

Density-dependent selection and the population ecology of relative fitness

Keywords: r/K selection, absolute fitness, eco-evo, competition-colonization trade-off, fluctuating selection, storage effect.

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.

10 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]. This variety is not necessarily problematic in itself, because different mea-
17 sures of fitness may be more useful in different circumstances. But any measure of fitness should
18 ultimately be grounded in the processes of birth and death which govern population biology
19 [Doebeli et al., 2017, Metcalf and Pavard, 2007]. While this grounding is clear for absolute fitness
20 measures like r and K , relative fitness seems largely divorced from population ecology.

21 In uncrowded populations, relative fitness simply represents differences in the intrinsic ex-
22 ponential growth rate r [Crow et al., 1970, pp. 26], with selection favoring greater r (r -selection).
23 In crowded populations, relative fitness models almost universally assume that total population
24 size N is fixed, or has some externally imposed time course. This is exemplified by the Wright-
25 Fisher model, in which time advances in discrete non-overlapping generations, and fitness can
26 be interpreted as a product of fertility and juvenile viability [Crow et al., 1970, pp. 185]. The
27 limitations of these relative fitness models are openly acknowledged, usually with an emphasis
28 on the difficulty of incorporating more of the life cycle “components” of fitness (e.g. [Ewens,
29 2004, pp. 276]). But more fundamentally, the constant- N , relative fitness description uncouples
30 selection and demography, at odds with the fact that the same birth/death events drive both.

31 The issue can be expressed more formally by revisiting MacArthur’s analysis of selection in
32 crowded populations [MacArthur and Wilson, 1967]. MacArthur considers a population con-
33 sisting of two types with densities n_1 and n_2 subject to density-dependent population growth
34 described by

$$\frac{dn_1}{dt} = f_1(n_1, n_2) \quad \frac{dn_2}{dt} = f_2(n_1, n_2). \quad (1)$$

Apart from the type densities, the environment is assumed to remain constant. 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).

The connection between constant- N relative fitness models and the broad class of density-regulated growth models considered by MacArthur (Eq. 1) is not clear, since the former only describe selection along lines defined by $n_1 + n_2 = N$ for each N (Fig. 1b). In particular, the f_1 and f_2 nullclines are not even defined. It is clear, however, that constant- N relative fitness models are not compatible with some of the most widely-used models of density-regulated population growth: 1) In the logistic model, the type with the greatest saturation population density excludes the others. 2) 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. 3) The Lotka-Volterra competition model also couples selection in crowded populations to changes in total density N (we return to this in section “ K -selection, c -selection and relative fitness”). 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 constant- N , relative fitness description has historically been justified as a short-term linear approximation [Ewens, 2004, pp. 277]. That is, within a sufficiently short time frame, population size can be treated as constant and selection quantified in terms of constant selection coefficients expressing relative fitness differences. Provided that selection is sufficiently weak and stable over time, this “short-term” assumption is not a major restriction. Yet it is increasingly

