Density-dependent selection and the limits of relative fitness

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Abstract

Selection is commonly described in terms of relative fitness. Yet when selection is strong, the ecological view of selection in density-regulated populations seems to be incompatible with widely-used, constant-density relative fitness models such as the Wright-Fisher. Here we analyze the population ecological limits of relative fitness using a novel generalization of the Wright-Fisher model in which population density depends dynamically on the demographic rates of the types present. Our model contains a "reproductive excess, and clearly distinguishes between density-dependent selection and selection-dependent density. These two effects are confounded in standard models of density-regulated population growth. Both effects 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 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)

Introduction

There are a variety of different measures of fitness. Some widely used examples in evolutionary ecology are expected lifetime reproductive ratio R_0, intrinsic population growth rate r, saturation population density (often labeled "K") (Benton and Grant, 2000), and invasion fitness (Metz et al., 1992). In addition, "relative fitness" is the standard in much of evolutionary biology, particularly evolutionary genetics, where attention is generally restricted to relative genotypic proportions (Barton et al., 2007, pp. 468). The variety of fitness measures is not problematic in itself, because different measures may be more useful in different circumstances. But it should be clear how the measure being used is connected to the processes of birth and death which govern population biology (Metcalf and Pavard, 2007; Doebeli et al., 2017). While such a connection is fairly clear for absolute fitness measures like r, relative fitness seems largely divorced from population biology. It has even been proposed that relative fitness be justified from measure theory, abandoning population biology altogether (Wagner, 2010). Given the ubiquitous use of relative fitness, it is important that we understand its population ecological basis, both to clarify its domain of applicability, and as part of the broader challenge of synthesizing ecology and evolution.

Constant relative fitness values can be justified as a linear approximation (Ewens, 2004, pp. 277) (Charlesworth, 1994, Chap. 4) which is close to exact provided that selection is sufficiently weak and stable over time. Yet strong, temporally-variable selection occurs widely in nature and the lab, including in wild *Drosophila*, where population density varies by orders of magnitude each seasonal cycle (Messer et al., 2016; Bergland et al., 2014). The question is whether relative fitness can be used when selection is not vanishingly weak. In general, age-structured populations that reproduce by outcrossing do not permit strong selection to be represented in terms of type-specific relative-fitness constants (Charlesworth, 1994, Chap. 4). We will therefore restrict our attention to asexual haploids with little or no

age structure, where it is easier to evaluate how the success or failure of the relative fitness description is tied to the underlying population ecological assumptions.

The basis of relative fitness is straightforward in the absence of crowding: it simply represents differences in intrinsic population growth rate. In discrete time, the change in frequency of type i is $\Delta p_i = \left(\frac{W_i}{\overline{W}} - 1\right) p_i$, where W_i is the intrinsic absolute growth factor of type i, and $\overline{W} = \sum_i W_i p_i$ is the population mean W. Here we can rescale W however we please and replace it with "relative fitness" w without affecting the ratio $\frac{W_i}{\overline{W}} = \frac{w_i}{\overline{w}}$. In continuous time, the canonical selection equation is $\frac{dp_i}{dt} = (r_i - \overline{r})p_i$, where W is replaced by the intrinsic exponential growth rate r (Crow et al., 1970, pp. 26). If there are two types present, a wildtype and a mutant for instance, then the continuous time canonical selection equation can be written as

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

where the constant selection coefficient s is the difference in r between types. The corresponding adaptive sweeps follow a logistic curve.

The difficulty with Eq. (1) arises in crowded populations. Since crowded and uncrowded conditions are so different, we expect that s will often depend on density (Travis et al., 2013). Eq. (1) is then no longer a complete description of selection — we would also need to specify a model for how density is changing. Note that frequency-dependent selection does not raise similar problems; Eq. (1) is still a complete description of selection even if its behavior is more complicated due to s depending on frequency. Population genetics traditionally evades the issue of density-dependent selection by simply assuming that total population density N has reached its equilibrium value, which is assumed to be a fixed constant. The selection coefficient s now abstractly parameterizes the rate at which selection changes relative frequencies, and no longer corresponds to differences in intrinsic growth rates r.

However, 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 saturation 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 saturation 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), even in the absence of age-structure and mating.

In light of this difficulty, the relative fitness description has been justified in broadly two different ways for crowded populations (we do not discuss Wagner's [2010] measure-theoretical justification, which is independent of population biology). 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 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

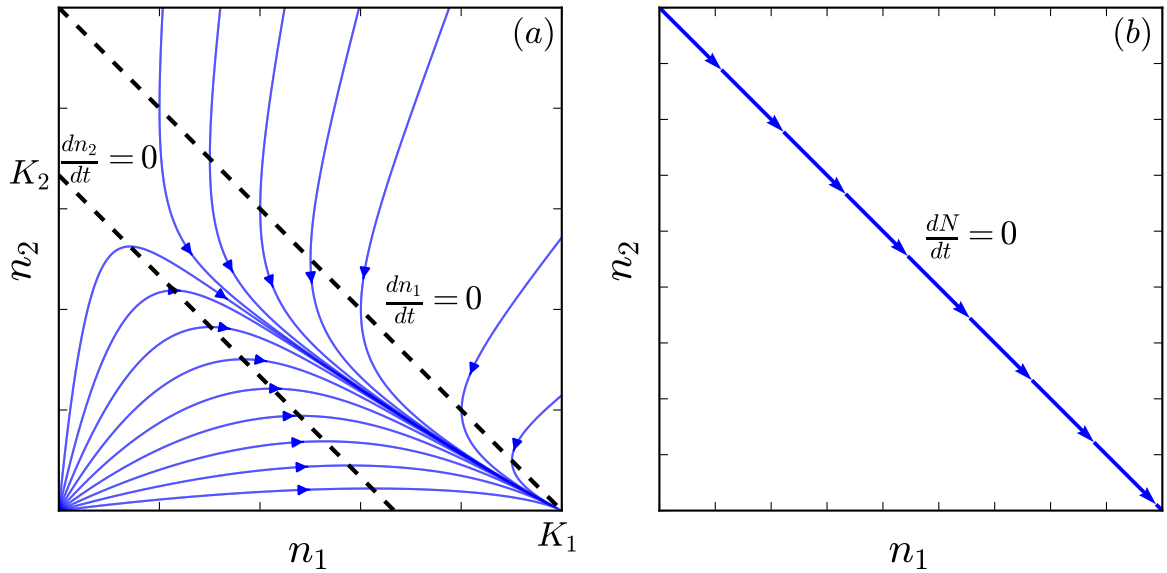

Figure 1: Selection in crowded environments shown as a phase diagram for the densities of two types n_1 and n_2. (a) The logistic model $\frac{dn_1}{dt} = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $\frac{dn_2}{dt} = r_2(1 - \frac{n_1+n_2}{K_2})n_1$ with $r_1 = r_2$ and $K_1 > K_2$. (b) The constant-N, relative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

