2v}{dR^2}\left(\frac{dR}{dN}\right) + \frac{dv}{dR}\frac{d^2R}{dN^2},$$

which gives after rearranging terms

$$\frac{d^2R}{dN^2} = -\frac{v''}{v'^3}. \tag{S22}$$

Eq. S22 determines the curvature of R as a function of N. Hence, Eq. S21 and Eq. S22 gives an expression for the first and second derivative of R in function of N, which we can use to substitute in the first and second derivative of g to N:

$$\frac{dg}{dN} = \frac{dg}{dR}\frac{dR}{dN} \quad \text{and} \quad \frac{d^2g}{dN^2} = \frac{d^2g}{dR^2}\left(\frac{dR}{dN}\right) + \frac{dg}{dR}\frac{d^2R}{dN^2}. \tag{S23}$$

For abiotic resources with type II functional response, function f and g become:

$$f(R) = \omega(R_0 - R) \quad \text{and} \quad g(R) = \frac{aR}{h+R}. \tag{S24}$$

In this case, $v(R)$ and its first and second derivative equal:

$$v(R) = \frac{\omega(R_0 - R)(h+R)}{aR} = \frac{\omega}{a}\left(\frac{hR_0}{R} - h + R_0 + R\right) \tag{S25a}$$

$$\frac{dv}{dR} = -\frac{\omega}{a}\left(\frac{hR_0}{R^2} + 1\right) \tag{S25b}$$

$$\frac{d^2v}{dR^2} = \frac{2\omega h R_0}{aR^3}. \tag{S25c}$$

From this it follows that $\frac{dR}{dN} < 0$ and $\frac{d^2R}{dN^2} > 0$. Thus, the resource equilibrium density is a decreasing convex function of consumer population density, just as in the case of the type I functional response.

From this we can determine the curvature of the per-capita growth rate by substituting the information given in Eq. S24 into Eq. S23. We get:

$$\begin{aligned} \frac{dg}{dR} &= \frac{ah}{(h+R)^2} \\ \frac{d^2g}{dR^2} &= -\frac{2ah}{(h+R)^3}. \end{aligned}$$

From this Eq. S23 becomes

$$\begin{aligned} \frac{d^2g}{dN^2} &= -\frac{2ah}{(h+R)^3}\cdot\left(\frac{1}{v'^2}\right) + \frac{ah}{(h+R)^2}\cdot\left(\frac{-v''}{v'^3}\right) \\ &= -\frac{ah}{v'^3(h+R)^3}(2v' + (h+R)v''). \end{aligned}$$

As $v' < 0$, it follows that $-\frac{ah}{v'^3(h+R)^3} > 0$. Hence $2v' + (h+R)v''$ determines the sign of $\frac{d^2g}{dN^2}$. Using information from Eq. S25, we can replace v' and v'' in $2v' + (h+R)v''$ and obtain:

$$\frac{2\omega}{a}\Big(\frac{h^2R_0}{R^3} - 1\Big).$$

Now $\frac{h^2R_0}{R^3} - 1 < 0 \Leftrightarrow \frac{R_0}{R^3} < \frac{1}{h^2}$. Hence, R decreases with N from R_0 at $N = 0$ until N is such that $R^3 = h^2R_0$. At $N = 0$, $R = R_0$, and we find that $\frac{h^2}{R_0^2} < 1 \Leftrightarrow h < R_0$. Note that the concavity in the density-regulation function stems from the concavity of the type II functional response of the consumer, not from the resource level itself, as the resource is a decreasing convex function of consumer population density.

S4 Fitting known density-regulation models to consumer dynamics with a type II functional response and abiotic resources

In order to compare the behaviour of Eq. S16 to existing population-regulation models, we take the same approach as Abrams (2009) and fitted these models to Eq. S16 using a least-squares approach. The respective ODEs were solved (function 'ode' of the 'deSolve' package in R version 3.4.4) and the model was fitted by minimizing the sum of squared residuals (Levenberg-Marquardt algorithm implemented in function 'nls.lm' of the 'minpack.lm' package in R). Specifically, we here consider the Beverton-Holt model (Eq. 8), the θ-logistic model (Gilpin and Ayala, 1973), the Hassel model (Hassell et al., 1976) and the Maynard Smith-Slatkin model (Maynard Smith and Slatkin, 1973) as possible candidates.

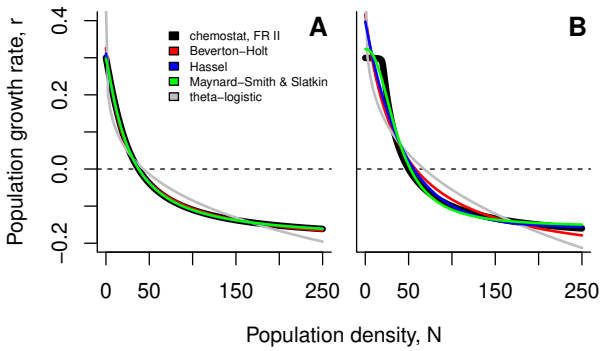

Figure S2: Fitting existing population growth models to the population growth function of consumer with a type II functional response feeding on abiotic resources (chemostat model). (A) High half-saturation constant and foraging rate ($h = 1000$, $a = 10$) (B) Low half-saturation constant and foraging rate ($h = 1$, $a = 5$). Parameter examples: $R_0 = 100000$, $\omega = 0.1$, $e = 0.1$, $d = 0.2$.

