Density-dependent selection and the limits of relative fitness

Abstract

new model of density-dependent selection by generalizing the fixed-density classic lottery model of territorial acquisition to accommodate arbitrary population densities.

We show that, with density dependence, co-existence is possible in the lottery model in a stable environment.

Inspired by natural *Drosophila* populations, we consider co-existence under strong, seasonally-fluctuating selection coupled to large cycles in population density, and show that co-existence (stable polymorphism) is promoted via a combination of the classic storage effect and density-regulated population growth.

Introduction

11   There are a variety of different measures of fitness. Some widely used examples in evolutionary

12   ecology are expected lifetime reproductive ratio R_0, intrinsic growth rate r, saturation population

13   density (often labeled "K") [Benton and Grant, 2000], and invasion fitness [Metz et al., 1992]. In

14   addition, "relative fitness" is the standard in much of evolutionary biology, particularly evolu-

15   tionary genetics, where attention is generally restricted to relative genotypic proportions [Barton

16   et al., 2007, pp. 468]. The variety of fitness measures is not problematic in itself, because different

17   measures may be more useful in different circumstances. But it should be clear how the measure

18   being used is connected to the processes of birth and death which govern population biology

19   [Doebeli et al., 2017, Metcalf and Pavard, 2007]. While such a connection is fairly clear for abso-

20   lute fitness measures like r, relative fitness seems largely divorced from population biology. It

21   has even been proposed that relative fitness be justified from more abstract measure-theoretical

22   arguments, abandoning population biology altogether [Wagner, 2010].

23   In uncrowded populations, relative fitness simply represents differences in intrinsic growth

24   rate. In continuous time, we have the canonical selection equation $\frac{dp_i}{dt} = (r_i - \bar{r})p_i$, where r_i is the

25   intrinsic exponential growth rate of type i, p_i is its frequency, and $\bar{r} = \sum_i r_i p_i$ is the population

26   mean r [Crow et al., 1970, pp. 26]. If there are two types present, a wildtype and a mutant for

27   instance, then Eq. (1) can be written as

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

28   where the constant selection coefficient s is the difference in r between types. The corresponding

29   adaptive sweeps follow a logistic curve.

30   The difficulty with Eq. (1) arises in crowded populations. It is then commonly assumed that

31   total population density N has reached its equilibrium value, which is assumed to be a fixed

32   constant. This is exemplified by the Wright-Fisher model. Yet MacArthur famously showed that

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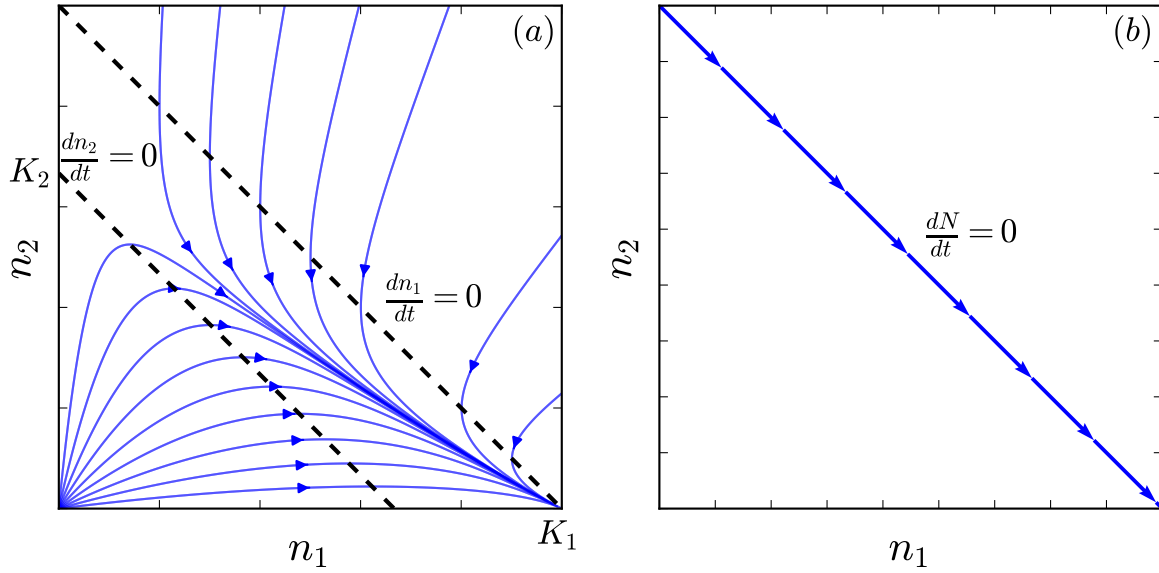
Figure 1: Selection in crowded environments shown as a phase diagram for the densities of two types n_1 and n_2. (a) The logistic model $\frac{dn_1}{dt} = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $\frac{dn_2}{dt} = r_2(1 - \frac{n_1+n_2}{K_2})n_1$ with $r_1 = r_2$ and $K_1 > K_2$. (b) The constant-N, relative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