from population density at the adult phase unless it is so strong that the reproductive excess is depleted. This justifies Eq. (1) because, for a population in demographic equilibrium, selective sweeps do 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. Kimura and Crow (1969) 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 Eq. (1) 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. Rather than attempting to make sense of relative fitness in existing standard models of population growth (e.g. (Kimura and Crow, 1969; Mallet, 2012)), we instead do the reverse, and attempt to make population eco-

logical sense of the widely-used Wright-Fisher relative-fitness model. Our starting point is the classic lottery model of territorial contest (Sale, 1977; Chesson and Warner, 1981). Like the Wright-Fisher model, the classic lottery assumes a saturated population with constant N, and fitness involves a product of fertility and juvenile viability (Crow et al., 1970, pp. 185), but unlike the Wright-Fisher model, generations can overlap. Our first task is to generalize the lottery model to create a variable-density version of the Wright-Fisher model with overlapping generations (sections "Model" and "Analytical approximation of the variable-density lottery").

Equipped with this new model, we turn to the evaluation of Eq. (1). We first discuss selection on the ability to contest territories, which behaves like a pure constant-N, relative fitness trait, and discuss how this fits with MacArthur's analysis of selection in crowded populations (section "K-selection and selection-dependent density"). We then consider selection on density-regulating traits (section "Density-regulating traits and the threat of strong selection"), and conclude by contrasting the classical density-dependent selection literature with our results ("Discussion").

Model

Assumptions and definitions

We assume that reproductively mature individuals ("adults") each 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 small type densities n_i/T).

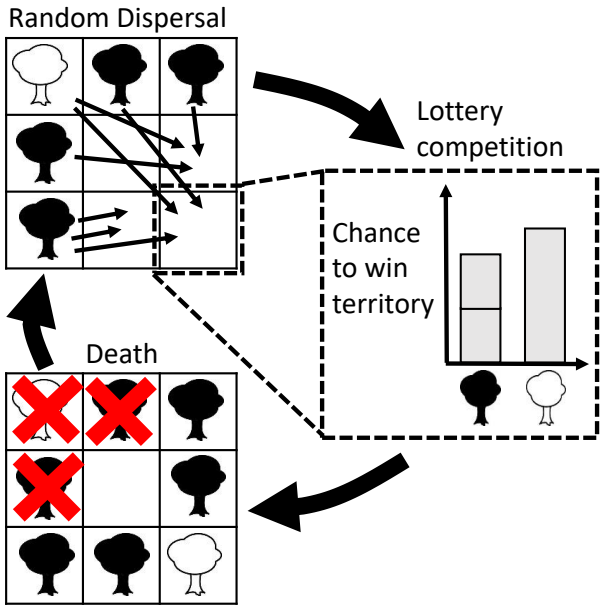

Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each unoccupied territory that receives a propagule (only illustrated in one territory). Each type has a probability proportional to $c_i x_i$ of securing a given territory, where c_i measures competitive ability and x_i is the number of propagules that disperse there. In the illustrated territory, the black type disperses more propagules but is a poorer competitor. Territories are then made available by deaths among those adults present at the start of the iteration (red crosses).

Each iteration, adults produce new offspring ("propagules"). These disperse at random, regardless of distance from their parents, and independently of each other (e.g. there is no avoidance of territories crowded with propagules). We assume that adults cannot be ousted by juveniles, so that propagules landing on occupied territories are doomed. We assume that each adult from type i produces a constant number b_i of successfully dispersing propagules; the number of propagules dispersing to unoccupied territories is then given by $m_i = b_i n_i U/T$. The total number of these propagules will be denoted $M = \sum_i m_i$. Note that due to our assumption of uniform dispersal, 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; Bolker and Pacala, 1999).

The number of propagules of the i'th type landing in any particular territory is denoted x_i. We assume that x_i follows a Poisson distribution $p_i(x_i) = l_i^{x_i} e^{-l_i}/x_i!$, where $l_i = m_i/U$ is the mean territorial propagule density for type i (the total propagule density will be denoted $L = \sum_i l_i$). This is strictly only an approximation of random dispersal, but it is an excellent approximation given our assumption that the n_i are large enough that drift can be ignored (Appendix A).

When multiple propagules land on the same territory, the victor is determined by lottery competition: type i wins a territory with probability $c_i x_i / \sum_j c_j x_j$, where c_i is a constant representing relative competitive ability (Fig. 2). We expect that a fraction $p_1(x_1) \ldots p_G(x_G)$ of the U unoccupied territories will have the propagule composition $x_1, \ldots, x_G$. Type i is expected to win a proportion $c_i x_i / \sum_j c_j x_j$ of these. Ignoring fluctuations about these two expectations (due to our no-drift, large n_i, large T approximation), type i's territorial acquisition is given by

$$\Delta_+ n_i = U \sum_{x_1,\ldots,x_G} \frac{c_i x_i}{\sum_j c_j x_j} p_1(x_1) \cdots p_G(x_G), \tag{2}$$

where the sum only includes territories with at least one propagule present.

Finally, we assume that adult mortality only occurs in adults present at the start of the iteration, and at a constant, type-specific per-capita rate $0 \leq d_i \leq 1$. Thus, the overall change in type abundances is

$$\Delta n_i = \Delta_+ n_i - d_i n_i. \tag{3}$$

Fig. 2 illustrates one iteration of the model.

Connection to the Wright-Fisher and classic lottery models

In the classic lottery model (Chesson and Warner, 1981), unoccupied territories are assumed to be saturated with propagules from every type $l_i \gg 1$. From the law of large numbers, the composition of propagules in each territory will then not deviate appreciably from the mean composition $l_1, l_2, \ldots, l_G$ (G is the number of types present), and so the probability that type i wins any particular unoccupied territory is approximately $c_i l_i / \sum_j c_j l_j$. Then the numbers of territories won by each type $\Delta_+ n_1, \Delta_+ n_2, \ldots, \Delta_+ n_G$ follow a multinomial distribution with U trials and success probabilities $\frac{c_1 l_1}{\sum_j c_j l_j}, \frac{c_2 l_2}{\sum_j c_j l_j}, \ldots, \frac{c_G l_G}{\sum_j c_j l_j}$, respectively. Type i is expected to win a proportion $c_i l_i / \sum_j c_j l_j$ of the U available territories, and deviations from this expected outcome are small (since T is large by assumption), giving

$$\Delta_+ n_i = \frac{c_i l_i}{\sum_j c_j l_j} U = \frac{c_i l_i}{\bar{c} L} U, \tag{4}$$

where $\bar{c} = \sum_j c_j m_j / M$ is the mean competitive ability for a randomly selected propagule. In section "Analytical approximation of the density-dependent lottery", we derive a generalization of Eq. (4) that accommodates arbitrary propagule densities l_i.

