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To cite this version:

Emanuel A Fronhofer, Lynn Govaert, Mary I O'Connor, Sebastian J Schreiber, Florian Altermatt. The shape of density dependence and the relationship between population growth, intraspecific competition and equilibrium population density. Oikos, 2023, 2024 (2), pp.e09824. 10.1111/oik.09824 . hal-04624339

HAL Id: hal-04624339
https://hal.umontpellier.fr/hal-04624339v1

Submitted on 25 Jun 2024

OIKOS

Research article

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

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Oikos
2024: e09824
doi: 10.1111/oik.09824

Subject Editor: Shurong Zhou
Editor-in-Chief: Dries Bonte
Accepted 15 October 2023

The logistic growth model is one of the most frequently used formalizations of density dependence affecting population growth, persistence and evolution. Ecological and evolutionary theory, and applications to understand population change over time often include this model. However, the assumptions and limitations of this popular model are often not well appreciated. Here, we briefly review past use of the logistic growth model and highlight limitations by deriving population growth models from underlying consumer–resource dynamics. We show that the logistic equation likely is not applicable to many biological systems. Rather, density-regulation functions are usually non-linear and may exhibit convex or concave curvatures depending on the biology of resources and consumers. In simple cases, the dynamics can be fully described by the Schoener model. More complex consumer dynamics show similarities to a Maynard Smith–Slatkin model. We show how population-level parameters, such as intrinsic rates of increase and equilibrium population densities are not independent, as often assumed. Rather, they are functions of the same underlying parameters. The commonly assumed positive relationship between equilibrium population density and competitive ability is typically invalid. We propose simple relationships between intrinsic rates of increase and equilibrium population densities that capture the essence of different consumer–resource systems. 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 as a test case for our theoretical predictions. Our results show that 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 relationships

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between model parameters, which has implications for theory and for formulating biologically sound and empirically testable predictions.

Keywords: Beverton–Holt model, carrying capacity, chemostat, consumer–resource interaction, density regulation, functional response, growth curve, K-selection, logistic growth, Maynard Smith–Slatkin model

Introduction

Population regulation and density dependence of population growth are at the core of fundamental but also controversial research in ecology (Turchin 1999, Henle et al. 2004, Sibly et al. 2005, Herrando-Pérez et al. 2012, Krebs 2015, Sæther 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-Pérez et al. 2012). This level of abstraction makes the interpretation of parameters challenging and may lead to paradoxical behaviours (Ginzburg 1992, Gabriel et al. 2005, Mallet 2012). Such 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:

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

Additional challenges arise when these parameters, especially the carrying capacity (K), are interpreted in an evolutionary context ('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 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. Recently, Reding-Roman et al. (2017) found positive $r - K$ relationships in microbial systems counter to their initial hypothesis, which led the authors to postulate 'trade-ups' and 'uberbugs' while discussing the relevance of these findings for cancer (Aktipis et al. 2013) and antibiotic resistance research (paper highlighted by Reznick and King 2017). Although these and related issues have been discussed in detail by Matessi and Gatto (1984), Reznick et al. (2002), Rueffler et al. (2006) and Mallet (2012), to name but a few, current empirical work continues to expect negative $r - K$ relationships (Fronhofer and Altermatt 2015, Reding-Roman et al. 2017) and some theory continues to use 'K' as an evolving trait (Lande et al. 2009, Burton et al. 2010, Engen and Sæther 2017, Fleischer et al. 2018).

In order to resolve some of the issues associated with the logistic growth model as described by Eq. 1, Mallet (2012), for instance, has promoted the use of Verhulst's original $r - \alpha$ formulation of logistic growth (Kostitzin 1937, 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:

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

From Eq. 2 it follows that the population density at equilibrium is $\hat{N} = r_0\alpha^{-1}$. 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 resource dynamics and especially consumer traits have to be taken into account in order to understand density-dependent selection (Fronhofer and Altermatt 2015). Such consumer–resource models provide a framework that can be used in an eco-evolutionary context (see McPeek 2017 for a detailed discussion) 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 empirical data is often not sufficient for confronting such models with data (Rosenbaum and Fronhofer 2023). In an attempt to simplify, some studies have explored under what conditions population level growth models (e.g. the logistic, Eq. 1–2) can be used to describe the underlying consumer–resource dynamics. For instance, consumer–resource dynamics potentially 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 (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 (2009b) 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 (see Abrams 2009c for an extension of this work to include multiple resources species). He showed that density dependence is non-linear if one assumes a Holling type II functional response for the consumer (Abrams 2002), but that this non-linearity is different from the θ-logistic model. He finally extended his work to include a type III functional response and non-linear numeric responses. Reynolds and Brassil (2013) discussed, extended and reinterpreted these findings. Recently, O'Dwyer (2018) used the same approach to discuss the general applicability of Lotka–Volterra equations. 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 mechanistic 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 Supporting information for a discussion of Lakin and Van Den Driessche 1977). We use these derivations to show how intrinsic rates of increase, competitive abilities and equilibrium population densities are non-independent and provide explicit relationships between those parameters. In addition, we highlight evolutionary consequences of these relationships and show the potential of deriving climate driven population growth models by discussing how to extend our results based on the metabolic theory of ecology (Brown et al. 2004) and multiple interacting species. Finally, we confront our theoretically derived growth models with time series data of population dynamics of microbial organisms, which are commonly used as model systems, using Bayesian inference.