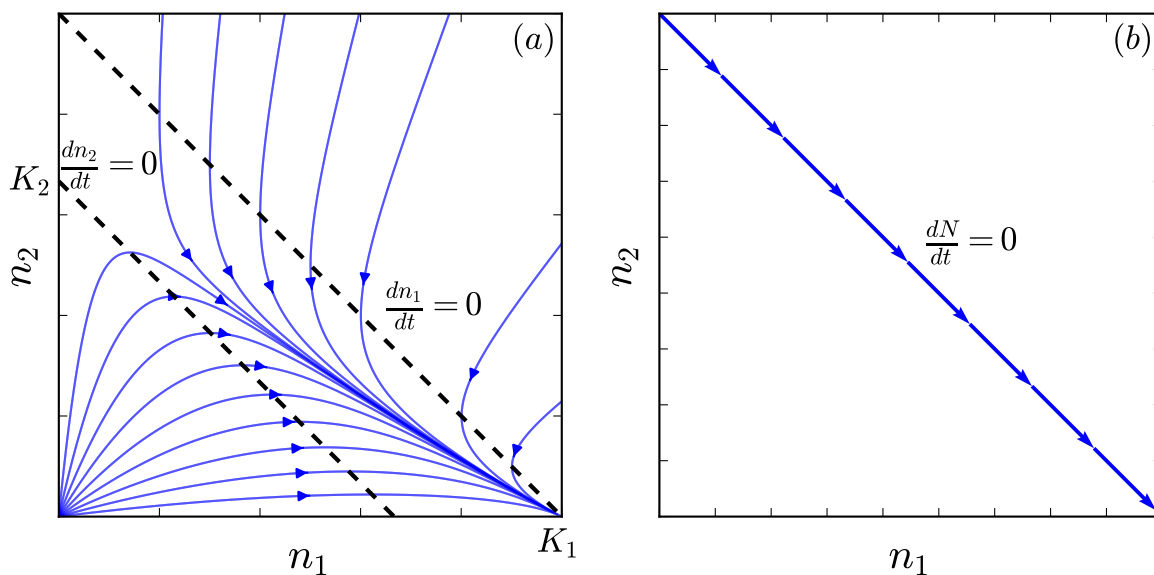


Figure 1: (a) MacArthur’s dynamical argument for how selection operates in crowded environments, illustrated using the logistic model $f_1 = r_1(1 - \frac{n_1+n_2}{K_1})n_1$ and $f_2 = r_2(1 - \frac{n_1+n_2}{K_2})n_1$ in Eq. (1). Here $r_1 = r_2$ and $K_1 > K_2$. (b) The constant- N , relative fitness description of selection.

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. These are not rare exceptions, but occur widely in nature and the lab, including in wild *Drosophila* [Messer et al., 2016]. The short-term approximation also precludes consideration of inherently long-term evolutionary processes like the management of genetic load and population extinction [Bertram et al., 2017]. 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. Thus, to summarize, there are important theoretical and practical reasons to deepen our understanding of the population-ecological foundations of relative fitness models.

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

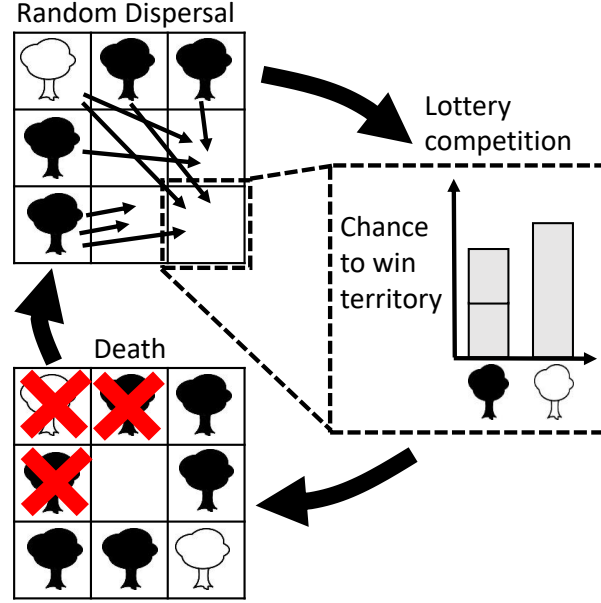


Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each unoccupied territory that receives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

101 maturity. In iteration t , the number of adults of the i 'th type is $n_i(t)$, the total number of adults
102 is $N(t) = \sum_i n_i(t)$, and the number of unoccupied territories is $U(t) = T - N(t)$.

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

107 Each iteration, adults produce new offspring ("propagules"), m_i of which disperse to un-
108 occupied territories. We assume that adults cannot be ousted from their territories, so that m_i
109 only includes propagules landing on unoccupied territories. Propagules disperse at random over
110 the unoccupied territories, regardless of distance from their parents, and independently of each
111 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]. In addition to random dispersal, we will compare our model to perfect directed dispersal, in which each propagule finds an unoccupied territory if one is available ($m_i = b_i$) [Chesson, 1983].

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 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 $p_1(x_1) \dots p_G(x_G)$ of the U unoccupied territories will have the propagule composition x_1, \dots, 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

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

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 $0 \leq d_i \leq 1$,

134 so that the overall change in type abundances is

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

135 Connection to the Wright-Fisher and classic lottery models

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

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

145 where $\bar{c} = \sum_j c_j m_j / M$ is the mean propagule competitive ability for a randomly selected propag-
 146 ule, $L = M/U$ is the total propagule density and $M = \sum_j m_j$ is the total number of propagules.