nected 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. 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 population ecological processes occurring in nature and experiments.

The relative fitness description has been justified in broadly two different ways for crowded populations (we do not address Wagner's [2010] measure theorical justification, which explicitly

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seeks to be independent of population biology and thus falls outside of our scope). First, if we only care about type frequencies, we can sometimes simply ignore N [Barton et al., 2007, pp. 468], because Eq. (1) is unaffected by changes in N if the mechanism regulating density applies equally to all types [Prout, 1980]. Yet, while this does allow us to relax the restrictive assumption of constant N, it does not address the assumption of constant s. In the examples from the previous paragraph, different types *are* affected by the regulation of density in different ways; indeed, the type-specific responses to density are at the center of MacArthur's argument and the literature on density-dependent selection that grew out of it.

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 [Crow et al., 1970, PAGE NUMBER]. Yet it is increasingly recognized that selection is not always weak, that it can fluctuate considerably over time [Messer et al., 2016], and that N can vary by orders of magnitude over a few generations as a routine feature of a population's ecology 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 like Wright-Fisher are the foundation for much of the population genetic literature, and are still widely used without considering the "short-term" restriction or the gulf with population ecology [Mallet, 2012]. Thus, it is important that we deepen our understanding of 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.

Here we introduce a novel model of density-dependent population growth based on territorial contests, and show that when this model reaches a demographic steady-state, the constant-N, relative fitness picture emerges. Our model is firmly grounded in population ecology, with fundamental parameters given by birth and death rates, and competitive ability. We show that this model can also be interpreted as a density-dependent generalization of the Wright-Fisher model with overlapping generations.

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 [Anderson, 1971]. This is largely an artifact of the models historically used in the density-dependent selection literature, which ignore relative contests.

Our model is essentially a density-dependent generalization of the classic ecological lottery model Chesson and Warner [1981]. In the lottery model, mature individuals ("adults") each require their own territory, whereas newborn individuals ("propagules") disperse to, and subsequently compete for, territories made available by the death of adults. Territorial contest among propagules leaves a single victorious adult per territory, the victor chosen at random from the propagules present, with probabilities weighted by a coefficient for each type representing competitive ability, akin to a weighted lottery [Sale, 1977].

The classic lottery model assumes a saturated population with constant N, and a large number of propagules dispersing to each territory (the Wright-Fisher model makes a similar "infinite propagule" assumption to justify sampling with replacement). As such, the lottery model breaks down at low densities (few propagules dispersing to each territory). 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

Basic assumptions

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 $U(t) = T - N(t)$.
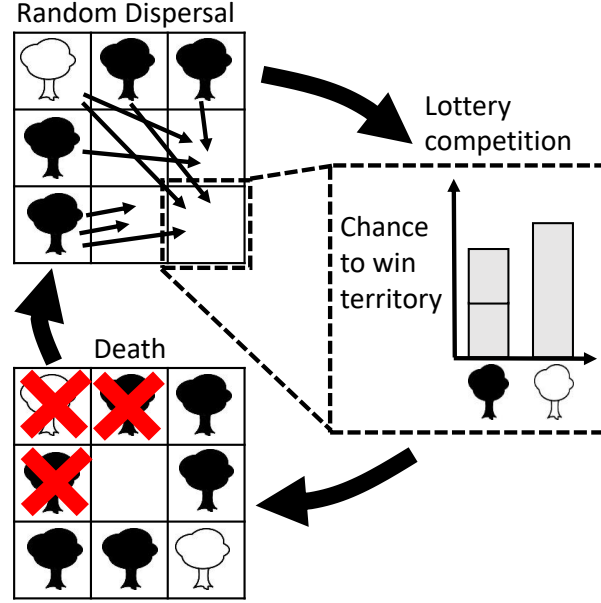
Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each unoccupied territory that receives 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).