Because the Maynard Smith-Slatkin model approximates the dynamics of Eq. S16 sufficiently well, we can use this model to analyse numerically how changes in consumer-resource parameters impact the parameters used in the Maynard Smith-Slatkin model (Fig. S3). We recapture the results laid out in the main text and show that strong concavity (determined by the shape parameter γ) mainly occurs at low values of the half-saturation constant (h) and specifically for low foraging rates (a).

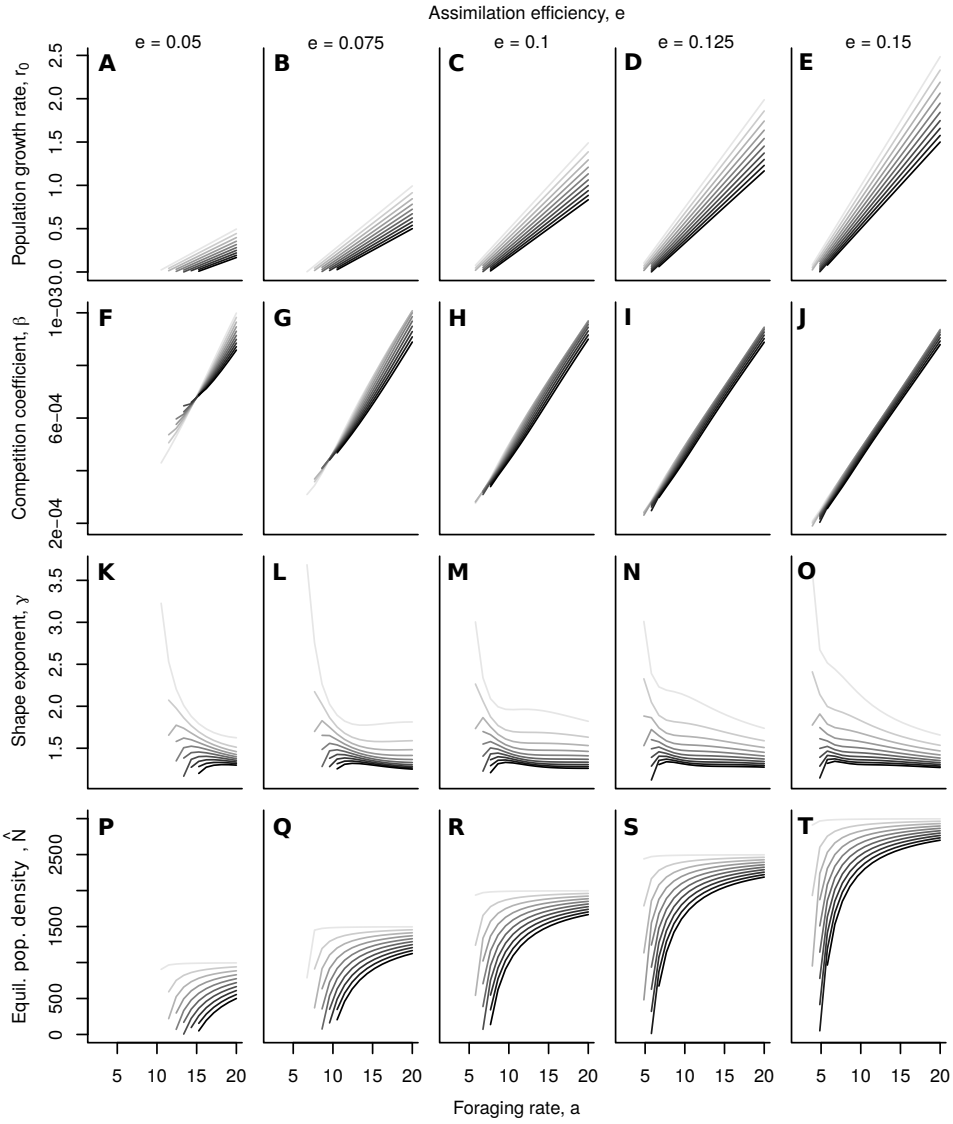

Figure S3: Correlations between consumer-resource parameters and the parameters of the Maynard Smith-Slatkin model for a consumer with a type II functional response feeding on abiotic resources. The Maynard Smith-Slatkin model was fitted using a least-squares approach to the respective realisation of Eq. S16. Darker shades of grey indicate higher parameter values of the half-saturation constant ($h \in [500, 50000]$). The assimilation efficiency ($e \in [0.05, 0.15]$) increases from left to right. Parameter examples: $a \in [2, 20]$, $R_0 = 100000$, $\omega = 0.1$, $d = 0.5$.