147 Eq. (4) breaks down for types with low propagule density ($l_i \ll 1$) because territorial acqui-
 148 sition is then not correctly represented by a lottery in each territory with the mean propagule
 149 density. Instead, a rare type's propagules only make it to a few territories where at least one of
 150 its propagule present. In our extension of the classic lottery model, we correct (Eq. 3) to account
 151 for this.

152 There is a close connection between the classic lottery model and the Wright-Fisher model
 153 of genetic drift [Svardal et al., 2015]. In the Wright-Fisher model, type abundances are sampled
 154 each generation from a multinomial distribution with success probabilities $w_i n_i / \sum_j w_j n_j$, where
 155 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

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.

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

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

where

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

175 and

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

176 Comparing Eq. (5) to Eq. (4), the classic lottery per-propagule success rate $c_i/\bar{c}L$ has been
 177 replaced by three separate terms. The first, e^{-L} , accounts for propagules which land alone on
 178 unoccupied territories; these territories are won without contest. The second, $R_i c_i/\bar{c}$ represents
 179 competitive victories when the i type is a rare invader in a high density population, determining
 180 its invasion fitness [Metz et al., 1992]. The third term, $A_i c_i/\bar{c}$, represents competitive victories
 181 when the i type is abundant. The relative importance of these three terms varies with both the
 182 overall propagule density L and the relative propagule frequencies m_i/M . If $l_i \gg 1$ for all types,
 183 we recover the classic lottery model (only the $A_i c_i/\bar{c}$ term remains, and $A_i \rightarrow 1/L$). Note that
 184 not all unoccupied territories are claimed each iteration, since under Poisson dispersal a fraction
 185 e^{-L} remain unoccupied; total population density thus obeys

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

186 Fig. 3 shows that Eq. (5) and its components closely approximate simulations of the density-
 187 dependent lottery model over a wide range of propagule densities. Two types are present, one
 188 of which is at low frequency. The growth of the low-frequency type relies crucially on the low-
 189 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
 190 type, which depends instead on high density territorial victories. Fig. 3 also shows the break-
 191 down of the classic lottery model at low propagule densities.

192 ***K*-selection, *c*-selection and relative fitness**

193 We now compare the density-dependent lottery model from the previous section with MacArthur's
 194 claims about selection in crowded environments.

As shown in the Introduction, MacArthur's argument revolves around the behaviour of eco-
 logical models of the general form Eq. 1, behaviour which depends on the relationship between

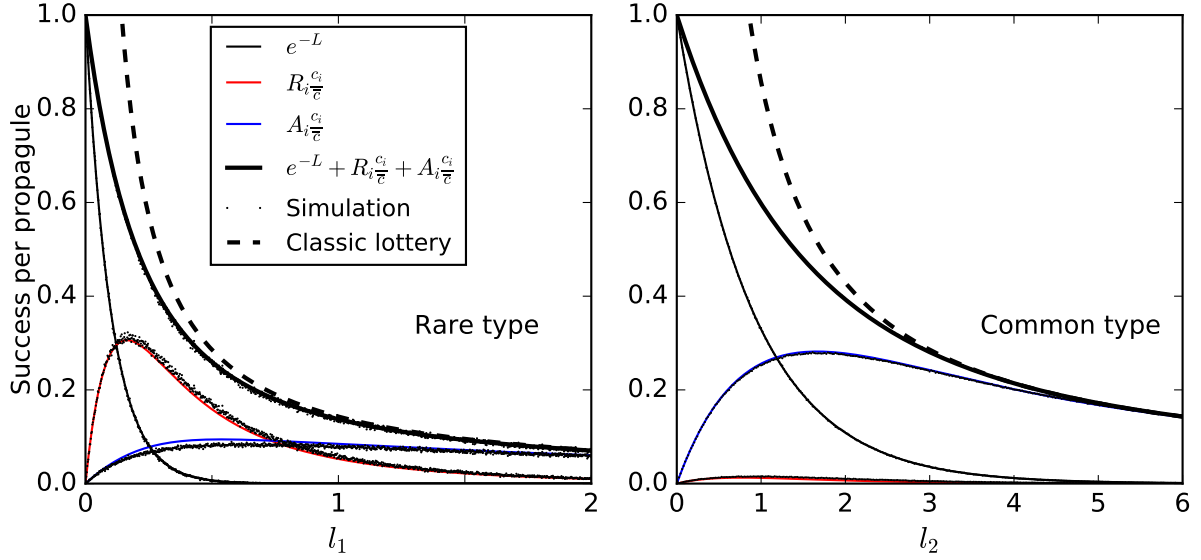


Figure 3: Comparison of mean field approximation Eq. (5) with simulations. Per-propagule success probability $\Delta_+ n_i / l_i U$ from the classic lottery model, individual-based simulations of random dispersal and lottery competition, and Eq. (5) and its three components. Two types are present, a 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 .