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 propag-

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ules 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).

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 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

155 our extension of the classic lottery model to arbitrary densities represents a density-dependent
156 generalization of the Wright-Fisher model.

Results

Mean-field approximation of the density-dependent lottery

159 Eq. (2) involves an expectation over the time-dependent dispersal distributions p_i, and is thus
160 too complicated to give intuition about the dynamics of density-dependent lottery competition.
161 We now evaluate this expectation using a "mean field" approximation.

162   Similarly to the high-l_i approximation of classic lottery model, we replace the x_i with appro-
163 priate mean values, although we cannot simply replace x_i with l_i. For a type with low propagule
164 density $l_i \ll 1$, we have $x_i = 1$ in the territories where its propagules land, and so its growth
165 comes entirely from territories which deviate appreciably from l_i. To account for this, we separate
166 Eq. (2) into $x_i = 1$ and $x_i > 1$ parts. Our more general mean field approximation only requires
167 that there are no large discrepancies in competitive ability (i.e. we do not have $c_i/c_j \gg 1$ for any
168 two types). We obtain (details in Appendix B)

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

169 where

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

170 and

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

171   Comparing Eq. (5) to Eq. (4), the classic lottery per-propagule success rate $c_i/\bar{c}L$ has been
172 replaced by three separate terms. The first, e^{-L}, accounts for propagules which land alone on
173 unoccupied territories; these territories are won without contest. The second, $R_i c_i/\bar{c}$ represents

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competitive victories when the i type is a rare invader in a high density population, determining
its 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 m_i/M. If $l_i \gg 1$ for all types,
we recover the classic lottery model (only the $A_i c_i / \bar{c}$ term remains, and $A_i \rightarrow 1/L$). Note that
not all unoccupied territories are claimed each iteration, since under Poisson dispersal a fraction
e^{-L} remain unoccupied; total population density thus obeys

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

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.

K-selection versus relative fitness

We now compare the density-dependent lottery model from the previous section with MacArthur's
analysis of selection in crowded environments [MacArthur and Wilson, 1967]. MacArthur con-
siders a population with two types that have densities n_1 and n_2 subject to density-dependent
growth described by

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

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
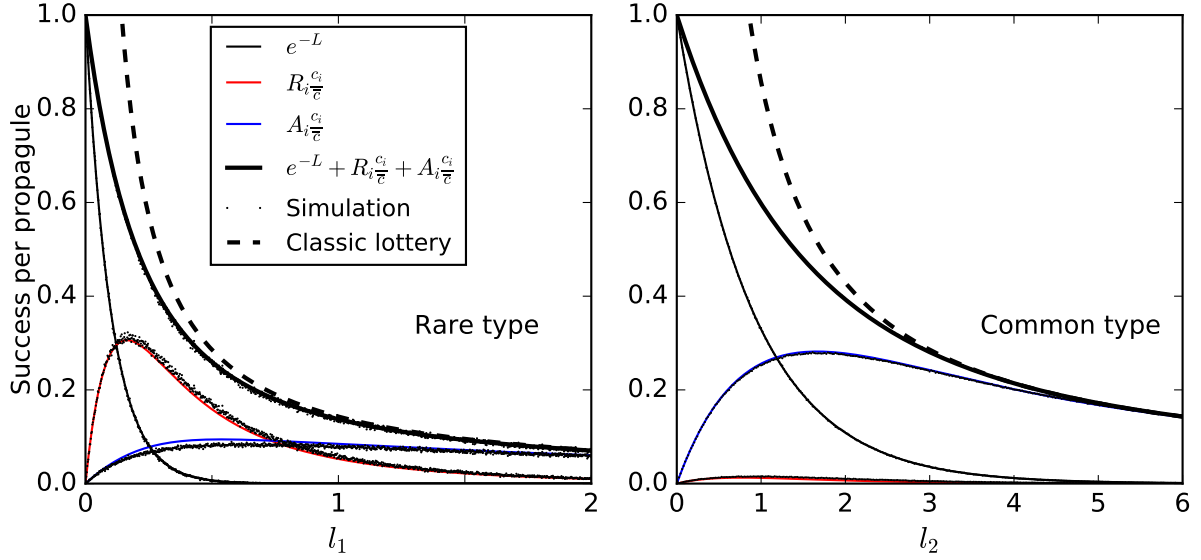outcome of selection is then determined by the relationship between these nullclines. Specifically,