Modelling populations using consumer–resource models

In order to derive population growth models and the density-regulation function capturing how per capita consumer population growth rates (r) change depending on population density (N), as well as to understand relationships between population-level parameters, 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 (see Hek 2010, O'Dwyer 2018 for critical discussions), that is, assuming that resources quickly equilibrate $\left(\frac{dR}{dt} = 0\right)$ and solving Eq. 3a for R, we obtain the resource equilibrium density $\hat{R}$ (piecewise defined, that is, $\hat{R} = 0$ if there is no positive equilibrium). The per capita consumer dynamics (density-regulation function) then become:

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

Throughout, we assume that the resource dynamics occur at a faster time scale than the consumer. If resources and consumers exhibit similar rates, dynamics may be more complex and it is likely appropriate to study the full consumer–resource model.

In order to understand how the form of the density-regulation function, that is, the function linking per capita population growth to population density (Eq. 4), depends on different consumer and resource characteristics (e.g. non-saturating consumers, saturating consumers, respectively, abiotic or biotic resources) we explore multiple functional forms of $f(R)$ and $g(R)$, including a chemostat model for resource growth ($f(R)$), as well as linear and type II (saturating) functional responses for the consumer ($g(R)$). See Table 1 for an overview of the model components used here. For simplicity, our work does not consider the possibility of predator-dependent functional responses (see Abrams 2014 for a discussion and overview), although these can be included in principle, for instance using a Beddington–DeAngelis functional response (Geritz and Gyllenberg 2012). Such a functional response may also be able to represent spatial variation and behavioural complexities (Cosner et al. 1999).

As a large part of the work introduced above, we stay in the realm of deterministic ordinary differential equations

Table 1. Model overview. Components and combinations of consumer–resource models used here. R is the resource population density. For chemostat resource population growth models ω is the flow rate into and out of the system and R_0 is the resource concentration flowing into the system. For biotic, that is Schoener, resource population growth models (for a justification of using this specific model, see main text), r_0 is the intrinsic rate of increase, d the death rate and β the intraspecific competition coefficient. In consumer functional responses (FR) a represents the foraging rate, while h is the half-saturation constant for saturating consumers. Here, we assume that non-saturating consumers follow a linear functional response, for simplicity. In the Supporting information we report results for the classical type I functional response of filter feeders (Jeschke et al. 2004), which is linear up to a saturation point.

	$g(R)=aR$	$g(R)=\frac{aR}{h+R}$
$f(R)=\omega R_0-\omega R$	Abiotic resources (chemostat model) linear consumer FR	Abiotic resources (chemostat model) saturating, type II FR
$f(R)=\left(\frac{r_0+d}{1+\beta R}-d\right)R$	Biotic resources (Schoener model) linear consumer FR	Biotic resources (Schoener model) saturating, type II FR

(ODEs), which have a long tradition in ecology and evolution. Of course, this implies that we are considering expected population sizes in continuous time systems and the equations may therefore be most appropriate for capturing the dynamics of biomass (Yodzis and Innes 1992). Nevertheless, over finite time frames, trajectories of corresponding individual-based models usually remain close to trajectories of the ODE whenever habitat size is sufficiently large (Kurtz 1981).

We start by exploring scenarios that are appropriate for basal biotic consumers feeding on abiotic resources. Then, we use these results to describe biotic resources fed upon by higher tropic level consumers and derive density-regulation functions, that is, the function linking per capita consumer growth to consumer density, describing the dynamics of the latter consumers. In all cases we show how population level parameters, specifically intrinsic rates of increase (r_0) and equilibrium population densities ($\hat{N}$), are impacted by and interrelated due to consumer traits such as parameters of the functional response ($g(R)$) as well as the assimilation coefficient (e) and the consumer's death rate (d).

A simple case: non-saturating consumers

Abiotic resources

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

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

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:

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

We here assume a linear functional response, that is, the consumer does not saturate. Clearly, this is a strong assumption and even filter feeders (Jeschke et al. 2004) may exhibit a saturation after an initially linear functional response. We treat this latter case in the Supporting information.

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

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

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):

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

with β being the intraspecific competition coefficient in analogy to α in Verhulst's model (Eq. 2). We will here always describe the parameters scaling per capita population growth rate with population density as intraspecific competitive ability. In the following, we will refer to Eq. 8 as the Schoener (1978) model.

In contrast to the logistic growth model (Eq. 1–2) the density-regulation function described by Eq. 8 is not linear (Fig. 1, Pástor et al. 2016). Rather, it is convex, implying a decreasing strength of density regulation with increasing population density. In other words, density-regulation reduces per capita population growth rate more quickly at low densities than at high densities (Fig. 1; note that here and in the following a concave shape implies a (local) negative second derivative while a convex shape implies a (local) positive second derivative). Importantly, this implies that already for very simple consumer–resource systems the logistic growth model does not hold (Lakin and Van Den Driessche 1977, see the Supporting information for a detailed discussion).

