Density-dependent selection and the limits of relative fitness

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1

Abstract

Relative fitness models are the basis of foundational in population genetics.

Yet the population ecological basis of relative fitness is poorly understood, and the classical ecology literature on selection in crowded populations seems to be incompatible with widely-used relative fitness models such as the Wright-Fisher. Here we develop a generalization of the Wright-Fisher model in which density depends dynamically on the demographic rates of the types present. We then explore the population ecology of relative fitness using this model as a reference point. Although density-dependent selection can cause relative fitness to break down, relative fitness models are fairly robust in populations close to demographic equilibrium. In particular, relative fitness only breaks down if selection is strong and density-dependent, and density is also selection-dependent. Our generalized Wright-Fisher model clearly distinguishes between three demographic parameters, each of whose behavior is, on its own, correctly described by relative fitness models. In contrast, the classical literature on density-dependent selection confounds them. We argue that selection-independent density is ecologically plausible for many species given the prevalence of reproductive excesses, an important aspect of selection omitted in many ecological models. Our model also offers a natural alternative to relative fitness when the latter is untenable, as is likely the case far from demographic equilibrium.

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 [Doebeli et al., 2017, Metcalf and Pavard, 2007]. 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 more abstract measure-theoretical arguments, abandoning population biology altogether [Wagner, 2010].

In age-structured, sexual populations, selection cannot in general be represented in terms of a single type-specific fitness parameter [Charlesworth, 1994, Chap. 4]. Relative fitness models can then be justified as a linear approximation in which selection is approximately constant [Ewens, 2004, pp. 277] [Charlesworth, 1994, Chap. 4]. Provided that selection is sufficiently weak and stable over time, this linear approximation is not a major restriction on the use of relative fitness. Yet it is increasingly recognized that selection is not always weak, that it can fluctuate strongly over time, and that N can vary by orders of magnitude over a few generations as a routine feature of a population's ecology [Messer et al., 2016]. These are not rare exceptions, but occur widely in nature and the lab, including in wild *Drosophila* [Bergland et al., 2014].

Nevertheless, relative fitness models are the foundation for much of the population genetic literature, and are still widely used without considering the "linear approximation" restriction or the poor integration with population ecology [Mallet, 2012]. Thus, it is important that we understand the population ecological basis of relative fitness models, both to gain insight into

⁴⁴ their domain of applicability, and as part of the broader challenge of synthesizing ecology and
⁴⁵ evolution.

⁴⁶ Our aim here is to explore in more depth where the population ecological limits of relative
⁴⁷ fitness lie. To do so, we set aside the complexities of age structure and mating, since we know
⁴⁸ that these can cause relative fitness to break down. In this simplest case of asexual haploids
⁴⁹ with no age structure, the primary threat to the relative fitness description of selection is the
⁵⁰ dependence of selection on population density.

⁵¹ To see this, first consider an uncrowded population. Relative fitness then simply represents
⁵² differences in intrinsic population growth rate. In discrete time, the change in frequency of
⁵³ 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
⁵⁴ $\overline{W} = \sum_i W_i p_i$ is the population mean W. Here we can rescale W however we please and replace
⁵⁵ it with "relative fitness" w without affecting the ratio $\frac{W_i}{\overline{W}} = \frac{w_i}{\overline{w}}$. In continuous time, the canonical
⁵⁶ selection equation is $\frac{dp_i}{dt} = (r_i - \bar{r})p_i$, where W is replaced by the intrinsic exponential growth
⁵⁷ rate r [Crow et al., 1970, pp. 26]. If there are two types present, a wildtype and a mutant for
⁵⁸ instance, then the continuous time canonical selection equation can be written as

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

⁵⁹ where the constant selection coefficient s is the difference in r between types. The corresponding
⁶⁰ adaptive sweeps follow a logistic curve.