S5 Consumer dynamics with a type II functional response and biotic resources

For a consumer-resource system with biotic resources (Eq. 8) and a consumer exhibiting a type II functional response, we can write:

$$\frac{dR}{dt} = \left(\frac{r_{0,R} + d_R}{1 + \beta_R R} - d_R\right) R - \frac{a}{h + R} RN \tag{S26a}$$

$$\frac{dN}{dt} = e\frac{a}{h + R} RN - d_N N. \tag{S26b}$$

Solving Eq. S26a to R results in two non-zero solutions:

$$\widehat{R}_{1,2} = \frac{-\beta_R d_R h - a\beta_R N + r_{0,R} \pm \sqrt{D}}{2\beta_R d_R}, \tag{S27}$$

with $D = (-\beta_R d_R h - a\beta_R N + r_{0,R})^2 + 4\beta_R d_R(-aN + hr_{0,R})$. Substituting the positive solution into Eq. S26b and simplifying this equation using similar steps as described in Supplementary Material S2 gives:

$$\frac{1}{N}\frac{dN}{dt} = \frac{-2ea(-aN + hr_{0,R})}{h(X - \sqrt{D}) - 2(-aN + hr_{0,R})} - d_N, \tag{S28}$$

with $X = -\beta_R d_R h - \beta_R aN + r_{0,R}$.

In order to find the equilibrium density, we solve this equation for N, giving the solutions: $\widehat{N} = 0$ and

$$\widehat{N} = \frac{-eh(-\beta_R d_N d_R h - d_N r_{0,R} + aer_{0,R})}{(d_N - ae)(-d_N + ea + \beta_R d_N h)} \tag{S29}$$

r_0 can be obtained by setting $N = 0$ in Eq. S28, which leads to

$$r_0 = \frac{ear_{0,R}}{h\beta_R d_R + r_{0,R}} - d_N \Leftrightarrow ea = \frac{1}{r_{0,R}}(r_0 + d_N)(h\beta_R d_R + r_{0,R}). \tag{S30}$$

Substituting r_0 into $\frac{1}{N}\frac{dN}{dt}$ by using Eq. S30 gives

$$\frac{1}{N}\frac{dN}{dt} = \frac{-2(r_0 + d_N)(\beta_R d_R h + r_{0,R})(-aN + hr_{0,R})}{hr_{0,R}[aN(-\beta_R + \frac{2}{hr_{0,R}}) - (\beta_R d_R h + r_{0,R})] - hr_{0,R}\sqrt{(\beta_R d_R h + r_{0,R})^2 + a^2\beta_R^2 N^2 - aN(-2\beta_R(-\beta_R d_R h + r_{0,R}) + 4\beta_R d_R)}} \tag{S31}$$

The previous equation can then be simplified by dividing by $\beta_R d_R h + r_{0,R}$:

$$\frac{1}{N}\frac{dN}{dt} = \frac{1}{hr_{0,R}} \frac{-2(r_0 + d_N)(-aN + hr_{0,R})}{\frac{aN}{\beta_R d_R h + r_{0,R}}(-\beta_R + \frac{2}{hr_{0,R}}) - 1 - \sqrt{1 - \frac{a^2\beta_R^2 N^2}{(\beta_R d_R h + r_{0,R})^2} - aN\frac{-2\beta_R(-\beta_R d_R h + r_{0,R}) + 4\beta_R d_R}{(\beta_R d_R h + r_{0,R})^2}}}, \tag{S32}$$

and by setting $\delta = \frac{-\beta_R d_R h + r_{0,R}}{\beta_R d_R h + r_{0,R}}$ and $\beta = \frac{a\beta_R}{\beta_R d_R h + r_{0,R}}$ we can rewrite the previous equation as follows:

$$\frac{1}{N}\frac{dN}{dt} = \frac{1}{hr_{0,R}} \frac{-2(r_0 + d_N)(-aN + hr_{0,R})}{-1 - \beta N(1 - \frac{2}{\beta_R h r_{0,R}}) - \sqrt{1 + \beta N(\beta N + 2\delta - \frac{4\beta d_R}{a\beta_R})}} \tag{S33}$$

which equals

$$\frac{1}{N}\frac{dN}{dt} = \frac{1}{hr_{0,R}} \frac{2(r_0 + d_N)(-aN + hr_{0,R})}{1 + \beta N(1 - \frac{2}{\beta_R h r_{0,R}}) + \sqrt{1 + \beta N(\beta N + 2\delta - \frac{4\beta d_R}{a\beta_R})}} \tag{S34}$$

S6 Fitting known density-regulation models to consumer dynamics with a type II functional response and biotic resources

For details of the fitting procedure see Supplementary Material S4.

