

# Density-dependent selection in evolutionary genetics: a lottery model of Grime's triangle

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## Abstract

Fitness is typically represented in heavily simplified terms in evolutionary genetics, often using  
3 constant selection coefficients. This excludes fundamental ecological factors such as dynamic  
population size or density-dependence from the most genetically-realistic treatments of evolu-  
tion, a problem that inspired MacArthur’s influential but problematic  $r/K$  theory. Following  
6 in the spirit of  $r/K$ -selection as a general-purpose theory of density-dependent selection, but  
grounding ourselves empirically in “primary strategy” trait classification schemes like Grime’s  
triangle, we develop a new model of density-dependent selection which revolves around terri-  
9 torial contests. To do so, we generalize the classic lottery model of territorial acquisition, which  
has primarily been used for studying species co-existence questions, to accommodate arbitrary  
densities. We use this density-dependent lottery model to predict the direction of trait evolution  
12 under different environmental conditions and thereby provide a mathematical underpinning for  
Grime’s verbal scheme. We revisit previous concepts of density-dependent selection, including  $r$   
and  $K$  selection, and argue that our model distinguishes between different aspects of fitness in a  
15 more natural and intuitive manner.

“...the concept of fitness is probably too complex to allow of a useful mathematical development. Since it enters fundamentally into many population genetics considerations, it is remarkable how little attention has been paid to it.” — Warren J. Ewens, *Mathematical Population Genetics I*, 2004

Evolutionary models differ greatly in their treatment of fitness. In models of genetic evolution, genotypes are typically assigned constant (or frequency-dependent) selection coefficients describing the change in their relative frequencies over time due to differences in viability. This considerably simplifies the mathematics of selection, facilitating greater genetic realism, and can be justified over sufficiently short time intervals (Ewens, 2004, p. 276). The emphasis here is on predicting how the course of allele frequencies over time depends on their selective effect, genetic drift and linkage. However, the resulting picture of evolution does not include even basic elements of the ecological underpinnings of selection, including dynamic population size and density-dependence.

By contrast, models of phenotypic trait evolution represent the change in phenotypic abundances over time using absolute fitness functions which describe how those traits affect survival and reproduction in particular ecological scenarios. This approach is powerful enough to model eco-evolutionary feedbacks between co-evolving traits, but is generally problem-specific and restricted to only a few traits at a time. These models emphasize invasion from low frequencies and co-existence over frequency trajectories over time. For instance, the adaptive dynamics approach revolves around the analysis of “invasion fitness” (Diekmann et al., 2004).

Far less work has been done to generalize beyond particular traits or ecological scenarios to models of fitness that still capture key distinctions between different forms of selection. Perhaps this is not surprising given that fitness is such a complex quantity, dependent on all of a phenotype’s functional traits (Violle et al., 2007) as well as its biotic and abiotic environment. In most cases, a detailed, trait-based, predictive model of fitness would be enormously complicated and have narrow applicability. It is therefore easy to doubt the feasibility of a simplified, general mathematical treatment of fitness (Ewens, 2004, p. 276). For example, MacArthur’s famous  $r/K$

scheme (MacArthur, 1962; MacArthur and Wilson, 1967) is now almost exclusively known as a framework for understanding life-history traits, and judged on its failure in that role (Boyce, 1984; Pianka, 1970; Reznick et al., 2002; Stearns, 1977). The  $r/K$  scheme's original purpose was as an extension of the existing population-genetic treatment of selection to account for population density (MacArthur, 1962), but few attempts have been made to develop it further as a mathematical analysis of the major different forms of selection.

Empirical studies of organismal traits have suggested the existence of a few "primary strategies" which reflect how different species have responded to selection (Winemiller et al., 2015). The most famous example is Grime's triangle (Grime, 1974, 1977, 1988; Westoby, 1998). Grime considered two broad determinants of population density: stress (persistent hardship e.g. due to resource scarcity, unfavorable temperatures or toxins) and disturbance (intermittent destruction of vegetation e.g. due to trampling, herbivory, pathogens, extreme weather or fire). The extremes of these two factors define three primary strategies denoted by C/S/R respectively (Fig. 1): competitors "C" excel in low stress, low disturbance environments; stress tolerators "S" excel in high stress, low disturbance environments; and ruderals "R" excel in low stress, high disturbance environments. Survival is not possible in high-stress, high-disturbance environments. Grime showed that measures of C, S and R across a wide range of plant species are anti-correlated, so that strong C-strategists are weak S and R strategists, and so on. Thus, plant species can be classified on a triangular C/S/R ternary plot (Grime, 1974). Similar trait classification schemes were proposed at a similar time for insects (Southwood, 1977), fishes (Winemiller and Rose, 1992), and zooplankton (Allan, 1976). While these schemes were largely verbal, modern hierarchical clustering techniques have revealed distinct clusters analogous to Grime's primary strategies in corals (Darling et al., 2012),

Trait classification schemes show empirically that, beneath the complicated details of trait variation, even among closely-related species, fitness is predominantly determined by a few key factors such as intrinsic reproductive rate or stress-tolerance. However, while trait classification schemes are firmly grounded in trait data, they are verbal and descriptive rather than mathemat-



Figure 1: Schematic of Grime’s triangle. The two axes show increasing levels of environmental stress and disturbance, respectively. Survival is not possible if the combination of stress and disturbance is too large (dashed line). This creates a triangle, each corner of which corresponds to a “primary strategy”.

ical, a recognized hindrance to their broader applicability (e.g. Tilman 2007).

The aim of this paper is explore the interplay between some major dimensions of fitness in a simplified, territorial model of growth, dispersal and competition. Building on the earlier  $r/K$  and  $C/S/R$  schemes, a central question is how fitness depends on the interaction between population density, intrinsic birth/death rates and competitive ability.

We broadly follow the spirit of MacArthur’s  $r/K$  selection scheme in that our model is intended to account for fundamentally different forms of selection without getting entangled in the intricacies of particular ecological scenarios. However, rather than building directly on MacArthur’s formalism and its later extensions using Lotka-Volterra equations to incorporate competition (“ $\alpha$ -selection”) (Case and Gilpin, 1974; Gill, 1974; Joshi et al., 2001), our model is devised more with Grime’s  $C/S/R$  scheme in mind, and represents a quantitative formalization of how  $C/S/R$  manifests at the level of within-population genotypic evolution (as opposed to phenotypic divergence between species). This choice is motivated in part by the substantial empirical support for  $C/S/R$ -like schemes, and in part by the failings of the  $r/K$  low/high density dichotomy — many growth ability traits will confer advantages at both low and high densities (more details in the Discussion).

As we will see, a generalized version of the classic lottery model of Chesson and Warner

87 (1981) is a convenient starting point for ecologically-grounded models of selection in evolution-  
ary genetics. In the classic lottery model, mature individuals (“adults”) each require their own  
territory, whereas newborn individuals (“propagules”) disperse to, and subsequently compete  
90 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  
(akin to a lottery; Sale 1977), with probabilities weighted by a coefficient for each type rep-  
93 resenting competitive ability. This representation of competition is much simpler than having  
coefficients for the pairwise effects of types on each other (e.g. the  $\alpha$  coefficients in the general-  
ized Lotka-Volterra equations), or than modeling resource consumption explicitly (Tilman, 1982).  
96 The classic lottery model is also closely connected to one of the central models of population  
genetics, the Wright-Fisher model of genetic drift.

However, the classic lottery model breaks down at low densities (that is, if there are only  
99 a few propagules dispersing to each territory; see “Model”). This was not a limitation in the  
lottery model’s original application to reef fishes, where a huge number of larvae from each  
species compete to secure territories each generation (Chesson and Warner, 1981), but is a critical  
102 limitation for studying density-dependent selection. We analytically extend the classic lottery  
model to correctly account for low density behavior.

