

Density-dependent selection and the limits of relative fitness

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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).

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Abstract

Selection is commonly described by assigning constant relative fitness values to genotypes. Yet population density is often regulated by crowding. Relative fitness may then depend on density, and selection can change density when it acts on a density-regulating trait. When strong density-dependent selection acts on a density-regulating trait, selection is no longer describable by density-independent relative fitnesses, even in demographically stable populations. These conditions are met in most previous models of density-dependent selection (e.g. “ K -selection” in the logistic and Lotka-Volterra models), suggesting that density-independent relative fitnesses must be replaced with more ecologically explicit absolute fitnesses unless selection is weak. Here we show that density-independent relative fitnesses can also accurately describe strong density-dependent selection under some conditions. We develop a novel model of density-regulated population growth with three ecologically intuitive traits: fecundity, mortality, and competitive ability. Our model, unlike the logistic or Lotka-Volterra, incorporates a density-dependent juvenile “reproductive excess”, which largely decouples density-dependent selection from the regulation of density. We find that density-independent relative fitnesses accurately describe strong selection acting on any one trait, even fecundity, which is both density-regulating and subject to density-dependent selection. Pleiotropic interactions between these traits recovers the familiar K -selection behavior. In such cases, or when the population is maintained far from demographic equilibrium, our model offers a possible alternative to relative fitness.

(215 words)

Introduction

There are a variety of different measures of fitness, such as expected lifetime reproductive ratio R_0 , intrinsic population growth rate r , equilibrium population density/carrying capacity (often labeled “ K ”) (Benton and Grant, 2000), and invasion fitness (Metz et al., 1992). In addition, “relative fitness” is widely used in evolutionary genetics, where the focus is on relative genotypic frequencies (Barton et al., 2007, pp. 468). The justification of any measure of fitness ultimately derives from how it is connected to the processes of birth and death which drive selection (Metcalf and Pavard 2007; Doebeli et al. 2017; Charlesworth 1994, pp. 178). While such a connection is clear for absolute fitness measures like r or R_0 , relative fitness has only weak justification from population ecology. It has even been proposed that relative fitness be justified from measure theory, abandoning population biology altogether (Wagner, 2010). Given the widespread use of relative fitness in evolutionary genetics, it is important to understand its population ecological basis, both to clarify its domain of applicability, and as part of the broader challenge of synthesizing ecology and evolution.

For haploids tracked in discrete time, the change in the abundance n_i of type i over a time step can be expressed as $\Delta n_i = (W_i - 1)n_i$ where W_i is “absolute fitness” (i.e. the abundance after one time step is $n'_i = W_i n_i$). The corresponding change in frequency is $\Delta p_i = \left(\frac{W_i}{\bar{W}} - 1\right) p_i$, where $\bar{W} = \sum_i W_i p_i$. In continuous time, the Malthusian parameter r_i replaces W_i and we have $\frac{dn_i}{dt} = r_i n_i$ and $\frac{dp_i}{dt} = (r_i - \bar{r})p_i$ (Crow et al., 1970). Note that we can replace the W_i with any set of values proportional to the W_i without affecting the ratio W_i/\bar{W} or Δp_i . These “relative fitness” values tell us how type frequencies change, but give no information about the dynamics of total population density $N = \sum_i n_i$ (Barton et al., 2007, pp. 468). Similarly in the continuous case, adding an arbitrary constant to the Malthusian parameters r_i has no effect on $\frac{dp_i}{dt}$ (these would then be relative log fitnesses).

Relative fitness is often parameterized in terms of selection coefficients which represent

the advantages of different types relative to each other. For instance, in continuous time $s = r_2 - r_1$ is the selection coefficient of type 2 relative to type 1. Assuming that only 2 and 1 are present, the change in frequency can be written as

$$\frac{dp_2}{dt} = sp_2(1 - p_2). \quad (1)$$

Thus, if r_1 and r_2 are constant, the frequency of the second type will grow logistically with a constant rate parameter s . We then say that selection is independent of frequency and density. The discrete time case is more complicated. Defining the selection coefficient by $W_2 = (1 + s)W_1$, and again assuming 1 and 2 are the only types present, we have

$$\Delta p_2 = \frac{W_2 - W_1}{\overline{W}} p_2(1 - p_2) = \frac{s}{1 + sp_2} p_2(1 - p_2). \quad (2)$$

We will refer to both the continuous and discrete time selection equations (1) and (2) throughout this paper, but the simpler continuous time case will be our point of comparison for the rest of this section.

In a constant environment, and in the absence of crowding, r_i is a constant “intrinsic” population growth rate. The interpretation of Eq. (1) is then simple: the selection coefficient s is simply the difference in intrinsic growth rates. However, growth cannot continue at a non-zero constant rate indefinitely: the population is not viable if $r_i < 0$, whereas $r_i > 0$ implies endlessly increasing population density. Thus, setting aside unviable populations, the increase in population density must be checked by crowding. This implies that the Malthusian parameters r_i eventually decline to zero (e.g. Begon et al. 1990, pp. 203). Selection can then be density-dependent, and indeed this is probably not uncommon, because crowded and uncrowded conditions can favor very different traits (Travis et al., 2013). Eq. (1) is then not a complete description of selection — it lacks an additional coupled equation describing the dynamics of N , on which s in Eq. (1) now depends. In general we cannot simply spec-

ify the dynamics of N independently, because those ecological dynamics are coupled with the evolutionary dynamics of type frequency (Travis et al., 2013). Thus, in the presence of density-dependent selection, the simple procedure of assigning constant relative fitness values to different types has to be replaced with an ecological description of absolute growth rates. Note that frequency-dependent selection does not raise a similar problem, because a complete description of selection still only requires us to model the type frequencies, not the ecological variable N as well.

In practice, many population genetic models simply ignore density dependence and assign a constant relative fitness to each type. Selection is typically interpreted as operating through viability, but the ecological processes underlying the regulation of population density are frequently left unspecified (e.g. Gillespie 2010; Nagylaki et al. 1992; Ewens 2004). Density either does not enter the model at all, or if finite-population size effects (“random genetic drift”) are important, then N is typically assumed to have reached some fixed equilibrium value (Fig. 1b; for some approaches to relaxing the constant N assumption in finite populations, see Lambert et al. 2005; Parsons and Quince 2007; Chotibut and Nelson 2017; Constable and McKane 2017).

A rather different picture emerges in more ecologically explicit studies of selection in density-regulated populations. Following Fisher’s suggestion that evolution tends to increase density in the long term (Fisher, 1930; Leon and Charlesworth, 1978; Lande et al., 2009), as well as the influential concept of K -selection (specifically, the idea that selection in crowded conditions favors greater equilibrium density; MacArthur 1962), many studies of density-regulated growth have focused on the response of density to selection (Kostitzin, 1939; MacArthur and Wilson, 1967; Roughgarden, 1979; Christiansen, 2004). Indeed, both N and s change during, and as a result of, adaptive sweeps in many of the most widely used models of density-regulated population growth. The latter includes simple birth-death (Kostitzin, 1939) and logistic models (Fig. 1a; MacArthur 1962; Roughgarden 1979; Boyce

1984), variants of these models using other functional forms for the absolute fitness penalties of crowding (Kimura, 1978; Charlesworth, 1971; Lande et al., 2009; Nagylaki, 1979; Lande et al., 2009), and the “ R^* rule” of resource competition theory (which states that the type able to deplete a shared limiting consumable resource to the lowest equilibrium density R^* excludes the others; Grover 1997). Density also changes in response to selection in the Lotka-Volterra competition model, at least during a sweep (except in special cases; Gill 1974; Smouse 1976; Mallet 2012).

The constant- N , constant- s description of selection also limits consideration of longer-term aspects of the interplay between evolution and ecology such as population extinction and trait evolution. A variety of approaches have been developed to address this in quantitative genetics (Burger and Lynch, 1995; Engen et al., 2013), population genetics (Bertram et al., 2017) and adaptive dynamics (Ferrière and Legendre, 2013; Dieckmann and Ferrière, 2004). Although density-dependent selection is pertinent to these longer-term issues, our focus here is 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.