The convexity of the density-regulation function we report is defined by the resources and their density-dependence. This is due to the principle of the inheritance of the curvature described by Abrams (2009b), stating that the curvature of the density-regulation function of a consumer with a linear functional (and numerical) response is identical to the

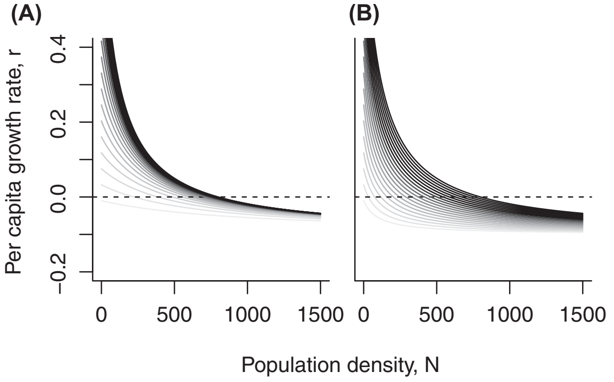

Figure 1. Density dependence for a non-saturating consumer (chemostat model for the resource and linear functional response for the consumer; Eq. 7). (A) Effect of changing the foraging rate (*a*) while keeping the assimilation efficiency constant ($e = 0.03$). (B) Effect of changing the assimilation efficiency parameter (*e*) while keeping the foraging rate constant ($a = 0.01$). In both panels, darker shades of grey indicate higher parameter values. Parameter values: $R_0 = 3000$, $\omega = 1$, $e \in [0.0003, 0.03]$, $a \in [0.001, 0.01]$, $d = 0.1$.

curvature of the density-regulation function of its resource. Indeed, resource density-dependence following the chemostat model is $\frac{1}{R}\frac{dR}{dt} = \omega\left(\frac{R_0}{R} - 1\right)$, which is a convex function.

We can also use Eq. 8 to study the relationship between population level parameters, such as the intrinsic rate of increase (r_0) and the equilibrium density ($\hat{N}$) of the consumer population. For non-saturating consumers the intrinsic rate of increase is

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

and the equilibrium density is obtained as

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

Importantly, this shows that intrinsic rates of increase (r_0; Eq. 9), competitive abilities ($\beta = \frac{a}{\omega}$; Eq. 8) and equilibrium population densities ($\hat{N}$; Eq. 10) depend on the same set of underlying parameters and are therefore not independent (Fig. 2). 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*). Counter to often made classical assumptions of a tradeoff between growth rates and equilibrium densities, populations of consumers best characterized by this model will always exhibit a positive relationship between equilibrium densities ($\hat{N}$) and intrinsic rates of increase, regardless of whether this is due to a change in foraging rate (*a*), assimilation efficiency (*e*), or death rate (*d*; Fig. 2). The increase will be linear for *e*, concave for *a*, and convex for *d*. If density-independent mortality (*d*) is very small, the effect of foraging rate (*a*) on the equilibrium population density ($\hat{N}$) is negligible and $\hat{N}$ only depends on the assimilation efficiency (*e*).

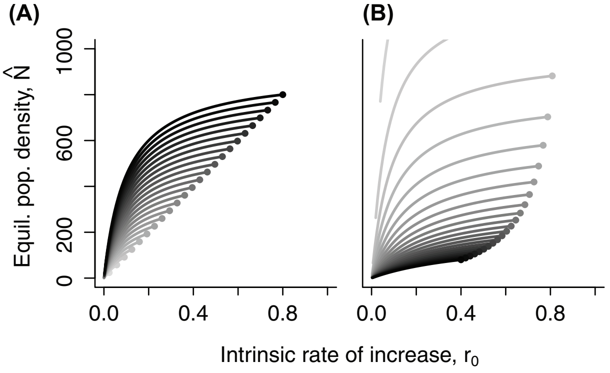

Figure 2. Relationship between intrinsic rate of increase (r_0) and equilibrium population density ($\hat{N}$) for consumers following a Schoener density-regulation function (chemostat model for the resource and linear functional response for the consumer; Eq. 7). (A) Effect of changing the foraging rate (*a*; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of *a*) and the assimilation efficiency (*e*; darker shades of grey indicate higher values of *e*) while the death rate is kept constant ($d = 0.1$). (B) Effect of changing the foraging rate (*a*; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of *a*) and the death rate (*d*; darker shades of grey indicate higher values of *d*) while the assimilation efficiency is kept constant ($e = 0.03$). Parameter values: $R_0 = 3000$, $\omega = 1$, $e \in [0.003, 0.03]$, $a \in [0.001, 0.01]$, $d \in [0.01, 0.5]$.

Our considerations up to now may best apply to filter feeding organisms, including branchiopods, some insect larvae, bryozoans, ascidians and molluscs, for example. It is important to note that, following Jeschke et al. (2004), even filter feeders do exhibit a saturation eventually. We explicitly treat this case in the Supporting information where we show that the resulting density-dependence is more complex and exhibits density independent growth at low densities (Supporting information) but follows the Schoener model for higher densities. Our results regarding the interrelationships between intrinsic rates of increase, competitive abilities and equilibrium population densities remain qualitatively unchanged (Supporting information).