There is a close connection between the classic lottery model and the Wright-Fisher model of genetic drift (Svardal et al., 2015). In the Wright-Fisher model, type abundances are sampled each generation from a multinomial distribution with success proba-

bilities $w_i n_i / \sum_j w_j n_j$, where w is relative fitness and the n_i are type abundances in the preceding generation. Population size N remains constant. This is equivalent to the classic lottery model with non-overlapping generations ($d_i = 1$ for all i) and relative fitness given by $w_i = b_i c_i$ i.e. a product of fertility and viability (Crow et al., 1970, pp. 185). Thus, the classic lottery model is essentially the Wright-Fisher model extended to allow overlapping generations, but ignoring drift. This means that our extension of the classic lottery model to arbitrary densities represents a variable-density generalization of the Wright-Fisher model (we also do not consider drift here).

Results

Analytical approximation of the variable-density lottery

Eq. (2) involves an expectation over the time-dependent dispersal distributions p_i, and is thus too complicated to give intuition about the dynamics of density-dependent lottery competition. We now evaluate this expectation.

Similarly to the high-l_i approximation of the classic lottery model, we replace the x_i with appropriate mean values, although we cannot simply replace x_i with l_i as in Eq. (4). The classic lottery model breaks down for types with low propagule density ($l_i \ll 1$) because territorial acquisition is then not correctly represented by a lottery in each territory with the mean propagule density. For a type with low propagule density $l_i \ll 1$, we have $x_i = 1$ in the territories where its propagules land, and so its growth comes entirely from territories which deviate appreciably from l_i. To account for this, we separate Eq. (2) into $x_i = 1$ and $x_i > 1$ parts. Our more general 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 (details

in Appendix B)

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

where

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

and

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

Comparing Eq. (5) to Eq. (4), the classic lottery per-propagule success rate $c_i/\overline{c}L$ has been replaced by three separate terms. The first, e^{-L}, accounts for propagules which land alone on unoccupied territories; these territories are won without contest. The second, $R_i c_i/\overline{c}$, represents competitive victories when the i type is a rare invader in a high density population (i.e. it determines invasion fitness (Metz et al., 1992)). The third term, $A_i c_i/\overline{c}$, represents competitive victories when the i type is abundant. 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 $A_i c_i/\overline{c}$ term remains, and $A_i \to 1/L$).

Fig. 3 shows that Eq. (5) 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 $R_i c_i/\overline{c}$. On the other hand, $R_i c_i/\overline{c}$ is negligible 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.

Eq. (5) takes a much simpler form if all types are competitively equivalent ($c_i = c$),

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

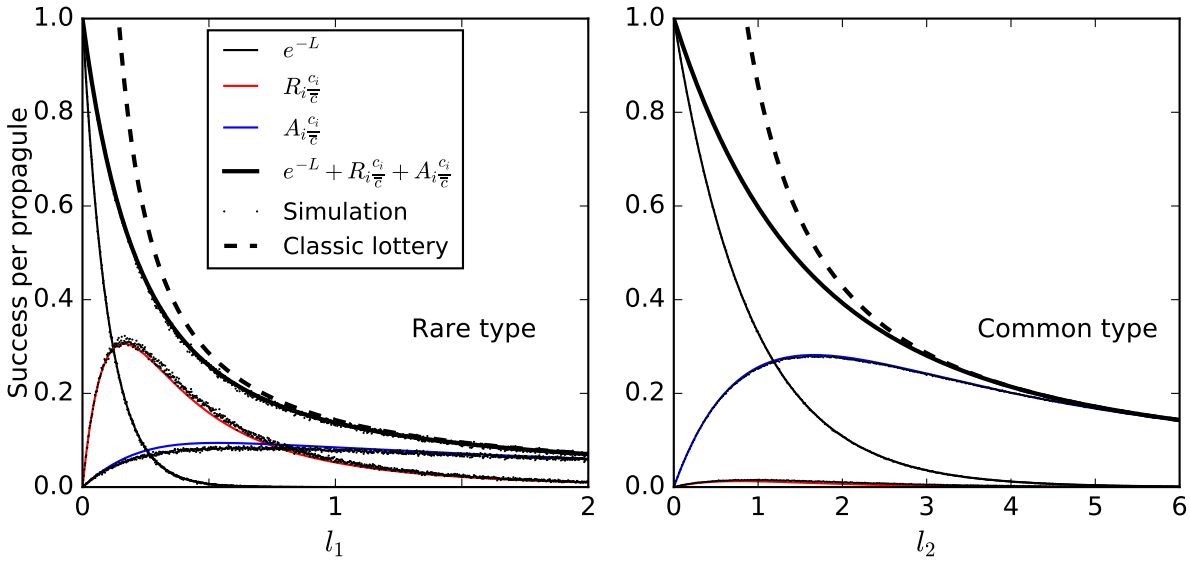

Figure 3: Comparison of the analytical approximation Eq. (5) with simulations. Per-propagule success probability $\Delta_+ n_i/l_i U$ from the classic lottery model, individual-based simulations of random dispersal and lottery competition, and Eq. (5) and its three components. Two types are present, a rare type with $c_1 = 1.5$, and a common type with $c_2 = 1$. Simulation points are almost invisible in for the common type due to near exact agreement with Eq. (5). Dashed lines in show the breakdown of the classic lottery model. Parameters: $m_1 = 10^4$ and $m_2 = 9 \times 10^4$ and U varies between 5×10^3 and 10^6.

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

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

Selection-dependent density and K-selection

Equipped with our variable-density lottery model, we now start evaluating the validity of Eq. (1). In this section we explore whether we should expect population density to vary as a result of selection (Prout, 1980). Since the idea that density does vary with selection is closely connected to the notion of "K-selection", we start by revisiting MacArthur's analysis of selection in crowded environments (MacArthur and Wilson, 1967).

MacArthur considers a population with two types that have densities n_1 and n_2 subject to density-dependent growth described by

$$\frac{dn_1}{dt} = f_1(n_1, n_2) \qquad \frac{dn_2}{dt} = f_2(n_1, n_2). \tag{8}$$

The environment is assumed to remain constant apart from the type densities. The functions f_1 and f_2 must decline to zero if n_1 or n_2 are sufficiently large, because no population has unlimited resources. This defines the 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. In other words, 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).