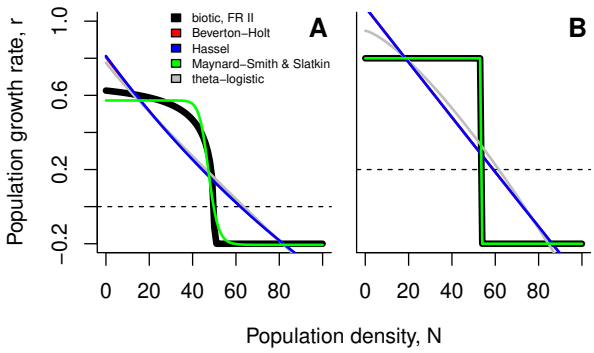

Figure S4: Fitting existing population growth models to the population growth function of consumer with a type II functional response feeding on biotic resources (Beverton-Holt model; Eq. 8). (A) High half-saturation constant and foraging rate ($h = 900$, $a = 9$) (B) Low half-saturation constant and foraging rate ($h = 1$, $a = 5$). Parameter examples: $r_{0,R} = 0.5$, $\beta_R = 0.001$, $d_R = 0.05$, $e = 0.1$, $d = 0.2$.

S7 Fitting population growth models to data

Study organism, experimental procedure and data collection

We used 7 strains of the freshwater ciliate *Tetrahymena thermophila* (strains: SB3539, B2086.2, A*III, CU438.1, A*V, CU427.4, CU428.2) originally obtained from the Cornell Tetrahymena Stock Center. These strains were kept for maintenance and during the experiments in protist medium (1 g dried *Lactuca sativa* powder in 1.6 L Volvic water) with *Serratia marcescens* as a food resource.

Growth experiments were carried out in 20 mL vials (Sarstedt) at 20 °C. 6 replicated growth curves of each *Tetrahymena* strain were started with 250 µL of protist culture (4 d old, at equilibrium) in 20 mL bacterized medium (10% *Serratia marcescens* from a 3 d old culture that had reached equilibrium). The growth experiment was followed over the course of 2 weeks and 2 mL of medium was replaced in each microcosm three times per week with freshly bacterized new medium.

Data was collected using video recording and analysis. At regular intervals (twice per day for the first two days, subsequently once per day or once every 2–3 days) the microcosms were sampled and the samples were placed on a counting slide (height: 0.5 mm) under a stereomicroscope (Perfex Pro 10) at a 2-fold magnification. Using a microscope camera (Perfex SC38800) videos were recorded for a total duration of 10 s at a rate of 15 frames per second imaging a volume of 31 µL. Videos were subsequently analysed using a customized version of the 'bemovi' package (Pennekamp et al., 2015) in R.

Model fitting

We used the 'rstan' package in R to solve the ODEs and fit the 4 potential growth models (logistic, Eq. 1; Beverton-Holt, Eq. 8; Eq. 11; Maynard Smith-Slatkin, Eq. 13). For a detailed description see Rosenbaum et al. (2018). To facilitate fitting, both data and model parameters (except δ in Eq. 11) were log-transformed, and, besides fitting the respective parameters of the ODEs we also fitted the initial density as a free parameter. Priors were chosen based on published data on *Tetrahymena* (Fronhofer and Altermatt, 2015; Fronhofer et al., 2017; Altermatt and Fronhofer, 2018). See below for the rstan model code.

