

Density-dependent selection and the limits of relative fitness

Jason Bertram ^{1,*}

Joanna Masel ¹

1. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721.

* Corresponding author; e-mail: jbertram@email.arizona.edu.

Keywords: Lottery model, competitive Lotka-Volterra, r/K -selection, interference competition, eco-evo.

Author contributions: JB and JM conceptualized the manuscript. JB did the formal analysis. JB wrote the manuscript with review and editing from JM.

Running title: Density-dependence and relative fitness

Acknowledgments: We thank Peter Chesson and Joachim Hermisson for many constructive comments on an earlier and quite different version of this manuscript. This work was financially supported by the National Science Foundation (DEB-1348262) and the John Templeton Foundation (60814).

Density-dependent selection and the limits of relative fitness

Abstract

[Needs revising] Selection is commonly described in terms of constant relative fitnesses. Yet when selection is strong, the ecological view of selection in density-regulated populations seems to be incompatible with constant-density relative fitnesses. Here we analyze the population ecological limits of relative fitness using a novel of density-dependent selection which contains a “reproductive excess. Our model clearly distinguishes between density-dependent selection and changes in density driven by selection. These two effects are confounded in standard models of density-regulated population growth, but both are necessary, in combination with strong selection, for relative fitness to break down in populations close to demographic equilibrium. Remarkably, both effects are not sufficient: we give an example of strong selection on a density-regulating trait subject to density-dependent selection that conforms to the density-independent relative fitness description almost exactly. We reiterate the importance of reproductive excesses in many species, which allows even strong selection to have no effect on density. Our model also offers a possible alternative to relative fitness when the latter is untenable, as is likely the case far from demographic equilibrium.

(191 words)

19 Introduction

20 There are a variety of different measures of fitness. Some widely used examples are expected
21 lifetime reproductive ratio R_0 , intrinsic population growth rate r , equilibrium population
22 density/carrying capacity (often labeled “ K ”) (Benton and Grant, 2000), and invasion fitness
23 (Metz et al., 1992). In addition, “relative fitness” is the standard in much of evolutionary
24 biology, particularly evolutionary genetics, where the focus is relative genotypic proportions
25 (Barton et al., 2007, pp. 468). The variety of fitness measures is not problematic in itself,
26 because different measures have different uses. But it should be clear how these measures
27 are connected to the processes of birth and death which ultimately drive selection (Metcalf
28 and Pavard, 2007; Doebeli et al., 2017). While such a connection is fairly clear for absolute
29 fitness measures like r , relative fitness is largely divorced from population ecology. It has even
30 been proposed that relative fitness be justified from measure theory, abandoning population
31 biology altogether (Wagner, 2010).

32 Constant relative fitness values are typically justified as an approximation that holds
33 when selection is sufficiently weak and stable over time (Kimura and Crow 1969; Ewens
34 2004, pp. 277; Charlesworth 1994, Chap. 4) and population density is either changing
35 either much faster or much slower than type frequencies (Otto and Day, 2011, Fig. 9.5).
36 Formally, these constant values are the leading terms in an expansion of a potentially com-
37 plicated relative fitness function which depends on density, frequency, age structure, and so
38 on. However, knowing that strong selection can break the relative fitness approximation in
39 toy models like the logistic (Kimura and Crow, 1969), or in highly complex age-structured
40 models (Charlesworth, 1994, Chap. 4) leaves important issues unresolved. For instance,
41 must we simply abandon relative fitness in important model systems like wild *Drosophila*,
42 where strong seasonally-alternating selection occurs in unison with “boom-bust” cycles in
43 population density (Messer et al., 2016; Bergland et al., 2014)? And if we do abandon rel-

44 ative fitness, are we compelled to develop customized absolute fitness models that capture
 45 the specific ecology of the system in question? Being able to assign relative fitness values
 46 to genotypes is a powerful idealization. It is therefore important that we understand the
 47 population ecological limits of this idealization when selection is not weak and demography
 48 is not stable, both to clarify its domain of applicability, and as part of the broader challenge
 49 of synthesizing ecology and evolution.

50 In the absence of crowding, relative fitness simply represents differences in intrinsic pop-
 51 ulation growth rate. In discrete time, the change in frequency of type i is $\Delta p_i = \left(\frac{W_i}{\bar{W}} - 1\right) p_i$,
 52 where W_i is the intrinsic absolute growth factor of type i , and $\bar{W} = \sum_i W_i p_i$ is the popula-
 53 tion mean W . The change in frequency depends only the relative ratio $\frac{W_i}{\bar{W}}$, not the absolute
 54 values of the growth factors W_i . Thus, we can replace the W_i with any set of values w_i that
 55 are proportional to the W_i ; these values are called “relative fitnesses”. The analogous for-
 56 mula in continuous time is $\frac{dp_i}{dt} = (r_i - \bar{r})p_i$, where W_i is replaced by the intrinsic exponential
 57 growth rate r_i (Crow et al., 1970, pp. 26), and the ratio $\frac{W_i}{\bar{W}}$ is replaced by the difference
 58 $r_i - \bar{r}$. In the particular case that there are two types present, a wildtype i and a mutant j
 59 for instance, then the continuous time equation takes the familiar form

$$\frac{dp_i}{dt} = sp_i(1 - p_i), \tag{1}$$

60 where $s = r_i - r_j$ is the selection coefficient.

61 This simple interpretation of relative fitness breaks down when we allow for population
 62 crowding. Since crowded and uncrowded conditions are so different, s will often depend on
 63 density (Travis et al., 2013). Eq. (1) is then no longer a complete description of selection
 64 — we would also need to specify a model for how density is changing. Note that frequency-
 65 dependent selection does not raise similar problems; Eq. (1) is still a complete description
 66 of selection even if its behavior is more complicated due to s depending on frequency. This

issue does not arise in many population genetics models because total population density N is assumed to have reached some fixed equilibrium value. The selection coefficient s then abstractly parameterizes the rate at which selection changes relative frequencies, and no longer corresponds to differences in intrinsic growth rates r .

Yet MacArthur famously argued that when population growth is density-regulated, selection in crowded populations is intimately connected to the ability to keep growing at higher densities than other types can tolerate (MacArthur and Wilson, 1967). The classic example is the logistic model, where the type with the greatest equilibrium population density “ K ” excludes the others (Fig. 1a). Similarly, the “ R^* rule”, a central tenet of resource competition theory, states that when growth is limited by a single homogeneous consumable resource, the type able to deplete the resource to the lowest equilibrium density R^* excludes the others (Grover, 1997). Differences in R^* will often entail differences in equilibrium density. The Lotka-Volterra competition model also couples selection in crowded populations to density except in special cases (Smouse, 1976; Mallet, 2012). In these examples, both N and s change during, and as a result of, adaptive sweeps. It would therefore seem that the ubiquitous constant- N , relative fitness description of selection is incompatible with a huge class of population ecological processes driving selection (Fig. 1b).

In light of this, the relative fitness description has been justified in broadly two different ways for crowded populations in the strong-selection, non-equilibrium demography regime. The first is to simply assume that selection is density-independent but relax the assumption of constant N by allowing density to change as a result of selective sweeps (Barton et al., 2007, pp. 468) (Prout, 1980). Obviously this does not address the problem that s can, in reality, depend on density. Type-specific responses to density are at the center of MacArthur’s argument and the density-dependent selection literature that grew out of it (e.g. (Roughgarden, 1979)). The second justification, which primarily grew out of a controversy over Haldane’s “cost of selection”, is to appeal to the existence of a “reproductive excess” of



Figure 1: Selection in crowded environments shown as a phase diagram for the densities of two types n_1 and n_2 . (a) The logistic model $\frac{dn_1}{dt} = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $\frac{dn_2}{dt} = r_2(1 - \frac{n_1+n_2}{K_2})n_2$ with $r_1 = r_2$ and $K_1 > K_2$. (b) The constant- N , relative fitness description of selection.

juveniles that are more fragile than their adult counterparts (Turner and Williamson, 1968; Kimura and Crow, 1969; Nei, 1971). Selection can then be concentrated at the juvenile phase, uncoupling selection from population density at the adult phase unless it is so strong that the reproductive excess is depleted. Selective sweeps then need not affect density, and so the density-dependence of selection does not matter. Unfortunately this reproductive excess literature is also poorly integrated with population ecology. For instance, Kimura and Crow (1969) simply took constant N as a requirement and then derived some variants of the logistic model that satisfy this requirement. Nei (1971) proposed a model with an explicit representation of reproductive excess, but used an unusual model of competition based on pair-wise interactions which was only defined for at most two different types. As a result, the role of reproductive excesses in justifying the use of relative fitness is still largely verbal.

Here we study the population ecology of relative fitness using a novel model of density-dependent population growth based on territorial contests. We restrict our attention to

asexual haploids with little or no age structure, since it is then easier to evaluate how the success or failure of the relative fitness description is tied to the underlying population ecological assumptions. Our starting point is the classic lottery model which was developed by ecologists to study competition driven by territorial contests in reef fishes and plants (Sale, 1977; Chesson and Warner, 1981). The classic lottery incorporates a reproductive excess, and fitness involves a product of fertility and juvenile viability akin to the population simplest population genetic models of selection (e.g. Crow et al. 1970, pp. 185). The classic lottery also assumes constant N , and generations can overlap. Our first task is to generalize the lottery model to create a variable-density lottery (sections “Model” and “Analytical approximation of the variable-density lottery”).

