

# 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 saturation density, relative fitness seems largely divorced from population  
21 ecology.

22 In uncrowded populations, relative fitness simply represents differences in the intrinsic ex-  
23 ponential growth rate  $r$  [Crow et al., 1970, pp. 26], with selection favoring greater  $r$  ( $r$ -selection).  
24 The situation is considerably more complicated in crowded populations. In this case, relative  
25 fitness models almost universally assume that total population size  $N$  is fixed, or has some ex-  
26 ternally imposed time course. This is exemplified by the Wright-Fisher model, in which time  
27 advances in discrete non-overlapping generations, and fitness can be interpreted as a product  
28 of fertility and juvenile viability [Crow et al., 1970, pp. 185]. The limitations of relative fitness  
29 models are openly acknowledged, usually with an emphasis on the difficulty of incorporating  
30 multiple life cycle “components” of fitness (e.g. [Ewens, 2004, pp. 276] [Prout, 1980]). But more  
31 fundamentally, the constant- $N$ , relative fitness description uncouples selection and demography,  
32 at odds with the fact that the same birth/death events drive both.

33 The issue can be expressed formally by revisiting MacArthur’s analysis of selection in crowded  
34 populations [MacArthur and Wilson, 1967]. MacArthur considers a population consisting of two

types with densities  $n_1$  and  $n_2$  subject to density-dependent population growth 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

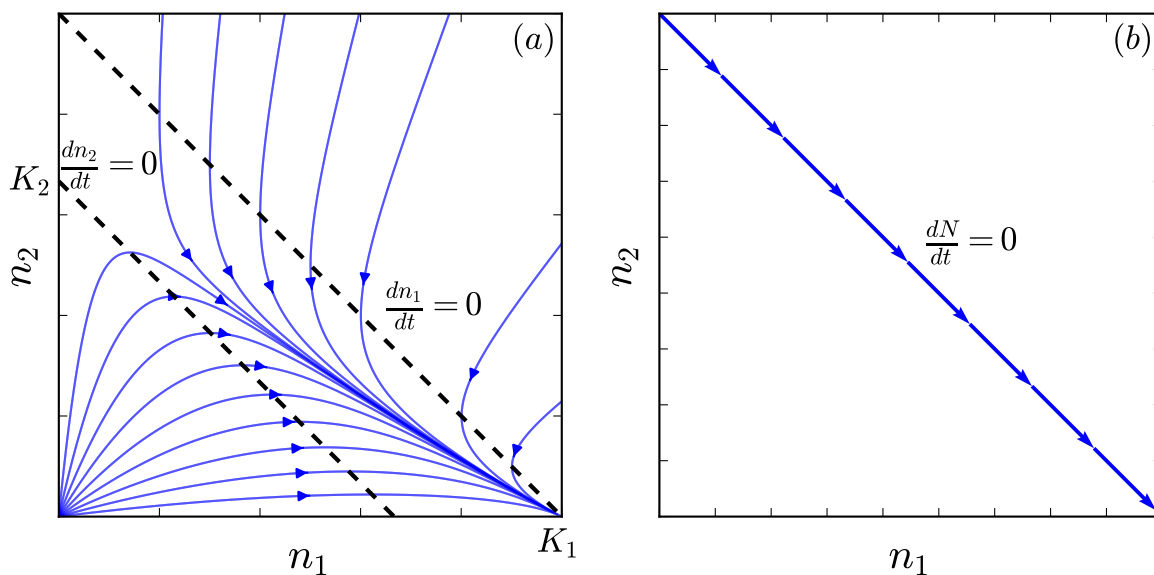


Figure 1: (a) MacArthur’s dynamical argument for how selection operates in crowded environments, illustrated using the logistic model  $f_1 = r_1(1 - \frac{n_1+n_2}{K_1})n_1$  and  $f_2 = r_2(1 - \frac{n_1+n_2}{K_2})n_1$  in Eq. (1). Here  $r_1 = r_2$  and  $K_1 > K_2$ . (b) The constant- $N$ , relative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

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 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 or the broader gulf with population ecology [Mallet, 2012]. Thus, it is important that we deepen our population-ecological understanding of relative fitness models, both to gain insight into their domain of applicability, and as part of the broad

challenge of synthesizing ecology and evolution.

