We need to talk about (sublinear) density dependence

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Abstract

Sublinear density dependence has been reported in numerous empirical studies, and yet it is seemingly incompatible with most resource-explicit models of competition. Reconciling this disconnect will likely necessitate substantive revision of the assumptions of mechanistic models and/or empirical methods, but it also presents rich opportunities for original research with wide-ranging implications.
Main

Density dependence as a central phenomenon

Negative density dependent population growth emerges when individuals compete for finite resources. It ‘creates’ the conditions for natural selection to drive evolution and underpins species coexistence and the maintenance of diversity. Countless studies in every conceivable system have demonstrated negative relationships between population growth and population size [1, 2]. We might reasonably consider it the first law of ecology and evolution. And yet, for such an ostensibly well studied phenomenon, a puzzling disconnect persists between empirical observations and the predictions of mechanistic theory.

A preponderant empirical pattern

The default phenomenological model of density dependence is the logistic growth model (and by extension to multi-species interactions, Lotka-Volterra), where per capita growth rate declines linearly with density [3]. Except in the vicinity of equilibria, however, per capita growth rates rarely respond additively to changes in density. A wide variety of alternative models for density dependence have been fit to empirical data, but one general form appears to emerge with surprising frequency. Sublinear (or convex) density dependence arises when per capita growth rate declines more slowly with increasing density [3, 4]. It is an inherent feature of several models that are a mainstay of plant and animal population modelling (e.g., Beverton-Holt and the Ricker model) [5], and has been observed across a broad spectrum of macro-organisms; in a recent high profile paper, the apparent parsimony of a sublinear model fitted to time-series of mammals, birds, fish and insects was invoked to explain positive diversity-stability relationships [4]. Leaving aside the limitations of fitting population models to coarse time-series, what makes the empirical preponderance of sublinear density dependence perplexing is that it is seemingly incompatible with most resource-explicit (i.e. mechanistic) models of competition.

Density dependence in consumer-resource models

Density-dependence in phenomenological population models is almost always implemented as a proxy for some underlying mechanism of competition, the most canonical example of which is the shared consumption of a limiting resource (regardless of whether the resource is exploited by individuals of the same or different species) [3]. As such, if a phenomenological model of negative density dependence has a mechanistic underpinning, we should expect it to be consistent with
a wide spectrum of consumer-resource interactions. To a first approximation, the corollary of
the density-dependent growth function in a consumer-resource model is the resource uptake
function or functional response. Following Holling [6] and a vast body of empirical research
[7], the resource uptake function in a consumer-resource model is typically drawn from one of
three functional forms: type I (linear increasing), type II (monotonically saturating, including
Michaelis-Menten or Monod function) or type III (sigmodial) (Fig 1A). Notwithstanding the
relaxation of standard simplifying assumptions (see below), as demonstrated by Abrams [8, 9]
and others [10–12], the emergent density-dependence in a consumer-resource model inherits
the functional form of the consumer’s resource uptake function. A type I functional response
translates to linear density dependence (i.e. logistic and Lotka-Volterra); type II translates
to concave density-dependence (i.e. an accelerating decline in per-capita growth rate as a
function of density); and type III gives rises to a density dependent function that is concave at
low densities but then switches to convex at higher densities (Fig 1B).

Evidently, none of ecology’s standard models of consumer resource dependence map to a purely
sublinear model of density dependence. Instead, all else being equal, sublinear density depen-
dence requires a resource uptake function that increases exponentially with resource availability
(i.e., resource uptake, and therefore growth, never saturates). Such a functional response is con-
sidered biologically unrealistic, hence why it has never been formalised with its own ‘type x’
label [3].

A mechanistic basis for sublinear density dependence?