In the section “Model”, we introduce the basic assumptions of our generalized lottery model.  
105 Analytical expressions for the change in genotype abundances over time are introduced in section  
“Mean field approximation”, with mathematical details relegated to the Appendices. In the  
following two sections, we then discuss the behavior of rare mutants (invasion and coexistence)  
108 and our formalization of Grime’s triangle.

## Model

We assume that the reproductively mature individuals in a population (“adults”) each require  
111 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 average time from birth to reproductive maturity. In iteration  $t$ , the number of adults of the  $i$ 'th genotype is  $n_i(t)$ , the total number of adults is  $N(t) = \sum_i n_i(t)$ , and the number of unoccupied territories is  $U(t) = T - N(t)$ .

Each iteration, adults produce new offspring ("propagules"),  $m_i$  of which disperse to unoccupied territories. We assume that adults cannot be ousted from occupied territories, and so only propagules landing on unoccupied territories are included in  $m_i$ . Propagules disperse at random uniformly, and independently of each other; all propagules have the same probability of landing on any of the  $U$  unoccupied territories. Thus, there is no interaction between propagules (e.g. avoidance of territories crowded with propagules). Loss of propagules during dispersal is subsumed into  $m_i$ . In general,  $m_i$  will increase with  $n_i$ , and will also depend on population density  $N$ . For example, if  $b_i$  is the number of successfully dispersing propagules produced per genotype  $i$  adult, then the loss of propagules due to dispersal to occupied territories implies  $m_i = b_i(1 - N/T)n_i$ , akin to Levins' competition-colonization model (Levins and Culver, 1971; Tilman, 1994). Here we assume  $m_i = b_i n_i$ , where  $b_i$  is a constant, meaning that all propagules land on unoccupied territories (a form of directed dispersal). This choice simplifies the mathematics without seriously restricting the generality of our analysis, since the results presented here are not sensitive to the specific functional form of  $m_i$ . Note that due to our assumption of uniform dispersal, the parameter  $b_i$  can be thought of as a measure of "colonization ability", which combines fecundity and dispersal ability (Bolker and Pacala, 1999; Levins and Culver, 1971; Tilman, 1994).

The number of individuals of the  $i$ 'th genotype landing in any particular territory is denoted  $x_i$ . Random dispersal implies that in the limit  $T \rightarrow \infty$ , with  $n_i/T$  held fixed,  $x_i$  is Poisson distributed with mean territorial propagule density  $l_i = m_i/U$  (this dispersal Poisson distribution is denoted  $p_i(x_i) = l_i^{x_i} e^{-l_i} / x_i!$ ). Although  $T$  is finite in our model, we assume that  $T$  and the  $n_i$  are large enough that  $x_i$  is Poisson-distributed to a good approximation (details in Appendix A). Note that the large  $n_i$ , large  $T$  approximation places no restrictions on our densities  $n_i/T$ , but it



Figure 2: Each iteration of our lottery model has three main elements. First, propagules are produced by adults which are dispersed at random over the unoccupied territories (only propagules landing on unoccupied territories are shown). Lottery competition then occurs in each unoccupied territory (competition in only one territory is illustrated): each genotype has a probability proportional to  $b_i n_i c_i$  of securing the territory. Then occupied territories are freed up by adult mortality. In Eq. (3) and most of the paper, only adults can die (red crosses), but we will also consider the case where juveniles die (blue cross; section “Primary strategies and Grime’s triangle”).



does preclude consideration of demographic stochasticity when  $n_i$  itself is very small.

When multiple propagules land on the same territory, they compete to secure the territory as they develop. This territorial contest is modeled as a weighted lottery: the probability that genotype  $i$  wins a territory by the next iteration, assuming that at least one of its propagules is present, is  $c_i x_i / \sum_j c_j x_j$ , where  $c_i$  is a constant representing relative competitive ability (Fig. 2).

In the classic lottery model (Chesson and Warner, 1981), unoccupied territories are assumed to be saturated with propagules from every genotype i.e.  $l_i \gg 1$  where  $l_i = m_i / U$  is the mean propagule density. From the law of large numbers, the composition of propagules in each territory will then not deviate appreciably from the mean composition  $l_1, l_2, \dots, l_G$  ( $G$  is the number of genotypes present), and so the probability that genotype  $i$  wins any particular unoccupied territory is approximately  $c_i l_i / \sum_j c_j l_j$ . Let  $\Delta_+ n_i$  denote the number of territories won by genotype  $i$ . Then  $\Delta_+ n_1, \Delta_+ n_2, \dots, \Delta_+ n_G$  follow a multinomial distribution with  $U$  trials and success probabilities  $\frac{c_1 l_1}{\sum_j c_j l_j}, \frac{c_2 l_2}{\sum_j c_j l_j}, \dots, \frac{c_G l_G}{\sum_j c_j l_j}$ , respectively. Genotype  $i$  is expected to win  $c_i l_i / \sum_j c_j l_j$  of the  $U$  available territories, and deviations from this expected outcome are small (since  $T$  is large by assumption), giving

$$\Delta_+ n_i(t) = \frac{c_i l_i}{\sum_j c_j l_j} U(t) = b_i n_i \frac{1}{L} \frac{c_i}{\bar{c}}, \quad (1)$$

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

There is a close connection between the classic lottery model and the Wright-Fisher model of genetic drift (Svardal et al., 2015). In the Wright-Fisher model, genotype abundances are sampled each generation from a multinomial distribution with success probabilities  $w_i n_i / \sum_j w_j n_j$ , where  $w$  is relative fitness and the  $n_i$  are genotype abundances in the preceding generation. Population size  $N$  remains constant. This is mathematically equivalent to the classic lottery model with non-overlapping generations ( $d_i = 1$  for all  $i$ ) and  $w_i = b_i c_i$ .

The classic lottery model allows us to replace the abstract Wright-Fisher relative fitnesses  $w_i$  with more ecologically-grounded fecundity, competitive ability and mortality parameters  $b_i, c_i$

and  $d_i$ , respectively. Since birth and death rates affect absolute abundances, this allows us to  
 165 evaluate selection at different densities (after appropriate extensions are made), in an otherwise  
 very similar model to the canonical Wright-Fisher model. Note that the classic lottery model,  
 and the present work, both ignore the stochastic drift in type frequencies (large  $T$  approximation)  
 168 which is the focus of the Wright-Fisher model.

In our extension of the classic lottery model, we do not restrict ourselves to high propagule  
 densities. Eq. (1) is nonsensical at low densities ( $l_i \ll 1$ ): genotype  $i$  can win at most  $m_i$  territories,  
 171 yet Eq. (1) demands  $c_i l_i / \sum_j c_j l_j$  of the  $U$  unoccupied territories, for any value of  $U$ . Intuitively, the  
 cause of this discrepancy is that individuals are discrete. Genotypes with few propagules depend  
 on the outcome of contests in territories where they have at least one propagule present, not  
 174 some small fraction of a propagule as would be implied by low propagule density  $l$  in the classic  
 lottery model. In other words, deviations from the mean propagule composition  $l_1, l_2, \dots, l_G$  are  
 important at low density.

177 Dispersal is Poisson, and so we expect that a fraction  $p_1(x_1) \dots p_G(x_G)$  of the  $U$  unoccu-  
 pied territories will have the propagule composition  $x_1, \dots, x_G$ . Genotype  $i$  is expected to win  
 $c_i x_i / \sum_j c_j x_j$  of these. Ignoring fluctuations about these two expectations (large  $T$  approximation),  
 180 genotype  $i$ '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 propag-  
 ule present.

183 For the majority of this manuscript we assume that mortality only occurs in adults (setting  
 aside the juvenile deaths implicit in territorial contest), and at a constant, genotype-specific per-  
 capita rate  $d_i$ , so that the overall change in genotype abundances is

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

This is reasonable approximation in the absence of disturbances; when we come to consider the effects of disturbances (Section “Primary strategies and Grime’s triangle”), we will incorporate disturbance-induced mortality in competing juveniles (Fig. 2).