⁶¹ The difficulty with Eq. (1) arises in crowded populations. Since crowded and uncrowded
⁶² conditions are so different, we expect that s will often depend on density (although empirical
⁶³ verification has proved challenging [Travis et al., 2013]). Eq. (1) is then no longer a complete de-
⁶⁴ scription of selection — we would also need to specify a model for how density is changing. Note
⁶⁵ that frequency-dependent selection does not raise similar problems; Eq. (1) is still a complete de-
⁶⁶ scription of selection even if its behavior is more complicated due to s depending on frequency.
⁶⁷ Standard population genetics evades the issue of density-dependent selection by simply assum-

ing that total population density N has reached its equilibrium value, which is assumed to be a fixed constant. The selection coefficient s now parameterizes the rate at which selection changes relative frequencies, but 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 [Mallet, 2012, Smouse, 1976]. 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 these difficulties, the relative fitness description has been justified in broadly three 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 [Roughgarden, 1979].

The second justification, which 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 [Kimura and Crow, 1969, Nei, 1971, Turner and Williamson, 1968]. Selection
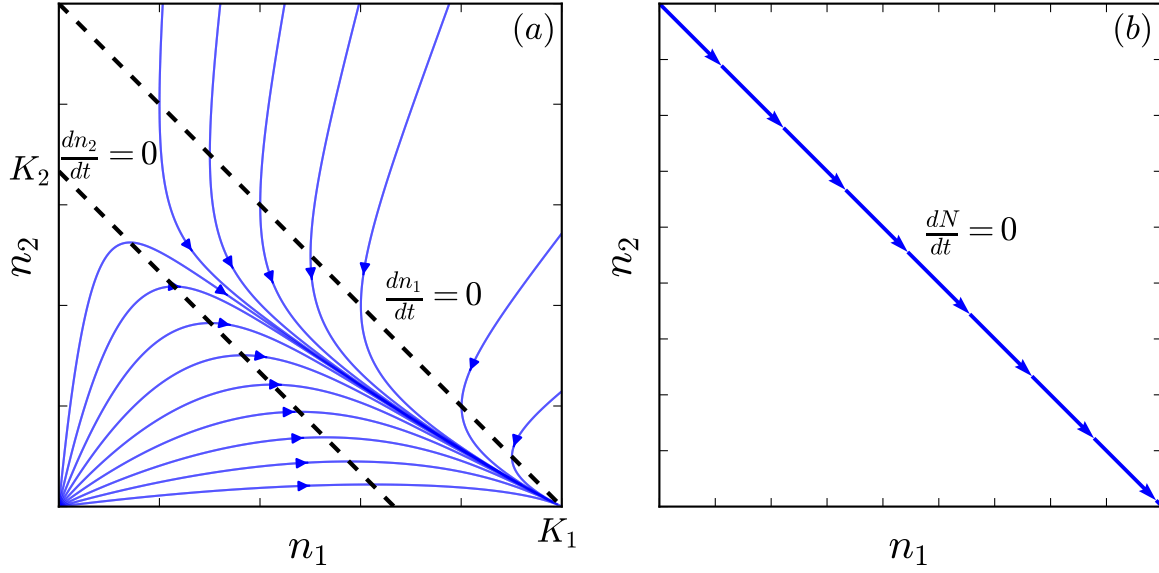
Figure 1: Selection in crowded environments shown as a phase diagram for the densities of two types n_1 and n_2. (a) The logistic model $\frac{dn_1}{dt} = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $\frac{dn_2}{dt} = r_2(1 - \frac{n_1+n_2}{K_2})n_1$ with $r_1 = r_2$ and $K_1 > K_2$. (b) The constant-N, relative fitness description of selection.

can then be concentrated at the juvenile phase, uncoupling selection from population density at the adult phase unless it is so strong that the reproductive excess is depleted. This justifies the use of Eq. (1) because, for a population in demographic equilibrium, selective sweeps do not affect density, and so it does not matter if selection is density-dependent. However, this reproductive excesses literature was focused on the evaluation of genetic load, and was poorly integrated with population ecology. Kimura and Crow [1969] took constant N as a requirement and then introduced some mathematical 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.

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 [Dieckmann and Ferrière, 2004, Ferriere and Legendre, 2013]. Although density-dependent selection is pertinent to these longer-term issues [Travis et al., 2013], 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.