To formalize the relationship between nullclines, MacArthur used the symbol "K" to

label the four intersection points of the nullclines with the n_1 and n_2 axes, specifically $f_1(K_{11}, 0) = 0$, $f_1(0, K_{12}) = 0$, $f_2(0, K_{22}) = 0$ and $f_2(K_{21}, 0) = 0$. 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 saturation densities akin to the K parameter in the logistic model; following widespread convention, we will refer to selection on these saturation densities as "K-selection" (Fig. 1a). 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

$$\begin{aligned} f_1(n_1, n_2) &= r_1(1 - \alpha_{11} n_1 - \alpha_{12} n_2) n_1 \\ f_2(n_1, n_2) &= r_2(1 - \alpha_{22} n_1 - \alpha_{21} n_2) n_2 \end{aligned} \tag{9}$$

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 (Fig. 4a).

Thus, when MacArthur concludes that "fitness is K" in crowded populations (MacArthur and Wilson, 1967, pp. 149), the meaning is 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) (Gill, 1974). This general idea is much broader than "K-selection" in the sense of selection for greater saturation density, and applies even if the nullclines are nonlinear to such an extent that the "K" values themselves do not give much information about the regions of high-density growth.

It is obvious from Eq. (9) that selection can favor a superior competitor in a crowded population even if its saturation density is the same as, or lower than that of the other types present. However, the Lotka-Volterra model still couples selection to population density (Smouse, 1976). Fig. 4a shows Lotka-Volterra selection between two types with the same

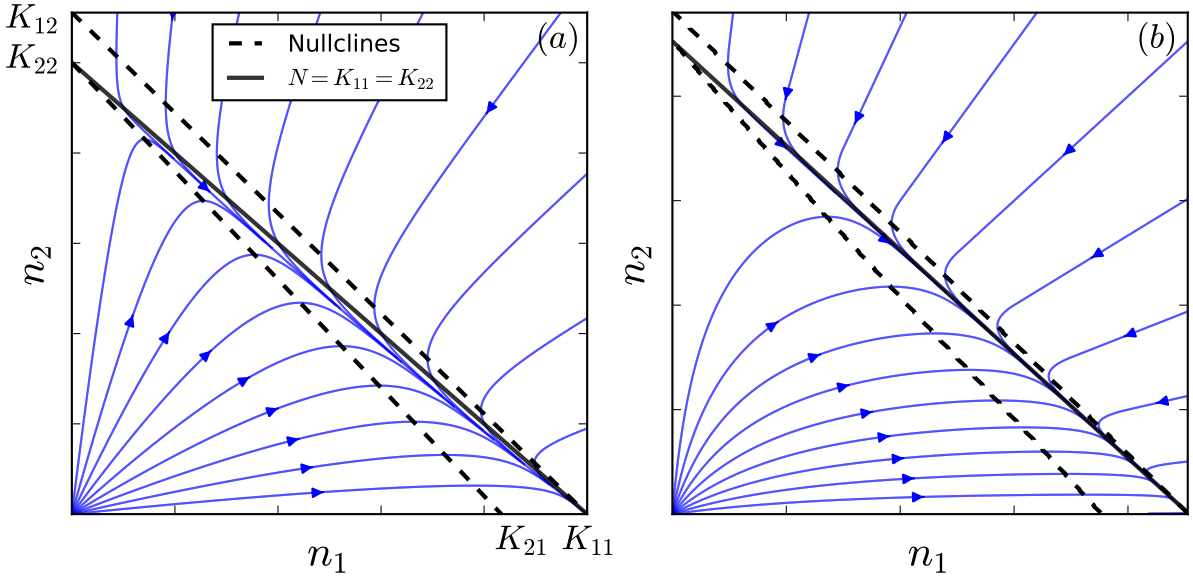

Figure 4: Selection between types with identical saturation density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 9) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. Trajectories do not follow the line $N = K_{11} = K_{22}$. (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 $N = K_{11} = K_{22}$.

saturation density ($\alpha_{11} = \alpha_{22}$, $\alpha_{21} > \alpha_{12}$). Even though the initial and final densities of a sweep are the same, density is not constant over a sweep. Only a highly restricted subset of r and α values will keep N constant over a selective sweep (further details in Appendix C). Intuitively, for one type to exclude another with the same saturation density, competitive suppression of growth between types must be stronger than competitive suppression of growth within types, causing a dip in N over the sweep.

By contrast, if one type in our density-dependent lottery model has a c advantage but the types are otherwise identical (so that each type has the same saturation density), the density trajectories converge on the line of constant density equal to the saturation density (Fig. 4b). Selection then occurs purely along this line, similarly to Fig. 1b. This occurs because c does not directly affect N: it only affects the relative likelihood for each type to win a contested territory, not whether a territory is contested in the first place (this can be seen formally in Eq. (7)). In other words, once the population reaches demographic equilibrium, it behaves indistinguishably from a constant-N relative fitness model. While quite different from classical growth models like the Lotka-Volterra, this is all perfectly consistent with MacArthur's general argument.

The constant-N behavior of c-selection arises from the role of c as a trait determining relative competitive success in territorial contests. As such, this behavior is a result of a reproductive excesses. By contrast, previous models of selection-independent density either used unusual models of competition (Kimura and Crow, 1969; Nei, 1971), or made restrictive parameter choices in the Lotka-Volterra model (Appendix C; Smouse 1976; Mallet 2012).

Density-regulating traits and the threat of strong selection

In the previous section we showed that c-selection and the regulation of population density are independent even though population growth is density-regulated in our variable-density lottery. Nevertheless, selection and density regulation *are* intimately connected in widely

used models of population growth, as well as for the lottery b and d traits.

To see why this connection potentially poses a threat to relative fitness, consider the simple birth-death model (Kostitzin, 1939, pp. 20) (Travis et al., 2013)

$$\frac{dn_i}{dt} = (b_i - \delta_i N)n_i \tag{10}$$

where δ_i is the per-capita increase in mortality rate due to crowding (for simplicity, there are no deaths when uncrowded), playing a similar role as K in the logistic model.

Starting from a monomorphic population, the frequency of a $\delta_i \to \delta_i(1-\epsilon)$ variant obeys

$$\frac{dp_i}{dt} = \epsilon\delta_i N p_i(1-p_i). \tag{11}$$

The selection coefficient $s = \epsilon\delta_i N$ thus depends on density (compare with Model III in Kimura and Crow (1969)). On the other hand, the frequency of a $b_i \to b_i(1+\epsilon)$ variant will exactly obey Eq. (1) with $s = \epsilon b_i$, independent of density.