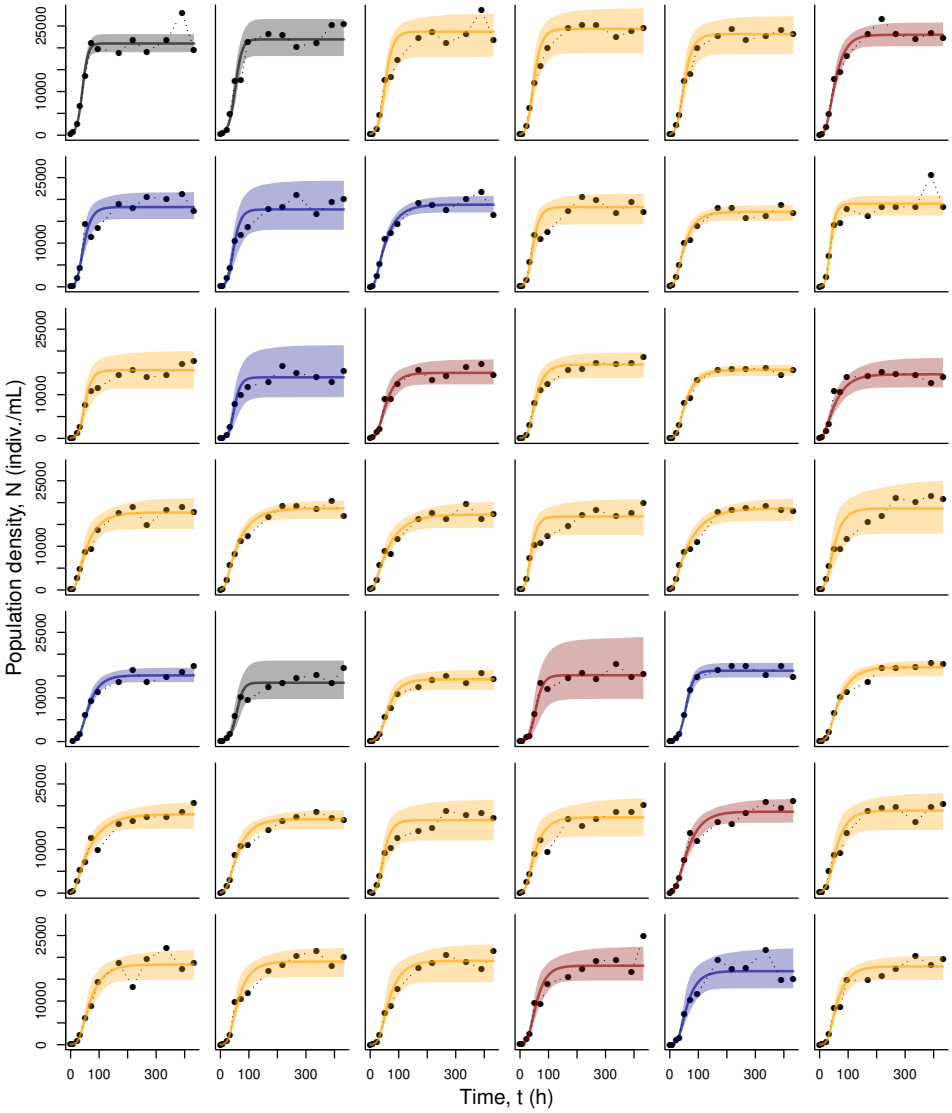

Figure S5: Fitting population growth models to *Tetrahymena thermophila* dynamics using Bayesian inference (see Supplementary Material S7 and Rosenbaum et al. (2018) for details). We fitted the logistic (black; Eq. 1), the Beverton-Holt model (blue; Eq. 8), Eq. 11 (orange) as well as the Maynard Smith-Slatkin model (red; Eq. 13) and compared fits using WAIC. Only the best fit is shown. Columns indicate technical replicates of growth curves, while rows show different genotypes of *Tetrahymena thermophila* (strains from top to bottom: SB3539, B2086.2, A*III, CU438.1, A*V, CU427.4, CU428.2).