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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.

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 growth of competitors at lower densities (moving the nullcline of competitors inwards) [Gill, 1974]. This general idea applies even if the nullclines are nonlinear to such an extent that the "K" values themselves do not give much information about the regions of high-density growth.

It is obvious from Eq. (8) that selection can favor a superior competitor in a crowded population even if its saturation density is the same as, or lower than that of the other types present. However, note that the Lotka-Volterra model still closely couples selection to population den-
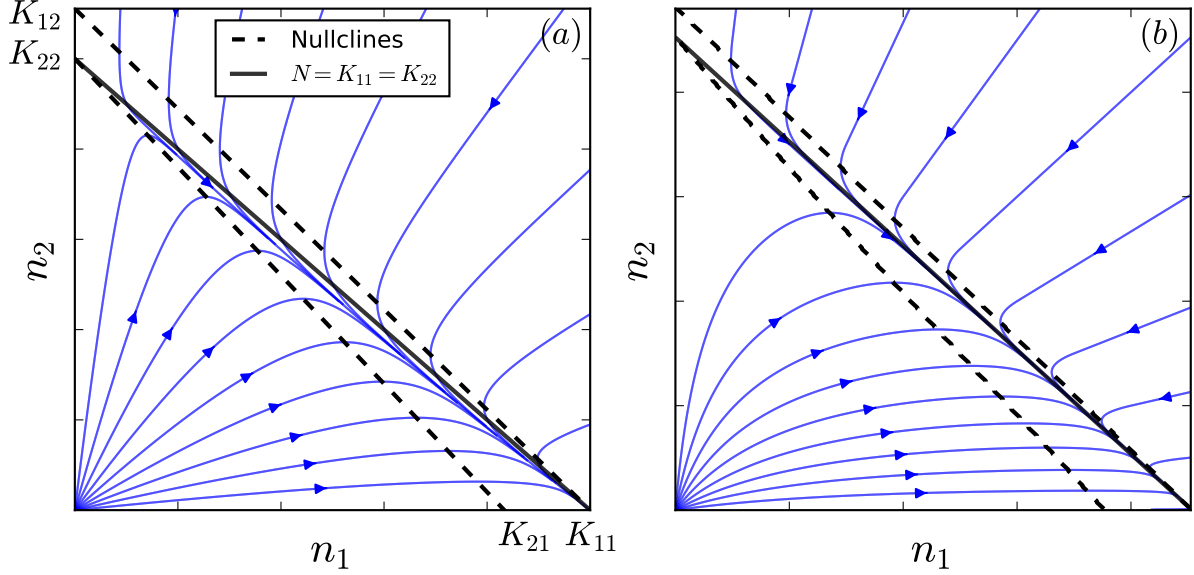
Figure 4: Selection between types with identical saturation density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 8) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. Trajectories do not follow the line $N = K_{11} = K_{22}$. (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 $N = K_{11} = K_{22}$.

sity. Fig. 4a shows Lotka-Volterra selection between two types with the same saturation density ($\alpha_{11} > \alpha_{22}$, $\alpha_{21} > \alpha_{12}$). Even though the initial and final densities of a sweep are the same, density is not constant during 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, inter-type competitive effects must be stronger than intra-type competitive effects, causing a dip in N over the sweep.