Biotic resources

Since the population dynamics of non-saturating consumers of a first trophic level can be described by the Schoener model (Eq. 8), we can investigate population dynamics of the next tropic level. We start by considering a non-saturating resource where *f*(*R*) can be described by Eq. 8 and a non-saturating consumer where *g*(*R*) is linear. Without repeating the previously described derivation, we can use the principle of the inheritance of the curvature as stated above (Abrams 2009b), and conclude that the population dynamics of any non-saturating consumers in a food chain with a basal abiotic resource will follow the Schoener model (Eq. 8).

A more complex case: saturating consumers

Abiotic resources

Up to now we have assumed a linear functional response for $g(R)$ (see the Supporting information for filter feeders in the strict sense following 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, when the consumer follows a saturating (type II) functional response ($g(R) = \frac{aR}{h+R}$, where h is the half-saturation constant).

Substituting the resource equilibrium (Supporting information for details) into the consumer equation results in a density-regulation function that is more complex than the Schoener model (Eq. 8; Fig. 1):

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

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

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

as the equilibrium density.

The density-regulation function may now exhibit both concave and convex sections (Fig. 3, Eq. 11, Supporting information) and depends on four 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 Supporting information and δ in Eq. 11, Fig. 3C). The density-regulation function is concave at low densities only if $\delta > 0$ (which is equivalent to $R_0 > h$; Supporting information). 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 before density regulation kicks in at high densities (Supporting information). By contrast, the larger the half-saturation constant is, the more the type II functional response will approach a linear shape ($\delta \to -2$). The latter case approaches the Schoener model (see the Supporting information for details). The effect of changing h on the density-regulation function is shown in the Supporting information.

As discussed in the Supporting information, Eq. 11 behaves in part similarly to existing density- regulation functions, specifically the continuous-time version of the Maynard Smith and Slatkin (1973) model:

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

In this model, the equilibrium density is $\hat{N} = \frac{1}{\beta}\left(\frac{r_0}{d}\right)^{\frac{1}{\gamma}}$. Via its shape exponent γ the Maynard Smith–Slatkin model (Eq. 13) is flexible enough (Bellows 1981) to reproduce both the convex and concave parts of the density-regulation function (Supporting information) qualitatively. Clearly, Eq. 11, 13 are structurally similar, since the exponent γ of Eq. 13 can partly reproduce the square-root dependency of consumer growth we find in Eq. 11. However, since the Maynard Smith–Slatkin model does not have fewer parameters than Eq. 11, it does not represent a more parsimonious alternative. In addition, tuning parameters like γ in Eq. 13 are difficult to interpret biologically.

As in the simplest case of non-saturating consumers, intrinsic rates of increase (r_0; Supporting information), competitive

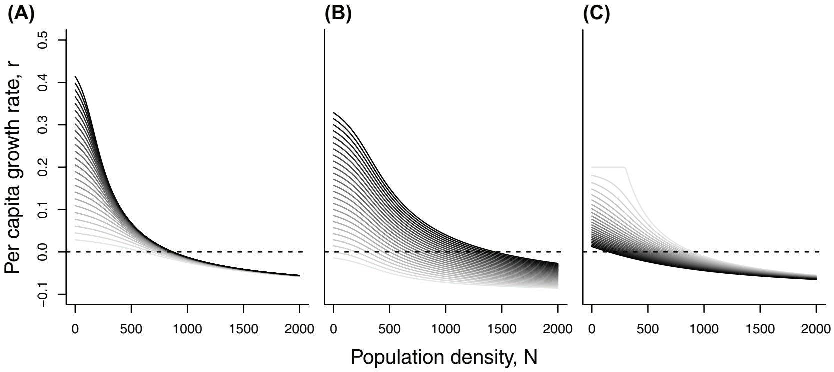

Figure 3. Density dependence for a consumer with a saturating, that is, type II, functional response (Supporting information) while resource remain abiotic. (A) Effect of changing the foraging rate (a) while keeping the assimilation efficiency ($e = 0.03$) and the half-saturation constant (h = 500) fixed. (B) Effect of changing the assimilation efficiency parameter (e) while keeping foraging rate ($a = 10$) and half-saturation constant ($h = 500$) fixed. (C) Effect of changing the half-saturation constant (h) while keeping foraging rate ($a = 10$) and assimilation efficiency ($e = 0.03$) fixed. In all panels darker shades of grey indicate higher parameter values. Parameter values: $R_0 = 3000$, $\omega = 1$, $e \in [0.01, 0.05]$, $a \in [5, 20]$, $h \in [0.1, 5000]$, $d = 0.1$.

abilities (β; Supporting information) and equilibrium population densities ($\hat{N}$; 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) and death rate (d). While competitive ability does not depend on the assimilation efficiency (e), equilibrium population densities and population growth rates increase with increasing assimilation efficiency. Therefore, as for non-saturating consumers, relationships between equilibrium population density ($\hat{N}$) and intrinsic rates of increase (r_0) will always be positive although the exact shape of the function will depend on which of the underlying consumer parameters is changing (Fig. 4).

Biotic resources

Consumers can also exhibit saturating functional responses ($g(R)$), while feeding on biotic resources. In this case, the Supporting information have to be adjusted (as shown in the Supporting information), which yields an even more complex density-regulation function (Fig. 5).

