Density-dependent selection and the limits of relative fitness

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1 Abstract

2 TBA

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 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 uncrowded populations, relative fitness simply represents differences in intrinsic 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, $\overline{W} = \sum_i W_i p_i$ 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 j and a mutant i 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

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conditions are so different, s will often depend on density and cannot be treated as a simple constant (the possible frequency-dependence of s is a separate issue, because this still leaves a closed model in terms of the frequencies). This issue is evaded 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 parameterizes the rate at which selection changes relative frequencies, but no longer corresponds to differences in intrinsic growth rates r.

Yet MacArthur famously showed 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 changes in N except in a few special cases (we return to this in section "K-selection, c-selection and relative fitness"). 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 the population ecological processes driving selection (Fig. 1b).

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 explicitly independent of population biology and thus falls outside of our scope). The first is to assume that selection is independent of density but still allow density to be affected by selection [Barton et al., 2007, pp. 468] [Prout, 1980]. While this allows us to relax the assumption of constant N, it does not address the problem that s can depend on density. In the examples from the previous paragraph, selection is density-dependent; indeed, the type-specific responses to density are at the center of MacArthur's argument and the density-dependent selection literature that grew out
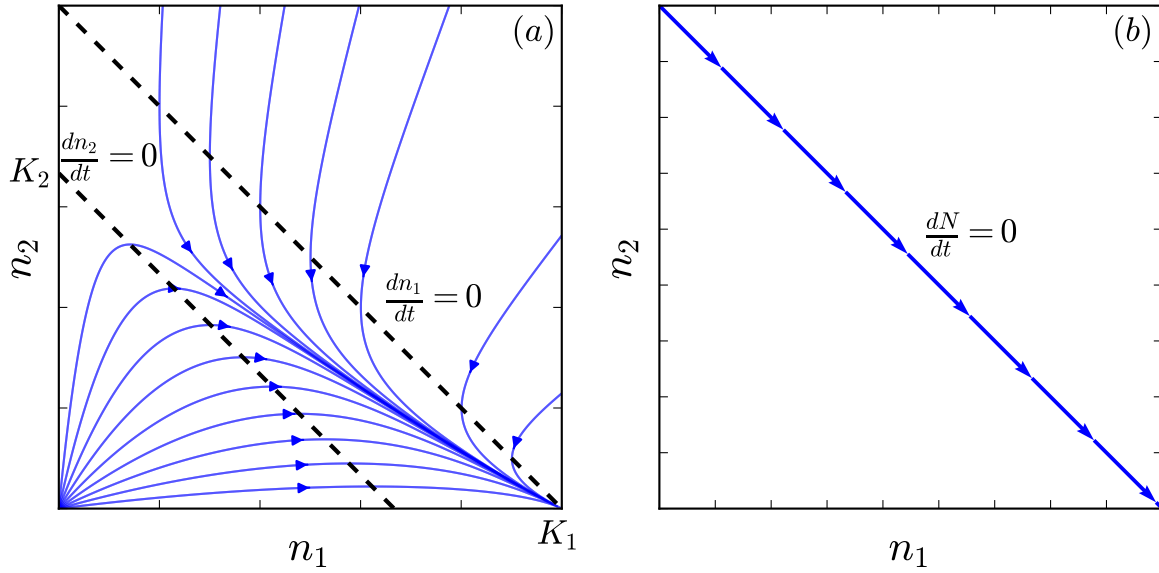
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Figure 1: Selection in crowded environments shown as a phase diagram for the densities of two types n_1 and n_2. (a) The logistic model $\frac{dn_1}{dt} = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $\frac{dn_2}{dt} = r_2(1 - \frac{n_1+n_2}{K_2})n_1$ with $r_1 = r_2$ and $K_1 > K_2$. (b) The constant-N, relative fitness description of selection.

of it [Roughgarden, 1979].

Second, constant N and s can both be seen as a short-term linear approximation [Ewens, 2004, pp. 277]. That is, within a sufficiently short time frame, N and s can be treated as constant. Provided that selection is sufficiently weak and stable over time, this "short-term" assumption is not a major restriction. Yet it is increasingly recognized that selection is not always weak, that it can fluctuate considerably 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 "short-term" restriction or the lack of integration with population ecology [Mallet, 2012]. Thus, it is important to understand the population ecological basis of relative fitness models, both to gain insight into their domain of applicability, and as part of the broader challenge of synthesizing ecology and evolution.

Another issue with the constant-N relative fitness description of selection is that it precludes

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consideration of longer-term aspects of the interplay between evolution and ecology such as population extinction. Adaptive dynamics currently provides a powerful framework for adresing the complex feedbacks between evolutionary change and population density [Diekmann et al., 2004]. However, the focus of adaptive dynamics is trait evolution rather than the underlying genetics, and in particular, selective sweeps are typically subsumed into effectively-instantaneous "trait substitutions". We emphasize that our focus here is the description of selection itself, which is particularly critical for making sense of evolution at the genetic level.