In practice the density dependence in Eq. (11) only matters if N changes substantially during a sweep. This can easily occur if a population is far from demographic equilibrium (we return to this scenario in the Discussion). However, even if N has reached equilibrium, it will change substantially over a δ-sweep if selection on δ is sufficiently strong. To quantify this effect, we need to account for how much N changes as a result of a δ-sweep beginning and ending in equilibrium (Kimura and Crow, 1969); from Eq. (10) we have an increase from $N_{\text{initial}} = b_i/\delta_i$ to $N_{\text{final}} = b_i/\delta_i(1-\epsilon) = N_{\text{initial}}/(1-\epsilon)$. The corresponding selection coefficient increases from $s_{\text{initial}} = \epsilon b_i$ to $s_{\text{final}} = s_{\text{initial}}/(1-\epsilon)$. Consequently, noticeable deviations from Eq. (1) occur with proportional changes to δ of order $\epsilon = 0.2$ and upwards i.e. selection must be quite strong (Fig. 5).

Let us now turn to selection on b and d in our lottery model. Recall that $m_i = b_i n_i U/T$,

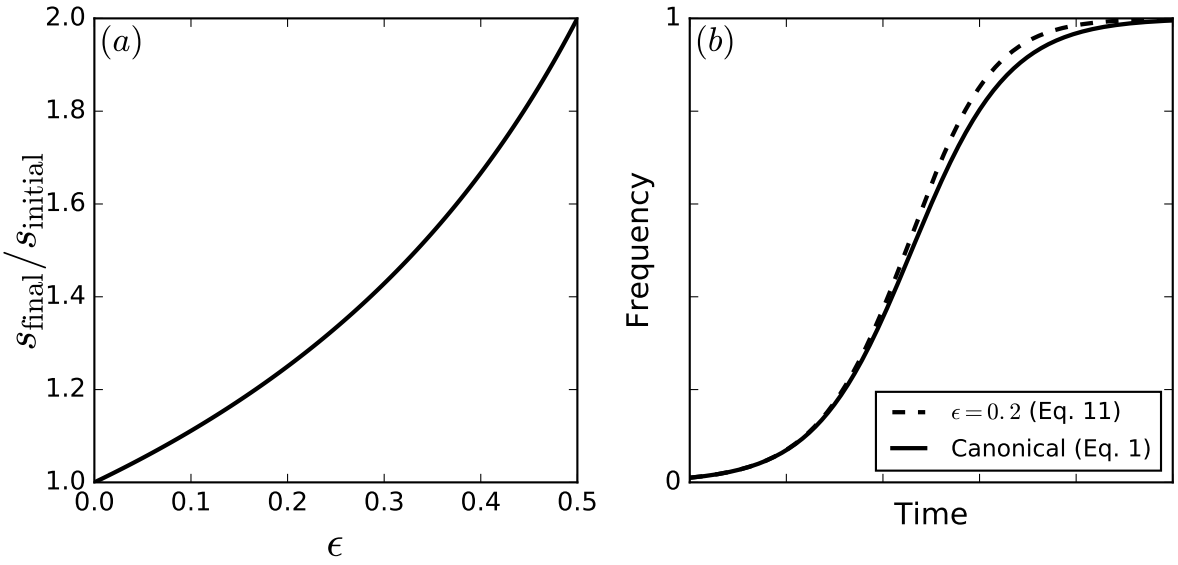

Figure 5: (a) Proportional change in the selection coefficient over a "K-like" sweep for a type that experiences proportionally $1 - \epsilon$ fewer deaths induced by crowding. The population is in demographic equilibrium at the start and end of the sweep. (b) Example equilibrium-to-equilibrium δ-sweep (Eq. 11) for $\epsilon = 0.2$ showing a noticeable deviation from the canonical selection equation.

and so $L = M/U = \bar{b}N/T$ where $\bar{b}$ is the population mean b. Thus, from Eq. (6) we have

$$\Delta n_i = \left(\frac{b_i}{\bar{b}} \frac{1 - e^{-\bar{b}N/T}}{N} (T - N) - d_i \right) n_i. \tag{12}$$

It can be seen that the mortality d is akin to the birth rate in Eq. (10), and so, while d does affect density, selection on d is density independent. Thus, d sweeps follow the canonical relative fitness model exactly (Fig. 6).

At first glance, b in Eq. (12) appears to be analogous to the δ in Eq. (10) because it regulates density and is multiplied by the density-dependent term $f(\bar{b}, N) = \frac{1-e^{-\bar{b}N/T}}{N}(T-N)$. This term declines from $\bar{b}$ at low density to zero at high density and as a result, selection on b is density-dependent. The source of this density-depedence is that the selective advantage from having greater b depends on the number of territories being contested; if almost all are occupied, then there is little advantage to having a greater b.

Nevertheless, the behavior of equilibrium-to-equilibrium b-sweeps are qualitatively different from the δ sweeps above. The reason is that b regulates density by controlling how many unoccupied territories receive propagules. Thus, greater b means more propagules contesting territories, but also more territories being contested. The net effect on $f(\bar{b}, N)$ is precisely zero in equilibrium: in a single-type equilibrium we have $b_i/\bar{b} = 1$ and so $f(\bar{b}, N) = d_i$ exactly at the beginning and end of a pure b sweep, even though the density N increases. Strictly speaking there is some deviation in $f(N)$ from d_i during the sweep, but this deviation is an order of magnitude smaller than for a δ sweep (the deviation due to a sweep with proportional effect $b_i \to b_i(1+\epsilon)$ is only of order ϵ^2, whereas the analogous effect in Fig. 5 is of order ϵ; see Appendix D for details). Since selection must already be quite strong for a δ sweep to threaten Eq. (1), we conclude that b sweeps also obey the canonical selection equation (to a close approximation).

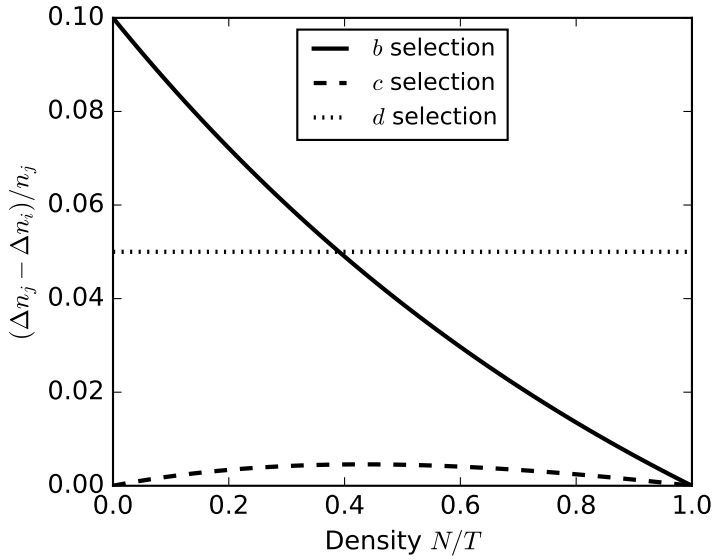

Figure 6: The density-dependence of selection in our variable-density lottery plotted as the selection coefficient $(\Delta n_j - \Delta n_i)/n_j$ experienced by an adaptive variant j present at the same frequency as a wildtype i. Here $b_i = 1$, $d_i = 0.5$ and $c_i = 1$. For b-selection we set $b_j = b_i(1 + \epsilon)$, 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 equilibrium density for the i type is ≈ 0.4.