Note that the competitive ability coefficients  $c_i$  represent a strictly relative aspect of fitness in the sense that they can only influence population size  $N$  indirectly by changing genotype frequencies. This can be seen by summing Eq. (3) over genotypes to get the change in population size  $N$ ,

$$\Delta N = U(1 - e^{-L}) - \sum_i d_i n_i, \quad (4)$$

which is independent of  $c_i$  (here  $L = \sum_j l_j$  is the overall propagule density). Unlike the classic lottery model, not all  $U$  unoccupied territories are claimed each iteration; a fraction  $e^{-L}$  remain unoccupied.

## 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.

Our approximation is similar to the high- $l_i$  approximation behind the classic lottery model in that we replace the  $x_i$  with appropriate mean values. However, we cannot simply replace  $x_i$  with  $l_i$  as in the classic lottery model. For a genotype with a low propagule density  $l_i \ll 1$ , we have  $x_i = 1$  in the few territories where its propagules land, and so its growth comes entirely from territories which deviate appreciably from  $l_i$ . In our more general approximation, territories with a single propagule from the focal genotype are handled separately. In place of the requirement of  $l_i \gg 1$  for all  $i$ , our approximation only requires that there are no large discrepancies in competitive ability (specifically, that we do not have  $c_i/c_j \gg 1$  for any two genotypes; further

discussion in section “Discussion”). We obtain (details in Appendix B)

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

210 where

$$R_i = \frac{\bar{c} e^{-l_i} (1 - e^{-(L-l_i)})}{c_i + \frac{L-1+e^{-L}}{1-(1+L)e^{-L}} \frac{\bar{c} L - c_i l_i}{L-l_i}}, \quad (6)$$

and

$$A_i = \frac{\bar{c} (1 - e^{-l_i})}{\frac{1-e^{-l_i}}{1-(1+l_i)e^{-l_i}} c_i l_i + \frac{1}{L-l_i} \left( L \frac{1-e^{-L}}{1-(1+L)e^{-L}} - l_i \frac{1-e^{-l_i}}{1-(1+l_i)e^{-l_i}} \right) \sum_{j \neq i} c_j l_j}. \quad (7)$$

Comparing Eq. (5) to Eq. (1), the classic lottery per-propagule success rate  $c_i/\bar{c}L$  has been  
 213 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  
 competitive victories when the  $i$  genotype is a rare invader in a high density population: from  
 216 Eq. (6),  $R_i \rightarrow 0$  when the  $i$  genotype is abundant ( $l_i \gg 1$ ), or other genotypes are collectively  
 rare ( $L - l_i \ll 1$ ). The third term,  $A_i c_i/\bar{c}$ , represents competitive victories when the  $i$  genotype  
 is abundant:  $A_i \rightarrow 0$  if  $l_i \ll 1$ . The relative importance of these three terms varies with both  
 219 the overall propagule density  $L$  and the relative propagule frequencies  $m_i/M$ . If  $l_i \gg 1$  for all  
 genotypes, we recover the classic lottery model (only the  $A_i c_i/\bar{c}$  term remains, and  $A_i \rightarrow 1/L$ ).  
 Thus, Eq. (5) generalizes the classic lottery model to account for arbitrary propagule densities  
 222 for each genotype.

Fig. 3 shows that Eq. (5) (and its components) closely approximate direct simulations of  
 random dispersal and lottery competition over a wide range of propagule densities (obtained by  
 225 varying  $U$ ). Two genotypes are present, one of which has a  $c$ -advantage and is at low frequency.  
 The growth of the low-frequency genotype relies crucially on the low-density competition term  
 $R_i c_i/\bar{c}$ , and also to a lesser extent on the high density competition term  $A_i c_i/\bar{c}$  if  $l_1$  is large  
 228 enough (Fig. 3b). On the other hand,  $R_i c_i/\bar{c}$  is negligible for the high-frequency genotype, which  
 depends instead on high density territorial victories (Fig. 3d). Fig. 3 also shows the breakdown

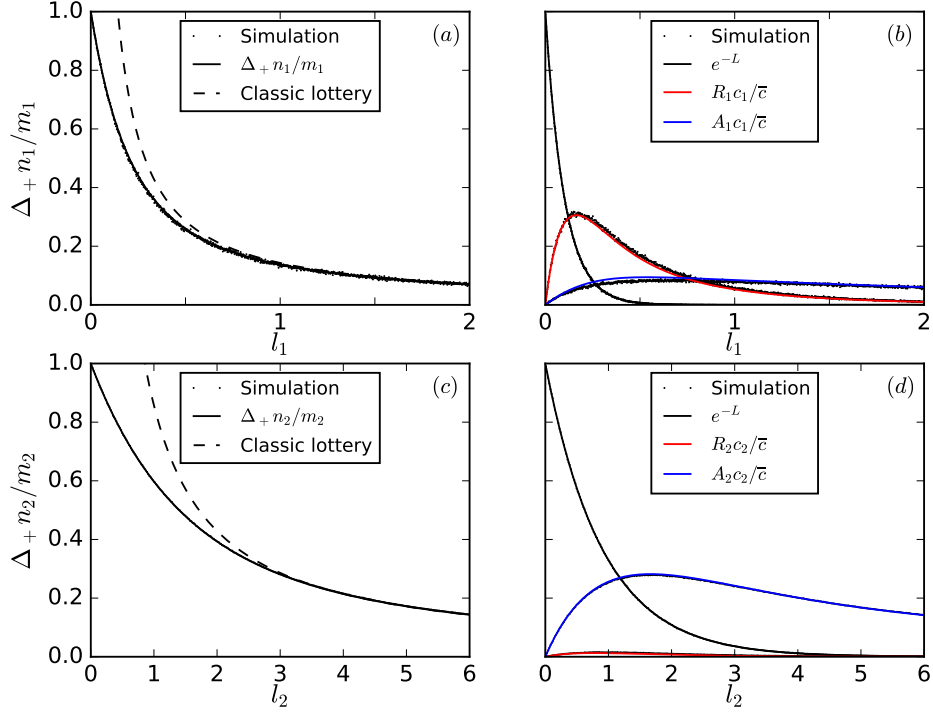


Figure 3: The change in genotype abundances in a density dependent lottery model is closely approximated by Eq. (5).  $\Delta_+ n_i / m_i$  from Eq. (5) (and its separate components) are shown, along with direct simulations of random dispersal and lottery competition over one iteration over a range of propagule densities (varied by changing  $U$  with the  $m_i$  fixed). Two genotypes are present. (a) and (b) show the low-frequency genotype with  $c$ -advantage ( $m_1/M = 0.1$ ,  $c_1 = 1.5$ ), (c) and (d) show the high-frequency predominant genotype ( $m_2/M = 0.9$ ,  $c_2 = 1$ ). Simulation points are almost invisible in (c) and (d) due to near exact agreement with Eq. (5). Dashed lines in (a) and (c) show the corresponding classic lottery model predictions.

of the classic lottery model at low densities (low  $l_1$  and  $l_2$ ).

### 231 Invasion of rare genotypes and coexistence

In our model (section “Model”), each genotype is defined by three traits:  $b$ ,  $c$  and  $d$ . To determine how these will evolve in a population where they are being modified by mutations, we need to know whether mutant lineages will grow (or decline) starting from low densities. In this section we discuss the behavior of rare genotypes predicted by Eq. (5).