Here we analyze the population ecology of relative fitness using a novel model of density-dependent population growth based on territorial contests. Rather attempting to make sense of relative fitness in the standard models of population growth mentioned above (e.g. Mallet [2012]), we instead do the reverse, and attempt to make population ecological sense of the widely-used Wright-Fisher, constant-N, 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]. Unlike the Wright-Fisher model, generations can overlap in the lottery model. We generalize the lottery model to allow population density to vary, and show that this model can be interpreted as a density-dependent generalization of the Wright-Fisher model with overlapping generations.

We show that when this model reaches a demographic steady-state, the constant-N, relative fitness picture emerges. Futhermore, we show that our model is entirely consistent with MacArthur's analysis of selection in crowded populations. In particular, we emphasize that MacArthur's argument does not justify the widespread intuition that selection in crowded environments is necessarily connected to achieving greater densities. This is largely an artifact of the models historically used in the density-dependent selection literature, which ignore relative contests.

Our first task is to analytically extend the classic lottery model to correctly account for low density behavior (sections "Model" and "Mean field approximation"). We then...

Model

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 t advances in discrete iterations, each representing the time from birth to reproductive maturity. In iteration t, the number of adults of the i'th type is $n_i(t)$, the total number of adults is $N(t) = \sum_i n_i(t)$, and the number of unoccupied territories is $U(t) = T - N(t)$.

We assume that the n_i are large enough that stochastic fluctuations in the n_i ("drift") can be ignored. In particular, we do not evaluate the initial stochastic behaviour of mutant lineages while they are at low abundance. We derive deterministic equations for the expected change in the n_i over time, leaving the evaluation of drift for future work.

Each iteration, adults produce new offspring ("propagules"), m_i of which disperse to unoccupied territories. We assume that adults cannot be ousted from their territories, so that m_i only includes propagules landing on unoccupied territories. Propagules disperse at random over the unoccupied territories, regardless of distance from their parents, and independently of each other. There is no interaction between propagules (e.g. avoidance of territories crowded with propagules). Loss of propagules during dispersal is subsumed into m_i. We assume that each adult produces a constant number b_i of successfully dispersing propagules; the loss of propagules due to dispersal to occupied territories then implies $m_i = b_i(1 - N/T)n_i$. 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 [Bolker and Pacala, 1999, Levins and Culver, 1971, Tilman, 1994].

The number of individuals 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 approximation becomes exact when the n_i are large enough that drift in n_i can be ignored (Appendix A).
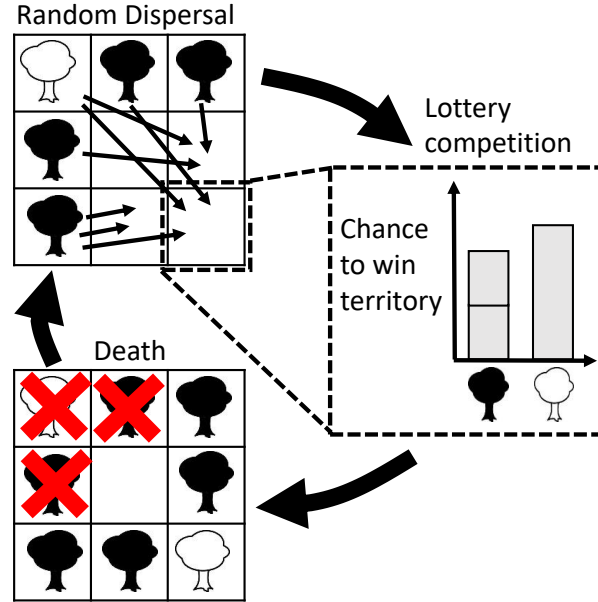
Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each unoccupied territory that receives 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).

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 T, large n_i approximation), type i's territorial acquisition is given by

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

in our extended lottery model, where the sum only includes territories with at least one propagule present.

Finally, we assume that mortality only occurs in adults (Fig. 2; setting aside the juvenile deaths implicit in territorial contest), and at a constant, type-specific per-capita rate $0 \leq d_i \leq 1$, so that the overall change in type abundances is

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

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

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by assumption), giving

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

where $\bar{c} = \sum_j c_j m_j / M$ is the mean propagule 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.

Eq. (4) 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. Instead, a rare type's propagules only make it to a few territories where at least one of its propagule present. In our extension of the classic lottery model, we correct (Eq. 3) to account for this.

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 fecundity 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 density-dependent generalization of the Wright-Fisher model.

Results

Mean-field approximation of the density-dependent 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 using a "mean field" approximation.

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

165 priate mean values, although we cannot simply replace x_i with l_i. For a type with low propagule

166 density $l_i \ll 1$, we have $x_i = 1$ in the territories where its propagules land, and so its growth

167 comes entirely from territories which deviate appreciably from l_i. To account for this, we separate

168 Eq. (2) into $x_i = 1$ and $x_i > 1$ parts. Our more general mean field approximation only requires

169 that there are no large discrepancies in competitive ability (i.e. we do not have $c_i/c_j \gg 1$ for any

170 two types). We obtain (details in Appendix B)

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

171 where

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

172 and

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

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

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

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

176 competitive victories when the i type is a rare invader in a high density population, determining

177 its invasion fitness [Metz et al., 1992]. The third term, $A_i c_i/\bar{c}$, represents competitive victories