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. Despite these differences, pure b, c and d sweeps starting and ending at equilibrium all obey the canonical selection equation. This rich variety of behaviors in relation to density is quite different from that found in the classical density-dependent selection literature (Roughgarden, 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 saturation 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 that they are density-dependent and cause density to change over a sweep (although N only dips temporarily during an α-sweep). Thus, strong selection is sufficient for relative fitness to break down in the classical view of density-dependent selection. Indeed, in the defense of Eq. (1) given by Kimura and Crow (1969), it was assumed that s will be a few percent at most. While this may be reasonable for adaptive mutations, there is no reason to expect selection on standing variation to be so weak, wild *Drosophila* being an obvious counter-example (Bergland et al., 2014).

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 Wright-Fisher model and similar viability selection heuristics actually capture an important ecological process.

We now turn to the breakdown of Eq. (1). We first discuss the problem shown in Fig. 5, which occurs when strong selection changes population density and is also density-dependent. In the variable-density lottery, this occurs if and only if types differ in more than one trait. 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 linear models that have become standard in discussions of density-dependent selection (Roughgarden, 1979; Christiansen, 2004; Mallet, 2012; Travis et al., 2013) actually represent a complicated form of the interaction between density and selection, and their parameters confound the

underlying issues.

While this is a conceptual reason to be wary of the classical density-dependent selection models, it is not clear how we should expect the trait variation in nature to align. For instance, 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 any interference competition are subsumed into the competitive ability c, which does not affect N.

Relative fitness models truly break down when N is far from equilibrium and selection is density-dependent (as seems likely; Travis et al. 2013). For example, wild *Drosophila* experience large seasonal boom-bust cycles in population density coupled to strong selection that drives large swings in allele frequency (Bergland et al., 2014). In this case there is no choice but to abandon relative fitness, and our model provides one potentially suitable option. Whether or not our density-dependent lottery model is a good description of *Drosophila* ecology, the close connection between our model and Wright-Fisher is useful, because drift in our model should behave broadly similarly. Thus, our model it should provide a useful starting point for analyzing evolution in this and other far-from-equilibrium situations.

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.

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Appendix A: Poisson approximation

For simplicity of presentation, we have assumed a Poisson distribution for the x_i as our model of dispersal. Strictly speaking, the total number of i propagules $\sum x_i$ (summed over unoccupied territories) is then no longer a constant m_i, but fluctuates between generations for a given mean m_i, which is more biologically realistic. Nevertheless, since we do not consider the random fluctuations in type abundances here, and for ease of comparison with the classic lottery model, we ignore the fluctuations in m_i. Instead we focus, on Poisson fluctuations in propagule composition in each territory.

In the exact model of random dispersal, the counts of a type's propagules across unocupied territories follows a multinomial distribution with dimension U, total number of trials equal to m_i, and equal probabilities $1/U$ for a propagule to land in a given territory. Thus, the x_i in different territories are not independent random variables. However, for sufficiently large U and m_i, this multinomial distribution for the x_i across territories is closely approximated by a product of independent Poisson distributions for each territory, each with rate parameter l_i (Arenbaev, 1977, Theorem 1). Since we are ignoring finite population size effects, we effectively have $T \to \infty$, in which case U can only be small enough to violate the Poisson approximation if there is vanishing population turnover, and then the dispersal distribution is irrelevant anyway. Likewise, in ignoring stochastic finite population size for the n_i, we have effectively already assumed that m_i is large enough to justify the Poisson approximation (the error scales as $1/\sqrt{m_i}$; Arenbaev 1977).

Appendix B: Derivation of growth equation

We separate the right hand side of Eq. (2) into three components $\Delta_+ n_i = \Delta_u n_i + \Delta_r n_i + \Delta_a n_i$ which vary in relative magnitude depending on the propagule densities l_i. 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.

Growth without competition

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

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

Competition when rare

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") i.e. $x_i = 1$ and $X_i \geq 1$ where $X_i = \sum_{j \neq i} x_j$ is the number of nonfocal propagules. The number of territories where this occurs is $U p_i(1) P(X_i \geq 1) = b_i n_i e^{-l_i}(1 - e^{-(L-l_i)})$. Thus

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

where $\langle\rangle_{\tilde{p}}$ denotes the expectation with respect to $\tilde{p}$, and $\tilde{p}$ is the probability distribution of nonfocal propagule abundances x_j *after* dispersal (the significance of evaluating after dispersal should become clearer below), in those territories where exactly one focal propagule, and at least one non-focal propagule, landed.

Our approximation is to replace x_j with its mean in the last term in Eq. (14),

$$\left\langle \frac{c_i}{c_i + \sum_{j\neq i} c_j x_j} \right\rangle_{\tilde{p}} \approx \frac{c_i}{c_i + \sum_{j\neq i} c_j \langle x_j \rangle_{\tilde{p}}}. \tag{15}$$

Below we justify this replacement by arguing that the standard deviation $\sigma_{\tilde{p}}(\sum_{j\neq i} c_j x_j)$ (with respect to $\tilde{p}$), is much smaller than $\langle \sum_{j\neq i} c_j x_j \rangle_{\tilde{p}}$. If this standard deviation is small as claimed, then the mean value gives an accurate representation of the values taken by $\sum_{j\neq i} c_j x_j$ across territories.