In light of the complications arising from density-dependence, the assignment of density-independent relative fitnesses has been justified as an approximation that holds when selection is weak and N changes slowly (Kimura and Crow 1969; Ewens 2004, pp. 277; Charlesworth 1994, Chap. 4). Under these conditions, s is approximately constant in Eq. (1), at least for some number of generations. If s depends only on density, not frequency, this approximate constancy can hold over entire selective sweeps (Otto and Day, 2011).

However, the preceding arguments do not imply that the constant relative fitness idealization of population genetics *only* applies when selection is weak and N is stable (or when selection is actually density-independent). The idealization of assigning relative fitness values to genotypes is powerful, and so it is important to understand the specifics of when

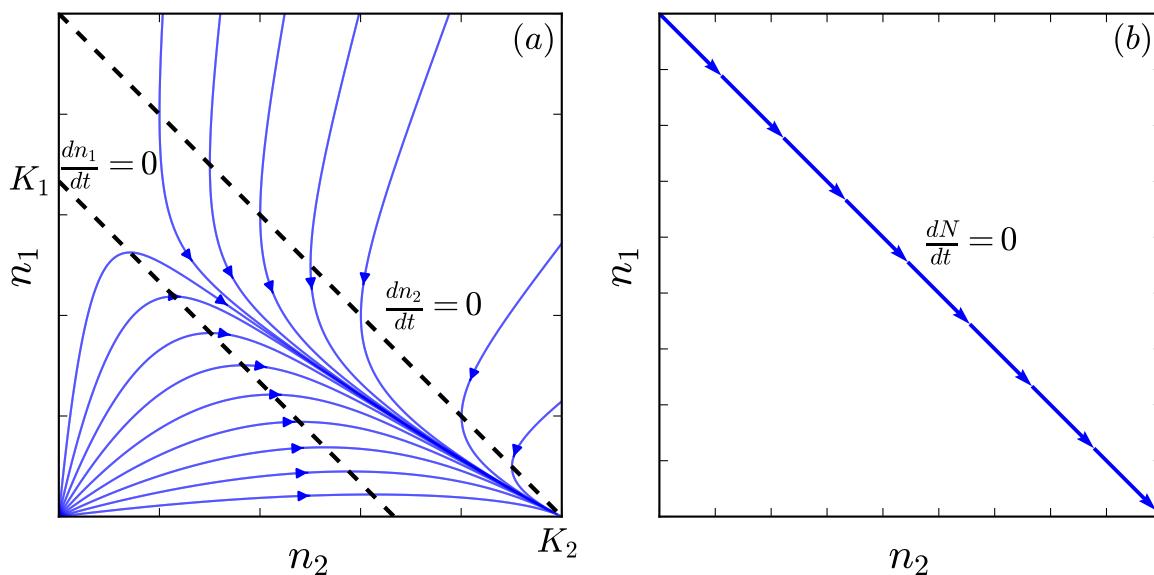


Figure 1: Phase diagram for the densities of two types n_1 and n_2 undergoing selection. (a) The logistic model $\frac{dn_1}{dt} = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $\frac{dn_2}{dt} = r_2(1 - \frac{n_1+n_2}{K_2})n_2$ with $r_1 = r_2$ and $K_2 > K_1$. (b) The constant- N , relative fitness description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

and how it succeeds or fails when selection is not weak, or N is not stable. For instance, in wild *Drosophila*, strong seasonally-alternating selection happens concurrently with large “boom-bust” density cycles (Messer et al., 2016; Bergland et al., 2014). Are we compelled to switch to a more ecologically-detailed model of selection based on Malthusian parameters or birth/death rates in this important model system? And if we make this switch, how much ecological detail do we need?

Here we argue that the simplified models of density-regulated growth mentioned above are potentially misleading in their representation of the interplay between selection and density. This ultimately derives from their failure to account for “reproductive excess”, that is, an excess of juveniles that experience stronger selection than their adult counterparts (Turner and Williamson, 1968). By allowing selection to be concentrated at a juvenile “bottleneck”, reproductive excess makes it possible for the density of adults to remain constant even under strong selection. Reproductive excess featured prominently in early debates

about the regulation of population density (e.g. Nicholson 1954), and also has a long history in evolutionary theory, particularly related to Haldane’s “cost of selection” (Haldane, 1957; Turner and Williamson, 1968). Additionally, reproductive excess is implicit in foundational evolutionary-genetic models like the Wright-Fisher, where each generation involves the production of an infinite number of zygotes, of which a constant number N are sampled to form the next generation of adults. Likewise in the Moran model, a juvenile is always available to replace a dead adult every iteration no matter how rapidly adults are dying, and as a result N remains constant.

Nevertheless, studies of density-dependent selection rarely incorporate reproductive excess. This requires that we model a finite, density-dependent excess, which is substantially more complicated than modeling either zero (e.g. logistic) or infinite (e.g. Wright-Fisher) reproductive excess. Nei’s “competitive selection” model incorporated a finite reproductive excess to help clarify the “cost of selection” (Nei, 1971; Nagylaki et al., 1992), but used an unusual representation of competition based on pairwise interactions defined for at most two different genotypes, and was also restricted to equal fertilities for each genotype.

In models with detailed age structure, it is often assumed that the density of a “critical age group” mediates the population’s response to crowding (Charlesworth, 1994, pp. 54). Reproductive excess is a special case corresponding to a critical pre-reproductive age group. A central result of the theory of density-regulated age-structured populations is that selection proceeds in the direction of increasing equilibrium density in the critical age group (Charlesworth, 1994, pp. 148). This is a form of the classical K -selection ideas discussed above, but restricted to the critical age group (juveniles, in this case). The interdependence of pre-reproductive selection and reproductive density is thus overlooked as a result of focusing on density in the critical age group.

We re-evaluate the validity of the constant relative fitness description of selection in a novel model of density-regulated population growth that has a finite reproductive excess.

Our model is inspired by the classic discrete-time 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), and which has some similarities to the Wright-Fisher model (Svardal et al., 2015). Each type is assumed to have three traits: fecundity b , mortality d , and competitive ability c . In each iteration of the classic lottery model, each type produces a large number of juveniles, such that N remains constant (infinite reproductive excess). Competitive ability c affects the probability of winning a territory, and behaves like a pure relative fitness trait. Thus, fitness involves a product of fertility and juvenile viability akin to standard population genetic models of selection (e.g. Crow et al. 1970, pp. 185). We relax the large-juvenile-number assumption of the lottery model to derive a variable-density lottery with a finite, density-dependent reproductive excess.

The properties of density-dependent selection in our model are strikingly different from the classical literature discussed above. The strong connection between crowding and selection for greater equilibrium density is broken: selection need not affect density at all. And when it does, the density-independent discrete-time selection equation (2) is almost exact even for strong selection, provided that any changes in density are driven only by selection (as opposed to large deviations from demographic equilibrium), and that selection occurs on only one of the traits b , c , or d . On the flip side, the constant relative fitness approximation fails when strong selection acts concurrently on two or more of these traits, or when the population is far from demographic equilibrium.

Model

Assumptions and definitions

We restrict our attention to asexual haploids, since it is then clearer how the properties of selection are tied to the underlying population ecological assumptions. We assume that

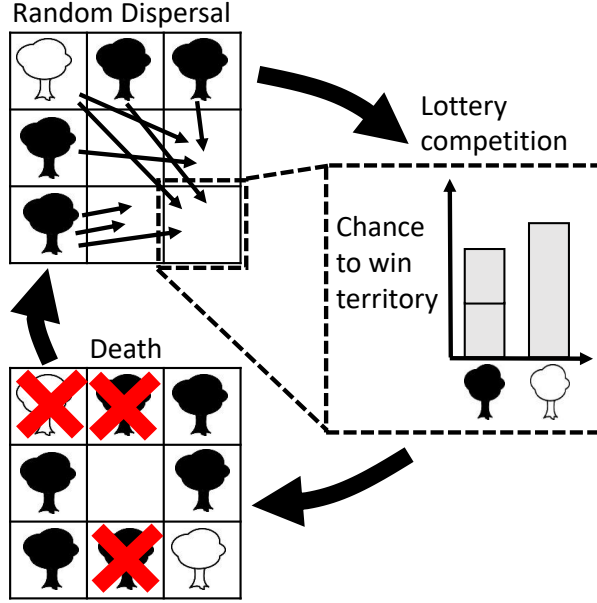


Figure 2: One iteration of our model. Propagules are dispersed by adults at random (only those propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each territory that receives more than one propagule (only illustrated in one territory). In a given territory, type i 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. Adult deaths make new territories available for the next iteration (red crosses).

reproductively mature individuals (“adults”) require their own territory to survive and re-
 produce. 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 $n_i/T \ll 1$.