178 when the i type is abundant. The relative importance of these three terms varies with both the

179 overall propagule density L and the relative propagule frequencies m_i/M. If $l_i \gg 1$ for all types,

180 we recover the classic lottery model (only the $A_i c_i/\bar{c}$ term remains, and $A_i \to 1/L$). Note that

181 not all unoccupied territories are claimed each iteration, since under Poisson dispersal a fraction

182 e^{-L} remain unoccupied; total population density thus obeys

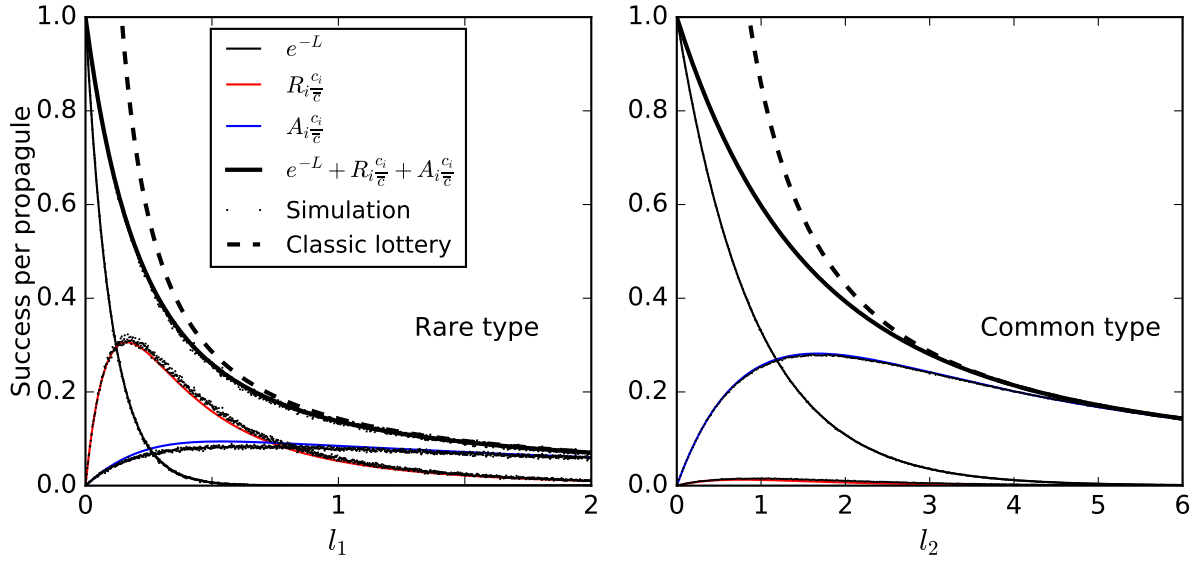$$\Delta N = (1 - e^{-L})U - \sum_i d_i n_i \tag{6}$$

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Figure 3: Comparison of mean field 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.

183   Fig. 3 shows that Eq. (5) and its components closely approximate simulations of the density-

184   dependent lottery model over a wide range of propagule densities. Two types are present, one

185   of which is at low frequency. The growth of the low-frequency type relies crucially on the low-

186   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

187   type, which depends instead on high density territorial victories. Fig. 3 also shows the break-

188   down of the classic lottery model at low propagule densities.

K-selection versus relative fitness

190   We now compare the density-dependent lottery model from the previous section with MacArthur's

191   analysis of selection in crowded environments [MacArthur and Wilson, 1967]. MacArthur con-

192   siders a population with two types that have densities n_1 and n_2 subject to density-dependent

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growth described by

$$\frac{dn_1}{dt} = f_1(n_1, n_2) \qquad \frac{dn_2}{dt} = f_2(n_1, n_2). \tag{7}$$

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

$$f_1(n_1, n_2) = r_1(1 - \alpha_{11}n_1 - \alpha_{12}n_2)n_1$$
$$f_2(n_1, n_2) = r_2(1 - \alpha_{22}n_1 - \alpha_{21}n_2)n_2 \tag{8}$$