Stan code

```
# stan rK model
stanmodelcode_rK = '
// function that caclulates r-K logistic population growth
functions{
  real[] odemodel(real t, real[] N, real[] p, real[] x_r, int[] x_i){
    // p[1]=r0, p[2]=K
    real dNdt[1];
    dNdt[1] = p[1] * (1 - (N[1]/p[2])) * N[1];
    return dNdt;
  }
}

data{
  int n;
  real log_N0;
  real log_N[n];
  real t0;
  real t[n];
}

transformed data {
  // not used here
  real x_r[0];
  int x_i[0];
}

parameters{
  real log_r;
  real log_K;
  real log_N0sim;
  real<lower=0> sdev;
}

transformed parameters{
  real p[2];
  real Nsim[n,1]; // simulated values, matrix. dim1 = time, dim2 = dim_ODE = 1
  real N0sim_dummy[1]; // a dummy because the ODE solver requires real[] instead of real

  // parameters for integrator
  p[1] = exp(log_r);
  p[2] = exp(log_K);
```

```
  N0sim_dummy[1] = exp(log_N0sim);  // see above

  // integrate ODE
  Nsim = integrate_ode_rk45(odemodel,N0sim_dummy,t0,t,p,x_r,x_i);
}

model{
  // priors
  log_r ~ normal(log(0.1), 1.5);
  log_K ~ normal(log(10000), 1);
  log_N0sim ~ normal(log(500),2);
  sdev ~ cauchy(0,1);

  // likelihood
  log_N0 ~ normal(log_N0sim,sdev);
  for (i in 1:n){
    log_N[i] ~ normal(log(Nsim[i,1]),sdev);
  }
}

// cacluate log lik to get waic
// from loo R package description
generated quantities {
  real log_lik[n];
  for (nn in 1:n){
    log_lik[nn] = normal_lpdf(log_N[nn] | log(Nsim[nn,1]), sdev);
  }
}
'
```

```
# stan BH model
stanmodelcode_BH = '
// function that caclulates BH population growth
functions{
  real[] odemodel(real t, real[] N, real[] p, real[] x_r, int[] x_i){
    // p[1]=r0, p[2]=d, p[3]=K
    real dNdt[1];
    dNdt[1] = ((p[1] + p[2])/(1 + ((p[1]/(p[3]*p[2])) * N[1])) - p[2])*N[1];
    return dNdt;
  }
}
```

```
data{
  int n;
  real log_N0;
  real log_N[n];
  real t0;
  real t[n];
}

transformed data {
  // not used here
  real x_r[0];
  int x_i[0];
}

parameters{
  real log_r;
  real log_d;
  real log_K;
  real log_N0sim;
  real<lower=0> sdev;
}


transformed parameters{
  real p[3];
  real Nsim[n,1]; // simulated values, matrix. dim1 = time, dim2 = dim_ODE = 1
  real N0sim_dummy[1]; // just a dummy because the ODE solver requires real[] instead of
    real

  // parameters for integrator
  p[1] = exp(log_r);
  p[2] = exp(log_d);
  p[3] = exp(log_K);
  N0sim_dummy[1] = exp(log_N0sim);  // see above

  // integrate ODE
  Nsim = integrate_ode_rk45(odemodel,N0sim_dummy,t0,t,p,x_r,x_i);
}

model{
  // priors
```

```
  log_r ~ normal(log(0.1), 1.5);
  log_K ~ normal(log(10000), 1);
  log_d ~ normal(log(0.1),1.5);
  log_N0sim ~ normal(log(500),2);
  sdev ~ cauchy(0,1);

  // likelihood
  log_N0 ~ normal(log_N0sim,sdev);
  for (i in 1:n){
    log_N[i] ~ normal(log(Nsim[i,1]),sdev);
  }
}

// cacluate log lik to get waic
// from loo R package description
generated quantities {
  real log_lik[n];
  for (nn in 1:n){
    log_lik[nn] = normal_lpdf(log_N[nn] | log(Nsim[nn,1]), sdev);
  }
}
'
```

```
# stan abiotic resources and consumer functional response type II model
stanmodelcode_abioticFR2 = '
// function that caclulates BH population growth
functions{
  real[] odemodel(real t, real[] N, real[] p, real[] x_r, int[] x_i){
    // p[1]=r0, p[2]=d, p[3]=K, p[4]=delta
    real dNdt[1];
    dNdt[1] = ( 2*(p[1]+p[2])/(1 + (4*p[1]*(p[1]+p[2]))/(p[3] * p[2] * (4*p[1]+2*p[2]+p
    [4]*p[2])) * N[1] + sqrt(1 + (4*p[1]*(p[1]+p[2]))/(p[3] * p[2] * (4*p[1]+2*p[2]+p[4]*
    p[2])) * N[1]*((4*p[1]*(p[1]+p[2]))/(p[3] * p[2] * (4*p[1]+2*p[2]+p[4]*p[2]))*N[1]-p
    [4])) ) - p[2] ) * N[1];
  return dNdt;
  }
}

data{
  int n;
  real log_N0;
```

```
  real log_N[n];
  real t0;
  real t[n];
}

transformed data {
  // not used here
  real x_r[0];
  int x_i[0];
}

parameters{
  real log_r;
  real log_d;
  real log_K;
  real <lower=-2,upper=2> delta;
  real log_N0sim;
  real<lower=0> sdev;
}


transformed parameters{
  real p[4];
  real Nsim[n,1]; // simulated values, matrix. dim1 = time, dim2 = dim_ODE = 1
  real N0sim_dummy[1]; // just a dummy because the ODE solver requires real[] instead of
    real

  // parameters for integrator
  p[1] = exp(log_r);
  p[2] = exp(log_d);
  p[3] = exp(log_K);
  p[4] = delta;
  N0sim_dummy[1] = exp(log_N0sim);  // see above

  // integrate ODE
  Nsim = integrate_ode_rk45(odemodel,N0sim_dummy,t0,t,p,x_r,x_i);
}

model{
  // priors
  log_r ~ normal(log(0.1), 1.5);
  log_K ~ normal(log(10000), 1);
```

```
  log_d ~ normal(log(0.1),1.5);
  delta ~ uniform(-2,2);
  log_N0sim ~ normal(log(500),2);
  sdev ~ cauchy(0,1);

  // likelihood
  log_N0 ~ normal(log_N0sim,sdev);
  for (i in 1:n){
    log_N[i] ~ normal(log(Nsim[i,1]),sdev);
  }
}

// cacluate log lik to get waic
// from loo R package description
generated quantities {
  real log_lik[n];
  for (nn in 1:n){
    log_lik[nn] = normal_lpdf(log_N[nn] | log(Nsim[nn,1]), sdev);
  }
}
'
```

```
# stan MSS model
stanmodelcode_MSS = '
// function that caclulates BH population growth
functions{
  real[] odemodel(real t, real[] N, real[] p, real[] x_r, int[] x_i){
    // p[1]=r0, p[2]=d, p[3]=K, p[4]=gamma
    real dNdt[1];
    dNdt[1] = ((p[1] + p[2])/(1 + ( ( 1/p[3] * (p[1]/p[2])^(1/p[4]) )  * N[1])^p[4]) - p
    [2])*N[1];
  return dNdt;
  }
}

data{
  int n;
  real log_N0;
  real log_N[n];
  real t0;
  real t[n];
```

```
}

transformed data {
  // not used here
  real x_r[0];
  int x_i[0];
}

parameters{
  real log_r;
  real log_d;
  real log_K;
  real log_N0sim;
  real log_gamma;
  real<lower=0> sdev;
}


transformed parameters{
  real p[4];
  real Nsim[n,1]; // simulated values, matrix. dim1 = time, dim2 = dim_ODE = 1
  real N0sim_dummy[1]; // just a dummy because the ODE solver requires real[] instead of
    real

  // parameters for integrator
  p[1] = exp(log_r);
  p[2] = exp(log_d);
  p[3] = exp(log_K);
  p[4] = exp(log_gamma);
  N0sim_dummy[1] = exp(log_N0sim);  // see above

  // integrate ODE
  Nsim = integrate_ode_rk45(odemodel,N0sim_dummy,t0,t,p,x_r,x_i);
}

model{
  log_r ~ normal(log(0.1), 1.5);
  log_K ~ normal(log(10000), 1);
  log_d ~ normal(log(0.1), 1.5);
  log_N0sim ~ normal(log(500),2);
  log_gamma ~ normal(log(1),0.3);
  sdev ~ cauchy(0,1);
```

```
  // likelihood, normal (maybe lognormal helpful)
  log_N0 ~ normal(log_N0sim,sdev);
  for (i in 1:n){
    log_N[i] ~ normal(log(Nsim[i,1]),sdev);
  }
}

// cacluate log lik to get waic
// from loo R package description
generated quantities {
  real log_lik[n];
  for (nn in 1:n){
    log_lik[nn] = normal_lpdf(log_N[nn] | log(Nsim[nn,1]), sdev);
  }
}
,
```