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

number of i propagules dispersing to unoccupied territories is $m_i = b_i n_i U/T$ (the factor U/T represents the loss of those propagules landing on occupied territories). Random dispersal is 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 of type i per unoccupied territory. The total propagule density per unoccupied territory 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

$$\Delta_+ n_i = U \sum_{x_1, \dots, x_G} \frac{c_i x_i}{\sum_i c_i x_i} p_1(x_1) \cdots p_G(x_G). \quad (3)$$

Here the sum only includes territories with at least one propagule present. Note that $\Delta_+ n_i$ denotes the *expected* territorial acquisition. Fluctuations about $\Delta_+ n_i$ (i.e. drift) will not be analyzed in this manuscript. Note that drift can become important if U is not sufficiently large even though n_i and T are large (by assumption); we do not consider this scenario on biological grounds, since it implies negligible population turnover.

Adult mortality occurs after lottery recruitment at a constant, type-specific per-capita rate $d_i \geq 1$, and can affect adults recruited in the current iteration, such that the new abundance at the end of the iteration is $(n_i + \Delta_+ n_i)/d_i$ (Fig. 2). In terms of absolute fitness, this can be written as

$$W_i = \frac{1}{d_i} \left(1 + \frac{\Delta_+ n_i}{n_i} \right). \quad (4)$$

Here $\frac{\Delta_+ n_i}{n_i}$ is the per-capita rate of territorial acquisition, and $1/d_i$ is the fraction of type i adults surviving to the next iteration.

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

$$\Delta_+ n_i = \frac{c_i l_i}{\sum_i c_i l_i} U = \frac{c_i l_i}{\bar{c} L} U, \quad (5)$$

where $\bar{c} = \sum_i c_i m_i / \sum_i m_i$ is the mean competitive ability for a randomly selected propagule. Note that all unoccupied territories are filled in a single iteration of the classic lottery model, whereas our more general model Eq. (3) allows for territories to be left unoccupied and hence also accommodates low propagule densities.

Results

Analytical approximation of the variable-density lottery

Here we evaluate the expectation in Eq. (3) to better understand the dynamics of density-dependent lottery competition. Similarly to the classic lottery model, we replace the x_i , which take different values in different territories, with “effective” mean values. However, since we want to allow for low propagule densities, we cannot simply replace the x_i with the means l_i as in the classic lottery. For a low density type, growth comes almost entirely from territories with $x_i = 1$, for which its mean density $l_i \ll 1$ is not representative. We

therefore separate Eq. (3) into $x_i = 1$ and $x_i > 1$ components, taking care to ensure that the effective mean approximations for these components are consistent with each other (details in Appendix A). The resulting variable-density approximation only requires that there are no large discrepancies in competitive ability (i.e. we do not have $c_i/c_j \gg 1$ for any two types). We obtain

$$\Delta_+ n_i \approx \left[e^{-L} + (R_i + A_i) \frac{c_i}{\bar{c}} \right] l_i U, \quad (6)$$

where

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

and

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

Comparing Eq. (6) to Eq. (5), the classic lottery per-propagule success rate $c_i/\bar{c}L$ has been replaced by three separate terms. The first, e^{-L} , accounts for propagules which land alone on unoccupied territories; these propagules secure the territories without contest. The second, $R_i c_i/\bar{c}$, represents competitive victories on territories where only a single i propagule lands, together with at least one other propagule from a different type (this term dominates the growth of a rare invader in a high density population and determines invasion fitness). The third term, $A_i c_i/\bar{c}$, represents competitive victories in territories where two or more i type propagules are present. The relative importance of these three terms varies with both the overall propagule density L and the relative propagule frequencies l_i/L . If $l_i \gg 1$ for all types, we recover the classic lottery model (only the $A_i c_i/\bar{c}$ term remains, and $A_i \rightarrow 1/L$).

Fig. 3 shows that Eq. (6) and its components closely approximate simulations of our variable-density lottery model over a wide range of propagule densities. Two types are present, one of which is at low frequency. The growth of the low-frequency type relies 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

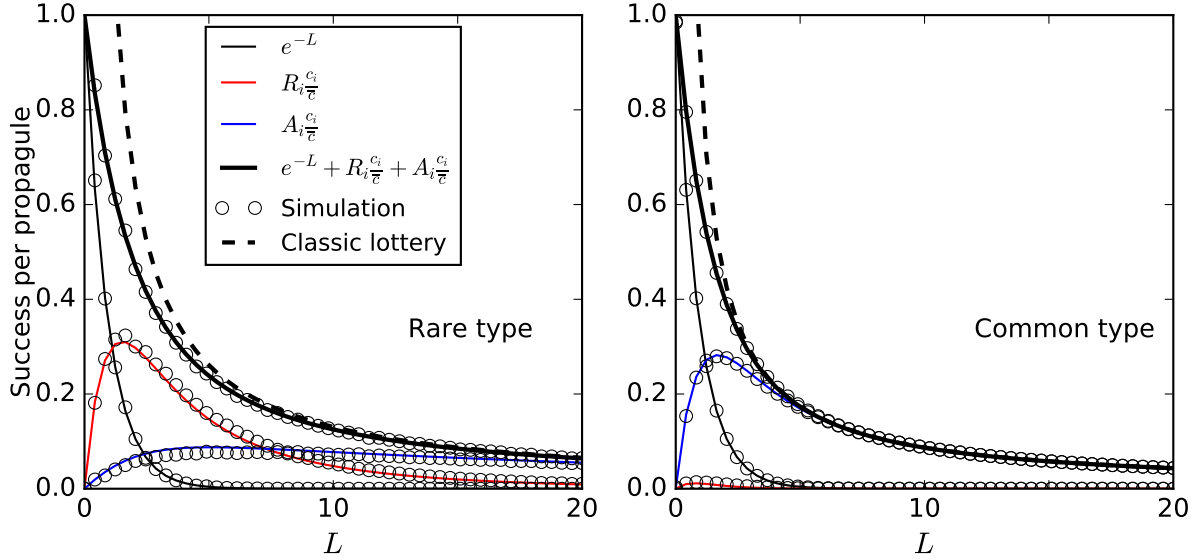


Figure 3: Comparison of Eq. (6), the classic lottery model, and simulations. The vertical axis is per-propagule success rate for all propagules $\Delta_+ n_i / m_i$, and for the three separate components in Eq. (6). Two types are present with $c_1 = 1$, $c_2 = 1.5$ and $l_2 / l_1 = 0.1$. Simulations 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 $c_i x_i / (c_1 x_1 + c_2 x_2)$. Dashed lines show the failure of the classic lottery model at low density.

for the high-frequency type, which depends instead on high density territorial victories. Fig. 3 also shows the breakdown of the classic lottery model at low propagule densities.

In the special case that all types are competitively equivalent (identical c_i), Eq. (6) takes a simpler form,

$$\Delta_+ n_i = \frac{l_i}{L} (1 - e^{-L}) U = \frac{b_i}{\bar{b}} \frac{1 - e^{-\bar{b}N/T}}{N} (T - N), \quad (7)$$

where we have used the fact that $L = \bar{b}N/T$ to make the dependence on b and N explicit (\bar{b} is the population mean b). Eq. (7) happens to be exact even though it is a special case of the approximation Eq. (6). This can be deduced directly from Eq. (3): $1 - e^{-L}$ is the fraction of territories 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.

By similar reasoning, the total number of territories acquired is given by

$$\Delta_+ N = (1 - e^{-L})U = (1 - e^{-\bar{b}N/T})(T - N). \quad (8)$$

This formula is also exact, but unlike Eq. (7), it also applies when the c_i differ between types.