While some simplifications are possible, the resulting density-regulation function remains unwieldy with its seven parameters (Supporting information). Clearly, if such complex dynamics need to be analysed in detail, it might be more appropriate to directly rely on the consumer–resource model, especially if data for resource dynamics are available. However, the Supporting information presents a density-regulation function that, interestingly, behaves similarly to the well known, continuous-time version of the Maynard Smith and Slatkin (1973) model (Supporting information), as already discussed for Eq. 11. While clearly more parsimonious than the Supporting information, the Maynard Smith–Slatkin model is not flexible enough to capture certain aspects, such as the asymmetry in the density-regulation functions one can observe in Fig. 5, especially the concavity for low densities and the step-like behaviour at higher densities which arises from the non-linearity of the functional response and resource density-regulation function (Supporting information).

Up to here, for abiotic and biotic resources and non-saturating consumers, the equilibrium density was always a monotonically increasing function of the intrinsic rate of increase. In contrast to these simpler consumer–resource systems, our analyses show that for saturating consumers feeding on biotic resources this relationship can take many forms: unimodal, monotonically decreasing or increasing and $\hat{N}$ and r_0 can even be independent of each other (Fig. 6). Changes in the foraging rate (a) may lead to positive or negative relationships which are globally unimodal (Fig. 6A). Interestingly, changes in the assimilation efficiency (e) may not impact $\hat{N}$ while increasing r_0 (Fig. 6A). Decreasing death rates (d) lead to an increasing relationship between $\hat{N}$ and r_0 (Fig. 6B). Clearly, the unimodal pattern is centrally impacted by the half-saturation constant (h; Fig. 6C): very low values of h can lead to negative relationships between $\hat{N}$ and r_0. Such a negative relationship is otherwise only possible in the Lakin and Van Den Driessche (1977) model (Supporting information).

Confronting population growth models with data

Above, we show that many consumers that are bottom–up regulated will exhibit non-linear density regulation (Fig. 1, 3, 5). For capturing dynamics at the consumer level, we offer alternatives to the logistic growth formulation: In the simplest case of non-saturating consumers and abiotic resources the dynamics of the consumer follow exactly the Schoener model (Eq. 8). For more complex cases involving

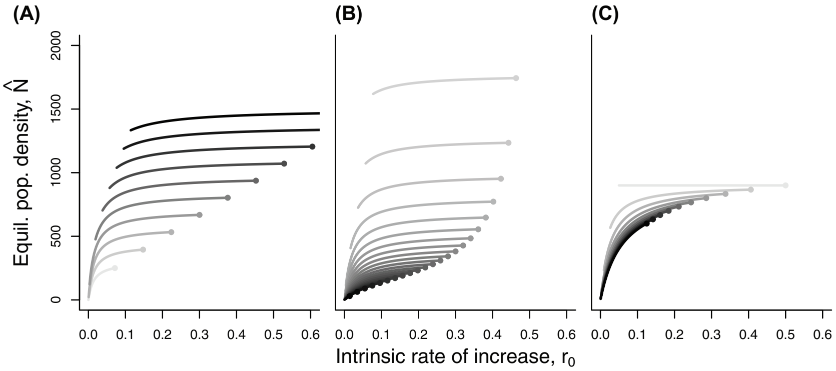

Figure 4. Relationship between intrinsic rate of increase (r_0) and equilibrium population density ($\hat{N}$) for consumers following Eq. 11 (chemostat model for the resource and saturating, that is, type II functional response for the consumer). (A) Effect of changing the foraging rate (a; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of a) and the assimilation efficiency (e; darker shades of grey indicate higher values of e) while the half-saturation constant and the death rate are kept constant ($h = 500$, $d = 0.1$). (B) Effect of changing the foraging rate (a; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of a) and the death rate (d; darker shades of grey indicate higher values of d) while the half-saturation constant and the assimilation efficiency are kept constant ($h = 500$, $e = 0.03$). (C) Effect of changing the foraging rate (a; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of a) and the half saturation constant (h; darker shades of grey indicate higher values of h) while the death rate and the assimilation efficiency are kept constant ($d = 0.1$, $e = 0.03$). Parameter values: $R_0 = 3000$, $\omega = 1$, $e \in [0.01, 0.05]$, $a \in [5, 20]$, $h \in [0.1, 5000]$, $d \in [0.01, 0.5]$.

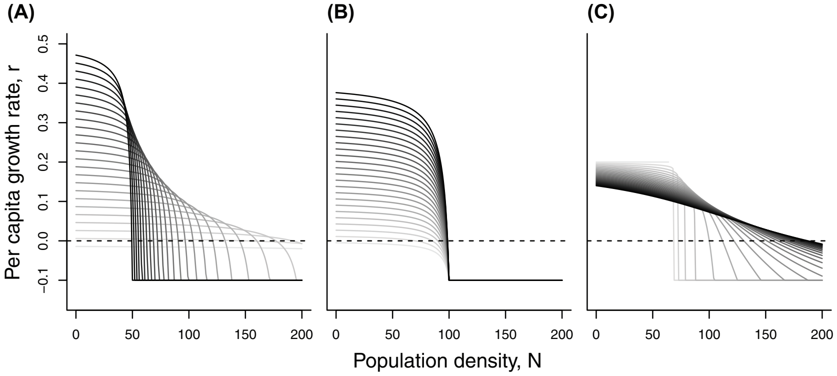

Figure 5. Density dependence for a consumer in a consumer–resource system with biotic resources (following the Schoener model; Eq. 8) and a saturating, that is, type II, functional response. (A) Effect of changing the foraging rate (a) while keeping assimilation efficiency (e = 0.03) and the half-saturation constant (h = 1000) fixed. (B) Effect of changing the assimilation efficiency parameter (e) while keeping foraging rate (a = 10) and half-saturation constant (h = 1000) fixed. (C) Effect of changing the half- saturation constant (h) while keeping foraging rate (a = 10) and assimilation efficiency (e = 0.03) fixed. In all three panels, darker shades of grey indicate higher parameter values. Parameter values: $r_{0,R} = 1$, $\beta_R = 0.001$, $d_R = 0.05$, $e \in [0.01, 0.05]$, $a \in [3, 20]$, $h \in [0, 5000]$, d = 0.1.