We first calculate $\langle x_j \rangle_{\tilde{p}}$. Let $X = \sum_j x_j$ denote the total number of propagules in a territory and $\mathbf{x}_i = (x_1, \ldots, x_{i-1}, x_{i+1} \ldots, x_G)$ denote the vector of non-focal abundances, so that $p(\mathbf{x}_i) = p_1(x_1) \cdots p_{i-1}(x_{i-1}) p_{i+1}(x_{i+1}) \cdots p_G(x_G)$. Then, $\tilde{p}$ is the probability distribution for $\mathbf{x}_i$ conditional on the territory having received $X \geq 2$ propagules, where $X_i = X - 1$ of them are nonfocal, giving

$$\tilde{p}(\mathbf{x}_i) = \sum_{X=2}^{\infty} P(X|X \geq 2) p(\mathbf{x}_i | X_i = X - 1) \tag{16}$$

Here the total number of propagules X follows a Poisson distribution with mean L, and we have $P(X|X \geq 2) = P(X)/P(X \geq 2) = P(X)/(1 - (1 + L)e^{-L})$. Thus,

$$\begin{aligned} \langle x_j \rangle_{\tilde{p}} &= \sum_{\mathbf{x}_i} \tilde{p}(\mathbf{x}_i) x_j \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - 1) x_j. \end{aligned} \tag{17}$$

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,

$$\begin{aligned}\langle x_j\rangle_{\tilde{p}} &= \frac{l_j}{1-(1+L)e^{-L}}\frac{1}{L-l_i}\sum_{X=2}^{\infty}P(X)(X-1)\\ &= \frac{l_j}{1-(1+L)e^{-L}}\frac{L-1+e^{-L}}{L-l_i},\end{aligned} \tag{18}$$

where the last line follows from $\sum_{X=2}^{\infty}P(X)(X-1)=\sum_{X=1}^{\infty}P(X)(X-1)=\sum_{X=1}^{\infty}P(X)X-\sum_{X=1}^{\infty}P(X)$.

Having evaluated the mean propagule numbers, we now evaluate the variance in propagule numbers to check that the mean value replacement in Eq. (15) is justified. This is complicated because the x_j are not independent with respect to $\tilde{p}$. Here we use the following approximation to give some insight into the magnitude of these fluctuations and also the nature of the correlations between the x_j. We replace $\tilde{p}$ with $\tilde{q}$, defined as the $\mathbf{x}_i$ Poisson dispersal probabilities conditional on $X_i \geq 1$ (which are independent). The distinction between $\tilde{p}$ and $\tilde{q}$ will be discussed further below. The $\tilde{q}$ approximation gives $\langle x_j\rangle_{\tilde{q}} = \langle x_j\rangle_p/C = l_j/C$, where $C = 1-e^{-(L-l_i)}$, with variances and covariances given by

$$\begin{aligned}\sigma^2_{\tilde{q}}(x_j) &= \langle x_j^2\rangle_{\tilde{q}} - \langle x_j\rangle^2_{\tilde{q}}\\ &= \frac{1}{C}\langle x_j^2\rangle_p - \frac{l_j^2}{C^2}\\ &= \frac{1}{C}(l_j^2+l_j) - \frac{l_j^2}{C^2}\\ &= \frac{l_j^2}{C}\left(1-\frac{1}{C}\right)+\frac{l_j}{C},\end{aligned} \tag{19}$$

and

$$\begin{aligned}\sigma_{\tilde{q}}(x_j, x_k) &= \langle x_j x_k \rangle_{\tilde{q}} - \langle x_j \rangle_{\tilde{q}} \langle x_k \rangle_{\tilde{q}} \\ &= \frac{1}{C} \langle x_j x_k \rangle_p - \frac{l_j l_k}{C^2} \\ &= \frac{l_j l_k}{C} \left(1 - \frac{1}{C}\right) \qquad\qquad j \neq k. \end{aligned} \tag{20}$$

The distinction between $\tilde{p}$ and $\tilde{q}$ is closely connected to why the exact dispersal probability distribution $\tilde{p}$ is evaluated *after* dispersal. $\tilde{p}$ assumes that one of the propagules present in a given territory after dispersal belongs to the focal type (a statement about propagule identity), whereas $\tilde{q}$ assumes that there is a focal propagule present before non-focal dispersal commences (a statement about propagule presence). As a result, if the focal type is rare, $\tilde{q}$ predicts that the mean propagule density is $L + 1$ in territories with one focal propagule. This is erroneous, because the mean number of propagules per territory when lottery competition commences is L, regardless of whether a focal propagule happens to be present. The discrepancy causes rare invaders evaluated under $\tilde{q}$ to have an intrinsic rarity disadvantage, which is absurd (i.e. even if b, c and d are identical, $\tilde{q}$ predicts that a rare type will decline in frequency). By contrast, Eq. (18) correctly predicts that there are on average $\sum_{j \neq i} \langle x_j \rangle_{\tilde{p}} \approx L - 1$ nonfocal propagules because $\tilde{p}$ accounts for potentially large negative covariances between the x_j "after dispersal". By neglecting the latter covariances, $\tilde{q}$ overestimates the fluctuations in $\sum_{j \neq i} c_j x_j$; thus $\tilde{q}$ gives an upper bound on the fluctuations. The discrepancy between $\tilde{q}$ and $\tilde{p}$ will be largest when L is of order 1 or smaller, because then the propagule assumed to already be present under $\tilde{q}$ is comparable to, or greater than, the entire propagule density.

Decomposing the variance in $\sum_{j\neq i} c_j x_j$,

$$\sigma^2_{\tilde{q}}(\sum_{j\neq i} c_j x_j) = \sum_{j\neq i}\left[c_j^2\sigma^2_{\tilde{q}}(x_j) + 2\sum_{k>j,k\neq i} c_j c_k \sigma_{\tilde{q}}(x_j, x_k)\right], \tag{21}$$

and using the fact that $\sigma_{\tilde{q}}(x_j, x_k)$ and the first term in Eq. (19) are negative because $C < 1$, we obtain an upper bound on the relative fluctuations in $\sum_{j\neq i} c_j x_j$,

$$\frac{\sigma(\sum_{j\neq i} c_j x_j)}{\langle\sum_{j\neq i} c_j x_j\rangle} = C^{1/2}\frac{\left(\sum_{j\neq i} c_j^2 l_j + (1-1/C)\left(\sum_{j\neq i} c_j l_j\right)^2\right)^{1/2}}{\sum_{j\neq i} c_j l_j} < C^{1/2}\frac{\left(\sum_{j\neq i} c_j^2 l_j\right)^{1/2}}{\sum_{j\neq i} c_j l_j}. \tag{22}$$

Suppose that the c_j are all of similar magnitude (their ratios are of order one). Then Eq. (22) is $\ll 1$ for the case when $L - l_i \ll 1$ (due to the factor of $C^{1/2}$), and also for the case when at least some of the nonfocal propagule densities are large $l_j \gg 1$ (since it is then of order $1/\sqrt{L - l_i}$). The worst case scenario occurs when $L - l_i$ is of order one. Then Eq. (22) gives a relative error of approximately 50%, which from our earlier discussion we know to be a substantial overestimate when L is of order 1. Our numerical results (Fig. 3) confirm that the relative errors are indeed small.

However, the relative fluctuations in $\sum_{j\neq i} c_j x_j$ can be large if some of the c_j are much larger than the others. Specifically, in the presence of a rare, extremely strong competitor ($c_j l_j \gg c_{j'} l_{j'}$ for all other nonfocal types j', and $l_j \ll 1$), then the RHS of Eq. (22) can be large and we cannot make the replacement Eq. (15).