Here we analyze 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 ecological sense of the widely-used Wright-Fisher relative-fitness model. Our starting point is the classic lottery model of territorial contest [Chesson and Warner, 1981, Sale, 1977]. 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").
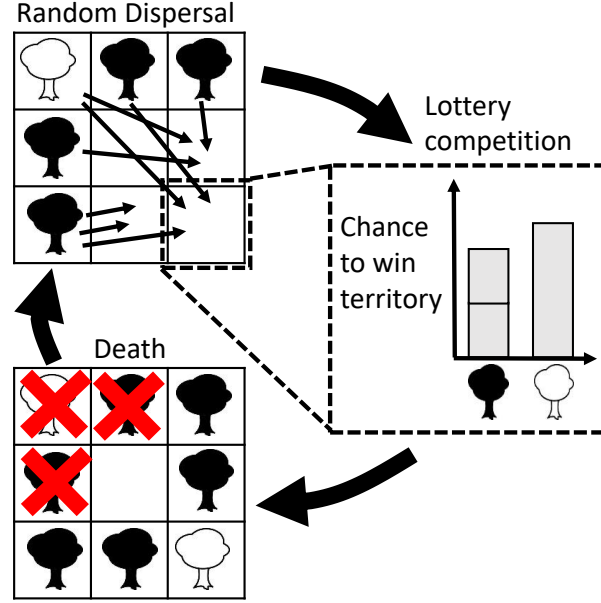
Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each unoccupied territory that receives 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).

Model

Assumptions and definitions

We assume that reproductively mature individuals ("adults") each require their own territory to survive and reproduce (Fig. 2). 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).

Each iteration, adults produce new offspring ("propagules"). These disperse at random,

8

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 $m_i = b_i n_i U / T$. 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 [Bolker and Pacala, 1999, Levins and Culver, 1971, Tilman, 1994].

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. 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 $c_i x_i / \sum_j c_j x_j$ 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

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

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

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

9

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 $c_i l_i / \sum_j c_j l_j$ 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, $L = M/U$ is the total propagule density and $M = \sum_j m_j$ is the total number of propagules. 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 probabilities $w_i n_i / \sum_j w_j n_j$, 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

191 Eq. (2) involves an expectation over the time-dependent dispersal distributions p_i, and is thus

192 too complicated to give intuition about the dynamics of density-dependent lottery competition.

193 We now evaluate this expectation.

194   Similarly to the high-l_i approximation of the classic lottery model, we replace the x_i with

195 appropriate mean values, although we cannot simply replace x_i with l_i as in Eq. (4). The classic

196 lottery model breaks down for types with low propagule density ($l_i \ll 1$) because territorial ac-

197 quisition is then not correctly represented by a lottery in each territory with the mean propagule

198 density. For a type with low propagule density $l_i \ll 1$, we have $x_i = 1$ in the territories where

199 its propagules land, and so its growth comes entirely from territories which deviate appreciably

200 from l_i. To account for this, we separate Eq. (2) into $x_i = 1$ and $x_i > 1$ parts. Our more general

201 approximation only requires that there are no large discrepancies in competitive ability (i.e. we

202 do not have $c_i/c_j \gg 1$ for any two types). We obtain (details in Appendix B)

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

203 where

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

204 and

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

205   Comparing Eq. (5) to Eq. (4), the classic lottery per-propagule success rate $c_i/\bar{c}L$ has been

206 replaced by three separate terms. The first, e^{-L}, accounts for propagules which land alone on

207 unoccupied territories; these territories are won without contest. The second, $R_i c_i/\bar{c}$, represents