Suppose that a population with a single genotype  $i$  is in equilibrium. Then  $R_i = 0$ ,  $\bar{c} = c_i$  and

237  $\Delta n_i = 0$ , and so Eq. (5) gives

$$b_i \left( e^{-L} + A_i \right) - d_i = 0, \quad (8)$$

where  $A_i = (1 - (1 + L)e^{-L})/L$ . Now suppose that a new genotype  $j$ , which is initially rare, appears in the population. Then  $A_j \ll R_j$ ,  $l_j \approx 0$  and  $\bar{c} \approx c_i$ , and so, from Eq. (5),  $n_j$  will increase

240 if

$$b_j \left( e^{-L} + R_j \frac{c_j}{c_i} \right) - d_j > 0, \quad (9)$$

where  $R_j \approx (1 - e^{-L}) / \left( \frac{c_j}{c_i} + \frac{L-1-e^{-L}}{1-(1+L)e^{-L}} \right)$ .

Combining Eqs. (8) and (9), we see that  $j$  will invade if it is superior in any one of the three  
 243 traits, but is otherwise identical to  $i$ . If the new genotype has the same competitive ability  $c_j = c_i$ , then  $R_j \approx A_i$  and Eqs. (8) and (9) imply that invasion occurs when  $b_j d_i - b_i d_j > 0$ , and in particular when  $b_j > b_i$  with  $d_j = d_i$ , or when  $d_j < d_i$  with  $b_j = b_i$ . In the case that the new  
 246 genotype has a different competitive ability but the same  $b_i$  and  $d_i$ , Eqs. (8) and (9) imply that invasion occurs when  $R_j c_j / c_i > A_i$ ; it is not hard to verify that this occurs if and only if  $c_j > c_i$  using the simplified expressions for  $A_i$  and  $R_j$  given after Eqs. (8) and (9) respectively. Moreover,  
 249 if  $j$  invades in any of these cases, it will eventually exclude  $i$ , since it is strictly superior.

Stable coexistence is possible between genotypes that are superior in different traits. Suppose that  $j$  is better at securing territories ( $c_j > c_i$ ), that  $i$  is better at producing propagules ( $b_i > b_j$ ),  
 252 and that  $d_i = d_j$ . Coexistence occurs if  $j$  will invade an  $i$ -dominated population, but  $i$  will also invade a  $j$ -dominated population ("mutual invasion"). If  $b_i$  is so large that  $L \gg 1$  when  $i$  is dominant, and  $b_j$  is so small that  $L \ll 1$  when  $j$  is dominant, then, combining Eqs. (8) and (9),  
 255 we find that  $i$  invades  $j$  because  $b_i > b_j$ , while  $j$  invades  $i$  provided that

$$b_j c_j R_j - b_i c_i A_i > 0. \quad (10)$$

Thus, coexistence occurs if  $c_j/c_i$  is large enough. This is a version of the classic competition-colonization trade-off (Levins and Culver, 1971; Tilman, 1994): the competitor ( $c$ -specialist) leaves

258 many territories unoccupied (low  $L$ ) due to its poor colonization ability (low  $b$ ), which the colo-  
nizer ( $b$ -specialist) can then exploit. A similar argument applies for coexistence between high- $c$   
and low- $d$  specialists; a “competition-longevity” trade-off (Tilman, 1994). Mutual invasibility is  
261 not possible between  $b$ - and  $d$ -specialists.

If the rare genotype  $j$  arises due to mutation, then its initial low-density behavior is more com-  
plicated than the above invasion analysis suggests. The mutant lineage starts with one individual  
264  $n_j = 1$ , and remains at low abundance for many generations after its initial appearance. During  
this period, the mutant abundance  $n_j$  will behave stochastically, and the deterministic equations  
(2) and (5) do not apply (section “Model”). However, if  $n_j$  becomes large enough, its behavior  
267 will become effectively deterministic, and governed by Eq. (5). For mutants with fitness greater  
than the population mean fitness, this occurs when  $n_j$  is of order  $1/s$  (Desai and Fisher, 2007),  
where the selection coefficient  $s$  is the mutant’s fitness advantage (i.e.  $s = \frac{\Delta n_i/n_i}{\sum_i \Delta n_i/n_i \times n_i/N} - 1$ ).  
270 Here we do not consider the initial stochastic behavior of novel mutants, and have restricted  
our attention to the earliest deterministic behavior of rare genotypes. In particular, for beneficial  
mutations we have only considered the case where  $s$  is large enough that deterministic behavior  
273 starts when  $n_j \ll N$ .

## Primary strategies and Grime’s triangle

We now discuss which changes in the traits  $b, c$  and  $d$  will be particularly favored under different  
276 environmental conditions. Of specific interest are Grime’s “disturbed”, “stressful” and “ideal”  
environments. To proceed, we need to map these verbally-defined environments to quantitative  
parameter regimes in our model.

279 The ideal environment is characterized by the near-absence of stress and disturbance. Con-  
sequently,  $d_i \ll 1$ , whereas  $b_i$  is potentially much larger than 1. From Eq. (4), the equi-  
librium value of  $L$  only depends on the ratio of birth and death rates. For one genotype,  
282  $L/(1 - e^{-L}) = b_i/d_i$ , and so the propagule density is high  $L \approx b_i/d_i \gg 1$ , and every unoc-  
cupied territory will be heavily contested. The population density is also high  $N/T \approx 1$  (since

$$L = b_i N / (N - T) = b_i / (1 - T/N).$$

Disturbed environments are characterized by unavoidably high extrinsic mortality caused by physical destruction. Environmental variability, and disturbances in particular, can be modeled as stochastic fluctuations in  $b$ ,  $c$  and  $d$  (Chesson and Warner, 1981). For simplicity, we do not pursue this more complicated stochastic approach. Instead, we represent disturbance by high constant mortality rates  $d_i$ , and extend this mortality to juveniles in the process of territorial contest (since disturbances do not only affect adults as in Eq. (3)). We assume that disturbances are equally damaging to adults and juveniles, so that only  $(1 - d_i)\Delta_+ n_i$  rather than  $\Delta_+ n_i$  territories are secured by genotype  $i$  each iteration. [More justification?] Disturbed environments then correspond to  $d_i$  being close to 1 for all genotypes (almost all adults and juveniles are killed each iteration). From Eq. (4), the single genotype equilibrium is given by  $L/(1 - e^{-L}) = d_i/[(1 - d_i)b_i]$ , and since  $L \ll 1$  and  $N/T \ll 1$  due to high mortality, we have  $L \approx 2(1 - d_i/[(1 - d_i)b_i])$ . Clearly  $b_i$  must be exceptionally large to ensure population persistence. The terms proportional to  $c_i/\bar{c}$  in Eq. (5) are then negligible, and  $\Delta_+ n_i$  depends primarily on  $b_i$ .

Stressful environments are more ambiguous, and have been the subject of an extensive debate in the plant ecology literature (the “Grime-Tilman” debate; Aerts 1999 and references therein). Severe stress inhibits growth and reproduction, so that  $b \ll 1$  (Grime, 1974, 1977). Mutations which appreciably improve  $b$  will be either non-existent or extremely unlikely, so  $b$  is constrained to remain low. In Grime’s view, under these conditions the rate at which propagules successfully develop to adulthood cannot appreciably exceed the mortality rate. This implies  $b/d \approx 1$  in our model, and so the propagule density  $L$  is suppressed to such low levels that there are essentially no territorial contests occurring.