Density regulation and selection in the variable-density lottery

Equipped with Eq. (6) we now outline the basic properties of the b , c and d traits. Adult density N is regulated by the birth and mortality rates b and d ; b controls the fraction of unoccupied territories that are contested (see Eq. (8)), while d controls adult mortality. Competitive ability c does not enter Eq. (8), and therefore does not regulate total adult density: c only affects the relative likelihood of winning a contested territory.

Selection in our variable-density lottery model is in general density-dependent, by which we mean that the discrete-time selection factor $(W_2 - W_1)/\bar{W}$ from Eq. (2) may depend on N . More specifically, as we show below, b - and c -selection are density-dependent, but d -selection is not. Note that 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 our 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.

The strength of b -selection declines with increasing density. When types differ in b only (b -selection), Eq. (6) simplifies to Eq. (7), and absolute fitness can be written as $W_i = (1 + \frac{b_i}{\bar{b}} f(\bar{b}, N))/d_i$ where $f(\bar{b}, N) = \frac{1 - e^{-\bar{b}N/T}}{N}(T - N)$ is a decreasing function of N . Thus, the selection factor $\frac{W_2 - W_1}{\bar{W}} = \frac{f(\bar{b}, N)}{1 + f(\bar{b}, N)} \frac{b_2 - b_1}{\bar{b}}$ declines with increasing density: the advantage of having greater b gets smaller the fewer territories there are to be claimed (Fig. 4).

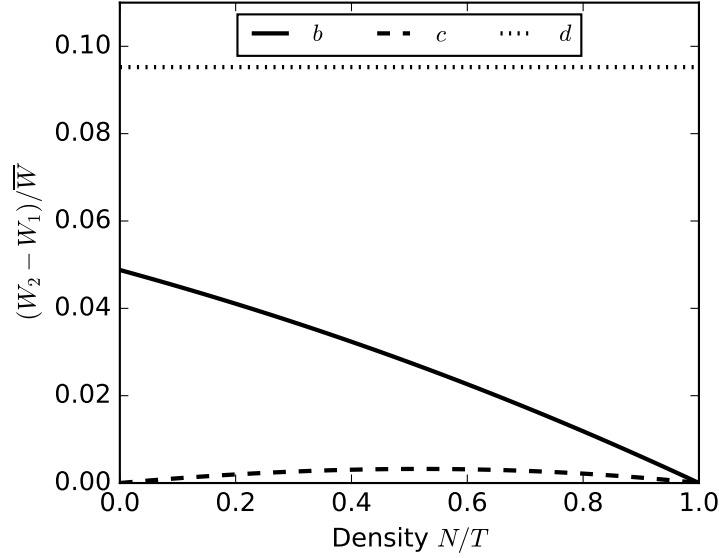


Figure 4: The density-dependence of selection in our variable-density lottery between an adaptive variant 2 and a wildtype variant 1 with at equal frequencies. Here $b_1 = 1$, $d_1 = 2$ and $c_1 = 1$. For b -selection we set $b_2 = b_1(1+\epsilon)$, and similarly for c and d , with $\epsilon = 0.1$. 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.

In the case of c -selection, Eq. (6) implies that $W_2 - W_1$ is proportional to $\frac{T-N}{T} [(R_2 + A_2)c_2 - (R_1 + A_1)c_1] / \bar{c}$. The strength of c -selection thus peaks at an intermediate density (Fig. 4), because most territories are claimed without contest at low density ($R_1, R_2, A_1, A_2 \rightarrow 0$), whereas at high density few unoccupied territories are available to be contested ($T - N \rightarrow 0$).

Selection on d is independent of density, because the density-dependent factor $1 + \frac{\Delta_+ n_i}{n_i}$ in Eq. (4) is the same for types that differ in d only.

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

We now turn to the issue of how density changes as a consequence of selection in our variable-density lottery, and in more familiar models of selection in density-regulated populations.

299 In the latter, selection under crowded conditions typically induces changes in equilibrium
300 density (see Introduction). In our variable-density lottery model, however, the competitive
301 ability trait c is not density-regulating, even though c contributes to fitness under crowded
302 conditions. Consequently, c -selection does not cause density to change. In this section we
303 compare this c -selection behavior with the previous literature, which we take to be exempli-
304 fied by MacArthur’s K -selection argument (MacArthur and Wilson, 1967).

305 MacArthur considered two types (with densities n_1 and n_2) in a constant environment
306 subject to density-dependent growth,

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

307 The outcome of selection is determined by the relationship between the nullclines $f_1(n_1, n_2) =$
308 0 and $f_2(n_1, n_2) = 0$. Specifically, a type will be excluded if its nullcline is completely
309 contained in the region bounded by the other type’s nullcline.

MacArthur used the four intersection points of the nullclines with the axes, defined by $f_1(K_{11}, 0) = 0$, $f_1(0, K_{12}) = 0$, $f_2(K_{21}, 0) = 0$ and $f_2(0, K_{22}) = 0$, to analyze each type’s exclusion or persistence. Note that only K_{11} and K_{22} are equilibrium densities akin to the K parameter in the logistic model; the other intersection points, K_{12} and K_{21} , are related to competition between types. For instance, in the Lotka-Volterra competition model we have

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

310 where $\alpha_{11} = 1/K_{11}$ and $\alpha_{22} = 1/K_{22}$ measure competitive effects within types, while $\alpha_{12} =$
311 $1/K_{12}$ and $\alpha_{21} = 1/K_{21}$ measure competitive effects between types. Hence, “fitness is K ”
312 in crowded populations (MacArthur and Wilson, 1967, pp. 149) in the sense that selection

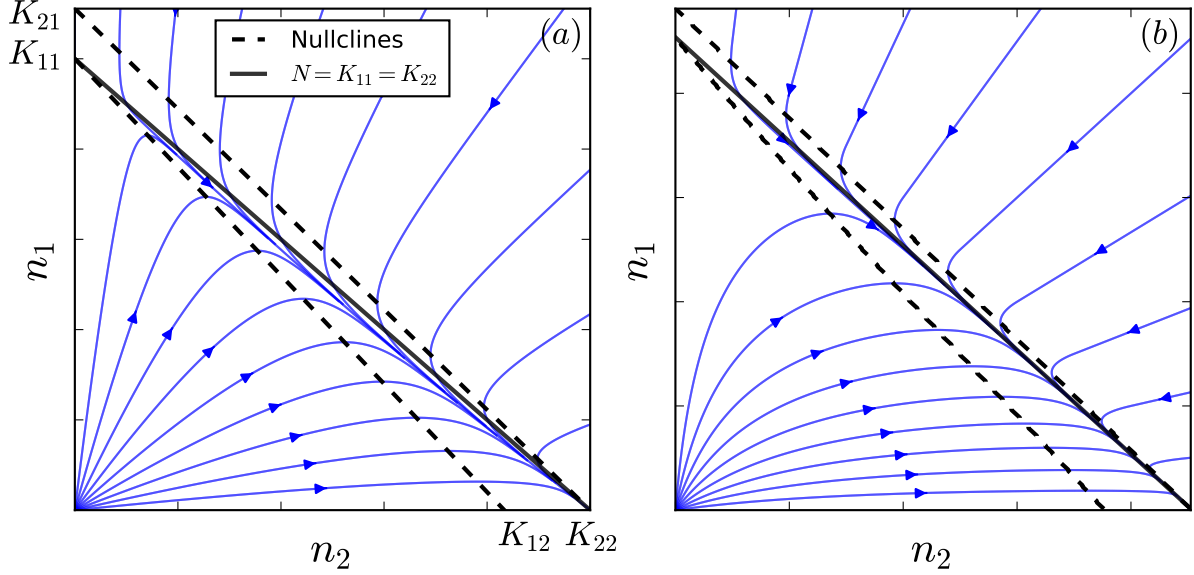


Figure 5: Selection between types with identical equilibrium density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 10) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. Trajectories do not follow the line $N = K_{11} = K_{22}$. (b) Lottery competition (Eq. 6) with $b_1 = b_2 = 5$, $d_1 = d_2 = 1.1$ and $c_1/c_2 = 5$. The lottery model nullclines are defined by $W_1 = 1$ (lower nullcline) and $W_2 = 1$ respectively in Eq. (4). For the discrete-time Eq. (6), trajectories are the flow lines of the vector field obtained by evaluating the direction of the local changes in n_1 and n_2 ; these converge on the line $N = K_{11} = K_{22}$.