the nullclines $f_1(n_1, n_2) = 0$ and $f_2(n_1, n_2) = 0$. To formalize this relationship, MacArthur used the symbol “ K ” to label the four intersection points of the nullclines with the n_1 and n_2 axes, specifically $f_1(K_{11}, 0) = 0$, $f_1(0, K_{12}) = 0$, $f_2(0, K_{22}) = 0$ and $f_2(K_{21}, 0) = 0$. These K values determine whether a region of higher-density growth exists for each type, provided that the nullclines are close to being straight lines. Note that only K_{11} and K_{22} are saturation densities akin to the K parameter in the logistic model; following widespread convention, we will refer to selection on these saturation densities as “ K -selection” (Fig. 1a). The other intersection points, K_{12} and K_{21} , are related to competition between types. For instance, in the Lotka-Volterra competition model we have

$$\begin{aligned}\frac{dn_1}{dt} &= r_1(1 - \alpha_{11}n_1 - \alpha_{12}n_2)n_1 = f_1(n_1, n_2) \\ \frac{dn_2}{dt} &= r_2(1 - \alpha_{22}n_1 - \alpha_{21}n_2)n_2 = f_2(n_1, n_2)\end{aligned}\tag{7}$$

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], it does not imply a dichotomy between r -selection (uncrowded) and K -selection (crowded) in the sense of selection for greater saturation density. MacArthur’s argument shows 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.

Constant- N relative fitness models are not compatible with K -selection, and must refer to the competitive effects summarized by K_{12} and K_{21} . We thus now restrict our attention to the case $K_{11} = K_{22}$. Fig. 4 shows two examples of selection between two types with the same saturation density. Fig. 4a shows exclusion by a superior Lotka-Volterra competitor ($\alpha_{21} > \alpha_{12}$). Even

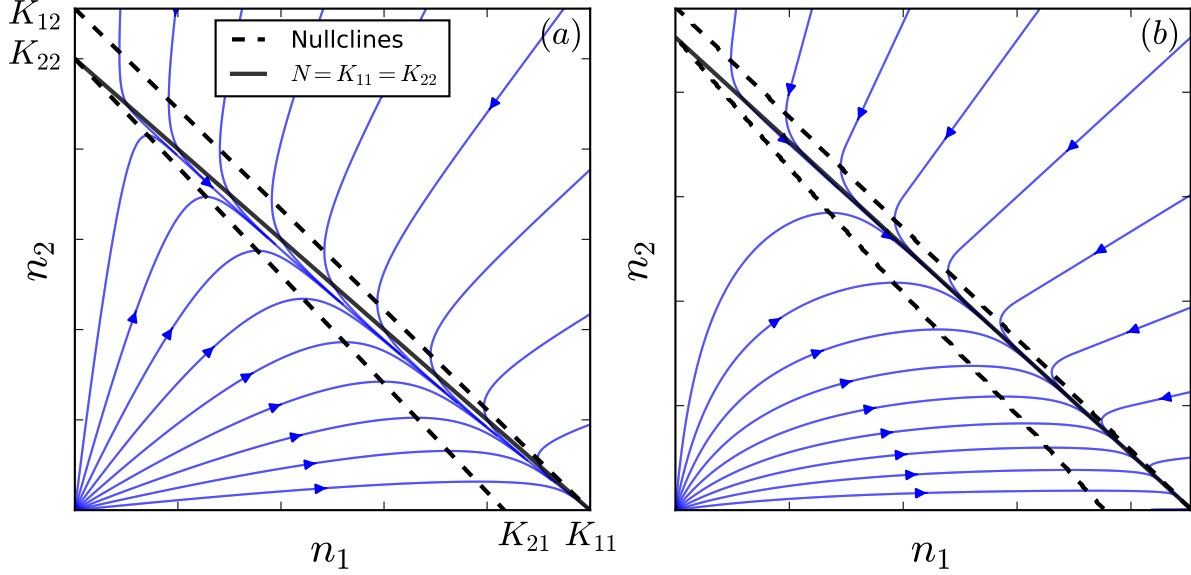


Figure 4: Selection between types with identical saturation density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 7) with $r_1 = r_2 = 1$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = 0.9$ and $\alpha_{21} = 1.2$. Trajectories do not follow the line $N = K_{11} = K_{22}$. (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 $N = K_{11} = K_{22}$.