The recent rise of adaptive dynamics has provided a powerful framework for modeling the interplay between long-term evolution and population ecology, including complex couplings between evolutionary change and population density. However, the focus of this latter work is on trait evolution rather than the underlying genetics, and in particular, the details of selective sweeps are typically subsumed into effectively instantaneous “trait substitutions” determined by invasion fitness. We emphasize that our focus here is on the description of selection itself, which is critical for evolutionary genetics i.e. for making sense of the change in allele frequencies over time.

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  $U(t) = T - N(t)$ .

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

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

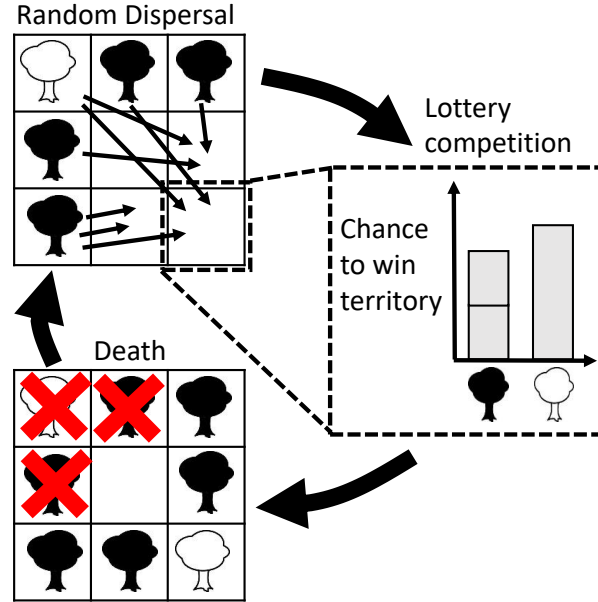


Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Some territories may receive zero propagules. Lottery competition then occurs in each unoccupied territory that receives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



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  $0 \leq d_i \leq 1$ , so that the overall change in type abundances is

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

## 145 Connection to the Wright-Fisher and classic lottery models

146 In the classic lottery model [Chesson and Warner, 1981], unoccupied territories are assumed  
 147 to be saturated with propagules from every type  $l_i \gg 1$ . From the law of large numbers, the  
 148 composition of propagules in each territory will then not deviate appreciably from the mean  
 149 composition  $l_1, l_2, \dots, l_G$  ( $G$  is the number of types present), and so the probability that type  $i$  wins  
 150 any particular unoccupied territory is approximately  $c_i l_i / \sum_j c_j l_j$ . Then the numbers of territories  
 151 won by each type  $\Delta_+ n_1, \Delta_+ n_2, \dots, \Delta_+ n_G$  follow a multinomial distribution with  $U$  trials and  
 152 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  
 153 the  $U$  available territories, and deviations from this expected outcome are small (since  $T$  is large  
 154 by assumption), giving

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

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

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

162 There is a close connection between the classic lottery model and the Wright-Fisher model  
 163 of genetic drift [Svardal et al., 2015]. In the Wright-Fisher model, type abundances are sampled  
 164 each generation from a multinomial distribution with success probabilities  $w_i n_i / \sum_j w_j n_j$ , where  
 165  $w$  is relative fitness and the  $n_i$  are type abundances in the preceding generation. Population  
 166 size  $N$  remains constant. This is equivalent to the classic lottery model with non-overlapping  
 167 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  
 168 viability [Crow et al., 1970, pp. 185]. Thus, the classic lottery model is essentially the Wright-  
 169 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