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; Gill 1974). However, even if the initial and final densities of an adaptive sweep in the Lotka-Volterra model are the same, N nevertheless does change transiently (Fig. 5a). Constant- N over a sweep only occurs for a highly restricted subset of r and α values (Appendix B; Mallet 2012; Gill 1974; Smouse 1976).

In contrast, density trajectories for c -selection in our variable-density lottery converge on a line of constant equilibrium density (Fig. 5b). This means that once N reaches demographic equilibrium, selective sweeps behave indistinguishably from a constant- N relative fitness model (Fig. 1b). Thus, for c -sweeps in a constant environment, the selection factor $(W_2 - W_1)/\bar{W}$ in Eq. (2) is density-independent. This uncoupling of density from c -selection arises

324 due to the presence of an excess of propagules which pay the cost of selection without affecting
 325 adult density (Nei, 1971).

326 **Density-regulating traits under strong selection**

327 For density to matter in Eq. (2), selection must be density-dependent and density must be
 328 changing. This can occur in a constant environment if selection acts on a density-regulating
 329 trait. Consider the simple birth-death model (Kostitzin, 1939)

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

330 where δ_i is per-capita mortality due to crowding. Starting from a type 1 population in
 331 equilibrium, a variant with $\delta_2 = \delta_1(1 - \epsilon)$ has density-dependent selection coefficient $s =$
 332 $\epsilon\delta_1 N$, which will change over the course of the sweep as N shifts from its initial type 1
 333 equilibrium to a type 2 equilibrium. The equilibrium densities at the beginning and end of
 334 the sweep are $N_{\text{initial}} = b_1/\delta_1$ and $N_{\text{final}} = b_1/(\delta_1(1 - \epsilon)) = N_{\text{initial}}/(1 - \epsilon)$ respectively, and
 335 so $s_{\text{initial}} = \epsilon b_1$ and $s_{\text{final}} = s_{\text{initial}}/(1 - \epsilon)$. Consequently, substantial deviations from Eq. (1)
 336 occur if there is sufficiently strong selection on δ (Fig. 6; Kimura 1978; Kimura and Crow
 337 1969).

338 In our variable density lottery, b regulates density and is subject to density-dependent
 339 selection, yet b -sweeps are qualitatively different from δ sweeps in the above example. Greater
 340 b means not only that more propagules contest the available territories, but also that a greater
 341 fraction of unoccupied territories receive propagules. Together, the net density-dependent
 342 effect on b -selection is negligible: in a single-type equilibrium we have $W_i = 1$ and $b_i/\bar{b} = 1$,
 343 and hence the density-dependence factor $f(\bar{b}, N) = \frac{1 - e^{-\bar{b}N/T}}{N}(T - N)$ in Eq. (7) has the same
 344 value $d_i - 1$ at the beginning and end of a b -sweep (recall that $\frac{W_2 - W_1}{\bar{W}} = \frac{f(\bar{b}, N)}{1 + f(\bar{b}, N)} \frac{b_2 - b_1}{\bar{b}}$ for
 345 b -selection). During the sweep there is some deviation in $f(\bar{b}, N)$, but this deviation is an

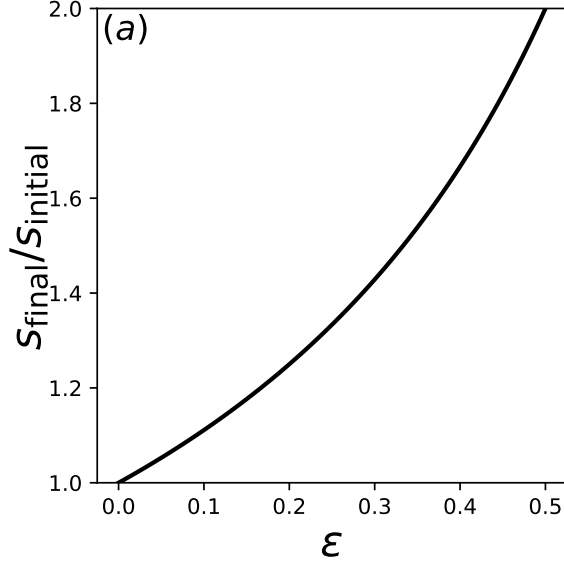


Figure 6: Change in the selection coefficient between the beginning and end of a sweep of a type that experiences proportionally $1 - \epsilon$ fold fewer crowding-induced deaths. The population is in demographic equilibrium at the start and end of the sweep.

order of magnitude smaller than for a δ sweep (the density-dependent deviation in Fig. 6 is of order ϵ , whereas the analogous effect for b sweep in our variable-density lottery is only of order ϵ^2 ; see Appendix C for details). Since selection must already be strong for a δ -sweep to invalidate Eq. (1), the density-independent model applies almost exactly for equilibrium b -sweeps (Fig. 7).

However, if selection acts simultaneously on more than one trait in our variable-density lottery, then evolution in a density-regulating trait can drive changes in the strength of selection on another trait subject to density-dependent selection. For instance, if selection acts simultaneously on b and d , then $f(\bar{b}, N)$ changes value from $d_1 - 1$ to $d_2 - 1$ over a sweep. The dynamics of density will then affect the selection factor $(W_2 - W_1)/\bar{W}$ and cause deviations analogous to selection on δ in the continuous time case (Fig. 8).

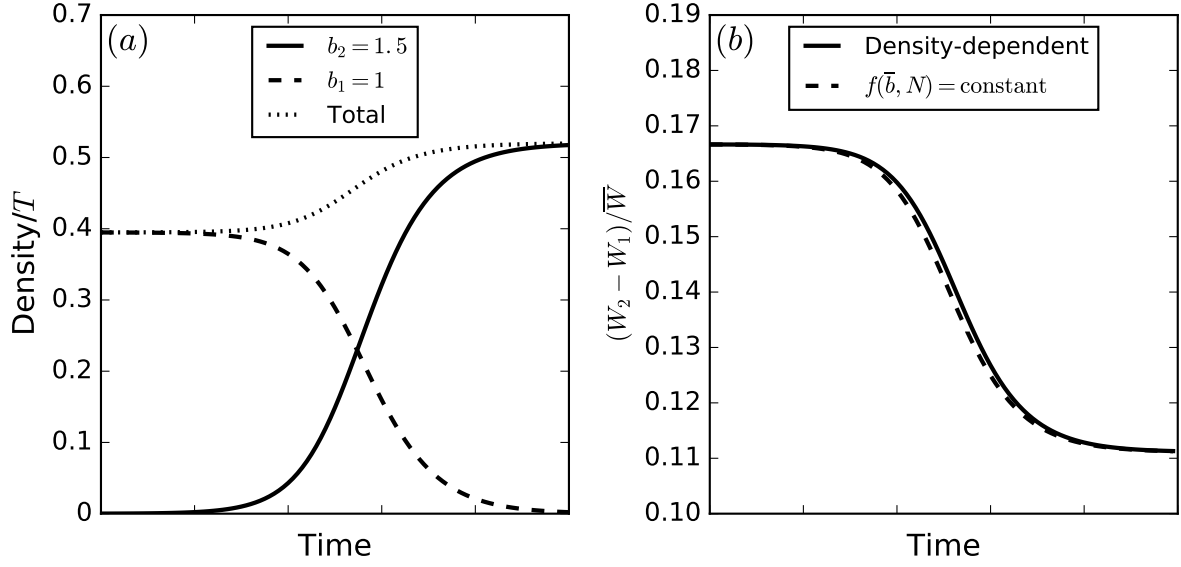


Figure 7: Equilibrium b -sweeps behave as though selection is independent of density even though b -selection is density-dependent in general. Panel (b) shows the density-dependent selection factor $(W_2 - W_1)/\bar{W}$ predicted by Eq. (6) (solid line) compared to the same selection factor with the density-dependence term $f(\bar{b}, N)$ held constant at its initial value (dashed line).