though the saturation densities are identical, the density trajectories do not follow a line of constant N . This is a general property of the Lotka-Volterra competition model; 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 a selective 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. 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. In

other words, c is a zero-sum relative fitness trait embedded within a non-zero-sum fitness model.

Thus, we can conclude that relative fitness models are perfectly consistent with MacArthur's claim that "fitness is K " in crowded populations, bearing in mind his broad use of the symbol " K ". However, inconsistency remains with standard growth models such as the Lotka-Volterra model. We revisit this issue in the Discussion.

Discussion

If s is small it doesn't matter anyway

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 are spatially localized (e.g. due to restricted movement through soils), resource competition and territorial acquisition effectively coincide, and in principle resource competition could be represented by a competitive ability c (or conversely, c should be derivable from resource competition). The situation is more complicated if the resources are well-mixed, since, in general, resource levels then need to be explicitly tracked. It seems plausible that explicit resource tracking may not be necessary when the focus is on the evolution of similar types that use identical resources rather than the stable co-existence of widely differing species with different resource preferences [Ram et al., 2016]. We are not aware of any attempts to delineate conditions under which explicit resource tracking is unnecessary even if it is assumed that community structure is ultimately determined by competition for consumable resources. More work is needed connecting resource competition models to the density-dependent selection literature, since most of the former has to date been focused on narrower issues of the role of competition at low resource availability and

in the absence of direct interactions between organisms at the same trophic level [Aerts, 1999, Davis et al., 1998, Tilman, 2007].

While our model can be applied to species rather than types (e.g. ecological invasions), our focus is type evolution i.e. the change in allele frequencies over time. Our assumption that there are no large c discrepancies (section “Mean field approximation”) amounts to a restriction on the amount of genetic variation in c in the population. Since beneficial mutation effect sizes will typically not be much larger than a few percent, large c discrepancies can only arise if the mutation rate is extremely large, and so the assumption will not be violated in most cases. However, this restriction could become important when looking at species interactions rather than type evolution.

In the introduction we mentioned the recurring difficulties with confounding selection and demography in population genetic inference. It seems that Eq. (5) or something similar (and hopefully more analytically tractable) is unavoidable for the analysis of time-course genetic data because, fundamentally, selective births and deaths affect both abundances and frequencies, not one or the other in isolation. Moreover, some aspects of allele frequency change are intrinsically 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 have $T \rightarrow \infty$, 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

$$\Delta_u n_i = U l_i e^{-L} = m_i e^{-L}. \quad (8)$$

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

$$\Delta_r n_i = m_i e^{-l_i} (1 - e^{-(L-l_i)}) \left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}}, \quad (9)$$

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. (9),

$$\left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}} \approx \frac{c_i}{c_i + \sum_{j \neq i} c_j \langle x_j \rangle_{\tilde{p}}}. \quad (10)$$

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

$$\begin{aligned}\tilde{p}(\mathbf{x}_i) &= p(\mathbf{x}_i | X \geq 2, x_i = 1) \\ &= \frac{P(\mathbf{x}_i, X \geq 2 | x_i = 1)}{P(X \geq 2)} \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) p(\mathbf{x}_i | X_i = X - 1),\end{aligned}\tag{11}$$

and so

$$\begin{aligned}\langle x_j \rangle_{\tilde{p}} &= \sum_{\mathbf{x}_i} \tilde{p}(\mathbf{x}_i) x_j \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - 1) x_j.\end{aligned}\tag{12}$$

The inner sum over \mathbf{x}_i is the mean number of propagules of a given nonfocal type j that will be found in a territory which received $X - 1$ nonfocal propagules in total, which is equal to $\frac{l_j}{L - l_i}(X - 1)$. Thus,

$$\begin{aligned}\langle x_j \rangle_{\tilde{p}} &= \frac{l_j}{1 - (1 + L)e^{-L}} \frac{1}{L - l_i} \sum_{k=2}^{\infty} P(X)(X - 1) \\ &= \frac{l_j}{1 - (1 + L)e^{-L}} \frac{L - 1 + e^{-L}}{L - l_i},\end{aligned}\tag{13}$$

378 where the last line follows from $\sum_{X=2}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)X -$
379 $\sum_{X=1}^{\infty} P(X)$.