S8 Temperature scaling of equilibrium densities

Substituting Eq. 14 for all biological rates, except the assimilation coefficient, e, which has been shown to be temperature independent (Del Giorgio and Cole, 1998; López-Urrutia and Morán, 2007), into Eq. 10 gives the expression of temperature dependent equilibrium population density of a filter feeding consumer feeding on abiotic resource:

$$\widehat{N}(T) = \frac{\omega(e_0 a_0 e^{-\frac{E_a}{kT}} R_0 - d_0 e^{-\frac{E_a}{kT}})}{a_0 e^{-\frac{E_a}{kT}} d_0 e^{-\frac{E_a}{kT}}}. \tag{S35}$$

Assuming that all activation energies E_a are identical, we can simplify this to

$$\widehat{N}(T) = \frac{\omega(e_0 a_0 R_0 - d_0)}{a_0 d_0} e^{\frac{E_a}{kT}}. \tag{S36}$$

More generally, in terms of density-dependence, we obtain for the capita growth rate of the consumer:

$$r(N,T) = \frac{e_0 a_0 e^{-\frac{E_a}{kT}} R_0}{1 + \frac{a_0 e^{-\frac{E_a}{kT}}}{\omega} N} - d_0 e^{-\frac{E_a}{kT}}. \tag{S37}$$

Under the same assumptions that all activation energies are identical, we can simplify the previous equation to:

$$r(N,T) = \frac{e_0 a_0 R_0}{e^{\frac{E_a}{kT}} + \frac{a_0}{\omega} N} - d_0 e^{-\frac{E_a}{kT}}. \tag{S38}$$

In analogy, temperature dependence of the equilibrium density can be investigated for type II functional responses and abiotic resources. In this case, we can use Eq. S12 and Eq. 14 to obtain:

$$\widehat{N}(T) = \frac{e_0 \omega}{d_0 e^{-\frac{E_a}{kT}}} \left(\frac{d_0 (R_0 + h_0 e^{\frac{E_a}{kT}}) - e_0 a_0 R_0}{d_0 - a_0 e_0} \right). \tag{S39}$$

Similarly, we can use Eq. S29 and Eq. 14 to obtain the temperature dependence of a consumer characterized by a type II functional response feeding on biotic resources. Without repeating the above derivation we obtain $\widehat{N}(T) = \widehat{N_0} e^{\frac{E_a}{kT}}$.

S9 Multi-species extensions

Multiple consumers

We here consider consumer-resource dynamics, where we have two consumer species feeding on one abiotic resource (similar to Eqs. 5 and 6 in the main text). In analogy to our previous considerations, we assume the following dynamics:

$$\frac{dR}{dt} = \omega R_0 - \omega R - a_1 N_1 R - a_2 N_2 R \tag{S40a}$$

$$\frac{dN_1}{dt} = e_1 a_1 R N_1 - d N_1 \tag{S40b}$$

$$\frac{dN_2}{dt} = e_2 a_2 R N_2 - d N_2. \tag{S40c}$$

Solving the resource for equilibrium we get:

$$\widehat{R} = \frac{\omega R_0}{\omega + a_1 N_1 + a_2 N_2}. \tag{S41}$$

We can now substitute Eq. S41 into Eq. S40b and get:

$$\begin{aligned} \frac{1}{N_1}\frac{dN_1}{dt} &= e_1 a_1 \widehat{R} - d \\ &= \frac{e_1 a_1 \omega R_0}{\omega + a_1 N_1 + a_2 N_2} - d \\ &= \frac{e_1 a_1 R_0}{1 + \frac{a_1}{\omega} N_1 + \frac{a_2}{\omega} N_2} - d. \end{aligned} \tag{S42}$$