The alternative view is that, while stressful environments imply lower  $b$  and support a lower number of individuals per unit area compared what is attainable in ideal environments, stressed populations are actually at high densities relative to the environmental carrying capacity, and are highly competitive (Taylor et al., 1990). In the particular case that stress is caused by scarcity of consumable resources, we might expect intense resource competition (for empirical support, see



	Ideal	Disturbance*	Stress (G)	Stress (HD)
Constraints	$d \ll 1$	$d \approx 1$	$b \ll 1$	$b \ll 1$
Other parameters	$b \gg d$	$b \gg d$	$b \approx d$	$b > d$
Density $N/T$	High	Low	Low	High
$\Delta_+ n_i \propto$	$b_i c_i$	$b_i$	$b_i$	$b_i c_i$
Evolution for	$\uparrow b, \uparrow c$	$\uparrow b, \downarrow d$	$\downarrow d$	$\uparrow c, \downarrow d$

Figure 4: The realization of Grime’s three environmental extremes in our model, as well as the high-density variant of the stressful environment. Shown are the mapping of each environment to our parameters, the approximate dependence of  $\Delta_+ n_i$  on  $b_i$  and  $c_i$ , as well as the corresponding expected evolutionary changes in  $b_i$ ,  $c_i$  and  $d_i$ . \*Mortality affects both adults and juveniles in the disturbed environment, with  $\Delta_+ n_i$  replaced by  $(1 - d_i)\Delta_+ n_i$  in Eq. (3).

Davis et al. 1998). Thus,  $b$  may actually appreciably exceed  $d$  under stressful conditions, even though the absolute value of  $b$  is small.

The mapping of different environments to our model parameters is summarized in the first two rows of Fig. 4. Also shown is the approximate dependence of  $\Delta_+ n_i$  on  $b_i$  and  $c_i$  for each environment (fourth row). These can be used infer the expected direction of evolution for the traits  $b$ ,  $c$  and  $d$  (fifth row) as follows.

As noted in the previous section, if beneficial mutations survive the low-abundance stochastic regime, they proceed to grow deterministically according to Eq. (5). The probability of surviving to deterministic abundances increases with the mutant fitness advantage, and is therefore typically on the order of one percent, whereas the fixation of neutral mutations is exceedingly unlikely (probability of order  $1/N$ ). Consequently, the direction of evolutionary change is determined by which trait changes are both available, and confer an appreciable benefit, where availability is subject to constraints imposed by the environment.

For example, in Grime’s interpretation of stressful environments,  $L$  is low, so competition is not important, and only mutants with greater  $b$  or lower  $d$  will have an appreciably greater  $\Delta n_i$ . Mutations in  $c$  are effectively neutral, and will rarely fix. However,  $b$  is constrained to be small. Thus, while some rare mutations may produce small improvements in  $b$ , it is much more likely that mutations lower  $d$ , making this the expected direction of evolutionary change.

Following Grime’s original argument for a triangular scheme (Grime, 1977), Fig. 5 repre-

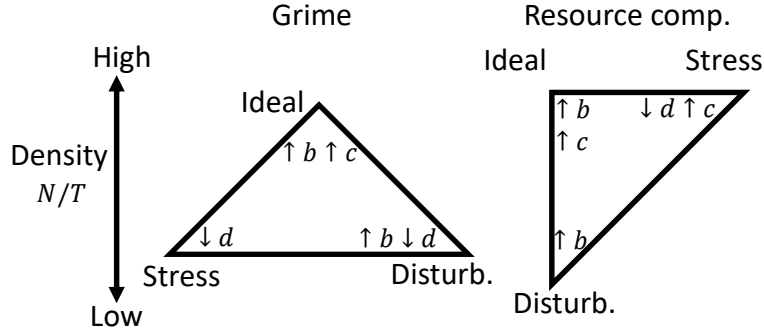


Figure 5: The realization of Grime’s triangle in our model. Schematic representation of the triangular space bounded by the low/high extremes of stress/disturbance. The low- $T$  interpretation of stress is also shown. The vertices of the triangles correspond to different environmental extremes. Selection favors different traits at each vertex, leading to different trait clusters.

sents each environmental extreme schematically as a vertex on a triangular space defined by perpendicular stress and disturbance axes. The ideal environment lies at the origin (no stress or disturbance), while the stressful and disturbed environments lie at the limits of survival on their respective axes. The hypotenuse connecting the stress and disturbance endpoints represents the limits of survival in the presence of a combination of stress and disturbance. The direction of evolutionary change is different at each vertex, leading to the emergence of different trait clusters or “primary strategies”.

How does Fig. 4 compare to empirical analyses of Grime’s C/S/R strategies? In our comparison we will stick to fishes, corals and plants, for which three-way primary strategy schemes are well developed (Darling et al., 2012; Grime, 1977; Winemiller and Rose, 1992). The connection of our model to fish strategies is necessarily more tentative, given that fishes are motile and not all territorial.

In disturbed environments, we predict evolution for higher  $b$  and lower  $d$ , but not higher  $c$ . Higher  $b$  means higher fecundity and/or dispersal ability (see “Model”). This is consistent with a ruderal strategy. Plant ruderals devote a large proportion of their productivity to seed production (Grime, 1977), whereas the analogous “opportunistic” fishes have large intrinsic growth rates (Winemiller and Rose, 1992). In corals, ruderals are distinguished by brood spawning (rather

than broadcast spawning; Darling et al. 2012). This corresponds to higher parental investment  
 348 and lower overall propagule production — counter-intuitively, a stereotypical “K-selected”, high-  
 density trait (Pianka, 1970). However, since broadcast spawners are vulnerable to an Allee effect  
 at the egg fertilization stage (Knowlton, 2001), brood spawning could actually be a way to ensure  
 351 high  $b$  at low densities (Darling et al., 2012). Lower  $d$  could be achieved by improved individual  
 resistance to physical destruction, but it is hard to reduce mortality in the face of severe dis-  
 turbances. Alternatively, shortening the time to reproductive maturity (the iteration time in our  
 354 model) is an effective way of reducing the chance of death per iteration,  $d$ , for a given frequency  
 of disturbance. An exceptionally short life cycle is probably the most defining characteristic of  
 ruderals (Darling et al., 2012; Grime, 1977; Winemiller and Rose, 1992). Note that if evolution  
 357 manages to appreciably reduce  $d$  for a given disturbance intensity, then the population no longer  
 lies at the extreme disturbance vertex of Grime’s triangle. Thus, ruderals are characterized by  
 both high  $b$  and high  $d$ , but there is a constant pressure for a shorter life cycle, extending the  
 360 limits of disturbance that can be tolerated.

In stressful environments, we predict evolution for lower  $d$ , and also for higher  $c$  in the high-  
 density interpretation of stressful environments. Low  $d$  is essential when  $b \ll 1$ , and stress  
 363 tolerant plants and corals have long life spans, allowing for long intervals between successful  
 recruitments (and episodic broadcast spawning in corals). For fishes, the “equilibrium” strategy  
 is the analogue of Grime’s stress tolerator. This strategy is associated with consumable resource  
 366 limitation, and is also characterized by long life span, as well as high parental investment in tiny  
 broods. This may reflect a high- $c$  strategy in the face of intense competition for severely limited  
 resources (the high-density interpretation).

369 In ideal environments, we predict evolution for higher  $b$  and  $c$ , but not lower  $d$ . In plants  
 and corals, a key mechanism for winning territorial contests (higher  $c$ ) is rapidly outgrowing  
 and “shading out” competitors; empirically, rapid individual growth is a defining feature of the  
 372 competitor trait cluster (Darling et al., 2012; Grime, 1977). The situation for  $b$  is more ambiguous.  
 Competitor strategies in plants and corals span a range of  $b$ . For fishes, the analogous “periodic”

strategy is characterized by enormous spawn sizes as well as rapid development (Winemiller et al., 2015; Winemiller and Rose, 1992). The role of  $b$  in ideal environments will be discussed further below.

## Cyclical birth and death rates

So we have only considered the low-frequency invasion behavior of Eq. (5). Here we start exploring its full time-dependent behaviour. The broader context for this section is the recurring difficulties in population genetic inference caused by the confounding of population demography and selection — selective sweeps generate similar genealogies to population bottlenecks (Barton, 1998). Current approaches attempt to treat selection and demography separately, typically fitting a demographic model to data on ostensibly neutral sites and then inferring selection against this demographic background, but with mixed success due to linkage (Schrider et al., 2016). Fitness models like Eq. (5) may help to address to these difficulties since they do not artificially separate the dynamics of abundance and frequency.