208 competitive victories when the i type is a rare invader in a high density population (i.e. it
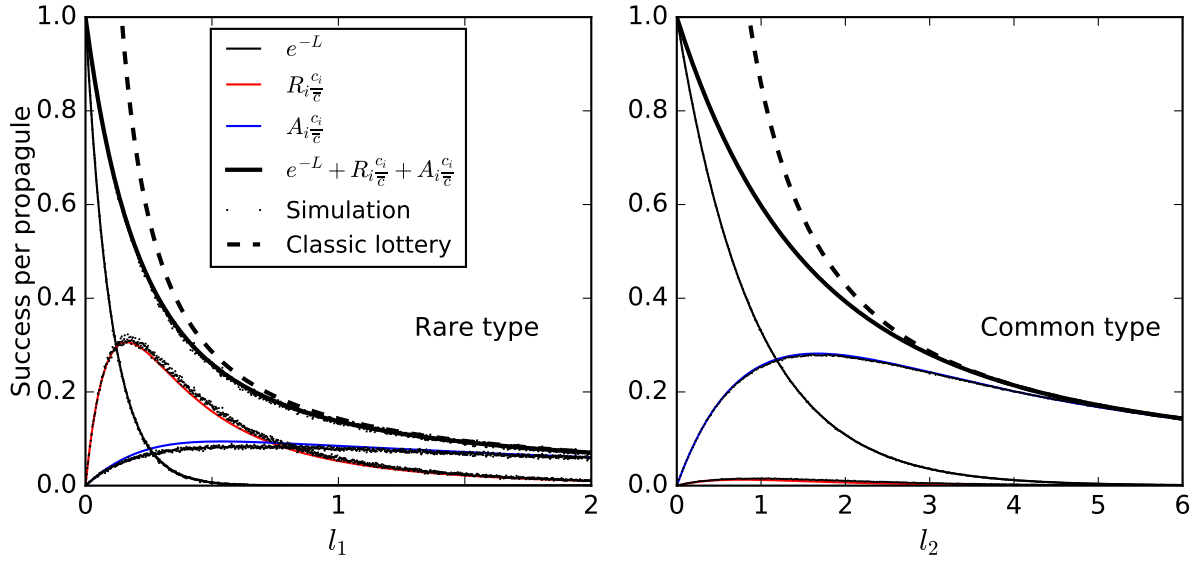
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Figure 3: Comparison of the analytical approximation Eq. (5) with simulations. Per-propagule success probability $\Delta_+ n_i / l_i U$ from the classic lottery model, individual-based simulations of random dispersal and lottery competition, and Eq. (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.

determines invasion fitness [Metz et al., 1992]). The third term, $A_i c_i / \bar{c}$, 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 $A_i c_i / \bar{c}$ term remains, and $A_i \to 1/L$).

Fig. 3 shows that Eq. (5) and its components closely approximate simulations of the density-dependent 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 for the high-frequency type, which depends instead on high density territorial victories. Fig. 3 also shows the break-down of the classic lottery model at low propagule densities.

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

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

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

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

13

238 (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

$$f_1(n_1, n_2) = r_1(1 - \alpha_{11}n_1 - \alpha_{12}n_2)n_1$$
$$f_2(n_1, n_2) = r_2(1 - \alpha_{22}n_1 - \alpha_{21}n_2)n_2 \qquad (9)$$

239 where $\alpha_{11} = 1/K_{11}$ and $\alpha_{22} = 1/K_{22}$ measure competitive effects within types, while $\alpha_{12} = 1/K_{12}$
240 and $\alpha_{21} = 1/K_{21}$ measure competitive effects between types (Fig. 4a).

241 Thus, when MacArthur concludes that "fitness is K" in crowded populations [MacArthur and
242 Wilson, 1967, pp. 149], the meaning is that selection either favors the ability to keep growing at
243 ever higher densities (moving a type's own nullcline outwards), or the ability to suppress the
244 growth of competitors at lower densities (moving the nullcline of competitors inwards) [Gill,
245 1974]. This general idea is much broader than "K-selection" in the sense of selection for greater
246 saturation density, and applies even if the nullclines are nonlinear to such an extent that the "K"
247 values themselves do not give much information about the regions of high-density growth.