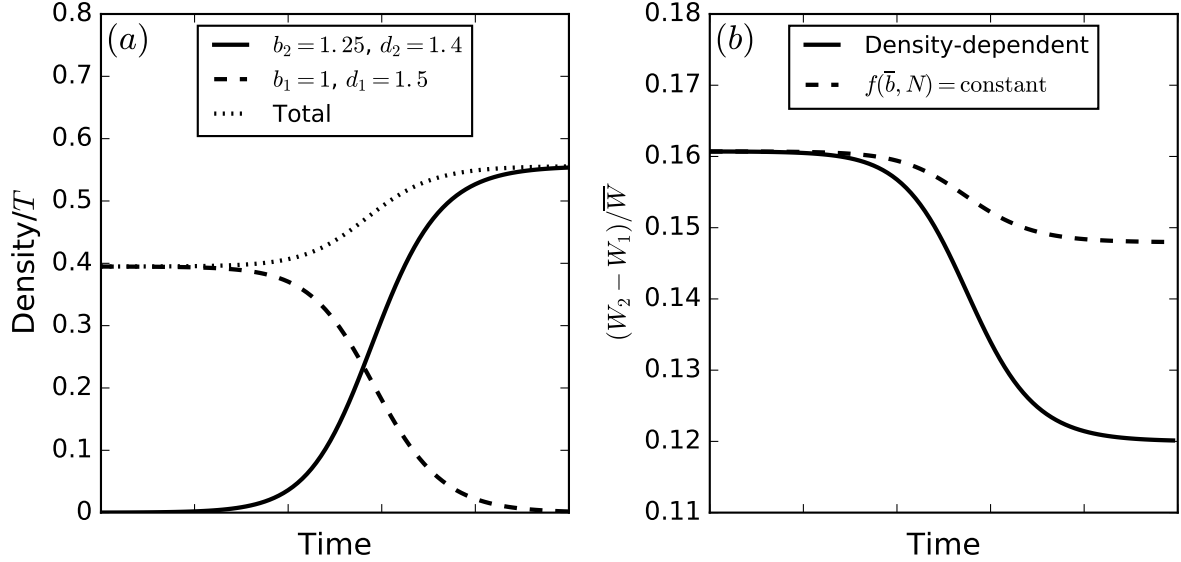


Figure 8: Simultaneous selection on b and d induces density-dependence in the selection factor $(W_2 - W_1)/\bar{W}$. Panel (b) shows the predictions of Eq. (7) (solid line) versus the same with the density-dependence factor $f(\bar{b}, N)$ held constant at its initial value.

Discussion

Summarizing the properties of selection in our 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 the differences between b , c and d , selection in a constant environment that only involves one of these traits obeys the density-independent relative fitness description of selection almost exactly (that is, $(W_2 - W_1)/\bar{W}$ in Eq. (2) is approximately independent of density). This density-independence breaks down when strong selection acts on more than one of b , c and d (Fig. 8). The c and d traits exemplify the two distinct directions in which density and selection can interact: selection may depend on density, and density may change in response to ongoing selection (Prout, 1980). The combination of both is necessary to invalidate the constant- s approximation. Remarkably, the b trait demonstrates that the combination is not sufficient; the density-dependence of b -selection effectively disappears over equilibrium-to-equilibrium b -sweeps.

The distinctive properties of selection in the variable-density lottery arise from a reproductive excess which appears when the number of propagules is greater than the number of available territories. Then only $\approx 1/L$ of the juveniles contesting unoccupied 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. Reproductive excess produces relative contests in which fitter types grow at the expense of others by preferentially filling the available adult “slots”. The number of available slots can remain fixed or change independently of selection at the juvenile stage. By ignoring reproductive excess, single life-stage models are biased to have total population density be more 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 making the full leap to complex age-structured models.

In practice, traits like b , c and d will often have pleiotropic interactions which mean that adaptive sweeps will behave similarly to the familiar “ δ sweeps” (“Density regulating traits under strong selection”). Thus, our analysis of the variable density lottery does not suggest that Eq. (1) and (2) should apply more broadly than previously thought. Rather, b , c and d represent a possible set of idealized fitness components mediating the interplay between selection and density in density-regulated populations. The conceptual distinctions they highlight will hopefully be useful regardless of the biological realism of the variable density lottery model.

Apart from familiar examples such as reef fishes (Chesson and Warner, 1981), many biological systems do not obviously satisfy the assumptions of our variable density lottery. However, even if competition occurs primarily via consumable resource exploitation, spatial localization of consumable resources (e.g. for plants due to restricted movement of nutrients through soils) will tend to create territorial contests similar to the lottery model, where resource competition only occurs locally and can be sensitive to contingencies such as the timing of propagule arrival (Bolker and Pacala, 1999). In this case, resource competition is effectively subsumed into a territorial competitive ability trait akin to c , which would likely affect N much more weakly than suggested by the R^* rule (assuming no pleiotropic interactions with b or d). Moreover, even in well-mixed populations, competition does not only involve indirect exploitation of shared resources, but also direct interference. Interference competition can dramatically alter the dynamics of resource exploitation (Case and Gilpin, 1974; Amarasekare, 2002), and is more likely than the exploitation of shared resource pools to involve relative contests akin to c -selection. For instance, sexual selection can be viewed as a form of relative interference competition between genotypes.

In the analysis presented here we have restricted our attention to selection in demographically stable populations. The largest deviations from the approximation of density-

independent selection (as represented by Eqs. (1) and (2)) will likely occur in populations far from demographic equilibrium e.g. as a result of a temporally-variable environment. This is because extremely strong selection to change population density by an amount comparable to environmental variability (see Fig. 6). By contrast, temporally-variable environments 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 (Lande et al., 2009).

This suggests that in systems like the wild *Drosophila* example mentioned in the Introduction, there may indeed be no choice but to abandon relative fitness. Our variable-density lottery could provide a useful starting point for analyzing evolution in this and other far-from-equilibrium situations for two reasons: 1) the b , c , d trait scheme neatly distinguishes between different aspects of the interplay between density and selection; 2) lottery models in general are mathematically similar to the Wright-Fisher model, which should facilitate the analysis of genetic drift when N is unstable.

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Appendix A: Growth equation derivation

Here we derive Eq. (6). Following the notation in the main text, the Poisson distributions for the x_i (or some subset of the x_i) will be denoted p , and we use P as a general shorthand for the probability of particular outcomes. We denote the vector of propagule abundances by $\mathbf{x} = (x_1, \dots, x_G)$ in a given territory, and the analogous vector of nonfocal abundances by $\mathbf{x}_i = (x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_G)$. The corresponding total propagule numbers are denoted $X = \sum_j x_j$ and $X_i = X - x_i$.

Similar to the classic lottery model, our approximation involves replacing the x_i with effective mean values. However, as discussed in the text preceding Eq. (6), it is important to treat the $x_i = 1$ case separately when allowing for low propagule densities. We thus start by separating the right hand side of Eq. (3) into three components

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

The relative magnitude of these components depends on the propagule densities l_i . The first component, $\Delta_u n_i$, accounts for territories where only one focal propagule is present ($x_i = 1$ and $x_j = 0$ for $j \neq i$; u stands for “uncontested”). The proportion of territories where this occurs is $l_i e^{-L}$, and so

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

The second component, $\Delta_r n_i$, accounts for territories where a single focal propagule is present along with at least one non-focal propagule (r stands for “rare”). The number of territories where this occurs is $U p_i(1) P(X_i \geq 1) = m_i e^{-l_i} (1 - e^{-(L-l_i)})$. Thus

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

554 where $\langle \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)}$ denotes the expectation with respect to the conditional probability
 555 distribution $p(\mathbf{x}|x_i = 1, X_i \geq 1)$ of propagule abundances in those territories where exactly
 556 one focal propagule, and at least one non-focal propagule, landed.