Equipped with this model, we turn to the evaluation of relative fitness. [Need to write outline, will do when structure is finalized]

Model

Assumptions and definitions

We assume that reproductively mature individuals (“adults”) require their own territory to survive and reproduce. All territories are identical, and the total number of territories is T . Time advances in discrete iterations, each representing the time from birth to reproductive maturity. In a given iteration, the number of adults of the i ’th type will be denoted by n_i , the total number of adults by $N = \sum_i n_i$, and the number of unoccupied territories by $U = T - N$. We assume that the n_i are large enough that stochastic fluctuations in the n_i (“drift”) can be ignored (with T also assumed large to allow for low type densities n_i/T).

Each iteration, adults produce propagules which disperse at random, independently of distance from their parents, and independently of each other. We assume that each adult from type i produces b_i propagules on average, so that the mean number of i propagules

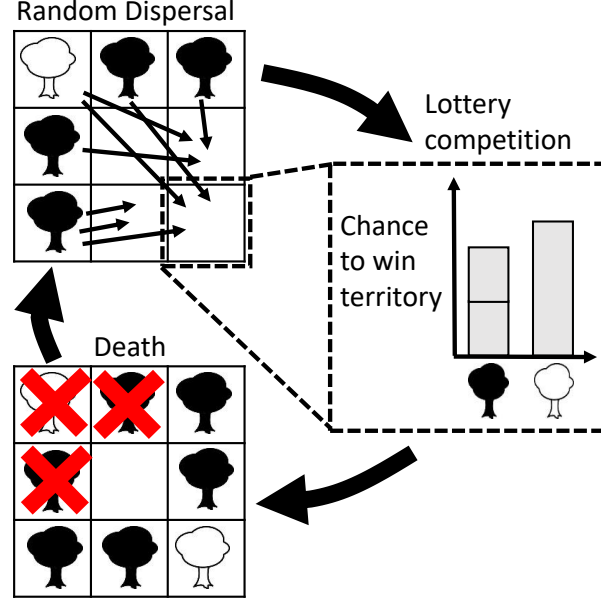


Figure 2: One iteration of our model. Propagules are dispersed by adults at random (only propagules landing on unoccupied territories are shown). Territories can receive zero propagules. Lottery competition then occurs in each territory that receives more than one propagule (only illustrated in one territory). In a given territory, each type has probability proportional to $c_i x_i$ of winning the territory, where c_i measures competitive ability and x_i is the number of i propagules present. In the illustrated territory, more black propagules are present, but white is a stronger competitor and has a higher probability of winning. Territories are made available for the next iteration by the death of adults present at the start of the iteration (red crosses).

dispersing to unoccupied territories is $m_i = b_i n_i U / T$. The parameter b_i can be thought of as a measure of “colonization ability”, which combines fecundity and dispersal ability (Levins and Culver, 1971; Tilman, 1994). Random dispersal is then modeled using a Poisson distribution $p_i(x_i) = l_i^{x_i} e^{-l_i} / x_i!$ for the number x_i of i propagules dispersing to any particular unoccupied territory, where $l_i = m_i / U$ is the mean propagule density in unoccupied territories. The total propagule density will be denoted $L = \sum_i l_i$.

We assume that adults cannot be ousted by juveniles, so that recruitment to adulthood occurs exclusively in unoccupied territories. When multiple propagules land on the same unoccupied territory, the winner is determined by lottery competition: type i wins a territory with probability $c_i x_i / \sum_i c_i x_i$, where c_i is a constant representing relative competitive ability (Fig. 2). Since the expected fraction of unoccupied territories with propagule composition x_1, \dots, x_G is $p_1(x_1) \cdots p_G(x_G)$ where G is the number of types present, and type i is expected to win a proportion $c_i x_i / \sum_i c_i x_i$ of these, type i ’s expected territorial acquisition is given by

$$\Delta_+ n_i = U \sum_{x_1, \dots, x_G} \frac{c_i x_i}{\sum_i c_i x_i} p_1(x_1) \cdots p_G(x_G). \quad (2)$$

Here the sum only includes territories with at least one propagule present. Since we do not consider drift here, we will not analyze the fluctuations around these two expectations.

Adult mortality only occurs in adults present at the start of the iteration, and at a constant, type-specific per-capita rate $0 \leq d_i \leq 1$ (Fig. 2). This gives an overall change in type abundances of

$$\Delta n_i = \Delta_+ n_i - d_i n_i. \quad (3)$$

Connection to the classic lottery model

In the classic lottery model (Chesson and Warner, 1981), unoccupied territories are assumed to be saturated with propagules from every type ($l_i \rightarrow \infty$ for all i). From the law of large

151 numbers, the composition of propagules in each territory will not deviate appreciably from
 152 the mean composition l_1, l_2, \dots, l_G . Type i is thus expected to win a proportion $c_i l_i / \sum_i c_i l_i$
 153 of the U available territories,

$$\Delta_+ n_i = \frac{c_i l_i}{\sum_i c_i l_i} U = \frac{c_i l_i}{\bar{c} L} U, \quad (4)$$

154 where $\bar{c} = \sum_i c_i m_i / \sum_i m_i$ is the mean competitive ability for a randomly selected propagule.
 155 Note that all unoccupied territories are filled in a single iteration of the classic lottery model,
 156 whereas our more general model Eq. (2) allows for territories to be left unoccupied and hence
 157 also accommodates low propagule densities.

158 Results

159 Analytical approximation of the variable-density lottery

160 Here we evaluate the expectation in Eq. (2) to better understand the dynamics of density-
 161 dependent lottery competition. Similarly to the classic lottery model, we replace the x_i ,
 162 which take different values in different territories, with “effective” mean values. However,
 163 since we want to allow for low propagule densities, we cannot simply replace the x_i with
 164 the means l_i as in the classic lottery. For a low density type, growth comes almost entirely
 165 from territories with $x_i = 1$, for which its mean density $l_i \ll 1$ is not representative. We
 166 therefore separate Eq. (2) into $x_i = 1$ and $x_i > 1$ components, taking care to ensure that the
 167 effective mean approximations for these components are consistent with each other (details
 168 in Appendix B). The resulting variable-density approximation only requires that there are
 169 no large discrepancies in competitive ability (i.e. we do not have $c_i/c_j \gg 1$ for any two
 170 types). We obtain

$$\Delta_+ n_i \approx \left[e^{-L} + (R_i + A_i) \frac{c_i}{\bar{c}} \right] l_i U, \quad (5)$$

171 where

$$R_i = \frac{\bar{c}e^{-l_i}(1 - e^{-(L-l_i)})}{c_i + \frac{\bar{c}L - c_i l_i}{L - l_i} \frac{L - 1 + e^{-L}}{1 - (1+L)e^{-L}}},$$

172 and

$$A_i = \frac{\bar{c}(1 - e^{-l_i})}{\frac{1 - e^{-l_i}}{1 - (1+l_i)e^{-l_i}} c_i l_i + \frac{\bar{c}L - c_i l_i}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1+L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1+l_i)e^{-l_i}} \right)}.$$

173 Comparing Eq. (5) to Eq. (4), the classic lottery per-propagule success rate $c_i/\bar{c}L$ has
 174 been replaced by three separate terms. The first, e^{-L} , accounts for propagules which land
 175 alone on unoccupied territories; these propagules secure the territories without contest. The
 176 second, $R_i c_i/\bar{c}$, represents competitive victories on territories where only a single i propagule
 177 lands, and at least one other propagule from a different type (this term dominates the
 178 growth of a rare invader in a high density population and determines invasion fitness). The
 179 third term, $A_i c_i/\bar{c}$, represents competitive victories in territories where two or more i type
 180 propagules are present. The relative importance of these three terms varies with both the
 181 overall propagule density L and the relative propagule frequencies l_i/L . If $l_i \gg 1$ for all
 182 types, we recover the classic lottery model (only the $A_i c_i/\bar{c}$ term remains, and $A_i \rightarrow 1/L$).

183 Fig. 3 shows that Eq. (5) and its components closely approximate simulations of our
 184 variable-density lottery model over a wide range of propagule densities. Two types are
 185 present, one of which is at low frequency. The growth of the low-frequency type relies
 186 crucially on the low-density competition term $R_i c_i/\bar{c}$. On the other hand, $R_i c_i/\bar{c}$ is negligible
 187 for the high-frequency type, which depends instead on high density territorial victories. Fig. 3
 188 also shows the breakdown of the classic lottery model at low propagule densities.