Similarly, substituting equation (S41) into equation (S40c) gives:

$$\frac{1}{N_2}\frac{dN_2}{dt} = \frac{e_2 a_2 R_0}{1 + \frac{a_1}{\omega} N_1 + \frac{a_2}{\omega} N_2} - d.$$

Hence, for a system with n consumer species, uniquely indexed with $i \in \{1, \ldots, n\}$, we get the consumer dynamics of species i:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_{0,i} + d}{1 + \sum_{j=1}^{n} \beta_j N_j} - d_i \tag{S43}$$

with $\beta_j = \frac{a_j}{\omega}$.

Multiple resources

There may also exist consumer-resource systems with multiple resources. We here consider a system with two abiotic resources, and one consumer species. This results in the following system of equations:

$$\frac{dR_1}{dt} = \omega_1 R_{0,1} - \omega_1 R_1 - a_1 N R_1 \tag{S44a}$$
$$\frac{dR_2}{dt} = \omega_2 R_{0,2} - \omega_2 R_2 - a_2 N R_2 \tag{S44b}$$
$$\frac{dN}{dt} = e_1 a_1 R_1 N + e_2 a_2 R_2 N - dN \tag{S44c}$$

Solving this system to resource equilibrium gives for $\widehat{R}_1 = \frac{\omega_1 R_{0,1}}{\omega_1 + a_1 N}$ and $\widehat{R}_2 = \frac{\omega_2 R_{0,2}}{\omega_2 + a_2 N}$. Substituting both resource equilibria into Eq. S44C gives:

$$\frac{1}{N}\frac{dN}{dt} = \frac{e_1 a_1 \omega_1 R_{0,1}}{\omega_1 + a_1 N} + \frac{e_2 a_2 \omega_2 R_{0,2}}{\omega_2 + a_2 N} - d.$$

Hence, for a system with multiple resources, uniquely indexed with $r \in \{1, \ldots, m\}$, we would find the following consumer dynamics:

$$\frac{1}{N}\frac{dN}{dt} = \sum_r \frac{e_r a_r R_{0,r}}{1 + \beta_r N} - d. \tag{S45}$$

However, when determining r_0 by setting $N = 0$, we get: $r_0 = \sum_r e_r a_r R_{0,r} - d$. Note that because of the different denominators we cannot easily substitute this into Eq. S45.

Multiple resources and multiple consumers

$$\frac{dR_1}{dt} = \omega_1 R_{0,1} - \omega_1 R_1 - a_{11} N_1 R_1 - a_{12} N_2 R_1 \tag{S46a}$$
$$\frac{dR_2}{dt} = \omega_2 R_{0,2} - \omega_2 R_2 - a_{21} N_1 R_2 - a_{22} N_2 R_2 \tag{S46b}$$
$$\frac{dN_1}{dt} = e_{11} a_{11} R_1 N_1 + e_{21} a_{21} R_2 N_1 - d_1 N_1 \tag{S46c}$$
$$\frac{dN_2}{dt} = e_{12} a_{12} R_1 N_2 + e_{22} a_{22} R_2 N_2 - d_2 N_2 \tag{S46d}$$

Solving to resource equilibrium gives $\widehat{R}_1 = \frac{\omega_1 R_{0,1}}{\omega_1 + a_{11} N_1 + a_{22} N_2}$ and $\widehat{R}_2 = \frac{\omega_2 R_{0,2}}{\omega_2 + a_{11} N_1 + a_{22} N_2}$. Substituting these resource equilibria into Eq. S46c gives:

$$\frac{1}{N}\frac{dN}{dt} = \frac{e_{11} a_{11} \omega_1 R_{0,1}}{\omega_1 + a_{11} N_1 + a_{22} N_2} + \frac{e_{21} a_{21} \omega_2 R_{0,2}}{\omega_2 + a_{11} N_1 + a_{22} N_2} - d_1.$$

Similarly, substituting $\widehat{R}_1$ and $\widehat{R}_2$ into Eq. S46d gives:

$$\frac{1}{N}\frac{dN}{dt} = \frac{e_{12}a_{12}\omega_1 R_{0,1}}{\omega_1 + a_{11}N_1 + a_{22}N_2} + \frac{e_{22}a_{22}\omega_2 R_{0,2}}{\omega_2 + a_{11}N_1 + a_{22}N_2} - d_1.$$

From this it follows that for a system with m resources and n consumers, the consumer dynamics of a consumer species i is given by the following equation:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \sum_r \frac{e_{i,r}a_{i,r}R_{0,r}}{1 + \sum_j \beta_{j,r}N_j} - d_i, \tag{S47}$$

where $\beta_{jr} = \frac{a_{jj}}{\omega_r}$. This is Eq. 18 found in the main text.

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