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

Type-specific responses to density and the strength of selection

We are now in a position to analyze the validity of relative fitness models 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 a sweep. This can easily occur if a population is far from demographic equilibrium (we return to this scenario in the Discussion). A more serious objection to Eq. (1) is that it is internally inconsistent even in crowded populations where N has reached equilibrium, because adaptive sweeps in density-dependent traits then induce a change in N and also change themselves in response to N. To quantify how serious this objection is, we need to account for how much
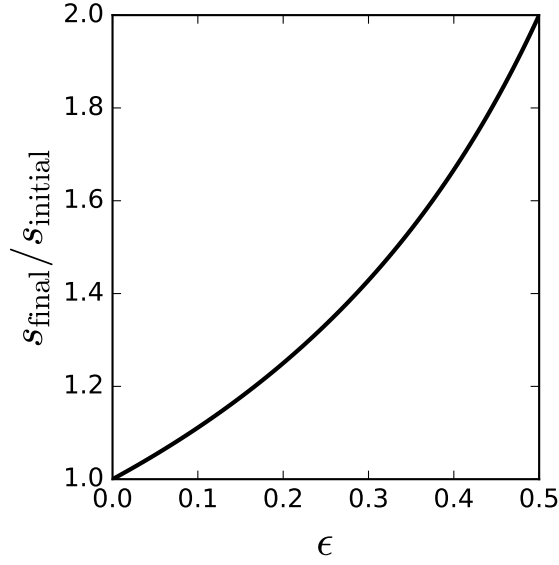
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Figure 5: Proportional change in the selection coefficient over a "K-selection"-type sweep for a type that experiences proportionally $1 - \epsilon$ fewer deaths induced by crowding. The population is in demographic equilibrium at the start of the sweep.

N changes over a sweep. In Eq. (9), the saturation density is $N = b_i/\delta_i$, and so the selection coefficient increases from s_{initial} to $s_{\text{final}} = s_{\text{initial}}/(1 - \epsilon)$ over a sweep (Fig. 5). Thus, Eq. (1) breaks down if selection is sufficiently strong on the density-dependent mortality rate, with proportional effects of $\epsilon > 0.2$ inducing substantial deviations from constant selection.

Let us now contrast the simple linearly density-dependent model Eq. (10) with our density-dependent lottery. As we have seen in our lottery model, the importance of c depends on density, yet since c has no effect on density, s is exactly constant for c sweeps. For b and d sweeps, s is also exactly consant, because the overall regulation of population density applies equally to all types [Prout, 1980]. To see this formally, we set c_i to be the same for all types in Eq. (5) which 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

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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.

The reason that our lottery model behaves so differently from Eq. (9) is that each type can respond differently to density via *c* without affecting the regulation of population density. That is, our lottery model separates density-dependent selection from "selection-dependent density" [Prout, 1980], two distinct effects that are conflated in simple growth models with linearly-density-dependent per-capita growth rates. If types in the lottery model differ in *c* as well as *b* or *d*, then the lottery model will exhibit similar complications as Fig. 5.

Discussion

It is important to recognize that MacArthur's argument does not imply a dichotomy between *r*-selection (uncrowded) and *K*-selection (crowded), with the latter taken to mean selection for greater saturation density. 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: 1) some types expand more rapidly in the absence of interactions between individuals or 2) some types are superior in their interactions with other types. Population density is a key factor controlling whether individuals interact, thereby setting the relative contributions of these forms of selection.

One potential limitation of our model as a general-purpose model of density-dependent selection is its restriction to interference competition between juveniles for durable resources (lottery recruitment to adulthood), analogous to the ubiquitous assumption of viability selection in population genetics [Ewens, 2004, p. 45]. In some respects this is the complement of consumable resource competition models, which restrict their attention to indirect exploitation competition, typically without age structure [Tilman, 1982]. In the particular case that consumable resources

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282 are spatially localized (e.g. due to restricted movement through soils), resource competition and

283 territorial acquisition effectively coincide, and in principle resource competition could be repre-

284 sented by a competitive ability c (or conversely, c should be derivable from resource competition).