189 In the special case that all types are competitively equivalent (identical c_i), Eq. (5) takes
 190 a simpler form,

$$\Delta_+ n_i = \frac{l_i}{L} (1 - e^{-L}) U. \quad (6)$$

191 This formula can also be deduced directly from Eq. (2): $1 - e^{-L}$ is the fraction of territories

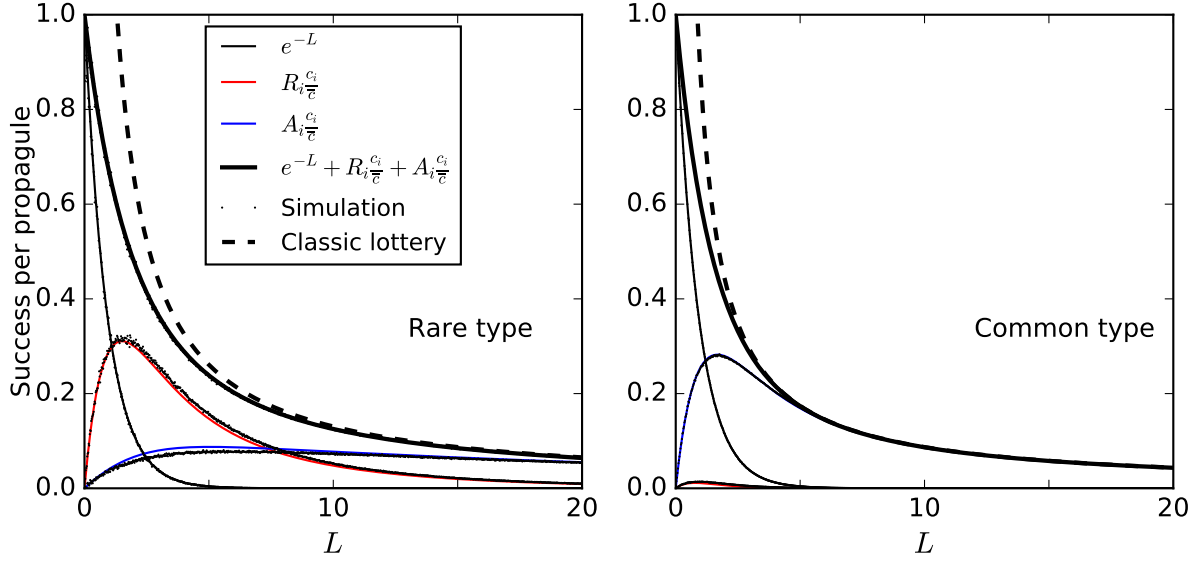


Figure 3: Comparison of Eq. (5), the classic lottery model, and simulations. The vertical axis is per-propagule success rate for all propagules $\Delta_+ n_i / m_i$, and for the three separate components in Eq. (5). Two types are present with $c_1 = 1$, $c_2 = 1.5$ and $l_2/l_1 = 0.1$. Simulations are conducted as follows: x_1, x_2 values are sampled $U = 10^5$ times from Poisson distributions with respective means l_1, l_2 , and the victorious type in each territory is then decided by random sampling weighted by the lottery win probabilities $c_i x_i / (c_1 x_1 + c_2 x_2)$. Simulation points are almost invisible for the common type due to near exact agreement with Eq. (5). Dashed lines show the failure of the classic lottery model at low density.

that receive at least one propagule under Poisson dispersal, $(1 - e^{-L})U$ is the total number of such territories, and type i is expected to receive a fraction l_i/L of these. Total population density thus grows according to

$$\Delta N = (1 - e^{-L})U - \sum_i d_i n_i \quad (7)$$

Density-dependent selection in the variable-density lottery

We now outline the basic properties of selection on b , c and d . The birth and mortality rates b and d are the traits which regulate density; b controls the fraction of unoccupied territories that are contested, while d controls adult mortality. Competitive ability c does not regulate density since it only affects the relative likelihood for each type to win a contested territory. Thus, selection between types which only differ in c occurs without causing N to change (Eq. (7) shows this formally).

Selection in the variable density lottery model is density-dependent, by which we mean that the selection coefficient, measured by the difference in per-capita growth rate $\Delta n_i/n_i$ between types, depends on N . Density-dependent selection is sometimes taken to mean a qualitative change in which types are fitter than others at different densities (Travis et al., 2013). While reversal in the order of fitnesses and co-existence driven by density-regulation are possible in the variable-density lottery (a special case of the competition-colonization trade-off; Levins and Culver 1971; Tilman 1994; Bolker and Pacala 1999), questions related to co-existence are tangential to our aims and will not be pursued further here.

Selection on c is density-dependent, with the strength of selection peaking at an intermediate density (Fig. 4). This intermediate peak occurs because at low density most territories are claimed without contest, whereas at high density few unoccupied territories are available to be contested. To see how selection on b and d depend on density, we write Eq. (6) in the

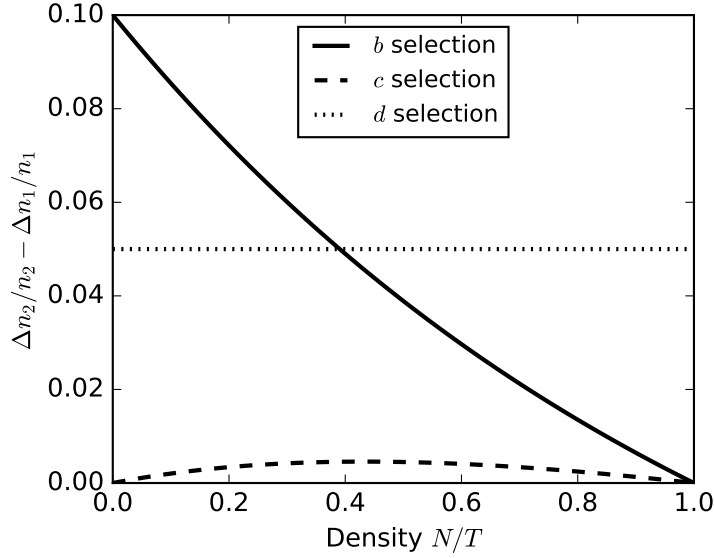


Figure 4: The density-dependence of selection in our variable-density lottery plotted as the difference in propagule success rate $\Delta n_2/n_2 - \Delta n_1/n_1$ between an adaptive variant 2 and a wildtype 1 with equal frequencies. Here $b_1 = 1$, $d_1 = 0.5$ and $c_1 = 1$. For b -selection we set $b_2 = b_1(1 + \epsilon)$, and similarly for c and d , with $\epsilon = 0.1$. d -selection is density-independent, b -selection gets weaker with lower territorial availability, while c -selection initially increases with density as territorial contests become more important, but eventually also declines as available territories become scarce. The wildtype equilibrium density is $n_1/T \approx 0.4$.

alternative form

$$\frac{\Delta n_i}{n_i} = \frac{b_i}{\bar{b}} \frac{1 - e^{-\bar{b}N/T}}{N} (T - N) - d_i, \quad (8)$$

where we have used that fact that $L = \bar{b}N/T$, and \bar{b} is the population mean b . It is clear d -selection is independent of density. On the other hand, the strength of b -selection declines with density because the advantage of having greater b gets smaller the fewer territories there are to be claimed (Fig. 4).

The response of density to selection; c -selection versus K -selection

We now turn to the issue of how density responds to selection, comparing the variable-density lottery and previous models of selection in density-regulated populations (Prout,

1980). Starting with some of the earliest work on the topic (Kostitzin, 1939; Christiansen, 2004), most previous models exhibit some form of “ K -selection” i.e. selection in crowded populations increases equilibrium density. This idea is intuitively appealing because births balance deaths at equilibrium, and adaptive mutants must overcome the existing balance to expand (Kostitzin, 1939, pp. 227). Yet, as we saw in the previous section, c -selection has no effect on population density in the variable-density lottery. To make sense of how c -selection fits with previous population growth models, we now revisit MacArthur’s general treatment of K -selection (MacArthur and Wilson, 1967).

MacArthur considered a population with two types that have densities n_1 and n_2 subject to density-dependent growth,

$$\frac{dn_1}{dt} = f_1(n_1, n_2) \quad \frac{dn_2}{dt} = f_2(n_1, n_2). \quad (9)$$

The environment is assumed to remain constant apart from changing type densities. The functions f_1 and f_2 must decline to zero if n_1 or n_2 are sufficiently large, because the resources required for growth are limited. This defines nullclines $f_1(n_1, n_2) = 0$ and $f_2(n_1, n_2) = 0$ in (n_1, n_2) space. The outcome of selection is then determined by the relationship between these nullclines. Specifically, a type will be excluded if its nullcline is completely contained in the region bounded by the other type’s nullcline. Thus, for a type to have the possibility of persisting, it must be able to keep growing to higher densities than the other type can tolerate in some region of (n_1, n_2) space (Fig. 1a).

MacArthur used “ K ” to label the four intersection points of the nullclines with the axes, specifically $f_1(K_{11}, 0) = 0$, $f_1(0, K_{12}) = 0$, $f_2(K_{21}, 0) = 0$ and $f_2(0, K_{22}) = 0$. These K values determine whether a region of higher-density growth exists for each type, provided that the nullclines are close to being straight lines. Note that only K_{11} and K_{22} are equilibrium densities akin to the K parameter in the logistic model (Fig. 1a). The other intersection

points, K_{12} and K_{21} , are related to competition between types. To be more concrete, in the Lotka-Volterra competition model we have

$$\begin{aligned} f_1(n_1, n_2) &= r_1(1 - \alpha_{11}n_1 - \alpha_{12}n_2)n_1 \\ f_2(n_1, n_2) &= r_2(1 - \alpha_{22}n_1 - \alpha_{21}n_2)n_2 \end{aligned} \tag{10}$$

where $\alpha_{11} = 1/K_{11}$ and $\alpha_{22} = 1/K_{22}$ measure competitive effects within types, while $\alpha_{12} = 1/K_{12}$ and $\alpha_{21} = 1/K_{21}$ measure competitive effects between types. Hence, “fitness is K ” in crowded populations (MacArthur and Wilson, 1967, pp. 149) in the sense that selection either favors the ability to keep growing at ever higher densities (moving a type’s own nullcline outwards), or the ability to suppress the growth of competitors at lower densities (moving the nullcline of competitors inwards). This general idea is much broader than selection for greater equilibrium density (Gill, 1974).