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

and

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

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

189 competitive victories when the  $i$  type is a rare invader in a high density population, determining  
 190 its invasion fitness [Metz et al., 1992]. The third term,  $A_i c_i / \bar{c}$ , represents competitive victories  
 191 when the  $i$  type is abundant. The relative importance of these three terms varies with both the  
 192 overall propagule density  $L$  and the relative propagule frequencies  $m_i / M$ . If  $l_i \gg 1$  for all types,  
 193 we recover the classic lottery model (only the  $A_i c_i / \bar{c}$  term remains, and  $A_i \rightarrow 1/L$ ). Note that  
 194 not all unoccupied territories are claimed each iteration, since under Poisson dispersal a fraction  
 195  $e^{-L}$  remain unoccupied; total population density thus obeys

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

196 Fig. 3 shows that Eq. (5) and its components closely approximate simulations of the density-  
 197 dependent lottery model over a wide range of propagule densities. Two types are present, one  
 198 of which is at low frequency. The growth of the low-frequency type relies crucially on the low-  
 199 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  
 200 type, which depends instead on high density territorial victories. Fig. 3 also shows the break-  
 201 down of the classic lottery model at low propagule densities.

## 202 **K-selection, c-selection and relative fitness**

203 We now compare the density-dependent lottery model from the previous section with MacArthur's  
 204 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  
 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 deter-  
 mine 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

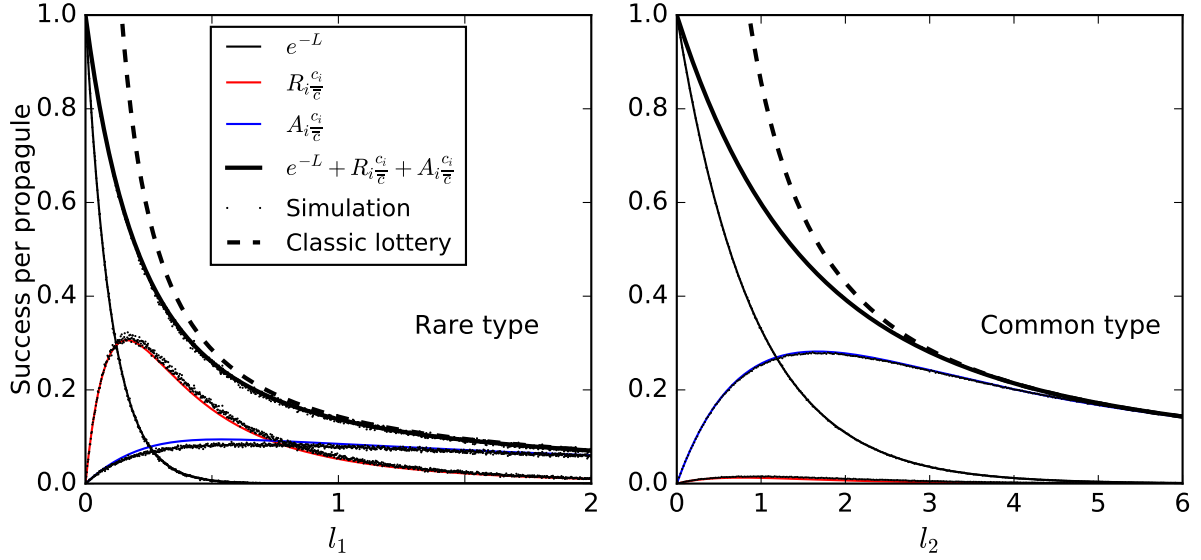


Figure 3: Comparison of mean field approximation Eq. (5) with simulations. Per-propagule success probability  $\Delta_+ n_i / l_i U$  from the classic lottery model, individual-based simulations of random dispersal and lottery competition, and Eq. (5) and its three components. Two types are present, 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  $5 \times 10^3$  and  $10^6$ .