Here we will not directly address these inference challenges, but will instead illustrate the complicated time-dependent behavior that can arise from Eq. (5) in an example where birth and death rates vary periodically with amplitude sufficient to cause large changes in population density. This is inspired by natural *Drosophila* populations, which expand rapidly in the warmer months when fruit is abundant, but largely die off in the colder months. Within this seasonal population density cycle, hundreds of polymorphisms also cycle in frequency (Bergland et al., 2014). Some of these polymorphisms may be adaptive and potentially millions of years old, suggesting stable coexistence (Bergland et al., 2014; Messer et al., 2016). Selection on allele frequencies thus occurs on the same time scale as population demography, a situation vastly more complicated than classical sweeps in demographically stable populations (Messer et al., 2016).

The classical population genetic treatment of fluctuating selection suggests that environmental fluctuations do not promote coexistence. Allele frequencies are successively multiplied by

relative fitness values for each environmental iteration, and so two alleles favored in different environments can only stably coexist if the product of fitnesses for one type exactly equals the product for the other (Dempster, 1955). Thus, stable coexistence still requires frequency dependent selection or heterozygote advantage (as is required in a constant environment).

This classical argument overlooks two general mechanisms by which fluctuating selection promotes coexistence. The first is the “storage effect”, which introduces a form of frequency dependent selection that promotes coexistence in the presence of environmental fluctuations but not in a constant environment. The storage effect occurs when some individuals are protected from selection; in the lottery model a fraction  $(1 - d_i)n_i$  of each type’s adults do not experience selection in a given iteration. Protection from selection promotes coexistence in fluctuating environments because abundant types cannot fully exploit environmental periods that favor them (since only a fraction of the rare type can be displaced), whereas rare types gain the full benefits of their favorable periods (far more adults from the abundant type die than can possibly be replaced by the rare types) (Chesson and Warner, 1981).

The second mechanism we will call the “bounded density effect”, since it is a consequence of the inhibition of reproduction at high population densities (Dempster’s (1955) argument ignores density-dependent effects). If there is growth from low to high density in each environmental cycle, then types that are abundant determine the time available for growth every cycle, with less time spent growing in cycles where they are favored, and more in cycles where they are not. This promotes coexistence even in the absence of frequency dependent selection (Yi and Dean, 2013).

Figure 6 shows the behavior of Eq. (5) for an example where  $b$  and  $d$  cycle between zero and positive values (“summers” with rapid growth and no mortality, and “winters” with mortality and no growth). Both the storage effect (adults are sheltered from selection during the summer growth phase) and the bounded density effect (expansion to high density occurs every cycle) are operating. Two types are present, a  $b$  specialist, which is better at rapidly growing in the summer (higher  $b$ ), and a  $d$  specialist which is better at surviving the winter (lower  $d$ ).

Neither type has an advantage over a full environmental cycle, and they stably coexist. This is

426 due to some combination of the storage and bounded population size effects (stable coexistence  
 between  $b$  and  $d$  specialists was not possible in a constant environment). It is clear that the  
 classic lottery model, which has a storage effect but no bounded population size effect, will  
 429 give very different coexistence predictions from our extension of it, because population size will  
 immediately return to capacity  $N = T$  in the first summer iteration, after which type frequencies  
 remain constant until the winter. The  $d$  specialist thus effectively has infinitely many propagules  
 432 to secure its winter frequency gains, an enormous advantage compared to the finite propagule  
 density dynamics in Fig. 6. Similar difficulties arise in previous models of how the storage effect  
 promotes genetic variation (Ellner and Hairston Jr, 1994), which assume that the total number  
 435 of offspring per iteration is constant. Beyond this observation, disentangling the storage and  
 bounded population size effects is not straightforward, and requires a more detailed discussion  
 of each effect than we have space for here. Our model is well suited for such a disentangling  
 438 since it extends the classic model of the storage effect to arbitrary population densities.

## Discussion

As discussed in “Primary strategies and Grime’s triangle”, adaptive evolution in the direction  
 441 predicted by our generalized lottery model produces traits consistent with Grime’s scheme, with  
 the possible exception of selection for  $b$  at high density, because the corresponding trait data is  
 ambiguous. Selection for  $b$  at high density is also counter to the expectations of MacArthur’s  
 444  $r/K$  dichotomy (MacArthur and Wilson, 1967), since  $b$  is closely related to the maximal, low-  
 density growth rate  $r = b - d$  (Pianka, 1972), yet in the  $r/K$  scheme, high density populations  
 should be subject to  $K$ , not  $r$ , selection.

447 It is not surprising that  $b$  can matter at high densities. In our model (or any lottery model of  
 competition),  $b$  matters at high densities because territorial contests among juveniles are intrinsi-  
 cally unpredictable. This is a realistic feature of the model. Even if one genotype is guaranteed to  
 450 win a territory in a “fair” contest (e.g. it is the most efficient exploiter of a limiting consumable

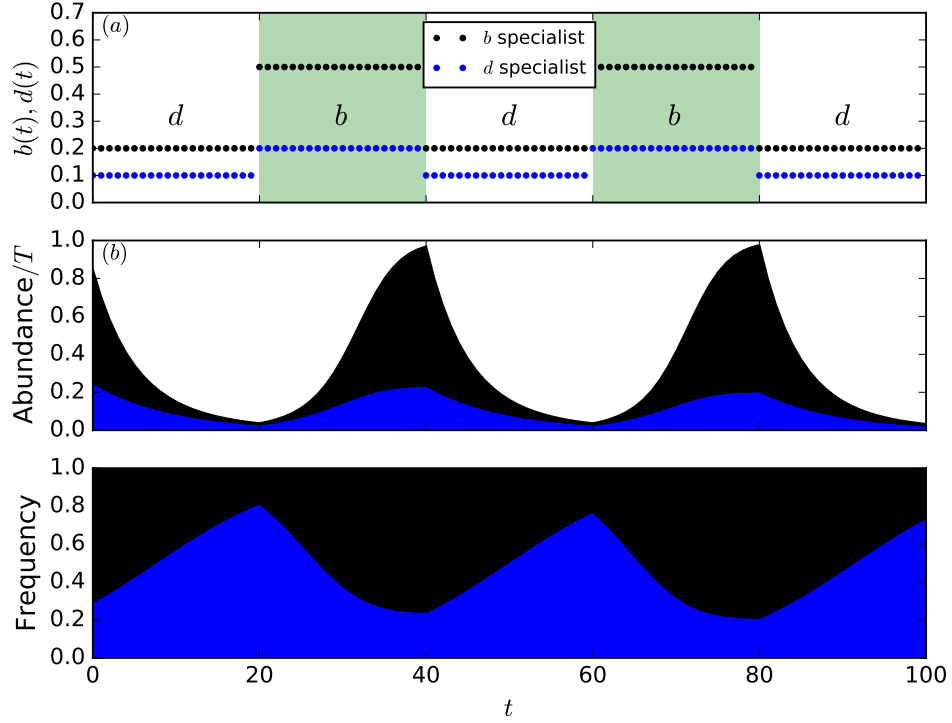


Figure 6: Stable coexistence between  $b$  and  $d$  specialists in a fluctuating environment. (a) Birth and death rates seasonally alternate being nonzero (white for winter, green for summer). The  $b$  specialist (black) has higher  $b$  and  $d$  ( $b = 0.5$ ,  $d = 0.2$ ) than the  $d$  specialist ( $b = 0.2$ ,  $d = 0.1$ ) (blue). (b) Both types grow during the positive  $b$  phase, and decline during the positive  $d$  phase, but the  $d$  specialist does so at a lower rate. Total height (blue+black) is population density  $N/T$ . (c) Summer favors the  $b$  specialist, winter the  $d$  specialist, and they stably coexist.

resource; Tilman 1982), inferior competitors can win by chance. For example, an inferior competitor's propagules may happen to arrive first, gaining a decisive developmental advantage. First arrivals are more likely to occur for genotypes with a fecundity and/or dispersal advantage, as represented by higher  $b$  in lottery models. The analogous intuition in the Wright-Fisher model is that fecundity confers a relative fitness advantage, even though population size is not changing. The logistic model for which  $r$  and  $K$  are named, does not capture this intuition.