Compared to simple birth-death models (Kostitzin, 1939) or variants of the logistic (Roughgarden, 1979), the Lotka-Volterra model clearly distinguishes between intra- and inter-type competitive effects. Thus, one type can displace another without having a greater equilibrium density (Fig. 5a). Nevertheless, selection drives transient changes in density in the Lotka-Volterra model even if the initial and final densities of a sweep are the same (constant density only occurs for a highly restricted subset of r and α values; further details in Appendix C; also see Mallet 2012; Smouse 1976). Intuitively, for one type to exclude the other, competitive suppression of growth between types must be stronger than competitive suppression of growth within types, causing N to dip over a sweep (Fig. 5a).

By contrast, density trajectories for c -selection in the variable-density lottery converge on a line of constant equilibrium density (Fig. 5b). This means that once the population reaches demographic equilibrium, it behaves indistinguishably from a constant- N relative fitness model (Fig. 1b). This complete uncoupling of density from c -selection arises due to

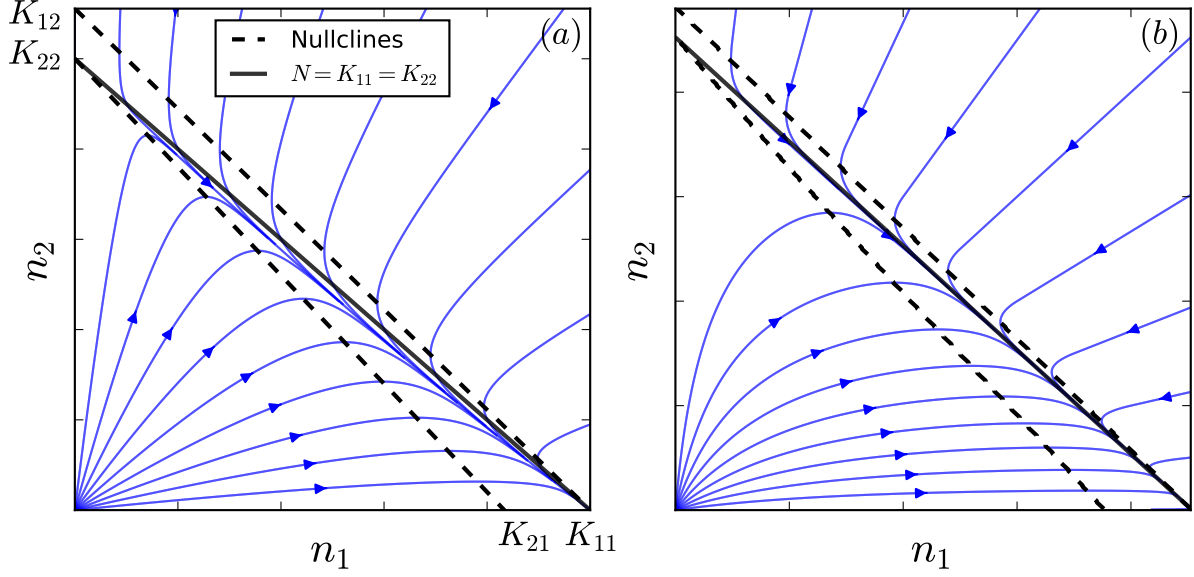


Figure 5: Selection between types with identical equilibrium density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 10) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. Trajectories do not follow the line $N = K_{11} = K_{22}$. (b) Lottery competition (Eq. 5) with $b_1 = b_2 = 5$, $d_1 = d_2 = 0.1$ and $c_1/c_2 = 5$. Trajectories converge on the line $N = K_{11} = K_{22}$.

the presence of an excess of propagules which pay the cost of selection without affecting adult density. As a result, Eq. (1) holds in equilibrium even though c -selection is density-dependent.

Density-regulating traits at equilibrium

The previous section underscores the fact that density must be affected by ongoing selection to threaten Eq. (1). We now turn to selection on density-regulating traits such as b and d in the variable density lottery.

As shown in Fig. 4, d -selection is independent of density; the selection coefficient for a d -variant with $d_2 = d_1(1 - \epsilon)$ is a constant $s = \epsilon d_1$. Thus, to threaten the assumption of density-independent s in an equilibrium population we require selection to act on a trait that is both density-dependent and density-regulating.

This is the case for b in the variable-density lottery. However, before we discuss this relatively complicated trait, it is helpful to summarize the threat to Eq. (1) in simpler models of density-regulated growth, as exemplified by the birth-death model (Kostitzin, 1939)

$$\frac{dn_i}{dt} = (b_i - \delta_i N)n_i. \quad (11)$$

Here δ_i is per-capita mortality due to crowding (for simplicity, there are no deaths when uncrowded). Starting from a type 1 population in equilibrium (we consider the non-equilibrium case in BLAH), a variant with $\delta_2 = \delta_1(1 - \epsilon)$ has density-dependent selection coefficient $s = \epsilon \delta_1 N$ in Eq. (1). This only affects the sweep if N changes substantially as the population shifts to the new equilibrium. From Eq. (11) we have $N_{\text{initial}} = b_1/\delta_1$ and $N_{\text{final}} = b_1/(\delta_1(1 - \epsilon)) = N_{\text{initial}}/(1 - \epsilon)$, and so $s_{\text{initial}} = \epsilon b_1$ and $s_{\text{final}} = s_{\text{initial}}/(1 - \epsilon)$. Consequently, substantial deviations from Eq. (1) occurs if there is sufficiently strong selection on δ (Fig. 6; Kimura and Crow 1969; Crow et al. 1970).

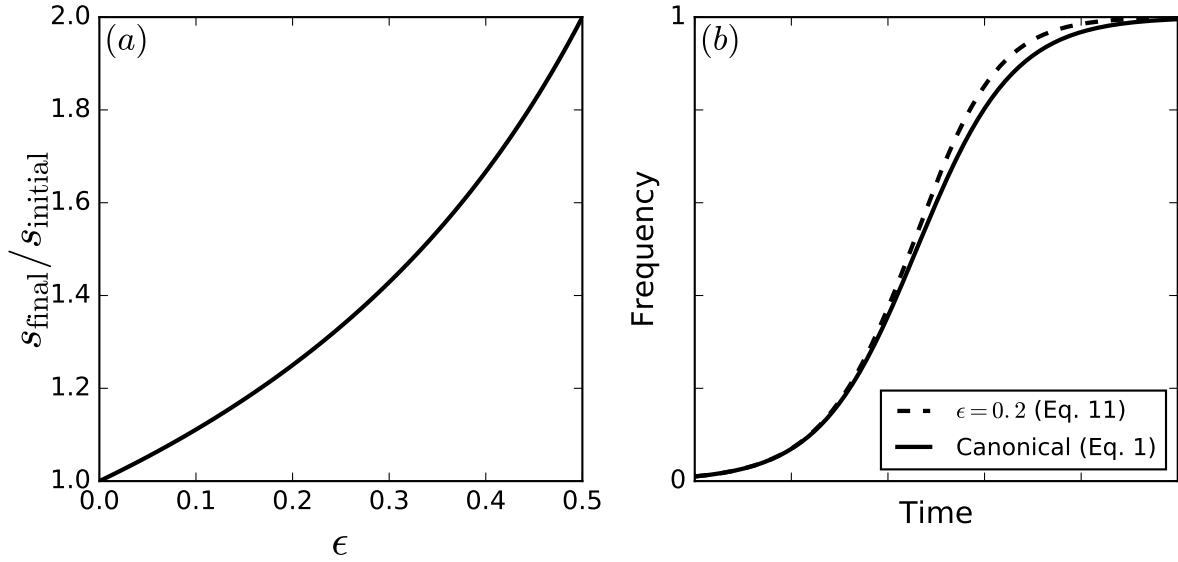


Figure 6: (a) Proportional change in the selection coefficient for a type that experiences proportionally $1 - \epsilon$ fewer deaths induced by crowding. The population is in demographic equilibrium at the start and end of the sweep. (b) Example equilibrium-to-equilibrium sweep.

Equilibrium-to-equilibrium b -sweeps in the variable-density lottery are qualitatively different from δ sweeps, because greater b not only means more propagules contesting territories, but also more territories being contested. Together, the net density-dependent effect on b -selection is zero; in Eq. (8), since $b_i/\bar{b} = 1$ in a single-type equilibrium, the density-dependence factor $f(\bar{b}, N) = \frac{1 - e^{-\bar{b}N/T}}{N}(T - N)$ is exactly equal to the constant mortality rate at the beginning and end of a b -sweep, even though b and density change. During the sweep there is some deviation in $f(\bar{b}, N)$, but this deviation is an order of magnitude smaller than for a δ sweep (the density-dependent deviation constant s in Fig. 6 is of order ϵ , whereas the analogous effect for b sweep in the variable-density lottery is only of order ϵ^2 ; see Appendix D for details). Since selection must already be strong for a δ -sweep to threaten Eq. (1), the density-independent model applies effectively exactly for equilibrium b -sweeps. Note, however, that the selection coefficient for b -sweeps (as defined by differences in $\Delta n_i/n_i$) does depend on frequency because of the $1/\bar{b}$ factor.