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 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  $\alpha$  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

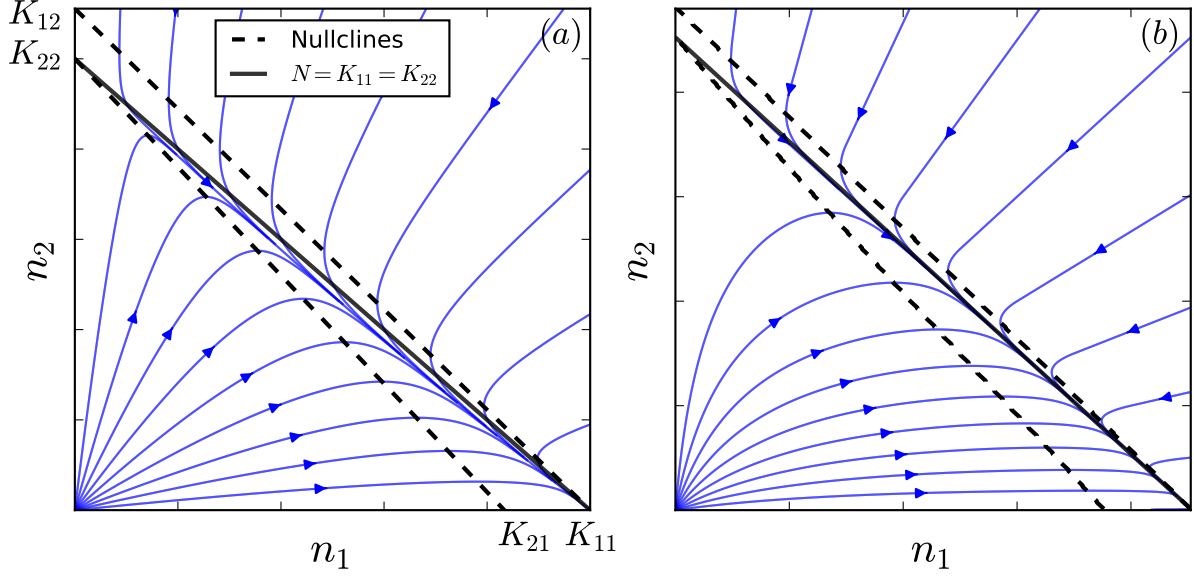


Figure 4: Selection between types with identical saturation density but different inter-type competitive ability. (a) Lotka-Volterra competition (Eq. 7) with  $r_1 = r_2 = 1$ ,  $\alpha_{11} = \alpha_{22} = 1$ ,  $\alpha_{12} = 0.9$  and  $\alpha_{21} = 1.2$ . Trajectories do not follow the line  $N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

in  $N$  due to the 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

356  $m_i$ , which is more biologically realistic. Nevertheless, since we do not consider the random fluc-  
 357 tuations in type abundances here, and for ease of comparison with the classic lottery model, we  
 358 ignore the fluctuations in  $m_i$ . Instead we focus, on Poisson fluctuations in propagule composition  
 359 in each territory.

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

## 372 **Appendix B: Derivation of growth equation**

373 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  
 374 vary in relative magnitude depending on the propagule densities  $l_i$ . Following the notation in  
 375 the main text, the Poisson distributions for the  $x_i$  (or some subset of the  $x_i$ ) will be denoted  $p$ ,  
 376 and we use  $P$  as a general shorthand for the probability of particular outcomes.

### 377 **Growth without competition**

378 The first component,  $\Delta_u n_i$ , accounts for territories where only one focal propagule is present  
 379  $x_i = 1$  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,

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

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

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).

## Competition when abundant

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

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

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

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

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

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

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

432 To calculate the relative fluctuations in  $\sum_{j \neq i} c_j x_j$ , we use a similar approximation as for  $\Delta_r n_i$ :  $\hat{p}$   
433 is approximated by  $\hat{q}$ , defined as the  $\mathbf{x}$  dispersal probabilities in a territory conditional on  $x_i > 2$   
434 (that is, treating the  $x_j$  as indepenent). All covariances between nonfocal types are now zero, so  
435 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

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

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

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

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

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

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

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

444 where  $A_i$  is defined in Eq. (6).

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

446 Here we show that under the Lotka-Volterra model of competition, total density  $N$  does not in  
447 general remain constant over a selective sweep in a crowded population even if the types have  
448 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

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

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

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

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

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