Confusingly, the term " $K$ -selection" sometimes refers generally to selection at high density (Pianka, 1972), encompassing both selection for higher saturation density (MacArthur and Wilson, 1967) and competitive ability (Gill, 1974). Contrary to an  $r/K$  dichotomy, empirical studies have shown that maximal growth rate and saturation density (measured by abundance) are positively correlated, both between species/strains (Fitzsimmons et al., 2010; Hendriks et al., 2005; Kuno, 1991; Luckinbill, 1979), and as a result of experimental evolution (Luckinbill, 1978, 1979). From the perspective of our model, this correlation is not surprising since the saturation density, which is determined by a balance between births and deaths, increases with  $b$ .

There is support for a negative relationship between competitive success at high density and maximal growth rate (Luckinbill, 1979), consistent with an  $r/K$  dichotomy. This could be driven by a tradeoff between individual size and reproductive rate. To avoid confusion with other forms of " $K$ -selection", selection for competitive ability has been called " $\alpha$ -selection" after the competition coefficients in the Lotka-Volterra equation (Case and Gilpin, 1974; Gill, 1974; Joshi et al., 2001). However, competitive success as measured by  $\alpha$  (i.e. the per-capita effect of one genotype on another genotype's growth rate) is only partly determined by individual competitive ability — in the presence of age-structured competition and territoriality, it also includes the ability of each genotype to produce contestants i.e.  $b$  in our model. Our  $c$  is strictly competitive ability only — as such, changes in  $c$  do not directly affect population density (section "Model"). The clean separation of a strictly-relative  $c$  parameter is particularly useful from an evolutionary genetics perspective, essentially embedding a zero-sum relative fitness trait within a non-zero-sum fitness model. This could have interesting applications for modeling the impacts



of intra-specific competition on species extinction, for example due to clonal interference (Desai and Fisher, 2007; Gerrish and Lenski, 1998) between *c*-strategists on the one hand, and *b*- and *d*-  
480 strategists on the other.

*K*-selection in the narrow logistic sense of selection for a greater environmental carrying capacity for given birth and death rates, sometimes referred to as “efficiency” (MacArthur and  
483 Wilson, 1967), could be represented in our model by smaller individual territorial requirements. To a first approximation, two co-occurring genotypes which differ by a small amount in their territorial requirements only should have the same fitness since the costs or benefits of a change in  
486 the amount of unoccupied territory is shared equally among genotypes via the propagule density per territory  $L$ . The situation is more complicated when the differences in territorial requirements become large enough that territorial contests can occur on different scales for different genotypes.  
489 We leave these complications for future work.

In the classic lottery model,  $b_i$  and  $c_i$  are essentially 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  
492 the case in our density- and frequency-dependent generalization, 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  
495 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 fluctuating environments our model would likely give similar co-existence  
498 predictions as Chesson and Warner (1981), which revolve around the “storage effect”, since we retain overlapping generations and competition at the juvenile phase only.

Our realization of Grime’s triangle (Fig. 4) differs from approaches which identify primary  
501 strategies as trait combinations which can co-exist (Bolker and Pacala, 1999), referring instead to the direction of adaptive trait evolution under different regimes of stress and disturbance, which  
504 is closer in spirit to Grime’s arguments (Grime, 1974, 1977). In addition, we have not assumed any

kind of trade-offs or pleiotropy between  $b$ ,  $c$  and  $d$ , only constraints imposed by the environment on the order of magnitude of  $b$  and  $d$ . As an example of a trade-off, corals which rapidly out-  
507 shade neighbors have a tall, branched morphology which is vulnerable to disturbances, and so, all else being equal, ideal environment  $c$ -strategists will suffer higher mortality from disturbances (Darling et al., 2012). Fig. 5 gives the same conclusion without invoking trade-offs; mutations  
510 which reduce disturbance vulnerability are essentially neutral under ideal conditions, leading to no improvements in mortality from disturbances, whereas  $c$  will tend to increase over time. Thus, while trade-offs may amplify specialization, and are sometimes invoked to explain primary  
513 strategy schemes (Aerts, 1999; MacArthur and Wilson, 1967; Winemiller and Rose, 1992), they are not necessary for it.

One limitation of our model as a general-purpose model of density-dependent selection is  
516 the restriction of competition 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 resource  
519 competition models, which restrict their attention to exploitation competition, typically without age structure (Tilman, 1982). In the particular case that resources are spatially localized (e.g. due to restricted movement through soils), resource competition and territorial acquisition effectively  
522 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.  
525 It seems plausible that explicit resource tracking may not be necessary when the focus is on the evolution of similar genotypes rather than the stable co-existence of widely differing species (Ram et al., 2016). We are not aware of any attempts to delineate conditions under which explicit  
528 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  
531 to date been focused on narrower issues of the role of competition at low resource availability

(Aerts, 1999; Davis et al., 1998; Tilman, 2007).

While our model can be applied to species rather than genotypes (e.g. ecological invasions),  
534 our focus is genotype evolution. 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  
537 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 genotype evolution.

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## Appendix A: Poisson approximation

For each genotype's dispersal, the counts of propagules across unoccupied territories follows a multinomial distribution with equal probabilities of landing in each territory. Thus, the  $x_i$  in different territories are not independent random variables. However, for sufficiently large  $T$ , holding  $n_i/T$  fixed, the Poisson limit theorem implies that this multinomial distribution for the  $x_i$  accross territories is closely approximated by a product of independent Poisson distributions for each territory, each with rate parameter  $l_i$  (large  $T$  implies large  $U$  except in the biologically uninteresting case that there is vanishing population turnover  $d_i \sim 1/T$ ).

Alternatively, we could have assumed a Poisson distribution for the  $x_i$  as our model of dispersal from the outset. The total number of genotype  $i$  propagules  $\sum x_i$  (summed over unoccupied territories) would then no longer be a constant  $m_i$ , but would fluctuate between generations for a given mean  $m_i$ , which is more biologically realistic. Nevertheless, for simplicity and ease of comparison with the classic lottery model, we ignore the possibility of fluctuations in  $m_i$  and focus instead on Poisson fluctuations propagule composition in each territory.

## 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

$$\Delta_u n_i = U l_i e^{-L} = m_i e^{-L}. \quad (11)$$



## 666 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  
 669  $X_i = \sum_{j \neq i} x_j$  is the number of nonfocal propagules. The number of territories where this occurs is  $Up_i(1)P(X_i \geq 1) = b_i n_i e^{-l_i}(1 - e^{-(L-l_i)})$ . Thus

$$\Delta_r n_i = m_i e^{-l_i}(1 - e^{-(L-l_i)}) \left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}}, \quad (12)$$

where  $\langle \rangle_{\tilde{p}}$  denotes the expectation with respect to  $\tilde{p}$ , and  $\tilde{p}$  is the probability distribution of  
 672 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. (12),

$$\left\langle \frac{c_i}{c_i + \sum_{j \neq i} c_j x_j} \right\rangle_{\tilde{p}} \approx \frac{c_i}{c_i + \sum_{j \neq i} c_j \langle x_j \rangle_{\tilde{p}}}. \quad (13)$$

675 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

$$\begin{aligned} \tilde{p}(\mathbf{x}_i) &= p(\mathbf{x}_i | X \geq 2, x_i = 1) \\ &= \frac{P(\mathbf{x}_i, X \geq 2 | x_i = 1)}{P(X \geq 2)} \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) p(\mathbf{x}_i | X_i = X - 1), \end{aligned} \quad (14)$$

and so

$$\begin{aligned}\langle x_j \rangle_{\tilde{p}} &= \sum_{\mathbf{x}_i} \tilde{p}(\mathbf{x}_i) x_j \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{X=2}^{\infty} P(X) \sum_{\mathbf{x}_i} p(\mathbf{x}_i | X_i = X - 1) x_j.\end{aligned}\quad (15)$$

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,

$$\begin{aligned}\langle x_j \rangle_{\tilde{p}} &= \frac{l_j}{1 - (1 + L)e^{-L}} \frac{1}{L - l_i} \sum_{k=2}^{\infty} P(X)(X - 1) \\ &= \frac{l_j}{1 - (1 + L)e^{-L}} \frac{L - 1 + e^{-L}}{L - l_i},\end{aligned}\quad (16)$$

where the last line follows from  $\sum_{X=2}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)(X - 1) = \sum_{X=1}^{\infty} P(X)X -$   
<sup>678</sup>  $\sum_{X=1}^{\infty} P(X)$ .