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

$$\Delta_a n_i = U(1 - (1 + l_i)e^{-l_i}) \left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{p(\mathbf{x}|x_i \geq 2)}. \quad (15)$$

559 To derive Eq. (6) we approximate the expectations in Eq. (14) and Eq. (15) by replacing
 560 x_i and the x_j with “effective” mean values as follows

$$\left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} \approx \frac{c_i}{c_i + \sum_{j \neq i} c_j \langle x_j \rangle_r}. \quad (16)$$

$$\left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{p(\mathbf{x}|x_i \geq 2)} \approx \frac{c_i \langle x_i \rangle_a}{\sum_j c_j \langle x_j \rangle_a}. \quad (17)$$

562 Here $\langle \rangle_r$ and $\langle \rangle_a$ are the effective means, which are defined in the following subsection.

563 The effective means $\langle \rangle_r$ and $\langle \rangle_a$

564 The decomposition Eq. (12) is exact and involves no additional assumptions. However this
 565 decomposition complicates our approximation procedure because the separate components
 566 in Eq. (12) must be approximated in a consistent manner.

567 To illustrate this consistency requirement, suppose that two identical types (same b , c
 568 and d) are present, the first with small density $l_1 \ll 1$ and the second with large density
 569 $l_2 \gg 1$. In this case, uncontested territories make up a negligible fraction of U ; the first
 570 type’s territorial acquisition is almost entirely due to $\Delta_r n_1$; and the second type’s territorial
 571 acquisition is almost entirely due to $\Delta_a n_2$. For consistency, the approximate per-capita

572 growth rates in (16) and (17) must be equal $\Delta_r n_1/m_1 = \Delta_a n_2/m_2$. Even small violations
 573 of this consistency condition would mean exponential growth of one type relative to the
 574 other. This behavior is pathological, because any single-type population can be arbitrarily
 575 partitioned into identical rare and common subtypes. Thus, predicted growth or decline
 576 would depend on an arbitrary assignment of rarity.

577 Suppose that we naively used the conditional distributions $p(\mathbf{x}|x_i = 1, X_i \geq 1)$ and
 578 $p(\mathbf{x}|x_i \geq 2)$ to calculate the effective means, such that $\langle \rangle_r = \langle \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)}$ and $\langle \rangle_a =$
 579 $\langle \rangle_{p(\mathbf{x}|x_i \geq 2)}$. Then, in the example from the previous paragraph ($l_1 \ll 1, l_2 \gg 1$), the right
 580 hand side of Eq. (16) would be $\approx 1/(l_2 + 1)$, and so $\Delta_r n_1/m_1 \approx 1/(l_2 + 1)$ in Eq. (14).
 581 Similarly, $\sum_j \langle x_j \rangle_a \approx l_2$ in Eq. (17), and so $\Delta_a n_2/m_2 \approx 1/l_2$. Thus, the rare type would be
 582 predicted to decline in frequency even though it has identical traits.

583 This pathological behavior occurs because the expected total density of propagules in the
 584 respective groups of territories are different; $\langle X \rangle_{p(\mathbf{x}|x_1=1, X_1 \geq 1)} \approx l_2 + 1 > \langle X \rangle_{p(\mathbf{x}|x_2 \geq 2)} \approx l_2$.
 585 As a result, the rare type's behavior is approximated as though it experiences more intense
 586 lottery competition than the common type, which cannot be the case since the two types are
 587 identical. The effective means must thus be taken in a way that ensures that the expected
 588 total propagule density is the same in Eq. (16) and Eq. (17).

589 We achieve this as follows. For nonfocal types $j \neq i$, we separately evaluate the X -
 590 dependence of the conditional dispersal probabilities to ensure that X has the same distri-
 591 bution for both $\langle \rangle_r$ and $\langle \rangle_a$. Specifically, we assume that X follows a Poisson distribution
 592 with rate parameter L , conditional on $X \geq 2$; this distribution will be denoted $P(X|X \geq 2)$.
 593 However, for the focal type i , we use the exact conditional dispersal distributions p to cal-
 594 culate the effective mean,

$$\langle x_i \rangle_r = 1, \quad \langle x_i \rangle_a = \langle x_i \rangle_{p(x_i|x_i \geq 2)}. \quad (18)$$

As we will see, these effective means are straightforward to calculate analytically, and ensure that the expected total propagule density $\langle x_i \rangle + \sum_{j \neq i} \langle x_j \rangle$ is the same in Eq. (16) and Eq. (17).

Starting with Eq. (16), we only need to evaluate $\langle x_j \rangle_r$ since $\langle x_i \rangle_r = 1$. To evaluate the X -dependence separately, we first hold X fixed to obtain

$$\sum_{x_j} p(x_j | x_i = 1, X) x_j = \frac{l_j}{L - l_i} (X - 1) \quad j \neq i. \quad (19)$$

The right hand side is obtained by observing that the sum on the left is the expected number of propagules with type j that will be found in a territory which received $X - 1$ nonfocal propagules in total. We then take the expectation with respect to $P(X | X \geq 2)$ to give

$$\begin{aligned} \langle x_j \rangle_r &= \frac{l_j}{L - l_i} \sum_{X=2}^{\infty} P(X | X \geq 2) (X - 1) \\ &= \frac{l_j}{L - l_i} \frac{L - 1 + e^{-L}}{1 - (1 + L)e^{-L}}, \end{aligned} \quad (20)$$

where the last line follows from $P(X | X \geq 2) = \frac{1}{1 - (1 + L)e^{-L}} P(X)$ and $\sum_{X=2}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)(X - 1) = L - 1 + e^{-L}$. Substituting Eqs. (16) and (20) into Eq. (14), we obtain

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{\bar{c}}, \quad (21)$$

where R_i is defined in Eq. (7).

Turning now to Eq. (17), from Eq. (18) the mean focal abundance is

$$\begin{aligned} \langle x_i \rangle_a &= \sum_{x_i} p(x_i | x_i \geq 2) x_i \\ &= \frac{1}{1 - (1 + l_i)e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i \\ &= l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}}. \end{aligned} \quad (22)$$

For nonfocal types $j \neq i$, we have analogously to Eq. (19),

$$\begin{aligned} \sum_{\mathbf{x}_i} p(\mathbf{x}_i | x_i \geq 2, X) x_j &= \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - x_i) x_j \\ &= \frac{l_j(X - x_i)}{L - l_i}. \end{aligned} \quad (23)$$

Again taking the expectation with respect to $P(X | X \geq 2)$ yields

$$\begin{aligned} \langle x_j \rangle_a &= \frac{l_j}{L - l_i} \left[\sum_{X=2}^{\infty} P(X | X \geq 2) X - \langle x_i \rangle_a \right] \\ &= \frac{l_j}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}} \right). \end{aligned} \quad (24)$$

Combining these results with Eqs. (15) and (17), we obtain

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \quad (25)$$

where A_i is defined in Eq. (7).

It is easily verified from Eqs. (20), (22) and (24) that the total expected propagule density is the same in Eq. (16) and Eq. (17) i.e. $\langle x_i \rangle_r + \sum_{j \neq i} \langle x_j \rangle_r = \langle x_i \rangle_a + \sum_{j \neq i} \langle x_j \rangle_a = \langle X \rangle_{P(X|X \geq 2)}$. As a result, Eq. (6) satisfies the consistency requirement (see Fig. 9).

Approximation limits

Having derived the approximation Eq. (6), we now evaluate its domain of validity. Eq. (6) relies on ignoring the fluctuations in x_i and x_j , such that we can replace them with constant effective mean values. To justify this, we show that the standard deviations $\sigma_{p(\mathbf{x}|x_i=1, X_i \geq 1)}(\sum_{j \neq i} c_j x_j)$ and $\sigma_{p(\mathbf{x}|x_i \geq 2)}(\sum_j c_j x_j)$ are small compared to the corresponding means $\langle \sum_{j \neq i} c_j x_j \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)}$ and $\langle \sum_j c_j x_j \rangle_{p(\mathbf{x}|x_i \geq 2)}$ in Eqs. (16) and (17). This result means that using the exact distributions $p(\mathbf{x}|x_i = 1, X_i \geq 1)$ and $p(\mathbf{x}|x_i \geq 2)$ for the effective means

612 would produce an accurate approximation of the components in (12) (though, as we have
 613 seen, not a consistent one). It is then clear that the effective means derived in the previous
 614 section will also give an accurate approximation since their magnitudes are similar to the
 615 exact means; this is obvious from the fact that the expected total number of propagules is
 616 of order $\min\{L, 2\}$ in both cases.