How then can we reconcile the apparent dissonance between theory and observation; does the
empirical evidence for sublinear density dependence require closer scrutiny or do the basic as-
sumption of mechanistic models need a radical rethink? Sublinear density dependence can in
fact emerge in consumer-resource models provided additional conditions are met. A combi-
nation of type I functional responses and continuous in flow and outflow of resources (as in
a classic chemostat model) provides one route [8, 11, 12]. The latter requirement, however,
seems improbable for the majority of natural systems, where resources are likely to undergo
substantial fluctuations across multiple timescales.

More plausibly, provided competitors have type III resource uptake functions and population
dynamics never stray far from equilibrium (right side of Fig 1B), the emergence of sublinear
density dependence is indeed possible. The key assumption here is that resources are held
sufficiently low that consumers never sample the concave-down portion of their uptake functions (left side of Fig 1B). Remarkably, given the importance of both conditions for a wide range of ecological processes and phenomena, robust evidence, both for or against, is sparse in the extreme (but see empirical support for unsaturated resource uptake rates in [13]).

Another possibility is that the numerical response capturing the conversion of resources into individuals/biomass takes a nonlinear functional form that translates, in concert with the resource uptake function, into sublinear density dependence. The convention is to treat the numerical response as directly proportional to the resource uptake function (see *quota* in the caption for Fig 1), but empirical evidence justifying this choice or an alternative nonlinear form is woefully limited [9].

Finally, regardless of the functional response, an abrupt form of sublinear density dependence can emerge in consumer-resource models if densities are perturbed above equilibrium. Provided mortality is independent of resource availability (a common assumption in consumer-resource models), the per capita growth rate is bounded below by the mortality rate (i.e., the responses in Fig 1B will flat line along the x-axis extended to the right). This behaviour may well contribute to the pervasiveness of sublinear fits to experimentally-derived data, where the widely adhered to recommendation (for statistical but not necessarily ecological purposes) is to sample densities well above equilibrium [14].

**Bridging the gap**

From the diversity-stability debate to higher-order interactions, density dependence is integrally relevant to many long-standing and emerging research themes in ecology. Which makes it all the more remarkable that there remains such a gulf in understanding of this central phenomenon. Nevertheless, it also means there are a wealth of opportunities for original and impactful basic research aimed at bridging the gap between mechanistic predictions and phenomenological observations. Does the rate of resource uptake accelerate at low resource concentrations for most organisms? Do real systems genuinely hover around equilibrium? Or even commonly exceed them? Is mortality rate resource-dependent? Answers to these questions, and many others, will not only shed much needed light on the nature of density-dependence but also provide a stronger foundation from which to tackle more complex phenomena.
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References


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**Figure 1:** Direct comparison of explicit resource-dependent (A) and emergent density-dependent (B) growth responses for consumer-resource models assuming logistic resource supply and type I (orange), type II (blue) or type III (green) resource uptake functions. Consumer resource models are of the form $\frac{dN}{dt} = N(\mu(R) - m)$; $\frac{dR}{dt} = rR(1 - \frac{R}{K}) - \mu(R)QN$, where $N$ is the density of the consumer, $R$ is the concentration of the resource, $\mu(R)$ is the resource dependent per capita growth rate, $m$ is the density independent mortality rate, $r$ is the intrinsic growth rate of the resource, $K$ is the carrying capacity of the resource, and $Q$ is the resource quota (amount of resource per individual consumer; an alternative formulation is use the reciprocal of $Q$ in the consumer equations, which then equates to the yield or numerical response described in the main text). $\mu(R)$ can take one of three forms: $\mu(R) = aR$ (type I); $\mu(R) = \frac{aR}{k+R}$ (type II); or $\mu(R) = \frac{aR^2}{k+R^2}$ (type III). For type I, $a$ is the linear slope of the relationship between resource uptake / growth and resource availability. For type II and III, $a$ is the maximum resource uptake / per-capita growth rate, and $k$ is the resource concentration at which growth is half its maximum. Density-dependent growth functions obtained by assuming a time-scale separation (resource dynamics much faster than consumer dynamics) and substituting resource concentration at equilibrium into consumer equations. Grey dashed lines in A and B denote the density independent mortality rate, $m$. 

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