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 $\langle x_j \rangle_{\tilde{q}} = \langle x_j \rangle_p / C = l_j / C$,

$$\begin{aligned}
\sigma_{\tilde{q}}^2(x_j) &= \langle x_j^2 \rangle_{\tilde{q}} - \langle x_j \rangle_{\tilde{q}}^2 \\
&= \frac{1}{C} \langle x_j^2 \rangle_p - \frac{l_j^2}{C^2} \\
&= \frac{1}{C} (l_j^2 + l_j) - \frac{l_j^2}{C^2} \\
&= \frac{l_j^2}{C} \left(1 - \frac{1}{C} \right) + \frac{l_j}{C},
\end{aligned} \tag{14}$$

and

$$\begin{aligned}
\sigma_{\tilde{q}}(x_j, x_k) &= \langle x_j x_k \rangle_{\tilde{q}} - \langle x_j \rangle_{\tilde{q}} \langle x_k \rangle_{\tilde{q}} \\
&= \frac{1}{C} \langle x_j x_k \rangle_p - \frac{l_j l_k}{C^2} \\
&= \frac{l_j l_k}{C} \left(1 - \frac{1}{C} \right),
\end{aligned} \tag{15}$$

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. (13) 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 $\sum_{j \neq i} c_j x_j$,

$$\sigma_{\tilde{q}}^2(\sum_{j \neq i} c_j x_j) = \sum_{j \neq i} \left[c_j^2 \sigma_{\tilde{q}}^2(x_j) + 2 \sum_{k > j, k \neq i} c_j c_k \sigma_{\tilde{q}}(x_j, x_k) \right], \quad (16)$$

and using the fact that $\sigma_{\tilde{q}}(x_j, x_k)$ and the first term in Eq. (14) are negative because $C < 1$, we obtain an upper bound on the relative fluctuations in $\sum_{j \neq i} c_j x_j$,

$$\frac{\sigma(\sum_{j \neq i} c_j x_j)}{\langle \sum_{j \neq i} c_j x_j \rangle} = C^{1/2} \frac{\left(\sum_{j \neq i} c_j^2 l_j + (1 - 1/C) \left(\sum_{j \neq i} c_j l_j \right)^2 \right)^{1/2}}{\sum_{j \neq i} c_j l_j} < C^{1/2} \frac{\left(\sum_{j \neq i} c_j^2 l_j \right)^{1/2}}{\sum_{j \neq i} c_j l_j}. \quad (17)$$

Suppose that the c_j are all of similar magnitude (their ratios are of order one). Then Eq. (17) is $\ll 1$ for the case when $L - l_i \ll 1$ (due to the factor of $C^{1/2}$), and also for the case when at least some of the nonfocal propagule densities are large $l_j \gg 1$ (since it is then of order $1/\sqrt{L - l_i}$). The worst case scenario occurs when $L - l_i$ is of order one. Then Eq. (17) gives a relative error of approximately 50%, which from our earlier discussion we know to be a substantial overestimate when L is of order 1. Our numerical results (Fig. 3) confirm that the relative errors are indeed small.

However, the relative fluctuations in $\sum_{j \neq i} c_j x_j$ can be large if some of the c_j are much larger than the others. Specifically, in the presence of a rare, extremely strong competitor ($c_j l_j \gg c_{j'} l_{j'}$ for all other nonfocal types j' , and $l_j \ll 1$), then the RHS of Eq. (17) can be large and we cannot make the replacement Eq. (10).

Substituting Eqs. (10) and (13) into Eq. (9), we obtain

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{C}, \quad (18)$$

where R_i is defined in Eq. (6).