248 It is obvious from Eq. (9) that selection can favor a superior competitor in a crowded popu-
249 lation even if its saturation density is the same as, or lower than that of the other types present.
250 However, the Lotka-Volterra model still couples selection to population density [Smouse, 1976].
251 Fig. 4a shows Lotka-Volterra selection between two types with the same saturation density
252 ($\alpha_{11} = \alpha_{22}$, $\alpha_{21} > \alpha_{12}$). Even though the initial and final densities of a sweep are the same,
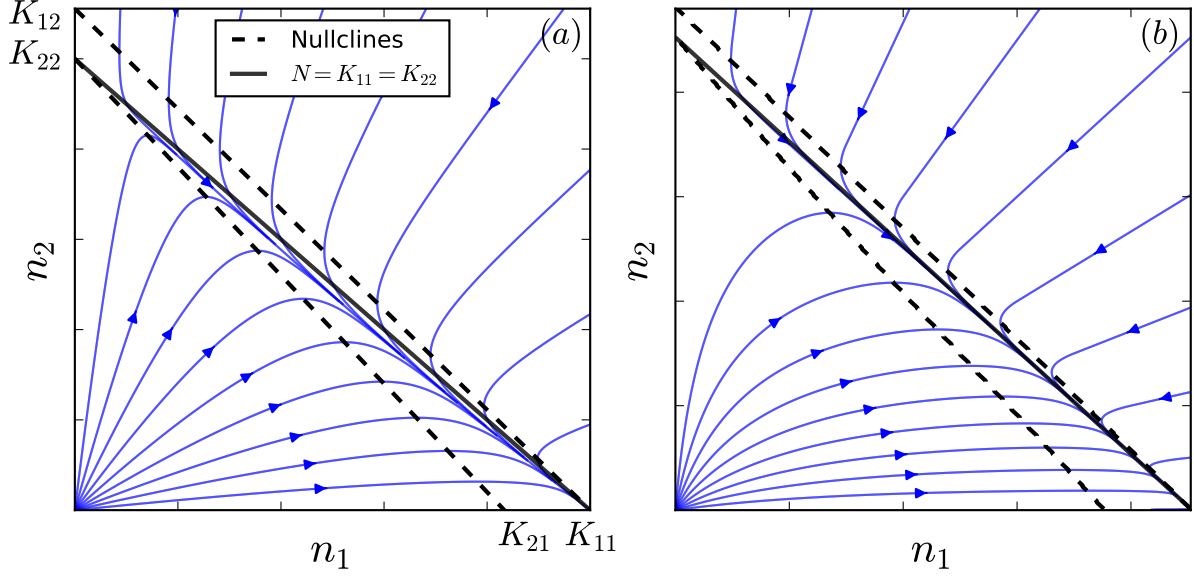
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Figure 4: Selection between types with identical saturation density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 9) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. 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 $N = K_{11} = K_{22}$.

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

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266 the Lotka-Volterra, this is all perfectly consistent with MacArthur's general argument.

267   The constant-N behavior of c-selection arises from the role of c as a trait determining relative

268 competitive success in territorial contests. As such, this behavior is a result of a reproductive

269 excesses Eq. (1). By contrast, previous models of selection-independent density either used un-

270 usual models of competition [Kimura and Crow, 1969, Nei, 1971], or made restrictive parameter

271 choices in the Lotka-Volterra model (Appendix C; Mallet 2012, Smouse 1976).

Density-regulating traits and the threat of strong selection

273 In the previous section we showed that selection and the regulation of population density can be

274 independent even if population growth is density-regulated. Nevertheless, selection and density

275 regulation *are* intimately connected in widely used models of population growth, as well as for

276 the b and d traits in our variable-density lottery model.

277   To see why this potentially poses a threat to relative fitness, consider the simple birth-death

278 model [Kostitzin, 1939, pp. 20] [Travis et al., 2013]

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

279 where δ_i is the per-capita increase in mortality rate due to crowding (for simplicity, there are no

280 deaths when uncrowded), playing a similar role as K in the logistic model.

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

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

282 The selection coefficient $s = \epsilon \delta_i N$ thus depends on density (compare with Model III in Kimura

283 and Crow [1969]). On the other hand, the frequency of a $b_i \to b_i(1 + \epsilon)$ variant will exactly obey