where $\alpha_{11} = 1/K_{11}$ and $\alpha_{22} = 1/K_{22}$ measure competitive effects within each type, while $\alpha_{12} = 1/K_{12}$ and $\alpha_{21} = 1/K_{21}$ measure competitive effects on the first type due to the second (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
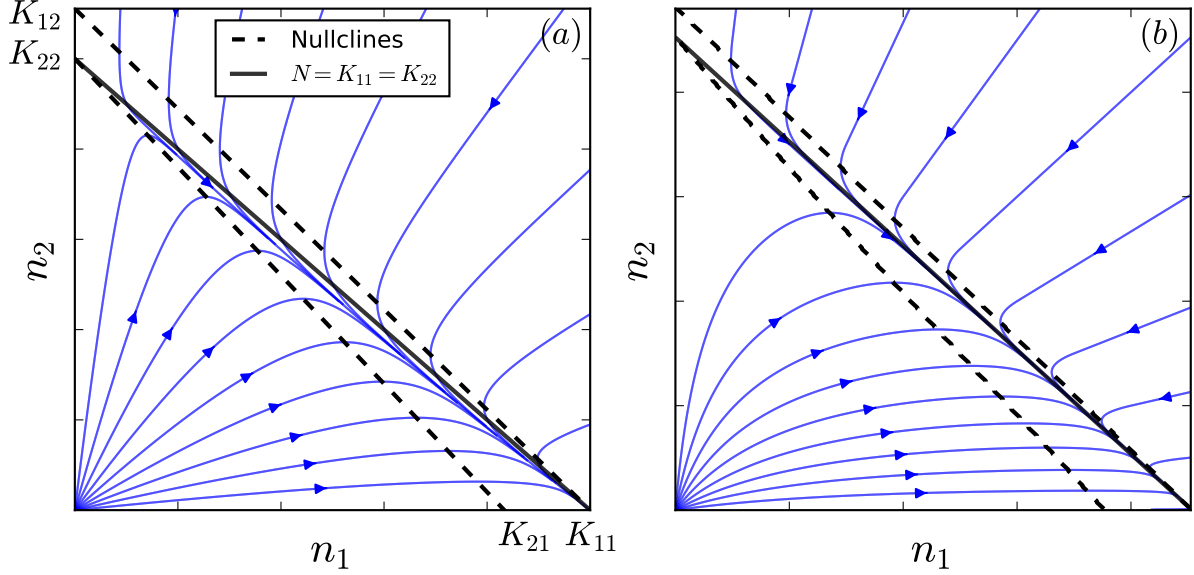
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Figure 4: Selection between types with identical saturation density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 8) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. 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 $N = K_{11} = K_{22}$.

²⁰⁷ growth of competitors at lower densities (moving the nullcline of competitors inwards) [Gill,

²⁰⁸ 1974]. This general idea applies even if the nullclines are nonlinear to such an extent that the "K"

²⁰⁹ values themselves do not give much information about the regions of high-density growth.

²¹⁰   It is obvious from Eq. (8) that selection can favor a superior competitor in a crowded popu-

²¹¹ lation even if its saturation density is the same as, or lower than that of the other types present.

²¹² However, note that the Lotka-Volterra model still closely couples selection to population density

²¹³ [Smouse, 1976]. Fig. 4a shows Lotka-Volterra selection between two types with the same satura-

²¹⁴ tion density ($\alpha_{11} > \alpha_{22}$, $\alpha_{21} > \alpha_{12}$). Even though the initial and final densities of a sweep are the

²¹⁵ same, density is not constant during a sweep. Only a highly restricted subset of r and α values

²¹⁶ will keep N constant over a selective sweep (further details in Appendix C). Intuitively, for one

²¹⁷ type to exclude another with the same saturation density, inter-type competitive effects must be

²¹⁸ stronger than intra-type competitive effects, causing a dip in N over the sweep.

²¹⁹   By contrast, if one type in our density-dependent lottery model has a c advantage but birth

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and death rates are identical, the density trajectories converge on the line of constant density equal to the saturation density Fig. 4b. Selection then occurs purely along this line, uncoupled from the density regulation of N. In other words, once the population reaches demographic equilibrium, it behaves indistinguishably from a constant-N relative fitness model. More generally, the competitive ability trait c does not directly affect population density (this can be seen formally in Eq. (6)), since c only affects which type wins a territory, not whether a territory is won at all. This is all perfectly consistent with MacArthur's general argument.

Density-dependent selection and the strength of selection

We are now in a position to analyze the validity of Eq. (1) more explicitly. In the previous section we showed that selection and the regulation of population density can be completely independent of each other even if population growth is density-regulated, and moreover that MacArthur's argument for the r/K scheme never precluded this possibility. Nevertheless, selection and density regulation *are* intimately connected in widely used models of population growth. To understand why this poses a problem for Eq. (1), consider the simple birth-death model [Kostitzin, 1939, pp. 20]

$$\frac{dn_i}{dt} = (b_i - \delta_i N)n_i \tag{9}$$

where δ_i is the per-capita increase in type i's mortality rate due to crowding (for simplicity, there are no deaths when uncrowded). Then, starting from a monomorphic population, the frequency of an adaptive δ-variant $\delta_i \to \delta_i(1 - \epsilon)$ obeys

$$\frac{dp_i}{dt} = \epsilon \delta_i N p_i(1 - p_i). \tag{10}$$

The selection coefficient $s = \epsilon \delta_i N$ thus depends on density (compare [Crow et al., 1970, pp. 29]). On the other hand, the frequency of an adaptive b-variant $b_i \to b_i(1 + \epsilon)$ will exactly obey Eq. (1) with $s = \epsilon b_i$, independent of density.