saturating consumers (non-linear functional responses) or biotic resources, Eq. 11 holds or the Maynard Smith–Slatkin model (Eq. 13) can be used as a heuristic description.

We will now consider how well these models perform when confronted with empirical data of a real biological system as a test example. 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 seven different genotypes, each replicated six times. We fit the logistic, the Schoener model, Eq. 11, and the Maynard Smith–Slatkin model to these dynamics using a Bayesian approach (trajectory matching; i.e. assuming pure observation error; see the Supporting information and Rosenbaum et al. (2019) 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 Schoener model or Eq. 11 to best describe the dynamics and therefore produce the best fit to the time-series data compared to other candidate models of density-dependent dynamics. Indeed, over the 42 growth curves the logistic model had, in general, the worst fit (in only 3 out of the 42 time-series the logistic was found to fit best using WAIC; for individual results see the Supporting information),

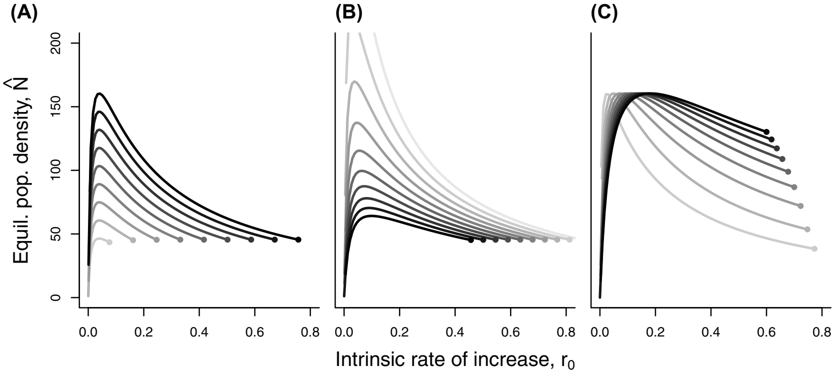

Figure 6. Relationship between intrinsic rate of increase (r_0) and equilibrium population density ($\hat{N}$) for saturating consumers feeding on biotic resources, that is, following the Supporting information (Schoener model for the resource and saturating, that is, type II functional response for the consumer). (A) Effect of changing the foraging rate (a; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of a) and the assimilation efficiency (e; darker shades of grey indicate higher values of e) while the half-saturation constant and the death rate are kept constant (h = 1000, d = 0.1). (B) Effect of changing the foraging rate (a; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of a) and the death rate (d; darker shades of grey indicate higher values of d) while the half-saturation constant and the assimilation efficiency are kept constant (h = 1000, e = 0.03). (C) Effect of changing the foraging rate (a; solid lines; dots represent the r_0 and $\hat{N}$ values for the highest value of a) and the half saturation constant (h; darker shades of grey indicate higher values of h) while the death rate and the assimilation efficiency are kept constant (d = 0.1, e = 0.03). Parameter values: $r_{0,R} = 1$, $\beta_R = 0.001$, $d_R = 0.05$, $e \in [0.01, 0.05]$, $a \in [3, 20]$, $h \in [0, 5000]$, $d \in [0.1, 0.5]$.

followed by the Schoener model (best fit in 7 out of 42 fits) and the Maynard Smith–Slatkin model (best fit in 6 out of 42 fits) while Eq. 11 performed best in 26 out of 42 cases (Fig. 7 for an example and the Supporting information for all fits). This finding is in good accordance with work showing that *Tetrahymena* may follow a type II functional response (Fronhofer and Altermatt 2015). Of course, this data set and the conclusions we can derive from the model fitting exercise are based on this specific case example and call for a more thorough test of our theoretical predictions across different taxa.

It is important to note that the models we use here are parameter-rich in comparison to the data, which may lead to overfitting. This becomes clear when using other information criteria such as LOO (leave- one-out cross-validation Vehtari et al. 2017), where our results for Fig. 7 remain qualitatively unchanged, however diagnostic values (Pareto k) indicate that fits may be sensitive to differences in model validation, that is, which data points are left out. One possibility to reduce the issue of overfitting is to fit multiple replicate time series at once using a joint likelihood function (see Rosenbaum and Fronhofer 2023 for more advanced fitting strategies).

Implications and extensions

Our derivations and the empirical support for Eq. 11 and the Schoener model in the specific case-example of the *Tetrahymena* system, clearly show the value of considering alternatives to the logistic growth model when modelling population dynamics with density-dependent rates. Even more importantly, our theoretical work highlights the underlying consumer–resource parameters being responsible for changes of and relationships between population level growth parameters (Fig. 2, 4, 6). In the following sections we discuss evolutionary consequences of our findings, and showcase extensions of our models to include temperature-dependence or multiple resource and consumer species.