411 Competition when abundant

412 The final contribution, $\Delta_a n_i$, accounts for territories where two or more focal propagules are
 413 present (a stands for “abundant”). Similarly to Eq. (9), we have

$$\Delta_a n_i = U(1 - (1 + l_i)e^{l_i}) \left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \quad (19)$$

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

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

$$\left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \approx \frac{c_i \langle x_i \rangle_{\hat{p}}}{\sum_j c_j \langle x_j \rangle_{\hat{p}}}. \quad (20)$$

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,

$$\begin{aligned} \langle x_i \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_i p(\mathbf{x} | x_i \geq 2) \\ &= \sum_{x_i} x_i p(x_i | x_i \geq 2) \\ &= \frac{1}{1 - (1 + l_i)e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i \\ &= l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}}. \end{aligned} \quad (21)$$

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

$$\begin{aligned}
\langle x_j \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_j p(\mathbf{x} | x_i \geq 2) \\
&= \sum_X P(X | x_i \geq 2) \sum_{\mathbf{x}} x_j p(\mathbf{x} | x_i \geq 2, X) \\
&= \sum_X P(X | x_i \geq 2) \sum_{x_i} p(x_i | x_i \geq 2, X) \sum_{\mathbf{x}_i} x_j p(\mathbf{x}_i | X_i = X - x_i) \\
&= \sum_X P(X | x_i \geq 2) \sum_{x_i} p(x_i | x_i \geq 2, X) \frac{l_j(X - x_i)}{L - l_i} \\
&= \frac{l_j}{L - l_i} \left[\sum_X P(X | x_i \geq 2) X - \sum_{x_i} p(x_i | x_i \geq 2) x_i \right] \\
&= \frac{l_j}{L - l_i} \left(L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}} \right). \tag{22}
\end{aligned}$$

418 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}
419 is approximated by \hat{q} , defined as the \mathbf{x} dispersal probabilities in a territory conditional on $x_i > 2$
420 (that is, treating the x_j as indepenent). All covariances between nonfocal types are now zero, so
421 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

$$\sigma_{\hat{q}}^2(x_i) = \frac{l_i}{D} \left(l_i + 1 - e^{-l_i} - \frac{l_i}{D} (1 - e^{-l_i})^2 \right), \tag{23}$$

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

$$\frac{\sigma_{\hat{q}}(\sum c_j x_j)}{\langle \sum c_j x_j \rangle} = \frac{\left(\sum_{j \neq i} c_j^2 l_j + c_i^2 \sigma_{\hat{q}}^2(x_i) \right)^{1/2}}{\sum_{j \neq i} c_j l_j + c_i l_i (1 - e^{-l_i}) / D}. \tag{24}$$

423 Similarly to Eq. (17), the RHS of Eq. (24) is $\ll 1$ for the case that $L \ll 1$ (due to a factor of
424 $D^{1/2}$), and also for the case when at least some of the propagule densities (focal or nonfocal) are
425 large — provided that c_i and the c_j are all of similar magnitude. Again, the worst case scenario
426 occurs when l_i and $L - l_i$ are of order 1, in which case Eq. (24) is around 35%, which is again
427 where the \hat{q} approximation produces the biggest overestimate of the fluctuations in \mathbf{x} . Similarly

428 to Eq. (17), the RHS of (24) will not be $\ll 1$ in the presence of a rare, extremely strong competitor.

429 Combining Eqs. (19) and (20), we obtain

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

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

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

432 Here we show that under the Lotka-Volterra model of competition, total density N does not in
433 general remain constant over a selective sweep in a crowded population even if the types have
434 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. (7), we obtain

$$\begin{aligned} \frac{dn_1}{dt} &= -r_1(\alpha_{12} - \alpha_{11})n_1n_2 \\ \frac{dn_2}{dt} &= -r_2(\alpha_{21} - \alpha_{22})n_1n_2 \end{aligned} \quad (26)$$

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

$$r_1(\alpha_{12} - \alpha_{11}) + r_2(\alpha_{21} - \alpha_{22}) = 0. \quad (27)$$

436 To get some intuition for Eq. (27), suppose that a mutant arises with improved competitive
437 ability but identical intrinsic growth rate and saturation density ($r_1 = r_2$ and $\alpha_{11} = \alpha_{22}$). This
438 could represent a mutation to an interference competition trait, for example [Gill, 1974]. Then,
439 according the above condition, for N to remain constant over the sweep, the mutant must find
440 the wildtype more tolerable than itself by exactly the same amount that the wildtype finds the
441 mutant less tolerable than itself. This condition, and Eq. (27) more generally, are so restrictive

442 that we can conclude that selective sweeps in the Lotka-Volterra competition model will generally
443 involve non-constant N .