Substituting Eqs. (15) and (18) into Eq. (14), we obtain

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{\bar{c}}, \tag{23}$$

where R_i is defined in Eq. (6).

Competition when abundant

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

$$\Delta_a n_i = U(1-(1+l_i)e^{l_i}) \left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \tag{24}$$

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

Again, we argue that the relative fluctuations in $\sum c_j x_j$ are much smaller than 1 (with respect to $\hat{p}$), so that,

$$\left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \approx \frac{c_i \langle x_i \rangle_{\hat{p}}}{\sum_j c_j \langle x_j \rangle_{\hat{p}}}. \tag{25}$$

Following a similar procedure as for $\Delta_r n_i$, where the vector of propagule abundances is denoted $\mathbf{x}$, the mean focal type abundance is,

$$\begin{aligned}
\langle x_i \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_i p(\mathbf{x}|x_i \geq 2) \\
&= \sum_{x_i} x_i p(x_i|x_i \geq 2) \\
&= \frac{1}{1-(1+l_i)e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i \\
&= l_i \frac{1-e^{-l_i}}{1-(1+l_i)e^{-l_i}}.
\end{aligned} \tag{26}$$

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

$$\begin{aligned}
\langle x_j \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_j p(\mathbf{x}|x_i \geq 2) \\
&= \sum_X P(X|x_i \geq 2) \sum_{\mathbf{x}} x_j p(\mathbf{x}|x_i \geq 2, X) \\
&= \sum_X P(X|x_i \geq 2) \sum_{x_i} p(x_i|x_i \geq 2, X) \sum_{\mathbf{x}_i} x_j p(\mathbf{x}_i|X_i = X - x_i) \\
&= \sum_X P(X|x_i \geq 2) \sum_{x_i} p(x_i|x_i \geq 2, X) \frac{l_j(X - x_i)}{L - l_i} \\
&= \frac{l_j}{L - l_i} \left[\sum_X P(X|x_i \geq 2) X - \sum_{x_i} p(x_i|x_i \geq 2) x_i \right] \\
&= \frac{l_j}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}} \right). \qquad (27)
\end{aligned}$$

In going from line 3 to 4, we used the same logic used to evaluate the inner sum in Eq. (17), and in going from 4 to 5 we have separately evaluated the contributions from the X and x_i terms in the numerator.

To calculate the standard deviation in $\sum_{j \neq i} c_j x_j$, we use a similar approximation as for $\Delta_r n_i$: $\hat{p}$ is approximated by $\hat{q}$, defined as the $\mathbf{x}$ dispersal probabilities in a territory conditional on $x_i > 2$ (that is, treating the x_j as independent). All covariances between nonfocal types are now zero, so that $\sigma^2_{\hat{q}}(\sum c_j x_j) = \sum c_j^2 \sigma^2_{\hat{q}}(x_j)$, where $\sigma^2_{\hat{q}}(x_j) = l_j$ for $j \neq i$, and

$$\sigma^2_{\hat{q}}(x_i) = \frac{l_i}{D} \left(l_i + 1 - e^{-l_i} - \frac{l_i}{D} \left(1 - e^{-l_i}\right)^2 \right), \qquad (28)$$

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

$$\frac{\sigma_{\hat{q}}(\sum c_j x_j)}{\langle \sum c_j x_j \rangle} = \frac{\left(\sum_{j \neq i} c_j^2 l_j + c_i^2 \sigma^2_{\hat{q}}(x_i) \right)^{1/2}}{\sum_{j \neq i} c_j l_j + c_i l_i (1 - e^{-l_i})/D}. \qquad (29)$$

Similarly to Eq. (22), the RHS of Eq. (29) is $\ll 1$ for the case that $L \ll 1$ (due to a

factor of $D^{1/2}$), and also for the case when at least some of the propagule densities (focal or nonfocal) are large — provided that c_i and the c_j are all of similar magnitude. Again, the worst case scenario occurs when l_i and $L - l_i$ are of order 1, in which case Eq. (29) is around 35%, which is again where the $\hat{q}$ approximation produces the biggest overestimate of the fluctuations in $\mathbf{x}$. Similarly to Eq. (22), the RHS of (29) will not be $\ll 1$ in the presence of a rare, extremely strong competitor.

Combining Eqs. (24) and (25), we obtain

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \tag{30}$$

where A_i is defined in Eq. (6).

Appendix C: 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 saturation 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. (9), we obtain

$$\begin{aligned} \frac{dn_1}{dt} &= r_1(\alpha_{11} - \alpha_{12}) n_1 n_2 \\ \frac{dn_2}{dt} &= r_2(\alpha_{22} - \alpha_{21}) n_1 n_2 \end{aligned} \tag{31}$$

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

$$r_1(\alpha_{\text{intra}} - \alpha_{12}) + r_2(\alpha_{\text{intra}} - \alpha_{21}) = 0. \tag{32}$$

To get some intuition for Eq. (32), suppose that a mutant arises with improved competitive ability but identical intrinsic growth rate and saturation 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

$$\sum_{ij} r_i(\alpha_{\text{intra}} - \alpha_{ij})p_i p_j = 0, \tag{33}$$

which depends on frequency and thus cannot be satisfied in general for constant inter-type coefficients α_{ij}. We conclude that selection in the Lotka-Volterra competition model will generally involve non-constant N.

Appendix D: 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

$$\begin{aligned} f_{\text{half}} = f(\frac{b_i+b_j}{2}, \frac{N_i+N_j}{2}) &= \frac{b_i+b_j}{2}\left(1 - \frac{D_i+D_j}{2}\right) \\ &= \frac{1}{4}(b_i+b_j)(2-D_i-D_j) \\ &= \frac{1}{4}(2d_i + b_i(1-D_j) + b_j(1-N_i)). \end{aligned} \tag{34}$$

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

$$\begin{aligned} \frac{f_{\text{half}}}{d_i} &= \frac{1}{4}\left(2 + \frac{b_i}{b_j} + \frac{b_j}{b_i}\right) \\ &= \frac{1}{4}\left(2 + \frac{1}{1+\epsilon} + 1 + \epsilon\right) \\ &= 1 + \frac{1}{4}(\epsilon^2 - \epsilon^3 + \ldots), \end{aligned} \tag{35}$$

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

By contrast, for a δ sweep in Eq. (10), the density-dependent term N increases by a factor of $\frac{1}{1-\epsilon} = 1 + \epsilon + \epsilon^2 + \ldots$. Thus, the deviations in $f(N)$ are an order of magnitude smaller than those shown in Fig. (5), and even proportional changes of order $\epsilon = 0.1$ will cause a negligible deviation from the canonical selection equation.