Evolutionary consequences

Besides being crucial to ecology, density dependence and resulting density-dependent selection represents 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). The shape of density dependence is also crucial for understanding the consequences of adaptive prey evolution (Abrams 2009a), which is a central topic in eco-evolutionary dynamics research (Yoshida et al. 2003, Hiltunen et al. 2014).

From an evolutionary point of view, Matessi and Gatto (1984) discuss that density-dependent selection ('*K*-selection') should minimize equilibrium resource availability rather than maximizing $\hat{N}$ (note parallels to R^* theory, Tilman 1980 and MacArthur's minimum principle, MacArthur 1969, Gatto 1990, Ghedini et al. 2018). As a consequence, assuming a Lotka–Volterra model with a basal resource and two

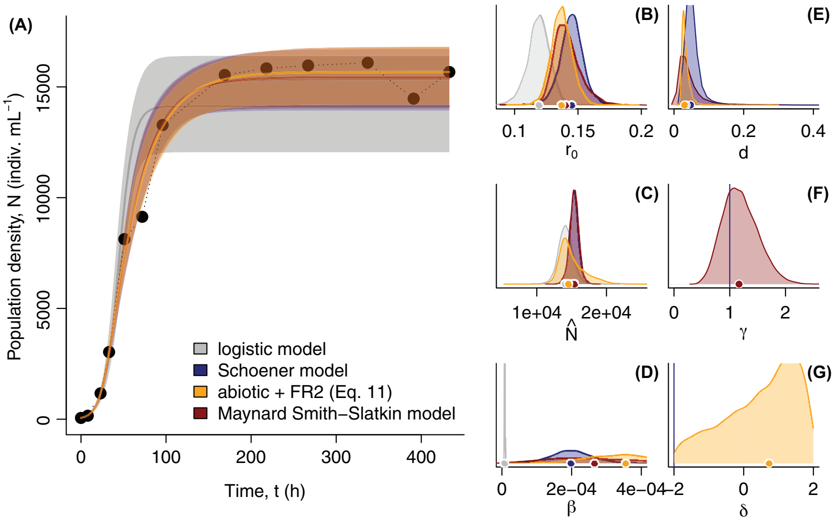

Figure 7. Fitting population growth models to *T. thermophila* dynamics using Bayesian inference (see the Supporting information and Rosenbaum et al. (2019) for details). We fitted the logistic (grey; Eq. 1), the Schoener model (blue; Eq. 8), Eq. 11 (orange), as well as the Maynard Smith–Slatkin model (red; Eq. 13) and compared fits using WAIC. Eq. 11 fitted best (WAIC = −19.21), but was very similar to both the Maynard Smith–Slatkin model (WAIC = −18.12) and to the Schoener model (WAIC = −16.81) while the logistic model clearly performed worst (WAIC = −2.38). As becomes clear in (A) the logistic model was not able to capture the asymmetry of the empirical growth curve well that approaches the equilibrium density more slowly than the logistic allows for. The panel shows medians and the 95th percentile of the posterior predictive distribution. (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 (F and the Supporting information). As a consequence, *T. thermophila* likely exhibits a type II functional response which is in good accordance with work by Fronhofer and Altermatt (2015).

competing consumers, Matessi and Gatto (1984) show that, at the consumer level, $\frac{d}{ea}$ will be minimized by evolution, as this strategy allows to reduce resource availability due to high values of e and/or a and low values of d and outcompete any other strategies. Therefore, density-dependent selection will increase r_0 (Eq. 9) and β, either leading to an increase or a decrease in equilibrium densities, depending on resource and consumer behaviour. Most importantly, an emerging negative relation between r_0 and $\hat{N}$ does not result from a tradeoff between population growth rates and competitive ability, as both parameters are always positively related. 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 non-saturating and saturating consumers, we find that for vanishingly small density-independent mortalities ($d \rightarrow 0$), the equilibrium population density ($\hat{N}$) 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 can evolution in the respective parameters (a or e) lead to a change in growth rate (r_0) without affecting the equilibrium population density ($\hat{N}$).

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 ($\hat{N}$). This result can be explained by our work if the protists exhibit a linear functional response (Fig. 2) or feed on abiotic resources (chemostat; Fig. 2, 4). 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 tradeoff 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.

Especially in the eco-evolutionary dynamics literature (Hendry 2017), it is often assumed that adaptation in the consumer will lead to increases in (equilibrium) population density. Correcting this view, Abrams (2019) has clarified that, adaptive population density declines can be predicted to occur regularly. In our work, adaptive population density decline, for instance, occurs in consumer–resource systems characterized by biotic resources and saturating consumers (unimodal $\hat{N} - r_0$ relationships; Fig. 6). Of course it should be noted that such declines may also happen in the other systems considered here: in Fig. 2, 4, 6 we have only considered that maximally two consumer parameter may change at once, this, of course, does not need to be the case. Additionally, the picture may be even more complicated by tradeoffs or relationships between the underlying consumer parameters (Kiørboe and Thomas 2020).