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

$$\begin{aligned}
\sigma_{\tilde{q}}^2(x_j) &= \langle x_j^2 \rangle_{\tilde{q}} - \langle x_j \rangle_{\tilde{q}}^2 \\
&= \frac{1}{C} \langle x_j^2 \rangle_p - \frac{l_j^2}{C^2} \\
&= \frac{1}{C} (l_j^2 + l_j) - \frac{l_j^2}{C^2} \\
&= \frac{l_j^2}{C} \left( 1 - \frac{1}{C} \right) + \frac{l_j}{C},
\end{aligned} \tag{17}$$

and

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

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. (16) 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  
693  $\tilde{q}$  is comparable to, or greater than, the entire propgaule density.

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

$$\sigma_{\tilde{q}}^2(\sum_{j \neq i} c_j x_j) = \sum_{j \neq i} \left[ c_j^2 \sigma_{\tilde{q}}^2(x_j) + 2 \sum_{k > j, k \neq i} c_j c_k \sigma_{\tilde{q}}(x_j, x_k) \right], \quad (19)$$

and using the fact that  $\sigma_{\tilde{q}}(x_j, x_k)$  and the first term in Eq. (17) are negative because  $C < 1$ , we  
696 obtain an upper bound on the relative fluctuations in  $\sum_{j \neq i} c_j x_j$ ,

$$\frac{\sigma(\sum_{j \neq i} c_j x_j)}{\langle \sum_{j \neq i} c_j x_j \rangle} = C^{1/2} \frac{\left( \sum_{j \neq i} c_j^2 l_j + (1 - 1/C) \left( \sum_{j \neq i} c_j l_j \right)^2 \right)^{1/2}}{\sum_{j \neq i} c_j l_j} < C^{1/2} \frac{\left( \sum_{j \neq i} c_j^2 l_j \right)^{1/2}}{\sum_{j \neq i} c_j l_j}. \quad (20)$$

Suppose that the  $c_j$  are all of similar magnitude (their ratios are of order one). Then Eq. (20)  
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  
699 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. (20) gives a relative error of  
approximately 50%, which from our earlier discussion we know to be a substantial overestimate  
702 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  
705 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 genotypes  $j'$ , and  $l_j \ll 1$ ), then the RHS of Eq. (20) can be large and we  
cannot make the replacement Eq. (13).

708 Substituting Eqs. (13) and (16) into Eq. (12), we obtain

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{C}, \quad (21)$$

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

## Competition when abundant

711 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. (12), we have

$$\Delta_a n_i = U(1 - (1 + l_i)e^{l_i}) \left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \quad (22)$$

where  $\hat{p}$  is the probability distribution of both focal and nonfocal propagaule abundances *after* 714 dispersal in those territories where at least two focal propagules landed.

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

$$\left\langle \frac{c_i x_i}{\sum_j c_j x_j} \right\rangle_{\hat{p}} \approx \frac{c_i \langle x_i \rangle_{\hat{p}}}{\sum_j c_j \langle x_j \rangle_{\hat{p}}}. \quad (23)$$

Following a similar procedure as for  $\Delta_r n_i$ , where the vector of propagule abundances is denoted  $\mathbf{x}$ , the mean focal genotype abundance is,

$$\begin{aligned} \langle x_i \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_i p(\mathbf{x} | x_i \geq 2) \\ &= \sum_{x_i} x_i p(x_i | x_i \geq 2) \\ &= \frac{1}{1 - (1 + l_i)e^{-l_i}} \sum_{x_i \geq 2} p(x_i) x_i \\ &= l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}}. \end{aligned} \quad (24)$$

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

$$\begin{aligned}
\langle x_j \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_j p(\mathbf{x} | x_i \geq 2) \\
&= \sum_X P(X | x_i \geq 2) \sum_{\mathbf{x}} x_j p(\mathbf{x} | x_i \geq 2, X) \\
&= \sum_X P(X | x_i \geq 2) \sum_{x_i} p(x_i | x_i \geq 2, X) \sum_{\mathbf{x}_i} x_j p(\mathbf{x}_i | X_i = X - x_i) \\
&= \sum_X P(X | x_i \geq 2) \sum_{x_i} p(x_i | x_i \geq 2, X) \frac{l_j(X - x_i)}{L - l_i} \\
&= \frac{l_j}{L - l_i} \left[ \sum_X P(X | x_i \geq 2) X - \sum_{x_i} p(x_i | x_i \geq 2) x_i \right] \\
&= \frac{l_j}{L - l_i} \left( L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}} \right). \tag{25}
\end{aligned}$$

717 To calculate the relative fluctuations in  $\sum_{j \neq i} c_j x_j$ , we use a similar approximation as for  $\Delta_r n_i$ :  $\hat{p}$   
is approximated by  $\hat{q}$ , defined as the  $\mathbf{x}$  dispersal probabilities in a territory conditional on  $x_i > 2$   
(that is, treating the  $x_j$  as independent). All covariances between nonfocal genotypes are now zero,  
720 so that  $\sigma_{\hat{q}}^2(\sum c_j x_j) = \sum c_j^2 \sigma_{\hat{q}}^2(x_j)$ , where  $\sigma_{\hat{q}}^2(x_j) = l_j$  for  $j \neq i$ , and

$$\sigma_{\hat{q}}^2(x_i) = \frac{l_i}{D} \left( l_i + 1 - e^{-l_i} - \frac{l_i}{D} (1 - e^{-l_i})^2 \right), \tag{26}$$

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

$$\frac{\sigma_{\hat{q}}(\sum c_j x_j)}{\langle \sum c_j x_j \rangle} = \frac{\left( \sum_{j \neq i} c_j^2 l_j + c_i^2 \sigma_{\hat{q}}^2(x_i) \right)^{1/2}}{\sum_{j \neq i} c_j l_j + c_i l_i (1 - e^{-l_i}) / D}. \tag{27}$$

Similarly to Eq. (20), the RHS of Eq. (27) is  $\ll 1$  for the case that  $L \ll 1$  (due to a factor of  
723  $D^{1/2}$ ), and also for the case when at least some of the propagule densities (focal or nonfocal) are  
large — provided that  $c_i$  and the  $c_j$  are all of similar magnitude. Again, the worst case scenario  
occurs when  $l_i$  and  $L - l_i$  are of order 1, in which case Eq. (27) is around 35%, which is again  
726 where the  $\hat{q}$  approximation produces the biggest overestimate of the fluctuations in  $\mathbf{x}$ . Similarly

to Eq. (20), the RHS of (27) will not be  $\ll 1$  in the presence of a rare, extremely strong competitor.

Combining Eqs. (22) and (23), we obtain

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \quad (28)$$

729 where  $A_i$  is defined in Eq. (7).