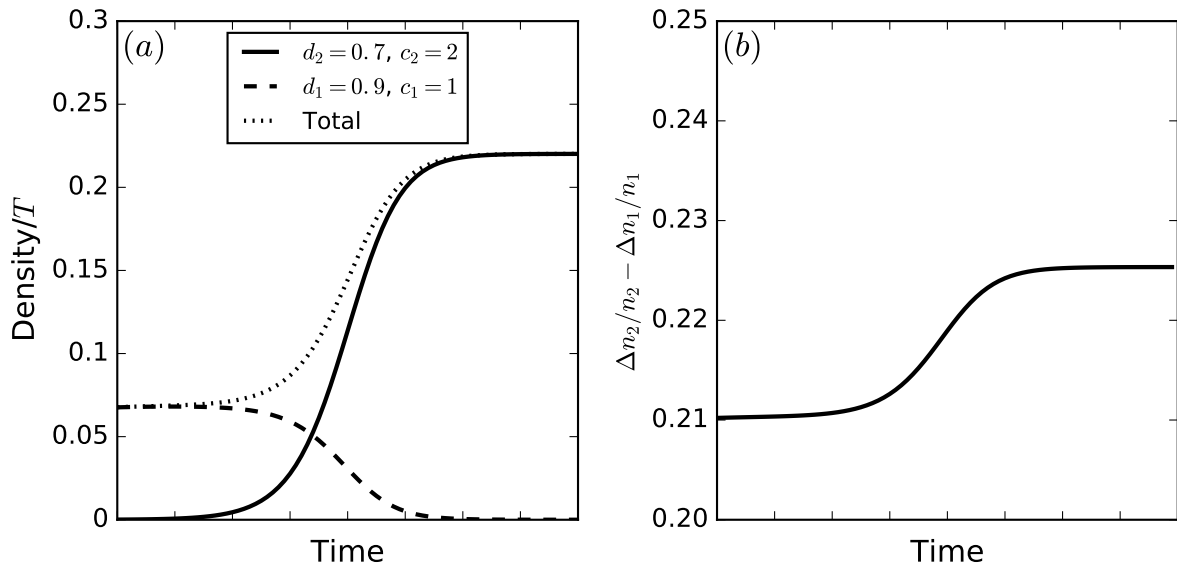


Figure 7: Simultaneous selection on d and c in the variable-density lottery model as predicted by Eq. (5). Selection is not constant over the sweep because d is density-regulating and c is density-dependent.

If selection acts simultaneously on more than one trait in the variable-density lottery, then evolution in a density-regulating trait can drive changes in the strength of selection on a trait subject to density-dependent selection (Fig. 7). This can produce behavior analogous to selection on δ in Fig. 6.

Discussion

Summarizing the three traits in the variable-density lottery model: (i) c -selection is density-dependent, but c does not regulate density; (ii) d regulates density, but d -selection is density-independent; (iii) b regulates density and b -selection is density-dependent. Yet despite these differences, pure b , c and d sweeps starting and ending at equilibrium all obey the density-independent relative fitness description of selection almost exactly. This behavior is quite different from that found in the classical density-dependent selection literature (Roughgar-

den, 1979; Christiansen, 2004).

To briefly review: based on a diploid, bi-allelic variant of the logistic model, the r/K scheme proposed a dichotomy between r -selection (uncrowded) and K -selection (crowded) (MacArthur, 1962), with the latter taken to mean selection for greater equilibrium density (Gill, 1974). A more general Lotka-Volterra model introduces the inter-type α_{ij} competition coefficients, with selection on these termed “ α -selection” (Gill, 1974; Joshi et al., 2001). Setting aside r which confers no selective advantage at equilibrium, we are left with K and α , which both behave like δ in Eq. (11) in that they are density-dependent and cause density to change over a sweep (although N only dips transiently during an α -sweep). Thus, strong selection is sufficient for relative fitness to break down in the classical view of density-dependent selection.

Our variable-density lottery model shows that it is not simply a lack of ecological realism that underlies the contrast between relative fitness and the classical view of density-dependent selection. Rather, in many population growth models, only one life-history stage is represented, and the competitive effects resulting from crowding appear as a reduction in absolute fitness that only depends on the type densities at this life-history stage (e.g. the n_i^2 and $n_i n_j$ terms in the Lotka Volterra equation). As noted in the introduction, this precludes selection concentrated at a fragile juvenile stage as a result of a reproductive excess (Chesson, 1983; Turner and Williamson, 1968; Kimura and Crow, 1969; Nei, 1971).

Reproductive excesses appear in the variable-density lottery model when the number of propagules is greater than the number of available territories. Then only $\approx 1/L$ of the juveniles contesting available territories survive to adulthood. Unlike the role of adult density n_i in single-life-stage models, it is the propagule densities l_i that represent the crowding that drives competition (a “critical age-group”; Charlesworth 1994, pp. 54). In general, reproductive excesses will tend to produce strictly-relative lottery-type contests in which fitter types grow at the expense of others by preferentially filling the available adult “slots”.

The number of slots can remain fixed or change independently of selection at the juvenile stage. By ignoring reproductive excesses, single life-stage models are biased to have total population density be sensitive to ongoing selection. In this respect, the viability selection heuristics that are common in population genetics (Gillespie, 2010, pp. 61) actually capture an important ecological process without jumping to the full complexity of age-structured models.

We now turn to the breakdown of the density-independent relative fitness assumption which occurs when strong selection changes population density and is also density-dependent (Fig. 6). In the variable-density lottery, this occurs if and only if types differ in more than one trait (Fig. 7). The c and d traits represent the two distinct directions in which density and selection interact: selection may depend on density, and density may depend on selection (Prout, 1980). The combination is necessary to pose a threat to Eq. (1). However, the b trait remarkably demonstrates that the combination is not sufficient, since the density-dependence of b -selection disappears over equilibrium-to-equilibrium b -sweeps. Thus, the simple differential/difference equations that have become standard in discussions of density-dependent selection (Roughgarden, 1979; Christiansen, 2004; Mallet, 2012; Travis et al., 2013) actually represent a confounded form of the interaction between density and selection.

While this is a conceptual reason to be wary of the classical density-dependent selection models, it is not clear what trait variation to expect in nature. Should we expect mutations to generally affect b , c and d independently of each other, or pleiotropically such that δ -like selection is prevalent? In the case of well-mixed indirect exploitation competition for consumable resources, the R^* rule suggests that δ -like selection will be prevalent. However, for many populations consumable resources are not well-mixed. Spatial localization of consumable resources (e.g. due to restricted movement of nutrients through soils) will tend to create a territorial situation similar to the lottery model, where resource competition only occurs locally and both it and interference competition are subsumed into the competitive

ability c , which does not affect N .

The above findings underscore that the most serious threat to relative fitness arises from deviations from demographic equilibrium. This can dramatically alter frequency trajectories for individual sweeps (e.g. Fig. 9.5 in Otto and Day (2011); Fig. 5 in Mallet (2012)), as well as the long-term outcomes of selection in fluctuating environments (Lande et al., 2009). This would suggest that in the wild *Drosophila* example mentioned in the Introduction, there is indeed no choice but to abandon relative fitness. The variable-density lottery could provide a useful starting point for analyzing evolution in this and other far-from-equilibrium situations. One convenient feature of our variable-density lottery (and lottery models in general) is a formal similarity to the Wright-Fisher model, which should facilitate the analysis of “density-dependent drift”.

Another issue with the constant- N relative fitness description of selection is that it precludes consideration of longer-term aspects of the interplay between evolution and ecology such as population extinction. A variety of approaches have been developed for dealing with these issues in quantitative genetics (Burger and Lynch, 1995; Engen et al., 2013), population genetics (Bertram et al., 2017) and adaptive dynamics (Ferriere and Legendre, 2013; Dieckmann and Ferrière, 2004). Although density-dependent selection is pertinent to these longer-term issues (Travis et al., 2013), our focus here has been the description of the time-dependent process by which selection changes allele frequencies. This is particularly critical for making sense of evolution at the genetic level, for which we now have abundant data.

References

- N. Barton, D. Briggs, J. Eisen, D. Goldstein, and N. Patel. *Evolution*. NY: Cold Spring Harbor Laboratory Press, 2007.
- T. Benton and A. Grant. Evolutionary fitness in ecology: comparing measures of fitness in

stochastic, density-dependent environments. *Evolutionary ecology research*, 2(6):769–789,
2000.

A. O. Bergland, E. L. Behrman, K. R. O’Brien, P. S. Schmidt, and D. A. Petrov. Genomic
evidence of rapid and stable adaptive oscillations over seasonal time scales in drosophila.
PLOS Genetics, 10(11):1–19, 11 2014. doi: 10.1371/journal.pgen.1004775.

J. Bertram, K. Gomez, and J. Masel. Predicting patterns of long-term adaptation and
extinction with population genetics. *Evolution*, 71(2):204–214, 2017.

B. M. Bolker and S. W. Pacala. Spatial moment equations for plant competition: Under-
standing spatial strategies and the advantages of short dispersal. *The American Naturalist*,
153(6):575–602, 1999. doi: 10.1086/303199.

R. Burger and M. Lynch. Evolution and extinction in a changing environment: a
quantitative-genetic analysis. *Evolution*, pages 151–163, 1995.

B. Charlesworth. *Evolution in age-structured populations*, volume 2. Cambridge University
Press Cambridge, 1994.

P. L. Chesson. *Coexistence of Competitors in a Stochastic Environment: The Storage Effect*,
pages 188–198. Springer Berlin Heidelberg, Berlin, Heidelberg, 1983. ISBN 978-3-642-
87893-0.

