

# We need to talk about (sublinear) density dependence

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## 1 **Abstract**

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

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## 7 **Main**

### 8 **Density dependence as a central phenomenon**

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

### 16 **A preponderant empirical pattern**

17 The default phenomenological model of density dependence is the logistic growth model (and by  
18 extension to multi-species interactions, Lotka-Volterra), where per capita growth rate declines  
19 linearly with density [3]. Except in the vicinity of equilibria, however, per capita growth rates  
20 rarely respond additively to changes in density. A wide variety of alternative models for density  
21 dependence have been fit to empirical data, but one general form appears to emerge with  
22 surprising frequency. Sublinear (or convex) density dependence arises when per capita growth  
23 rate declines more slowly with increasing density [3, 4]. It is an inherent feature of several  
24 models that are a mainstay of plant and animal population modelling (e.g., Beverton-Holt and  
25 the Ricker model) [5], and has been observed across a broad spectrum of macro-organisms; in a  
26 recent high profile paper, the apparent parsimony of a sublinear model fitted to time-series of  
27 mammals, birds, fish and insects was invoked to explain positive diversity-stability relationships  
28 [4]. Leaving aside the limitations of fitting population models to coarse time-series, what makes  
29 the empirical preponderance of sublinear density dependence perplexing is that it is seemingly  
30 incompatible with most resource-explicit (i.e. mechanistic) models of competition.

### 31 **Density dependence in consumer-resource models**

32 Density-dependence in phenomenological population models is almost always implemented as  
33 a proxy for some underlying mechanism of competition, the most canonical example of which is  
34 the shared consumption of a limiting resource (regardless of whether the resource is exploited by  
35 individuals of the same or different species) [3]. As such, if a phenomenological model of negative  
36 density dependence has a mechanistic underpinning, we should expect it to be consistent with

37 a wide spectrum of consumer-resource interactions. To a first approximation, the corollary of  
38 the density-dependent growth function in a consumer-resource model is the resource uptake  
39 function or functional response. Following Holling [6] and a vast body of empirical research  
40 [7], the resource uptake function in a consumer-resource model is typically drawn from one of  
41 three functional forms: type I (linear increasing), type II (monotonically saturating, including  
42 Michaelis-Menten or Monod function) or type III (sigmoidal) (Fig 1A). Notwithstanding the  
43 relaxation of standard simplifying assumptions (see below), as demonstrated by Abrams [8, 9]  
44 and others [10–12], the emergent density-dependence in a consumer-resource model inherits  
45 the functional form of the consumer’s resource uptake function. A type I functional response  
46 translates to linear density dependence (i.e. logistic and Lotka-Volterra); type II translates  
47 to concave density-dependence (i.e. an accelerating decline in per-capita growth rate as a  
48 function of density); and type III gives rises to a density dependent function that is concave at  
49 low densities but then switches to convex at higher densities (Fig 1B).

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

### 56 **A mechanistic basis for sublinear density dependence?**

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

65 More plausibly, provided competitors have type III resource uptake functions *and* population  
66 dynamics never stray far from equilibrium (right side of Fig 1B), the emergence of sublinear  
67 density dependence is indeed possible. The key assumption here is that resources are held

68 sufficiently low that consumers never sample the concave-down portion of their uptake functions  
69 (left side of Fig 1B). Remarkably, given the importance of both conditions for a wide range  
70 of ecological processes and phenomena, robust evidence, both for or against, is sparse in the  
71 extreme (but see empirical support for unsaturated resource uptake rates in [13]).

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

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

## 86 **Bridging the gap**

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

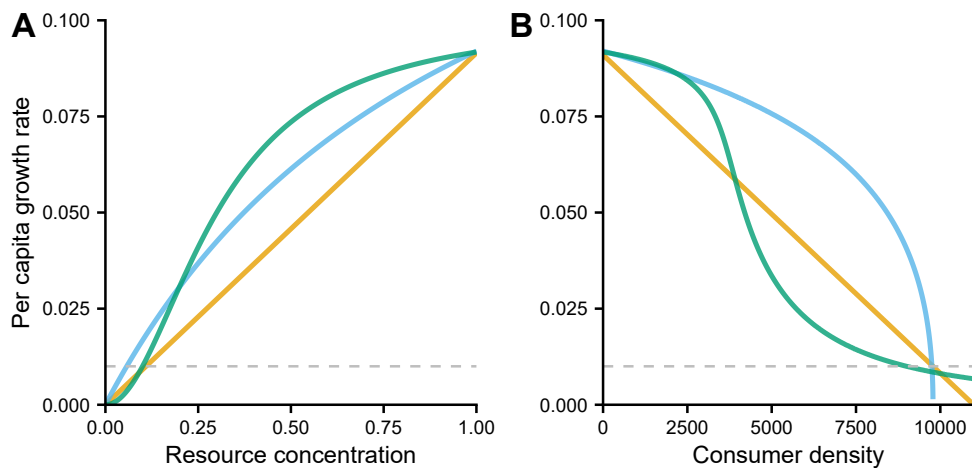
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## 102 **References**

- 103 [1] Harrison, S. and Cappuccino, N. (1995) Using density-manipulation experiments to study  
104 population regulation. In N. Cappuccino and P.W. Price, eds., *Population dynamics: new*  
105 *approaches and synthesis*. Academic Press, San Diego, pp. 131–147
- 106 [2] Brook, B.W. and Bradshaw, C.J. (2006) Strength of evidence for density dependence in  
107 abundance time series of 1198 species. *Ecology* 87, 1445–1451
- 108 [3] Case, T.J. (1997) *Illustrated Guide to Theoretical Ecology*. Oxford University Press
- 109 [4] Hatton, I.A. *et al.* (2024) Diversity begets stability: Sublinear growth and competitive  
110 coexistence across ecosystems. *Science* 383, eadg8488
- 111 [5] Stouffer, D.B. (2022) A critical examination of models of annual-plant population dynamics  
112 and density-dependent fecundity. *Methods in Ecology and Evolution* 13, 2516–2530
- 113 [6] Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal  
114 predation of the european pine sawfly<sup>1</sup>. *The Canadian Entomologist* 91, 293–320
- 115 [7] Uiterwaal, S.F. *et al.* (2022) Forage database: A compilation of functional responses for  
116 consumers and parasitoids. *Ecology* 103, e3706
- 117 [8] Abrams, P.A. (2009) Determining the functional form of density dependence: deductive  
118 approaches for consumer-resource systems having a single resource. *The American Natu-*  
119 *ralist* 174, 321–330
- 120 [9] Abrams, P.A. (2022) *Competition theory in ecology*. Oxford University Press
- 121 [10] O’Dwyer, J.P. (2018) Whence lotka-volterra? conservation laws and integrable systems in  
122 ecology. *Theoretical Ecology* 11, 441–452

- 123 [11] Letten, A.D. and Stouffer, D.B. (2019) The mechanistic basis for higher-order interactions  
124 and non-additivity in competitive communities. *Ecology letters* 22, 423–436
- 125 [12] Fronhofer, E.A. *et al.* (2023) The shape of density dependence and the relationship between  
126 population growth, intraspecific competition and equilibrium population density. *Oikos* ,  
127 e09824
- 128 [13] Coblenz, K.E. *et al.* (2023) Predator feeding rates may often be unsaturated under typical  
129 prey densities. *Ecology Letters* 26, 302–312
- 130 [14] Inouye, B.D. (2001) Response surface experimental designs for investigating interspecific  
131 competition. *Ecology* 82, 2696–2706



**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  $\mu(R) = \frac{aR^2}{k^2+R^2}$  (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,  $m$ .