In practice the density dependence in Eq. (10) only matters if N changes substantially during
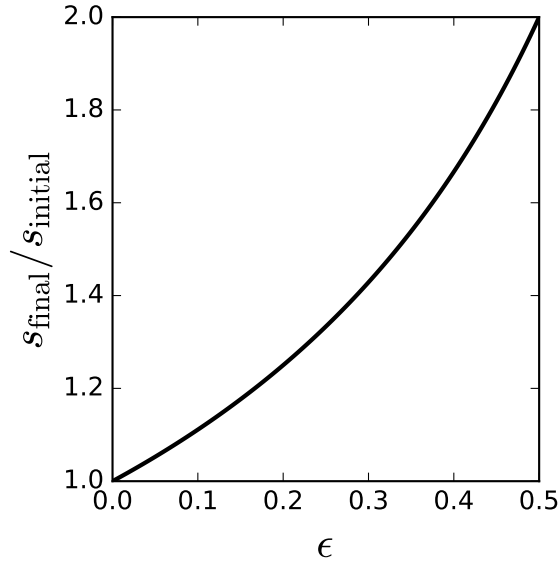
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Figure 5: Proportional change in the selection coefficient over a "*K*-selection"-type sweep for a type that experiences proportionally $1 - \epsilon$ fewer deaths induced by crowding. The population is in demographic equilibrium at the start of the sweep.

242 a sweep. This can easily occur if a population is far from demographic equilibrium (we return

243 to this scenario in the Discussion). A more serious objection to Eq. (1) is that it is internally

244 inconsistent even in crowded populations where N has reached equilibrium, because adaptive

245 sweeps in density-dependent traits then induce a change in N and also change themselves in

246 response to N. To quantify how serious this objection is, we need to account for how much

247 N changes over a sweep. In Eq. (9), the saturation density is $N = b_i/\delta_i$, and so the selection

248 coefficient increases from s_{initial} to $s_{\text{final}} = s_{\text{initial}}/(1 - \epsilon)$ over a sweep (Fig. 5). Thus, Eq. (1)

249 breaks down if selection is sufficiently strong on the density-dependent mortality rate, with

250 proportional effects of $\epsilon > 0.2$ inducing substantial deviations from constant selection.

251 Let us now contrast the simple linearly density-dependent model Eq. (10) with our density-

252 dependent lottery. As we have seen in our lottery model, the importance of c depends on density,

253 yet since c has no effect on density, s is exactly constant for c sweeps. For b and d sweeps, s is

254 also exactly consant, because the overall regulation of population density applies equally to all

255 types [Prout, 1980]. To see this formally, we set c_i to be the same for all types in Eq. (5) which

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yields

$$\Delta n_i = \frac{m_i}{M}(1 - e^{-L})U - d_i n_i = \left(b_i \frac{1 - e^{-L}}{L} - d_i \right) n_i. \tag{11}$$

Thus, the density-regulation of population size occurs via the juvenile recruitment fraction $(1 - e^{L})/L$. This applies uniformly to all types and therefore does not induce density-dependence in selective advantages related to b or d. Note that our lottery model accounts for two key aspects of the interaction between selection and demography: selection is density-dependent, and density will change as a result of selection on absolute fitness traits. And yet pure b, c and d sweeps all obey Eq. (1) exactly.

Discussion

It is widely recognized that the evolutionary description of selection is poorly integrated with the ecological literature on population growth [Mallet, 2012]. Typically this is cast as a narrow focus on frequencies on the part of evolutionary geneticists, who, perhaps out of necessity, omit the complexities of population ecology. While there may be some truth to this, we argue that part of the reason for the disconnect between the evolutionary geneticist's selection and the ecologist's selection is that relative fitness models actually contain important ecological processes omitted in many ecological models, including the classical Lotka-Volterra and logistic models. To illustrate, we highlight two important properties of our extended lottery model.

First, our lottery model contains a "reproductive excess" [any good suggestions for citations here, Joanna?] that allows selection (and competition) to occur among juveniles without affecting population density at the adult stage. This excess appears when the number of propagules produced is greater than the number of available territories. By contrast, in classical ecological growth models only one life-history stage is represented and selection is intrinsically connected to the effects of each type's adult density on the other. These are restrictive assumptions — it is often the case that competition and selection are concentrated at the more fragile juvenile stage [Chesson, 1983]. Reproductive excesses tend to produce strictly-relative lottery-type contests in

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²⁸⁰ which fitter types can grow at the expense of others by preferentially filling the available adult

²⁸¹ "slots". The number of slots can remain fixed or change independently of the large amount of

²⁸² selection occurring at the juvenile stage. Reproductive excesses expand the domain of validity of

²⁸³ Eq. (1) by facilitating selection-independent density [Prout, 1980].

²⁸⁴ Second, density is regulated by fecundity b and mortality d traits that are affected equally

²⁸⁵ by density. There are only so many territories, and all territories are equally available to all

²⁸⁶ types. This removes the density-dependence that would make selection on b and d exhibit the

²⁸⁷ difficulties shown in Fig. 5 without removing density-dependent selection from the model as

²⁸⁸ whole via c (by contrast, [Barton et al., 2007, pp. 468] allows density to depend on selection but

²⁸⁹ removes density-dependent selection entirely). Although standard ecological models do have

²⁹⁰ type-specific regulation of density (setting aside special parameter choices [Mallet, 2012]), it is

²⁹¹ not obvious that we should expect this as a general rule. Much of our intuition about type-

²⁹² specific regulation of density (and density-dependent selection in general) is grounded in the

²⁹³ logistic model and its diploid bi-allelic variants [Roughgarden, 1979], which should hardly be

²⁹⁴ regarded as universal [Christiansen, 2004, Mallet, 2012]. Consumable resource models are a

²⁹⁵ better guide, because they explicitly model the processes underlying an important form of com-

²⁹⁶ petition. Density regulation is type-specific in well-mixed resource competition models, but for

²⁹⁷ many populations consumable resources are not well-mixed. Spatial localization of consumable

²⁹⁸ resources (e.g. due to restricted movement of nutrients through soils) will tend to create a terri-

²⁹⁹ torial situation similar to the lottery model, where resource competition only occurs locally and

³⁰⁰ is subsumed into the competitive ability c. Density regulation will then apply at the population

³⁰¹ level similarly to the lottery model, allowing N to change via b or d without affecting Eq. (1).