P. L. Chesson and R. R. Warner. Environmental variability promotes coexistence in lottery
competitive systems. *American Naturalist*, pages 923–943, 1981.

F. Christiansen. Density dependent selection. In *Evolution of Population Biology: Modern
Synthesis*, pages 139–155. Cambridge University Press, 2004.

J. F. Crow, M. Kimura, et al. *An introduction to population genetics theory*. New York,
Evanston and London: Harper & Row, Publishers, 1970.

- 405 U. Dieckmann and R. Ferrière. Adaptive dynamics and evolving biodiversity. 2004.
- 406 M. Doebeli, Y. Ispolatov, and B. Simon. Towards a mechanistic foundation of evolutionary
407 theory. *eLife*, 6:e23804, feb 2017. ISSN 2050-084X. doi: 10.7554/eLife.23804.
- 408 S. Engen, R. Lande, and B.-E. Saether. A quantitative genetic model of r - and k -selection in
409 a fluctuating population. *The American Naturalist*, 181(6):725–736, 2013. ISSN 00030147,
410 15375323. URL <http://www.jstor.org/stable/10.1086/670257>.
- 411 W. J. Ewens. *Mathematical Population Genetics 1: Theoretical Introduction*. Springer
412 Science & Business Media, 2004.
- 413 R. Ferriere and S. Legendre. Eco-evolutionary feedbacks, adaptive dynamics and evolutionary
414 rescue theory. *Phil. Trans. R. Soc. B*, 368(1610):20120081, 2013.
- 415 D. E. Gill. Intrinsic rate of increase, saturation density, and competitive ability. ii. the
416 evolution of competitive ability. *American Naturalist*, 108:103–116, 1974.
- 417 J. H. Gillespie. *Population genetics: a concise guide (2nd Ed.)*. John Hopkins University
418 Press, 2010.
- 419 J. P. Grover. *Resource competition*, volume 19. Springer Science & Business Media, 1997.
- 420 A. Joshi, N. Prasad, and M. Shakarad. K -selection, α -selection, effectiveness, and tolerance
421 in competition: density-dependent selection revisited. *Journal of Genetics*, 80(2):63–75,
422 2001.
- 423 M. Kimura and J. F. Crow. Natural selection and gene substitution. *Genetics Research*, 13
424 (2):127–141, 1969.
- 425 V. A. Kostitzin. *Mathematical biology*. George G. Harrap And Company Ltd.; London, 1939.

- 426 R. Lande, S. Engen, and B.-E. Sæther. An evolutionary maximum principle for density-
 427 dependent population dynamics in a fluctuating environment. *Philosophical Transactions*
 428 *of the Royal Society B: Biological Sciences*, 364(1523):1511–1518, 2009.
- 429 R. Levins and D. Culver. Regional coexistence of species and competition between rare
 430 species. *Proceedings of the National Academy of Sciences*, 68(6):1246–1248, 1971.
- 431 R. H. MacArthur. Some generalized theorems of natural selection. *Proceedings of the National*
 432 *Academy of Sciences*, 48(11):1893–1897, 1962.
- 433 R. H. MacArthur and E. O. Wilson. *Theory of Island Biogeography*. Princeton University
 434 Press, 1967.
- 435 J. Mallet. The struggle for existence. how the notion of carrying capacity, k , obscures the
 436 links between demography, darwinian evolution and speciation. *Evol Ecol Res*, 14:627–665,
 437 2012.
- 438 P. W. Messer, S. P. Ellner, and N. G. Hairston. Can population genetics adapt to rapid
 439 evolution? *Trends in Genetics*, 32(7):408–418, 2016.
- 440 C. J. E. Metcalf and S. Pavard. Why evolutionary biologists should be demographers.
 441 *Trends in Ecology and Evolution*, 22(4):205 – 212, 2007. ISSN 0169-5347. doi:
 442 <https://doi.org/10.1016/j.tree.2006.12.001>.
- 443 J. A. Metz, R. M. Nisbet, and S. A. Geritz. How should we define fitness for general ecological
 444 scenarios? *Trends in Ecology & Evolution*, 7(6):198–202, 1992.
- 445 M. Nei. Fertility excess necessary for gene substitution in regulated populations. *Genetics*,
 446 68(1):169, 1971.
- 447 S. P. Otto and T. Day. *A biologist’s guide to mathematical modeling in ecology and evolution*.
 448 Princeton University Press, 2011.

- 449 T. Prout. Some relationships between density-independent selection and density-dependent
450 population growth. *Evol. Biol*, 13:1–68, 1980.
- 451 J. Roughgarden. Theory of population genetics and evolutionary ecology: an introduction.
452 1979.
- 453 P. F. Sale. Maintenance of high diversity in coral reef fish communities. *The American*
454 *Naturalist*, 111(978):337–359, 1977.
- 455 P. E. Smouse. The implications of density-dependent population growth for frequency-and
456 density-dependent selection. *The American Naturalist*, 110(975):849–860, 1976.
- 457 D. Tilman. Competition and biodiversity in spatially structured habitats. *Ecology*, 75(1):
458 2–16, 1994.
- 459 J. Travis, J. Leips, and F. H. Rodd. Evolution in population parameters: Density-dependent
460 selection or density-dependent fitness? *The American Naturalist*, 181(S1):S9–S20, 2013.
461 doi: 10.1086/669970.
- 462 J. Turner and M. Williamson. Population size, natural selection and the genetic load. *Nature*,
463 218(5142):700–700, 1968.
- 464 G. P. Wagner. The measurement theory of fitness. *Evolution*, 64(5):1358–1376, 2010.

465 **Appendix A: Growth equation derivation**

466 In this appendix we derive Eq. (5). Following the notation in the main text, the Poisson
467 distributions for the x_i (or some subset of the x_i) will be denoted p , and we use P as a
468 general shorthand for the probability of particular outcomes.

469 We start by separating the right hand side of Eq. (2) into three components

$$\Delta_+ n_i = \Delta_u n_i + \Delta_r n_i + \Delta_a n_i, \quad (12)$$

470 which vary in relative magnitude depending on the propagule densities l_i . The first compo-
 471 nent, $\Delta_u n_i$, accounts for territories where only one focal propagule is present ($x_i = 1$ and
 472 $x_j = 0$ for $j \neq i$; u stands for “uncontested”). The proportion of territories where this occurs
 473 is $l_i e^{-L}$, and so

$$\Delta_u n_i = U l_i e^{-L} = m_i e^{-L}. \quad (13)$$

474 The second component, $\Delta_r n_i$, accounts for territories where a single focal propagule is
 475 present along with at least one non-focal propagule ($x_i = 1$ and $X_i \geq 1$ where $X_i = \sum_{j \neq i} x_j$
 476 is the number of nonfocal propagules; r stands for “rare”). The number of territories where
 477 this occurs is $U p_i(1) P(X_i \geq 1) = m_i e^{-l_i} (1 - e^{-(L-l_i)})$. Thus

$$\Delta_r n_i = m_i e^{-l_i} (1 - e^{-(L-l_i)}) \left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}}, \quad (14)$$

478 where $\langle \rangle_{\tilde{p}}$ denotes the expectation with respect to the probability distribution \tilde{p} of nonfocal
 479 propagule abundances x_j , in those territories where exactly one focal propagule, and at least
 480 one non-focal propagule, landed.

481 The final contribution, $\Delta_a n_i$, accounts for territories where two or more focal propagules
 482 are present ($x_i \geq 2$; a stands for “abundant”). Similar to Eq. (14), we have

$$\Delta_a n_i = U (1 - (1 + l_i) e^{-l_i}) \left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \quad (15)$$

483 where \hat{p} is the probability distribution of both focal and nonfocal propagule abundances in
 484 those territories where at least two focal propagules landed.

To derive Eq. (5) we approximate the expectations in Eq. (14) and Eq. (15) by replacing x_i and the x_j with “effective” mean values as follows

$$\left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}} \approx \frac{c_i}{c_i + \sum_{j \neq i} c_j \langle x_j \rangle_{\tilde{q}}}. \quad (16)$$

$$\left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \approx \frac{c_i \langle x_i \rangle_{\hat{q}}}{\sum_j c_j \langle x_j \rangle_{\hat{q}}}. \quad (17)$$

Here the effective means $\langle \rangle_{\tilde{q}}$ and $\langle \rangle_{\hat{q}}$ are taken with respect to new distributions \tilde{q} and \hat{q} , respectively. In the following subsection we define \tilde{q} and \hat{q} and explain our reasoning for using these distributions to take the effective means.

The effective distributions \tilde{q} and \hat{q}

The approximations (16) and (17) must be consistent between rare and common types. To illustrate, suppose that two identical types (same b , c and d) are present, with low $l_1 \ll 1$ and high density $l_2 \approx L \gg 1$ respectively. Since L is large, uncontested territories make up a negligible fraction of the total. The rare type grows almost entirely due to $\Delta_r n_1$, while the common type grows almost entirely due to $\Delta_a n_2$. To ensure consistency, the approximate per-capita growth rates implied by the approximations (16) and (17) must be equal $\Delta_r n_1 / m_1 = \Delta_a n_2 / m_2$. Even small violations of this consistency condition would mean exponential growth of one type relative to the other. This behavior is clearly pathological, because any single-type population can be arbitrarily partitioned into identical rare and common subtypes. Thus, predicted growth or decline would depend on an arbitrary assignment of rarity.