285 The situation is more complicated if the resources are well-mixed, since, in general, resource lev-

286 els then need to be explicitly tracked. It seems plausible that explicit resource tracking may not

287 be necessary when the focus is on the evolution of similar types that use identical resources

288 rather than the stable co-existence of widely differing species with different resource preferences

289 [Ram et al., 2016]. We are not aware of any attempts to delineate conditions under which explicit

290 resource tracking is unnecessary even if it is assumed that community structure is ultimately

291 determined by competition for consumable resources. More work is needed connecting resource

292 competition models to the density-dependent selection literature, since most of the former has to

293 date been focused on narrower issues of the role of competition at low resource availability and

294 in the absence of direct interactions between organisms at the same trophic level [Aerts, 1999,

295 Davis et al., 1998, Tilman, 2007].

296   While our model can be applied to species rather than types (e.g. ecological invasions), our

297 focus is type evolution i.e. the change in allele frequencies over time. Our assumption that there

298 are no large c discrepancies (section "Mean field approximation") amounts to a restriction on

299 the amount of genetic variation in c in the population. Since beneficial mutation effect sizes

300 will typically not be much larger than a few percent, large c discrepancies can only arise if

301 the mutation rate is extremely large, and so the assumption will not be violated in most cases.

302 However, this restriction could become important when looking at species interactions rather

303 than type evolution.

304   In the introduction we mentioned the recurring difficulties with confounding selection and

305 demography in population genetic inference. It seems that Eq. (5) or something similar (and

306 hopefully more analytically tractable) is unavoidable for the analysis of time-course genetic data

307 because, fundamentally, selective births and deaths affect both abundances and frequencies, not

308 one or the other in isolation. Moreover, some aspects of allele frequency change are intrinsically

18

density-dependent. In the classic lottery model, which as we have seen is essentially the Wright-Fisher model with overlapping generations, b_i and c_i are equivalent in the sense that the number of territorial victories only depends on the product $b_i c_i$ (see "Model"). This is no longer the case in our extension, where b and c specialists can co-exist. This "colonization-competition trade-off" is well known in the co-existence literature [Tilman, 1994]. It and similar forms of "spatial co-existence" in stable environments have previously been modeled either with Levin's qualitative representation of competition [Levins and Culver, 1971, Tilman, 1994], as opposed to the quantitative c of lottery competition, or with a more sophisticated treatment of space (non-uniform dispersal; Bolker and Pacala 1999, Shmida and Ellner 1984). In cyclical environments, polymorphisms can be stabilized by the bounded density effect, which is completely lost if there is an exclusive focus on allele frequencies [Yi and Dean, 2013]. We leave the details of how our model might be applied to inference problems, including the crucial issue of its genetic drift predictions (providing a null model for neutral sites), for future work.

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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

22

404 have $T \to \infty$, in which case U can be only be small enough to violate the Poisson approximation if

405 there is vanishing population turnover, and then the dispersal distribution is irrelevant anyway.

406 Likewise, in ignoring stochastic finite population size for the n_i, we have effectively already

407 assumed that m_i is large enough to justify the Poisson approximation (the error scales as $1/\sqrt{m_i}$;

408 Arenbaev 1977).

Appendix B: Derivation of growth equation

410 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

411 vary in relative magnitude depending on the propagule densities l_i. Following the notation in

412 the main text, the Poisson distributions for the x_i (or some subset of the x_i) will be denoted p,

413 and we use P as a general shorthand for the probability of particular outcomes.

Growth without competition

415 The first component, $\Delta_u n_i$, accounts for territories where only one focal propagule is present

416 $x_i = 1$ and $x_j = 0$ for $j \neq i$ (u stands for "uncontested"). The proportion of territories where this

417 occurs is $l_i e^{-L}$, and so

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

Competition when rare

419 The second component, $\Delta_r n_i$, accounts for territories where a single focal propagule is present

420 along with at least one non-focal propagule (r stands for "rare") i.e. $x_i = 1$ and $X_i \geq 1$ where

421 $X_i = \sum_{j \neq i} x_j$ is the number of nonfocal propagules. The number of territories where this occurs