³⁰² Relative fitness breaks down if strong selection occurs in a way that changes population

³⁰³ density and is also density-dependent (Fig. 5). In our lottery model, the latter can only occur if

³⁰⁴ types differ in c as well as b or d. The reason for this is that density-dependent (c) and density-

³⁰⁵ determining traits (b and d) are completely separate.

³⁰⁶ It is interesting to compare this separation of traits with the r/K scheme, often presented as a

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dichotomy between r-selection (uncrowded) and K-selection (crowded), with the latter taken to mean selection for greater saturation density (e.g. [Gill, 1974]). As we have seen, MacArthur's argument does not justify this dichotomy at all. A better dichotomy is between interaction-dependent selection and interaction-independent selection. That is, selective shifts in frequency are a result of differences in absolute growth rates, but these differences can arise in two logically distinct ways: i) some types expand more rapidly in the absence of interactions between individuals or ii) some types are superior in their interactions with other types. In our the lottery model, b and d are interaction-independent traits (both within and between types), whereas c is entirely about interactions between types. This logical distinction captures the essence of crowding, namely that crowding forces you to displace others in order to grow. Composite parameters like K and R^* conflate the regulation of density (factors which cause density trajectories to move "outwards" in Fig. 1a) with interaction-dependent displacement (factors which cause density trajectories to move diagonally in Fig. 1b).

Relative fitness models truly breaks down if N is far from equilibrium and selection is density-dependent. For example, wild *Drosophila* experience huge 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. Our density-dependent lottery model may not be a particularly good description of *Drosophila* ecology, but the close connection between our model and Wright-Fisher is particularly 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 from-from-equilibrium situations.

Acknowledgments

References

NK Arenbaev. Asymptotic behavior of the multinomial distribution. *Theory of Probability & Its Applications*, 21(4):805–810, 1977.

NH Barton, DEG Briggs, JA Eisen, DB Goldstein, and NH Patel. *Evolution*. NY: Cold Spring Harbor Laboratory Press, 2007.

TG Benton and A Grant. Evolutionary fitness in ecology: comparing measures of fitness in stochastic, density-dependent environments. *Evolutionary ecology research*, 2(6):769–789, 2000.

Alan O. Bergland, Emily L. Behrman, Katherine R. O'Brien, Paul S. Schmidt, and Dmitri A. Petrov. Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in drosophila. *PLOS Genetics*, 10(11):1–19, 11 2014. doi: 10.1371/journal.pgen.1004775.

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

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

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

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

James F Crow, Motoo Kimura, et al. An introduction to population genetics theory. *An introduction to population genetics theory.*, 1970.

Odo Diekmann et al. A beginner's guide to adaptive dynamics. *Banach Center Publications*, 63: 47–86, 2004.

Michael Doebeli, Yaroslav Ispolatov, and Burt Simon. Towards a mechanistic foundation of evolutionary theory. *eLife*, 6:e23804, feb 2017. ISSN 2050-084X. doi: 10.7554/eLife.23804.

Warren J Ewens. *Mathematical Population Genetics 1: Theoretical Introduction*. Springer Science & Business Media, 2004.

Douglas E Gill. Intrinsic rate of increase, saturation density, and competitive ability. ii. the evolution of competitive ability. *American Naturalist*, 108:103–116, 1974.

James P Grover. *Resource competition*, volume 19. Springer Science & Business Media, 1997.

Vladimir Alexandrovitch Kostitzin. *Mathematical biology*. George G. Harrap And Company Ltd.; London, 1939.

Richard Levins and David Culver. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences*, 68(6):1246–1248, 1971.

Robert H MacArthur and Edward O Wilson. *Theory of Island Biogeography*. Princeton University Press, 1967.

James Mallet. The struggle for existence. how the notion of carrying capacity, k, obscures the links between demography, darwinian evolution and speciation. 2012.

Philipp W Messer, Stephen P Ellner, and Nelson G Hairston. Can population genetics adapt to rapid evolution? *Trends in Genetics*, 32(7):408–418, 2016.

C. Jessica E. Metcalf and Samuel Pavard. Why evolutionary biologists should be demographers. *Trends in Ecology and Evolution*, 22(4):205 – 212, 2007. ISSN 0169-5347. doi: https://doi.org/10.1016/j.tree.2006.12.001.

Johan AJ Metz, Roger M Nisbet, and Stefan AH Geritz. How should we define 'fitness' for general ecological scenarios? *Trends in Ecology & Evolution*, 7(6):198–202, 1992.