We first consider the means and standard deviations in Eq. (16). We have
 $\langle x_j \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} = l_j/C$, where $C = 1 - e^{-(L-l_i)}$, and the corresponding variances and
 covariances are given by

$$\begin{aligned} \sigma_{p(\mathbf{x}|x_i=1, X_i \geq 1)}^2(x_j) &= \langle x_j^2 \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} - \langle x_j \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)}^2 \\ &= \frac{l_j^2 + l_j}{C} - \frac{l_j^2}{C^2} \\ &= \left(1 - \frac{1}{C}\right) \frac{l_j^2}{C} + \frac{l_j}{C}, \end{aligned} \quad (26)$$

and

$$\begin{aligned} \sigma_{p(\mathbf{x}|x_i=1, X_i \geq 1)}(x_j, x_k) &= \langle x_j x_k \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} - \langle x_j \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} \langle x_k \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} \\ &= \frac{1}{C} \langle x_j x_k \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)} - \frac{l_j l_k}{C^2} \\ &= \left(1 - \frac{1}{C}\right) \frac{l_j l_k}{C} \quad j \neq k. \end{aligned} \quad (27)$$

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

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

618 we obtain

$$\frac{\sigma_{p(\mathbf{x}|x_i=1, X_i \geq 1)}(\sum_{j \neq i} c_j x_j)}{\langle \sum_{j \neq i} c_j x_j \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)}} = C^{1/2} \frac{\left(\sum_{j \neq i} c_j^2 l_j + (1 - \frac{1}{C}) \left(\sum_{j \neq i} c_j l_j \right)^2 \right)^{1/2}}{\sum_{j \neq i} c_j l_j}. \quad (29)$$

619 Eq. (29) shows that, when the c_j have similar magnitudes (their ratios are of order one),
 620 Eq. (16) is an excellent approximation. The right hand side of Eq. (29) is then approximately
 621 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 high nonfocal densities. The
 622 worst case scenario occurs when $L - l_i$ is of order one, and it can be directly verified that
 623 Eq. (16) is then still a good approximation (see Fig. 9).

624 Turning to Eq. (17), all covariances between nonfocal types are now zero, so that
 625 $\sigma_{p(\mathbf{x}|x_i \geq 2)}^2(\sum c_j x_j) = \sum c_j^2 \sigma_{p(\mathbf{x}|x_i \geq 2)}^2(x_j)$. For nonfocal types ($j \neq i$) $\sigma_{p(\mathbf{x}|x_i \geq 2)}^2(x_j) = l_j$, whereas
 626 for the focal type we have

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

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

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

628 Similarly to Eq. (29), the right hand side of Eq. (31) is small for both low and high nonfocal
 629 densities provided that the c_j have similar magnitudes. Again, the worst case scenario occurs
 630 when l_i and $L - l_i$ are of order 1, but Eq. (17) is still a good approximation in this case
 631 (Fig. 9).

632 In both Eqs. (29) and (31), the standard deviation in $\sum_{j \neq i} c_j x_j$ can be large relative to
 633 its mean if some of the c_j are much larger than the others. Specifically, in the presence of
 634 a rare, strong competitor ($c_j l_j \gg c_{j'} l_{j'}$ for all other nonfocal types j' , and $l_j \ll 1$), then the

right hand side of Eqs. (29) and (31) can be large and we cannot make the replacement
 Eq. (16). Fig. 9 shows the breakdown of the effective mean approximation when there are
 large differences in c .

Appendix B: Total density under Lotka-Volterra competition

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

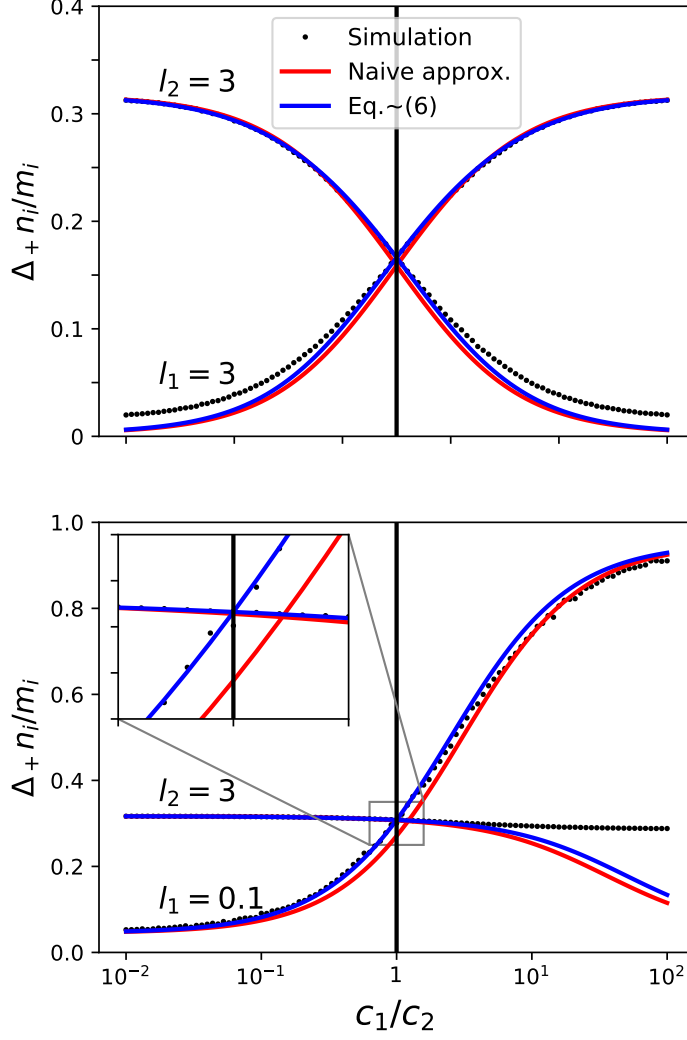


Figure 9: Comparison of our effective mean approximation Eq. (6) with simulations, and also with the naive $\langle \rangle_r = \langle \rangle_{p(\mathbf{x}|x_i=1, X_i \geq 1)}$ and $\langle \rangle_a = \langle \rangle_{p(\mathbf{x}|x_i \geq 2)}$ approximation, as a function of the relative c difference between two types. Eq. (6) breaks down in the presence of large c differences. The inset shows the pathology of the naive approximation — growth rates for rare and common types are not equal in the neutral case $c_1 = c_2$. Simulation procedure is the same as in Fig. 3, with $U = 10^5$.

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 under strong selection” we argued that the density-dependent factor $f(\bar{b}, N) = \frac{1 - e^{-\bar{b}N/T}}{N}(T - N)$ is unchanged at the beginning and end points of an equilibrium to equilibrium sweep of a type with higher 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 approximation 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 $b_2 = b_1(1 + \epsilon)$, and we denote the initial and final densities by D_1 and D_2 respectively, where we have

$f_{\text{initial}} = b_1(1 - D_1) = d_1 - 1 = f_{\text{final}} = b_2(1 - D_2)$. We obtain

$$\begin{aligned}
 f_{\text{half}} &= f\left(\frac{b_1 + b_2}{2}, \frac{N_1 + N_2}{2}\right) = \frac{b_1 + b_2}{2} \left(1 - \frac{D_1 + D_2}{2}\right) \\
 &= \frac{1}{4}(b_1 + b_2)(2 - D_1 - D_2) \\
 &= \frac{1}{4}(2(d_1 - 1) + b_1(1 - D_2) + b_2(1 - D_1)). \tag{35}
 \end{aligned}$$

Dividing by $d_1 - 1$, the proportional deviation in $f(N)$ at the midpoint of the sweep is

$$\begin{aligned}
 \frac{f_{\text{half}}}{d_1 - 1} &= \frac{1}{4} \left(2 + \frac{b_1}{b_2} + \frac{b_2}{b_1}\right) \\
 &= \frac{1}{4} \left(2 + \frac{1}{1 + \epsilon} + 1 + \epsilon\right) \\
 &= 1 + \frac{1}{4}(\epsilon^2 - \epsilon^3 + \dots), \tag{36}
 \end{aligned}$$

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

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