422 is $U p_i(1) P(X_i \geq 1) = b_i n_i e^{-l_i}(1 - e^{-(L-l_i)})$. Thus

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

23

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),

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

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 $\mathbf{x}_i = (x_1, \dots, x_{i-1}, x_{i+1} \dots, x_G)$ denote the vector of non-focal abundances, so that $p(\mathbf{x}_i) = p_1(x_1) \dots p_{i-1}(x_{i-1}) p_{i+1}(x_{i+1}) \dots p_G(x_G)$. Then, $\tilde{p}$ can be written as

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

and so

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

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

24

$\frac{l_j}{L-l_i}(X-1)$. Thus,

$$
\begin{aligned}
\langle x_j \rangle_{\tilde{p}} &= \frac{l_j}{1-(1+L)e^{-L}} \frac{1}{L-l_i} \sum_{k=2}^{\infty} P(X)(X-1) \\
&= \frac{l_j}{1-(1+L)e^{-L}} \frac{L-1+e^{-L}}{L-l_i},
\end{aligned}
\tag{17}
$$

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

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 when L is of order 1 or smaller, because then the propagule assumed to already be present under $\tilde{q}$ is comparable to, or greater than, the entire propgaule density.

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

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

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

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

Suppose that the c_j are all of similar magnitude (their ratios are of order one). Then Eq. (21) is $\ll 1$ for the case when $L - l_i \ll 1$ (due to the factor of $C^{1/2}$), and also for the case when at least some of the nonfocal propagule densities are large $l_j \gg 1$ (since it is then of order $1/\sqrt{L - l_i}$).

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

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

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

455 small.

456   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

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

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

459 make the replacement Eq. (14).

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

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

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

Competition when abundant

463 The final contribution, $\Delta_a n_i$, accounts for territories where two or more focal propagules are

464 present (a stands for "abundant"). Similarly to Eq. (13), we have

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

465 where $\hat{p}$ is the probability distribution of both focal and nonfocal propagule abundances *after*

466 dispersal in those territories where at least two focal propagules landed.

467   Again, we argue that the relative fluctuations in $\sum c_j x_j$ are much smaller than 1 (with respect

468 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

27

$\mathbf{x}$, the mean focal type abundance is,

$$\langle x_i \rangle_{\hat{p}} = \sum_{\mathbf{x}} x_i p(\mathbf{x}|x_i \geq 2)$$

$$= \sum_{x_i} x_i p(x_i|x_i \geq 2)$$

$$= \frac{1}{1 - (1 + l_i)e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i$$

$$= l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}}. \tag{25}$$

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

$$\langle x_j \rangle_{\hat{p}} = \sum_{\mathbf{x}} x_j p(\mathbf{x}|x_i \geq 2)$$

$$= \sum_{X} P(X|x_i \geq 2) \sum_{\mathbf{x}} x_j p(\mathbf{x}|x_i \geq 2, X)$$

$$= \sum_{X} P(X|x_i \geq 2) \sum_{x_i} p(x_i|x_i \geq 2, X) \sum_{x_i} x_j p(\mathbf{x}_i|X_i = X - x_i)$$

$$= \sum_{X} P(X|x_i \geq 2) \sum_{x_i} p(x_i|x_i \geq 2, X) \frac{l_j(X - x_i)}{L - l_i}$$

$$= \frac{l_j}{L - l_i} \left[\sum_{X} P(X|x_i \geq 2)X - \sum_{x_i} p(x_i|x_i \geq 2)x_i \right]$$

$$= \frac{l_j}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}} \right). \tag{26}$$

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

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

29

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

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

487 To get some intuition for Eq. (31), suppose that a mutant arises with improved competitive

488 ability but identical intrinsic growth rate and saturation density ($r_1 = r_2$ and $\alpha_{11} = \alpha_{22}$). This

489 could represent a mutation to an interference competition trait, for example [Gill, 1974]. Then,

490 according the above condition, for N to remain constant over the sweep, the mutant must find

491 the wildtype more tolerable than itself by exactly the same amount that the wildtype finds the

492 mutant less tolerable than itself. This condition, and Eq. (31) more generally, are so restrictive

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

494 involve non-constant N.