376 Timothy Prout. Some relationships between density-independent selection and density-
377 dependent population growth. *Evol. Biol*, 13:1–68, 1980.

378 Jonathan Roughgarden. Theory of population genetics and evolutionary ecology: an introduc-
379 tion. 1979.

380 Peter F. Sale. Maintenance of high diversity in coral reef fish communities. *The American Natural-
381 ist*, 111(978):337–359, 1977.

382 Peter E Smouse. The implications of density-dependent population growth for frequency-and
383 density-dependent selection. *The American Naturalist*, 110(975):849–860, 1976.

384 Hannes Svardal, Claus Rueffler, and Joachim Hermisson. A general condition for adaptive genetic
385 polymorphism in temporally and spatially heterogeneous environments. *Theoretical Population
386 Biology*, 99:76 – 97, 2015. ISSN 0040-5809. doi: http://dx.doi.org/10.1016/j.tpb.2014.11.002.

387 David Tilman. Competition and biodiversity in spatially structured habitats. *Ecology*, 75(1):2–16,
388 1994.

389 Günter P Wagner. The measurement theory of fitness. *Evolution*, 64(5):1358–1376, 2010.

Appendix A: Poisson approximation

391 For simplicity of presentation, we have assumed a Poisson distribution for the x_i as our model
392 of dispersal. Strictly speaking, the total number of i propagules $\sum x_i$ (summed over unoccupied
393 territories) is then no longer a constant m_i, but fluctuates between generations for a given mean
394 m_i, which is more biologically realistic. Nevertheless, since we do not consider the random fluc-
395 tuations in type abundances here, and for ease of comparison with the classic lottery model, we
396 ignore the fluctuations in m_i. Instead we focus, on Poisson fluctuations in propagule composition
397 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).

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

$$\Delta_u n_i = U l_i e^{-L} = m_i e^{-L}. \tag{12}$$

23

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

$$\Delta_r n_i = m_i e^{-l_i}(1 - e^{-(L-l_i)}) \left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}},$$ (13)

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. (13),

$$\left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}} \approx \frac{c_i}{c_i + \sum_{j \neq i} c_j \langle x_j \rangle_{\tilde{p}}}.$$ (14)

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 $\langle \sum_{j \neq i} c_j x_j \rangle_{\tilde{p}}$.

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

$$\begin{aligned}
\tilde{p}(\mathbf{x}_i) &= p(\mathbf{x}_i | X \geq 2, x_i = 1) \\
&= \frac{P(\mathbf{x}_i, X \geq 2 | x_i = 1)}{P(X \geq 2)} \\
&= \frac{1}{1 - (1+L)e^{-L}} \sum_{X=2}^{\infty} P(X) p(\mathbf{x}_i | X_i = X - 1),
\end{aligned}$$ (15)

and so

$$\langle x_j \rangle_{\tilde{p}} = \sum_{\mathbf{x}_i} \tilde{p}(\mathbf{x}_i) x_j$$

$$= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - 1) x_j. \qquad (16)$$

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,

$$\langle x_j \rangle_{\tilde{p}} = \frac{l_j}{1 - (1+L)e^{-L}} \frac{1}{L - l_i} \sum_{k=2}^{\infty} P(X)(X-1)$$

$$= \frac{l_j}{1 - (1+L)e^{-L}} \frac{L - 1 + e^{-L}}{L - l_i}, \qquad (17)$$

430 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 - $

431 $\sum_{X=1}^{\infty} P(X)$.

The exact analysis of the fluctuations in $\sum_{j \neq i} c_j x_j$ is complicated because the x_j are not independent 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 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 $\langle x_j \rangle_{\tilde{q}} = \langle x_j \rangle_p / C = l_j / C$,

$$\begin{aligned}
\sigma_{\tilde{q}}^2(x_j) &= \langle x_j^2 \rangle_{\tilde{q}} - \langle x_j \rangle_{\tilde{q}}^2 \\
&= \frac{1}{C} \langle x_j^2 \rangle_p - \frac{l_j^2}{C^2} \\
&= \frac{1}{C}(l_j^2 + l_j) - \frac{l_j^2}{C^2} \\
&= \frac{l_j^2}{C}\left(1 - \frac{1}{C}\right) + \frac{l_j}{C},
\end{aligned} \tag{18}$$

and

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

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

The exact distribution $\tilde{p}$ assumes that exactly one of the propagules present in a given site after dispersal belongs to the focal type, whereas $\tilde{q}$ assumes that there is a focal propagule present before non-focal dispersal commences. As a result, $\tilde{q}$ predicts that the mean propagule density is greater than L (in sites with only one focal propagule is present) when the focal type is rare and the propagule density is high. This is erroneous, because the mean number of propagules in every site is L by definition. Specifically, if $L - l_i \approx L \gg 1$, then the mean propagule density predicted by $\tilde{q}$ is approximately $L + 1$. The discrepancy causes rare invaders to have an intrinsic rarity disadvantage (territorial contests under $\tilde{q}$ are more intense than they should be). In contrast, Eq. (17) 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 covariences, $\tilde{q}$ 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

26

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

446 $\tilde{q}$ is comparable to, or greater than, the entire propgaule density.