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 (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 (Supporting information).

Ecological extensions

Besides having consequences for evolutionary considerations, our work has implications for instance in the context of global change research (for a concrete example see the Supporting information). Linking consumer–resource parameters and population level quantities (like equilibrium densities or population growth rates) explicitly is at the centre of efforts to understand how populations behave under changing climatic conditions, specifically changing temperatures (Gilbert et al. 2014, Uszko et al. 2017, Bernhardt et al. 2018).

Finally, 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, one can expand our work to multiple species (see the Supporting information for some examples). For example, Abrams (2009c) presents an extension of Abrams (2009b) to include multiple resource species (O'Dwyer 2018).

Discussion and conclusion

Our theoretical 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 ($\hat{N}$) are not independent, but are all functions of consumer traits such as foraging rate and assimilation efficiency (Fig. 2, 4, 6). Contrary to the idea that growth rates and equilibrium densities are negatively related, we show that various relationships must be expected, depending on the underlying consumer–resource dynamics.

In accordance with previous work (Thieme 2003, Johst et al. 2008, Abrams 2009b, Reynolds and Brassil 2013) we show that 1) the logistic model (Eq. 1–2) assuming linear density dependence may only be appropriate under very specific conditions, such as competition for spatial resources like nesting sites or territories (Mallet 2012, O'Dwyer 2018), and that 2) most ecological systems will rather follow concave or convex density-regulation functions. As discussed in Abrams (2009b), 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 non-saturating consumers, and generally organisms with linear functional responses, follow a convex density-regulation function that is exactly described by a continuous-time version of the Schoener model (Eq. 8, Thieme 2003, Pástor et al. 2016, for example) when feeding on a resource that is appropriately described by a chemostat model. For filter feeders in the sense of Jeschke et al. (2004), we provide a derivation in the Supporting information. 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 may be heuristically described by a continuous-time version of the Maynard Smith–Slatkin model (Eq. 13).

It is interesting to note that, following Abrams (2009b), resource dynamics and especially the curvature of their density-regulation function is crucial for understanding consumer density-dependence, especially when consumer functional- and numerical responses are linear. This implies that, if resource dynamics were to follow a linear density-regulation function as in the logistic model, for example because the resource is limited by space (Mallet 2012), then a consumer with a linear functional response would also be following logistic growth. Extensions of this specific case to consumers with saturating functional responses can be found in Reynolds and Brassil (2013), for example. By contrast, our results hold for the case of abiotic basal resources that are regulated by fluxes.

Based on our theoretical work, we predict non-saturating consumers to generally exhibit a positive relationship between growth rates, competitive abilities and equilibrium population densities (Fig. 2). The form of this relationship will depend on whether higher growth rates are achieved by increasing foraging rates or by increasing assimilation efficiencies (Fig. 2). For foraging strategies that are characterized by a type II, that is, saturating functional response while keeping the resources abiotic, we show that the appropriate density-regulation function can be both concave and convex (Fig. 3). Increasing foraging rates and assimilation coefficients will still increase both growth rates and equilibrium densities (Fig. 4), 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. Specifically, changing foraging rates and half-saturation constants may lead to non-monotonic relationships between growth rates and equilibrium densities (Fig. 6). These considerations highlight that population growth and competitive ability are related, usually positively, and that equilibrium densities are a result of underlying consumer–resource dynamics that may change positively or negatively with population growth and competitive ability. This has important implications for evolutionary considerations as discussed above. Recent microbial work has started to explore the underlying genetic basis of $r - K$ relationships (Wei and Zhang 2019).

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 *Chlamydomonas* maintained in a 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. 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 non-saturating consumers and abiotic resources, which is rather surprising, 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 relationships. 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. For a detailed discussion of the impact of the shape of density dependence in basic and applied ecology see Abrams 2009c.

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). Including a more behavioural and physiological focus, the pace-of-life syndrome (POLS) hypothesis represents a relevant development towards more biological complexity of $r - K$ selection thinking (Réale et al. 2010, Montiglio et al. 2018). Furthermore, our models 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) treat 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 non-saturating consumers and abiotic resources the continuous-time version of the Schoener model can be derived (Abrams 1977, Schoener 1978). 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. Importantly, a precise understanding of the shape of density-dependence is highly relevant for understanding population responses to global change and environmental variation (Lawson et al. 2015) and eco-evolutionary dynamics in general (Govaert et al. 2019). 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 and relationships between equilibrium density and population growth are treated in ecology, evolution and beyond (Aktipis et al. 2013).

Acknowledgements – We thank Peter Abrams and François Massol for valuable comments on the previous versions of the text. This is publication ISEM-2023-233 of the Institut des Sciences de l'Evolution - Montpellier.

Funding – FA received funding from the Swiss National Science Foundation Grant no. PP00P3, 179089 and the University of Zurich Research Priority Programme 'URPP Global Change and Biodiversity'. SJS is supported by US NSF DMS-1716803.

Author contributions

Emanuel A. Fronhofer: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Lynn Govaert**: Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Mary I. O'Connor**: Conceptualization (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Sebastian J. Schreiber**: Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Florian Altermatt**: Conceptualization (supporting); Resources (lead); Supervision (supporting); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo Repository: https://doi.org/10.5281/zenodo.7702324 (Fronhofer et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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