284 Eq. (1) with $s = \epsilon b_i$, independent of density.

285   In practice the density dependence in Eq. (11) only matters if N changes substantially during

286 a sweep. This can easily occur if a population is far from demographic equilibrium (we return
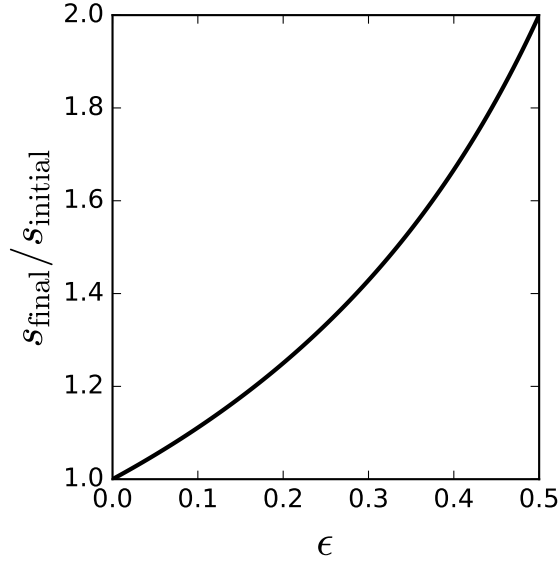
Figure 5: Proportional change in the selection coefficient over a "*K*-like" sweep for a type that experiences proportionally $1 - \epsilon$ fewer deaths induced by crowding. The population is in demographic equilibrium at the start and end of the sweep.

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, substantial deviations from Eq. (1) occur with proportional changes to δ of order $\epsilon = 0.1$ and upwards (Fig. 5).

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

17

298 fitness model exactly.

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

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

Discussion

317 Summarizing the three traits in the variable-density lottery model: (i) c-selection is density-
318 dependent, but c does not regulate density; (ii) d regulates density, but d-selection is density-
319 independent; (iii) b regulates density and b-selection is density-dependent. Despite these differ-
320 ences, pure b, c and d sweeps starting and ending at equilibrium all obey the canonical selection
321 equation. This rich variety of behaviors in relation to density is quite different from that found
322 in the classical density-dependent selection literature [Christiansen, 2004, Roughgarden, 1979].

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 necessary to assume that s will be a few percent at most.

Our variable-density lottery model shows that it is not simply a lack of ecological realism that underlies the incompatibility of relative fitness with 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, Kimura and Crow, 1969, Nei, 1971, Turner and Williamson, 1968].

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 on-

19

going 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 [Christiansen, 2004, Mallet, 2012, Roughgarden, 1979, 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.

Acknowledgments

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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 unoccupied 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 be 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).

25

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, in those territories where exactly one focal propagule, and at least one non-focal propagule, landed.

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

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

26

508 Below we justify this replacement by arguing that the standard deviation $\sigma_{\tilde{p}}(\sum_{j \neq i} c_j x_j)$ (with

509 respect to $\tilde{p}$), is much smaller than $\langle \sum_{j \neq i} c_j x_j \rangle_{\tilde{p}}$.

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 $p(\mathbf{x}_i) =$

$p_1(x_1) \ldots p_{i-1}(x_{i-1}) p_{i+1}(x_{i+1}) \ldots p_G(x_G)$. Then, $\tilde{p}$ can be written as

$$
\begin{aligned}
\tilde{p}(\mathbf{x}_i) &= p(\mathbf{x}_i | X \geq 2, x_i = 1) \\
&= \frac{P(\mathbf{x}_i, X \geq 2 | x_i = 1)}{P(X \geq 2)} \\
&= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) p(\mathbf{x}_i | X_i = X - 1),
\end{aligned}
\tag{16}
$$

and so

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

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,

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

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

511 $\sum_{X=1}^{\infty} P(X)$.

The exact analysis of the fluctuations in $\sum_{j \neq i} c_j x_j$ is complicated because the x_j are not inde-

pendent with respect to $\tilde{p}$. These fluctuations are part of the "drift" in type abundances which

we leave for future work. Here we use the following approximation to give some insight into the

27

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 $\tilde{p}$ with $\tilde{q}$ will be discussed further below. The $\tilde{q}$ approximation gives $\langle x_j \rangle_{\tilde{q}} = \langle x_j \rangle_p / C = l_j / C$,

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

and

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

512   where $C = 1 - e^{-(L - l_i)}$ and $j \neq k$.