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

$$\sigma_{\tilde{q}}^2\left(\sum_{j \neq i} c_j x_j\right) = \sum_{j \neq i}\left[c_j^2 \sigma_{\tilde{q}}^2(x_j) + 2 \sum_{k>j, k \neq i} c_j c_k \sigma_{\tilde{q}}(x_j, x_k)\right], \tag{20}$$

448 and using the fact that $\sigma_{\tilde{q}}(x_j, x_k)$ and the first term in Eq. (18) are negative because $C < 1$, we

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

$$\frac{\sigma\left(\sum_{j \neq i} c_j x_j\right)}{\left\langle\sum_{j \neq i} c_j x_j\right\rangle} = C^{1/2} \frac{\left(\sum_{j \neq i} c_j^2 l_j + (1 - 1/C)\left(\sum_{j \neq i} c_j l_j\right)^2\right)^{1/2}}{\sum_{j \neq i} c_j l_j} < C^{1/2} \frac{\left(\sum_{j \neq i} c_j^2 l_j\right)^{1/2}}{\sum_{j \neq i} c_j l_j}. \tag{21}$$

450   Suppose that the c_j are all of similar magnitude (their ratios are of order one). Then Eq. (21)

451 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

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

453 The worst case scenario occurs when $L - l_i$ is of order one. Then Eq. (21) gives a relative error of

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

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

456 small.

457   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

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

459 for all other nonfocal types j', and $l_j \ll 1$), then the RHS of Eq. (21) can be large and we cannot

460 make the replacement Eq. (14).

461   Substituting Eqs. (14) and (17) into Eq. (13), we obtain

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{\bar{c}}, \tag{22}$$

462 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. (13), we have

$$\Delta_a n_i = U(1 - (1 + l_i)e^{l_i}) \left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \tag{23}$$

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,

$$\left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \approx \frac{c_i \langle x_i \rangle_{\hat{p}}}{\sum_j c_j \langle x_j \rangle_{\hat{p}}}. \tag{24}$$

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,

$$\begin{aligned}
\langle x_i \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_i p(\mathbf{x}|x_i \geq 2) \\
&= \sum_{x_i} x_i p(x_i|x_i \geq 2) \\
&= \frac{1}{1 - (1 + l_i)e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i \\
&= l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}}.
\end{aligned} \tag{25}$$

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

$$
\begin{aligned}
\langle x_j \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_j p(\mathbf{x}|x_i \geq 2) \\
&= \sum_X P(X|x_i \geq 2) \sum_{\mathbf{x}} x_j p(\mathbf{x}|x_i \geq 2, X) \\
&= \sum_X P(X|x_i \geq 2) \sum_{x_i} p(x_i|x_i \geq 2, X) \sum_{\mathbf{x}_i} x_j p(\mathbf{x}_i|X_i = X - x_i) \\
&= \sum_X P(X|x_i \geq 2) \sum_{x_i} p(x_i|x_i \geq 2, X) \frac{l_j(X - x_i)}{L - l_i} \\
&= \frac{l_j}{L - l_i} \left[\sum_X P(X|x_i \geq 2) X - \sum_{x_i} p(x_i|x_i \geq 2) x_i \right] \\
&= \frac{l_j}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}} \right).
\end{aligned}
\tag{26}
$$

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

$$
\sigma_{\hat{q}}^2(x_i) = \frac{l_i}{D} \left(l_i + 1 - e^{-l_i} - \frac{l_i}{D} \left(1 - e^{-l_i} \right)^2 \right),
\tag{27}
$$

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

$$
\frac{\sigma_{\hat{q}}(\sum c_j x_j)}{\langle \sum c_j x_j \rangle} = \frac{\left(\sum_{j \neq i} c_j^2 l_j + c_i^2 \sigma_{\hat{q}}^2(x_i) \right)^{1/2}}{\sum_{j \neq i} c_j l_j + c_i l_i (1 - e^{-l_i})/D}.
\tag{28}
$$

Similarly to Eq. (21), the RHS of Eq. (28) 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. (28) is around 35%, which is again where the $\hat{q}$ approximation produces the biggest overestimate of the fluctuations in $\mathbf{x}$. Similarly

to Eq. (21), the RHS of (28) will not be $\ll 1$ in the presence of a rare, extremely strong competitor.

Combining Eqs. (23) and (24), we obtain

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \tag{29}$$

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.

We assume $\alpha_{11} = \alpha_{22}$ and $N = 1/\alpha_{11}$ 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. (8), we obtain

$$\begin{aligned}
\frac{dn_1}{dt} &= -r_1(\alpha_{12} - \alpha_{11})n_1 n_2 \\
\frac{dn_2}{dt} &= -r_2(\alpha_{21} - \alpha_{22})n_1 n_2
\end{aligned} \tag{30}$$

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

$$r_1(\alpha_{12} - \alpha_{11}) + r_2(\alpha_{21} - \alpha_{22}) = 0. \tag{31}$$

To get some intuition for Eq. (31), 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. This condition, and Eq. (31) more generally, are so restrictive

494   that we can conclude that selective sweeps in the Lotka-Volterra competition model will generally

495   involve non-constant N.