For example, suppose that we use \tilde{p} and \hat{p} to calculate the effective means. The right hand side of Eq. (16) is then approximately $1/(L+1)$, and since $l_1 \ll 1$ and $L \gg 1$ we have $\Delta_r n_1 \approx 1/(L+1)$ in Eq. (14). Similarly, for the common type, $\sum_j \langle x_j \rangle_{\hat{p}} = L$ in Eq. (17),

506 and so $\Delta_a n_2 \approx 1/L$. Thus, the identical rare type is pathologically predicted to decline in
 507 frequency.

508 The effective distributions \tilde{q} and \hat{q} are devised to avoid this pathology. The idea is to
 509 make the approximation that the distribution for the total number of propagules per territory
 510 is the same in all territories. This is only an approximation because conditioning on focal
 511 propagules being present does change the distribution of X in the corresponding subset of
 512 territories (in the above example, the mean propagule density across all territories is L , but
 513 in the territories responsible for the growth of the rare type we have $\langle X \rangle_{\tilde{p}} = L + 1$).

514 More formally, let \mathbf{x} denote the vector of propagule abundances (x_1, \dots, x_G) in a given
 515 territory, and $\mathbf{x}_i = (x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_G)$ similarly denote the vector of non-focal abun-
 516 dances, so that $p(\mathbf{x}_i) = p_1(x_1) \cdots p_{i-1}(x_{i-1}) p_{i+1}(x_{i+1}) \cdots p_G(x_G)$. The corresponding total
 517 propagule numbers are denoted $X = \sum_j x_j$ and $X_i = X - x_i$. Then, in territories where one
 518 focal propagule and at least one non-focal propagule are present, the effective distribution
 519 is defined by

$$\tilde{q}(\mathbf{x}_i) = \sum_{X=2}^{\infty} P(X|X \geq 2) p(\mathbf{x}_i|X_i = X - 1), \quad (18)$$

520 where the total number of propagules X follows a Poisson distribution with mean L , and
 521 $P(X|X \geq 2) = P(X)/P(X \geq 2) = P(X)/(1 - (1 + L)e^{-L})$. Similarly, in territories where
 522 more than one focal propagule is present, the effective distribution is defined by

$$\hat{q}(\mathbf{x}) = \sum_{X=2}^{\infty} P(X|X \geq 2) p(\mathbf{x}|x_i \geq 2, X). \quad (19)$$

523 Calculating the effective means

Here we calculate the effective means, starting with the $\Delta_r n_i$ component. We have

$$\begin{aligned}\langle x_j \rangle_{\tilde{q}} &= \sum_{\mathbf{x}_i} \tilde{q}(\mathbf{x}_i) x_j \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - 1) x_j.\end{aligned}\quad (20)$$

The inner sum over \mathbf{x}_i is the mean number of propagules of a given nonfocal type j that will be found in a territory which received $X - 1$ nonfocal propagules in total, which is equal to $\frac{l_j}{L - l_i}(X - 1)$. Thus,

$$\begin{aligned}\langle x_j \rangle_{\tilde{q}} &= \frac{l_j}{1 - (1 + L)e^{-L}} \frac{1}{L - l_i} \sum_{X=2}^{\infty} P(X)(X - 1) \\ &= \frac{l_j}{1 - (1 + L)e^{-L}} \frac{L - 1 + e^{-L}}{L - l_i},\end{aligned}\quad (21)$$

524 where the last line follows from $\sum_{X=2}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)X -$
525 $\sum_{X=1}^{\infty} P(X)$. Substituting Eqs. (16) and (21) into Eq. (14), we obtain

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{\bar{c}}, \quad (22)$$

526 where R_i is defined in Eq. (6).

Turning now to the $\Delta_a n_i$ component, the mean focal abundance is

$$\begin{aligned}
\langle x_i \rangle_{\hat{q}} &= \sum_{\mathbf{x}} \hat{q}(\mathbf{x}) x_i \\
&= \sum_{x_i} p(x_i | x_i \geq 2) x_i \\
&= \frac{1}{1 - (1 + l_i) e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i \\
&= l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i) e^{-l_i}}.
\end{aligned} \tag{23}$$

For nonfocal types $j \neq i$, we have

$$\begin{aligned}
\langle x_j \rangle_{\hat{q}} &= \sum_{X=2}^{\infty} P(X | X \geq 2) \sum_{\mathbf{x}} p(\mathbf{x} | x_i \geq 2, X) x_j \\
&= \sum_{X=2}^{\infty} P(X | X \geq 2) \sum_{x_i} p(x_i | x_i \geq 2, X) \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - x_i) x_j \\
&= \sum_{X=2}^{\infty} P(X | X \geq 2) \sum_{x_i} p(x_i | x_i \geq 2, X) \frac{l_j (X - x_i)}{L - l_i} \\
&= \frac{l_j}{L - l_i} \left[\sum_{X=2}^{\infty} P(X | X \geq 2) X - \sum_{x_i} p(x_i | x_i \geq 2) x_i \right] \\
&= \frac{l_j}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1 + L) e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i) e^{-l_i}} \right).
\end{aligned} \tag{24}$$

527 In going from line 2 to 3, we used the same logic used to evaluate the inner sum in Eq. (20),
528 and in going from 3 to 4 we have separately evaluated the contributions from the X and x_i
529 terms in the numerator. Combining these results with Eqs. (15) and (17), we obtain

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \tag{25}$$

530 where A_i is defined in Eq. (6).

Approximation limits

Eq. (16) and (17) must not only be consistent with each other, they must also be individually good approximations. Here we evaluate these approximations.

The fundamental requirement for making the replacement in Eqs. (16) and (17) is that we can ignore the fluctuations in the x_i and hence replace them with a constant effective mean value. Mathematically, we require that the standard deviations $\sigma_{\tilde{q}}(\sum_{j \neq i} c_j x_j)$ and $\sigma_{\hat{q}}(\sum_j c_j x_j)$ must be sufficiently small compared to the corresponding means $\langle \sum_{j \neq i} c_j x_j \rangle_{\tilde{q}}$ and $\langle \sum_j c_j x_j \rangle_{\hat{q}}$ in Eqs. (16) and (17) respectively.

To evaluate these standard deviations, we will work with \tilde{p} and \hat{p} distributions instead of \tilde{q} and \hat{q} . This is mathematically much simpler because the x_i are independent under \tilde{p} and \hat{p} , and is justified by the fact that \tilde{p} and \hat{p} are closely related to \tilde{q} and \hat{q} respectively, and so we expect the relevant means and standard deviations will be similar.

Starting with Eq. (16), we have $\langle x_j \rangle_{\tilde{p}} = l_j/C$, where $C = 1 - e^{-(L-l_i)}$, and the corresponding variances and covariances are given by

$$\begin{aligned} \sigma_{\tilde{p}}^2(x_j) &= \langle x_j^2 \rangle_{\tilde{p}} - \langle x_j \rangle_{\tilde{p}}^2 \\ &= \frac{l_j^2 + l_j}{C} - \frac{l_j^2}{C^2} \\ &= \left(1 - \frac{1}{C}\right) \frac{l_j^2}{C} + \frac{l_j}{C}, \end{aligned} \tag{26}$$

and

$$\begin{aligned} \sigma_{\tilde{p}}(x_j, x_k) &= \langle x_j x_k \rangle_{\tilde{p}} - \langle x_j \rangle_{\tilde{p}} \langle x_k \rangle_{\tilde{p}} \\ &= \frac{1}{C} \langle x_j x_k \rangle_p - \frac{l_j l_k}{C^2} \\ &= \left(1 - \frac{1}{C}\right) \frac{l_j l_k}{C} \quad j \neq k. \end{aligned} \tag{27}$$

543 Note that $1 - 1/C$ is negative because $C < 1$. Decomposing the variance in $\sum_{j \neq i} c_j x_j$,

$$\sigma_{\hat{p}}^2(\sum_{j \neq i} c_j x_j) = \sum_{j \neq i} \left[c_j^2 \sigma_{\hat{p}}^2(x_j) + 2 \sum_{k > j, k \neq i} c_j c_k \sigma_{\hat{p}}(x_j, x_k) \right], \quad (28)$$

544 we obtain

$$\frac{\sigma(\sum_{j \neq i} c_j x_j)}{\langle \sum_{j \neq i} c_j x_j \rangle} = C^{1/2} \frac{\left(\sum_{j \neq i} c_j^2 l_j + (1 - \frac{1}{C}) \left(\sum_{j \neq i} c_j l_j \right)^2 \right)^{1/2}}{\sum_{j \neq i} c_j l_j}. \quad (29)$$

545 Eq. (29) reveals two key points. First, when the c_j have similar magnitudes (their ratios
 546 are of order one), Eq. (16) is an excellent approximation. In this case, the right hand side of
 547 Eq. (29) is approximately equal to $C^{1/2} \left(\frac{1}{L-l_i} + 1 - \frac{1}{C} \right)^{1/2}$, which is small for both low and
 548 high nonfocal densities. The worst case scenario occurs when $L - l_i$ is of order one, and it
 549 can be directly verified that Eq. (16) is then still a good approximation (see Fig. 8). Second,
 550 if some of the c_j are much larger than the others, the relative fluctuations in $\sum_{j \neq i} c_j x_j$ can
 551 be large. Specifically, in the presence of a rare, strong competitor ($c_j l_j \gg c_{j'} l_{j'}$ for all other
 552 nonfocal types j' , and $l_j \ll 1$), then the right hand side of Eq. (29) can be large and we
 553 cannot make the replacement Eq. (16). Fig. 8 shows the breakdown of the effective mean
 554 approximation when there are large differences in c .