513   The exact distribution $\tilde{p}$ assumes that exactly one of the propagules present in a given site

514   after dispersal belongs to the focal type, whereas $\tilde{q}$ assumes that there is a focal propagule

515   present before non-focal dispersal commences. As a result, $\tilde{q}$ predicts that the mean propagule

516   density is greater than L (in sites with only one focal propagule is present) when the focal

517   type is rare and the propagule density is high. This is erroneous, because the mean number

518   of propagules in every site is L by definition. Specifically, if $L - l_i \approx L \gg 1$, then the mean

519   propagule density predicted by $\tilde{q}$ is approximately $L + 1$. The discrepancy causes rare invaders

520   to have an intrinsic rarity disadvantage (territorial contests under $\tilde{q}$ are more intense than they

521   should be). In contrast, Eq. (18) correctly predicts that there are on average $\sum_{j \neq i} \langle x_j \rangle_{\tilde{p}} \approx L - 1$

522 nonfocal propagules because $\tilde{p}$ accounts for potentially large negative covariances between the x_j

523 "after dispersal". By neglecting the latter covariences, $\tilde{q}$ overestimates the fluctuations in $\sum_{j\neq i} c_j x_j$;

524 thus $\tilde{q}$ gives an upper bound on the fluctuations. The discrepancy between $\tilde{q}$ and $\tilde{p}$ will be largest

525 when L is of order 1 or smaller, because then the propagule assumed to already be present under

526 $\tilde{q}$ is comparable to, or greater than, the entire propgaule density.

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

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

528 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

529 obtain an upper bound on the relative fluctuations in $\sum_{j\neq i} c_j x_j$,

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

530 Suppose that the c_j are all of similar magnitude (their ratios are of order one). Then Eq. (22)

531 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

532 some of the nonfocal propagule densities are large $l_j \gg 1$ (since it is then of order $1/\sqrt{L - l_i}$).

533 The worst case scenario occurs when $L - l_i$ is of order one. Then Eq. (22) gives a relative error of

534 approximately 50%, which from our earlier discussion we know to be a substantial overestimate

535 when L is of order 1. Our numerical results (Fig. 3) confirm that the relative errors are indeed

536 small.

537 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

538 than the others. Specifically, in the presence of a rare, extremely strong competitor ($c_j l_j \gg c_{j'} l_{j'}$

539 for all other nonfocal types j', and $l_j \ll 1$), then the RHS of Eq. (22) can be large and we cannot

540 make the replacement Eq. (15).

29

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

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

(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

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

(24)

where $\hat{p}$ is the probability distribution of both focal and nonfocal propagaule 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,

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

(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,

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

(26)

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

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

To calculate the relative fluctuations 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 indepenent). All covariances between nonfocal types are now zero, so that $\sigma_{\hat{q}}^2(\sum c_j x_j) = \sum c_j^2 \sigma_{\hat{q}}^2(x_j)$, where $\sigma_{\hat{q}}^2(x_j) = l_j$ for $j \neq i$, and

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

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

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

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

560 to Eq. (22), the RHS of (29) will not be $\ll 1$ in the presence of a rare, extremely strong competitor.

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

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

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

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

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

    We assume equal effects of crowding within types $\alpha_{11} = \alpha_{22} = \alpha_{\mathrm{intra}}$ and $N = 1/\alpha_{\mathrm{intra}}$ 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

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

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

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

569 To get some intuition for Eq. (32), suppose that a mutant arises with improved competitive
570 ability but identical intrinsic growth rate and saturation density ($r_1 = r_2$ and $\alpha_{11} = \alpha_{22}$). This
571 could represent a mutation to an interference competition trait, for example [Gill, 1974]. Then,
572 according the above condition, for N to remain constant over the sweep, the mutant must find

32

 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 $f(\overline{b}, N)$ is unchanged at the beginning and end points of an equilibrium-

 to-equilibrium b. Here we estimate the magnitude of the deviation in $f(\overline{b}, N)$ during the sweep.

For simplicity, we introduce the notation $D = N/T$ and assume that D is small. We can thus make the approximation $1 - e^{-\overline{b}D} \approx \overline{b}D$ and $f(\overline{b}, N) \approx \overline{b}(1 - D)$. 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 $f(\overline{b}, N)$ 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

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

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

585 By contrast, for a δ sweep in Eq. (10), the density-dependent term N increases by a factor

586 of $\frac{1}{1-\epsilon} = 1 + \epsilon + \epsilon^2 + \ldots$. Thus, the deviations in $f(N)$ are an order of magnitude smaller than

587 those shown in Fig. (5), and even proportional changes of order $\epsilon = 0.1$ will cause a negligible

588 deviation from the canonical selection equation.