555 Turning now to Eq. (17), all covariances between nonfocal types are now zero, so that
 556 $\sigma_{\hat{p}}^2(\sum c_j x_j) = \sum c_j^2 \sigma_{\hat{p}}^2(x_j)$, where $\sigma_{\hat{p}}^2(x_j) = l_j$ for $j \neq i$. Here

$$\sigma_{\hat{p}}^2(x_i) = \frac{l_i}{D} \left(l_i + 1 - e^{-l_i} - \frac{l_i}{D} (1 - e^{-l_i})^2 \right), \quad (30)$$

557 where $D = 1 - (1 + l_i)e^{-l_i}$, and

$$\frac{\sigma_{\hat{p}}(\sum c_j x_j)}{\langle \sum c_j x_j \rangle} = \frac{\left(\sum_{j \neq i} c_j^2 l_j + c_i^2 \sigma_{\hat{p}}^2(x_i) \right)^{1/2}}{\sum_{j \neq i} c_j l_j + c_i l_i (1 - e^{-l_i})/D}. \quad (31)$$

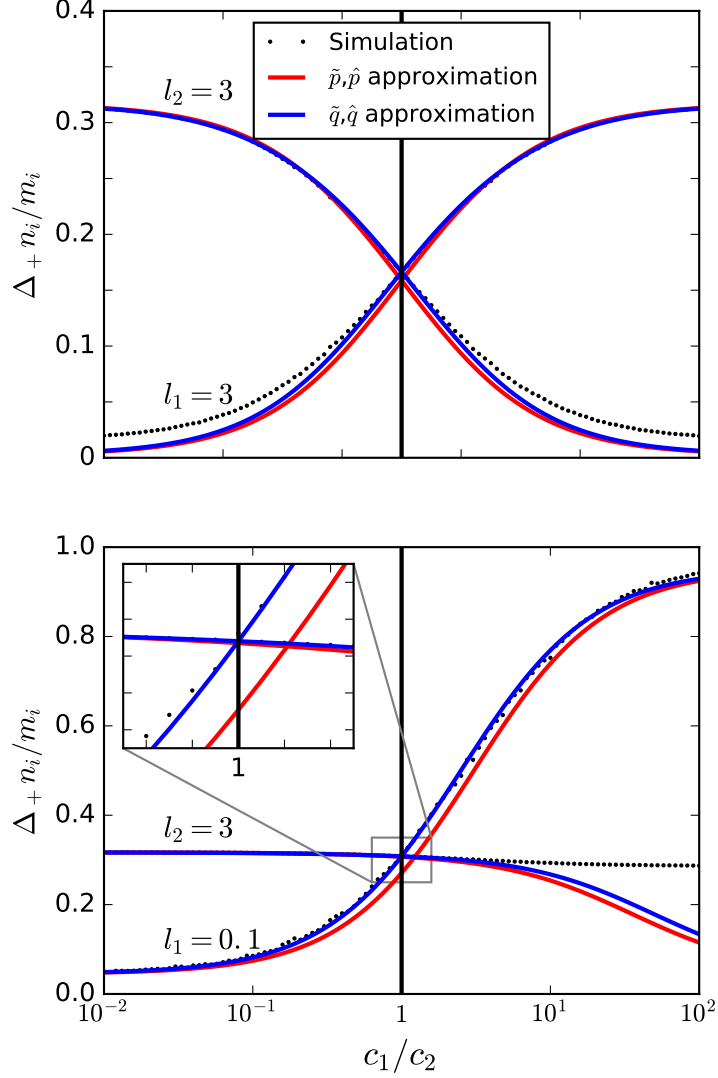


Figure 8: Comparison of our \tilde{q}, \hat{q} approximation with simulations, and also with the naive \tilde{p}, \hat{p} approximation, as a function of the relative c difference between two types. Our approximation breaks down in the presence of large c differences. The inset shows the pathology of the \tilde{p}, \hat{p} approximation — growth rates are not equal in the neutral case $c = 1$. Simulation procedure is the same as in Fig. 3, with $U = 10^5$.

Similarly to Eq. (29), the right hand side of Eq. (31) is small for both low and high nonfocal densities. Again, the worst case scenario occurs when l_i and $L - l_i$ are of order 1, but Eq. (17) is still a good approximation in this case. Again, the approximation breaks down in the presence of a rare, strong competitor (Fig. 8).

Appendix B: Total density in the Lotka-Volterra competition model

Here we show that under the Lotka-Volterra model of competition, total density N does not in general remain constant over a selective sweep in a crowded population even if the types have the same equilibrium density (for a related discussion on the density- and frequency-dependence of selection in the Lotka-Volterra model, see (Smouse, 1976; Mallet, 2012)).

We assume equal effects of crowding within types $\alpha_{11} = \alpha_{22} = \alpha_{\text{intra}}$ and $N = 1/\alpha_{\text{intra}}$ and check whether it is then possible for $\frac{dN}{dt}$ to be zero in the sweep ($n_1, n_2 \neq 0$). Substituting these conditions into Eq. (10), we obtain

$$\begin{aligned}\frac{dn_1}{dt} &= r_1(\alpha_{11} - \alpha_{12})n_1n_2 \\ \frac{dn_2}{dt} &= r_2(\alpha_{22} - \alpha_{21})n_1n_2\end{aligned}\tag{32}$$

Adding these together, $\frac{dN}{dt}$ can only be zero if

$$r_1(\alpha_{\text{intra}} - \alpha_{12}) + r_2(\alpha_{\text{intra}} - \alpha_{21}) = 0.\tag{33}$$

To get some intuition for Eq. (33), suppose that a mutant arises with improved competitive ability but identical intrinsic growth rate and equilibrium density ($r_1 = r_2$ and $\alpha_{11} = \alpha_{22}$). This could represent a mutation to an interference competition trait, for example (Gill,

1974). Then, according the above condition, for N to remain constant over the sweep, the mutant must find the wildtype more tolerable than itself by exactly the same amount that the wildtype finds the mutant less tolerable than itself.

Even if we persuaded ourselves that this balance of inter-type interactions is plausible in some circumstances, when multiple types are present the requirement for constant N becomes

$$\sum_{ij} r_i(\alpha_{\text{intra}} - \alpha_{ij})p_i p_j = 0, \quad (34)$$

which depends on frequency and thus cannot be satisfied in general for constant inter-type coefficients α_{ij} . Therefore, Lotka-Volterra selection will generally involve non-constant N .

Appendix C: Density-dependence of b -selection

In section “Density-regulating traits and the threat of strong selection” we argued that the density-dependent factor $f(\bar{b}, N)$ is unchanged at the beginning and end points of an equilibrium-to-equilibrium b . Here we estimate the magnitude of the deviation in $f(\bar{b}, N)$ during the sweep.

For simplicity, we introduce the notation $D = N/T$ and assume that D is small. We can thus make the approximation $1 - e^{-\bar{b}D} \approx \bar{b}D$ and $f(\bar{b}, N) \approx \bar{b}(1 - D)$. We expect this to be a conservative approximate based on the worst case scenario, because N is most sensitive to an increase in b in this low-density linear regime. We first calculate the value of $f(\bar{b}, N)$ at the halfway point in a sweep, where the halfway point is estimated with simple linear averages for b and N . The sweep is driven by a b variant with $b_j = b_i(1 + \epsilon)$, and we denote the corresponding initial and final densities by D_i and D_j respectively, where we

have $d_i = b_i(1 - D_i) = b_j(1 - D_j)$. We obtain

$$\begin{aligned}
f_{\text{half}} &= f\left(\frac{b_i + b_j}{2}, \frac{N_i + N_j}{2}\right) = \frac{b_i + b_j}{2} \left(1 - \frac{D_i + D_j}{2}\right) \\
&= \frac{1}{4}(b_i + b_j)(2 - D_i - D_j) \\
&= \frac{1}{4}(2d_i + b_i(1 - D_j) + b_j(1 - N_i)). \tag{35}
\end{aligned}$$

Dividing by d_i , the proportional deviation in $f(N)$ at the midpoint of the sweep is

$$\begin{aligned}
\frac{f_{\text{half}}}{d_i} &= \frac{1}{4} \left(2 + \frac{b_i}{b_j} + \frac{b_j}{b_i}\right) \\
&= \frac{1}{4} \left(2 + \frac{1}{1 + \epsilon} + 1 + \epsilon\right) \\
&= 1 + \frac{1}{4}(\epsilon^2 - \epsilon^3 + \dots), \tag{36}
\end{aligned}$$

585 where we have used the Taylor expansion $\frac{1}{1+\epsilon} = 1 - \epsilon + \epsilon^2 - \epsilon^3 + \dots$

586 By contrast, for a δ sweep in Eq. (11), the density-dependent term N increases by a
587 factor of $\frac{1}{1-\epsilon} = 1 + \epsilon + \epsilon^2 + \dots$. Thus, the deviations in $f(N)$ are an order of magnitude
588 smaller than those shown in Fig. (6).