

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

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*Manuscript elements:* Figure 1, figure 2, table 1, online appendices A and B (including figure A1 and figure A2). Figure 2 is to print in color.

*Keywords:* Examples, model, template, guidelines.

*Manuscript type:* Article.

Prepared using the suggested L<sup>A</sup>T<sub>E</sub>X template for *Am. Nat.*

## **Abstract**

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

## Introduction

Evolutionary models differ greatly in their treatment of fitness. In models of genetic evolu-  
9 tion, 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  
12 be justified over sufficiently short time intervals (Ewens, 2012, p. 276). However, selection can  
have very different effects when operating on different types of traits, and evolutionary changes  
in one population can lead to complicated ecological responses.

15 By contrast, models of phenotypic trait evolution represent the change in phenotypic abun-  
dances 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  
18 eco-evolutionary feedbacks between co-evolving traits, but is generally problem-specific and re-  
stricted to only a few traits at a time.

Far less work has been done to model fitness in more general terms than particular traits or  
21 ecological scenarios, while still capturing 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  
24 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, 2012, p. 276). Even MacArthur’s famous  $r/K$  selection  
27 scheme 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). In spite of the r/K scheme's original purpose as an extension of the existing population-genetic treatment of selection to account for population density (MacArthur, 1962), comparatively few attempts have been made to develop it further as a mathematical analysis of the major different forms of selection.

Nevertheless, there are strong indications there are broader principles governing the operation of selection. In many groups of organisms, including corals (Darling et al., 2012), insects (Southwood, 1977), fishes (Winemiller and Rose, 1992), zooplankton (Allan, 1976) and plants (Grime, 1988), different species can be divided into a small number of distinct trait clusters corresponding to fundamentally distinct "primary strategies" (Winemiller et al., 2015). The most famous example is Grime's plant trait classification scheme (Grime, 1974, 1977, 1988). 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: 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). Trait classification schemes for other organisms are broadly analogous to Grime's scheme (Winemiller et al., 2015).

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 mathematical, a recognized hinderance 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, spatially-homogeneous model of genotype 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 primarily with Grime’s C/S/R scheme in mind, and represents a quantitative formalization of how C/S/R manifests at the level of genotype evolution (as opposed to divergence between species). This choice is motivated in part by the substantial empirical support for the C/S/R scheme, 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, in which case r- and K- selection will effectively coincide (more details in the Discussion).

In section

## Model

We assume that each individual in a population requires its own territory to survive and reproduce (a site-occupancy model). All territories are identical, and the total number of territories is  $K$ . Time  $t$  advances in discrete iterations, each representing the average time from birth to reproductive maturity. In iteration  $t$ , the number of reproductively mature individuals (henceforth called “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  $U(t) = K - N(t)$ .

Each iteration, adults produce  $m_i$  new offspring (henceforth called “propagules”) which disperse at random over the  $U$  unoccupied territories (no dispersal limitation). We assume adults

cannot be ousted from occupied territories, so only propagules landing on occupied territories  
 81 are included in  $m_i$ . More generally,  $m_i$  does not include propagules which never even begin the  
 development cycle. For simplicity, we assume  $m_i = b_i n_i$ , where  $b_i$  is a constant, genotype-specific  
 birth rate.

84 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  $K \rightarrow \infty$ , with  $n_i/K$  held fixed,  $x_i$  is Poisson  
 distributed with mean territorial propagule density  $l_i = m_i/U$ . Although  $K$  is finite in our  
 87 model, we assume that  $K$  and the  $n_i$  are large enough that  $x_i$  is Poisson-distributed to a good  
 approximation (details in Appendix A). This dispersal Poisson distribution is denoted  $p_i(x_i)$ .  
 Note that the large  $n_i$ , large  $K$  approximation places no restrictions on our densities  $n_i/K$ , but it  
 90 does preclude consideration of demographic stochasticity when  $n_i$  itself is very small (this will  
 be discussed further in Section ).

When multiple propagules land on the same territory, they compete to secure the territory  
 93 as they develop. This territorial contest is modeled as a weighted lottery: the probability that  
 genotype  $i$  wins a given territory by the next iteration is  $c_i x_i / \sum_j c_j x_j$  where  $c_i$  is a constant  
 representing relative competitive ability.

96 The increase in  $n_i$  over one iteration due to territorial acquisition,  $\Delta_+ n_i$ , is the sum of genotype  
 $i$ 's victories over all  $U$  unoccupied territories. Since  $p_1(x_1) \dots p_G(x_G)$  is equal to the proportion  
 of unoccupied territories with  $x_1, \dots, x_G$  of the respective propagules (again, we assume that  $K$   
 99 is large enough that fluctuations in this proportion are negligible), this sum can be replaced by  
 an expectation over the  $p_i$ . This gives

$$\Delta_+ n_i(t) = U(t) \sum_{x_1, \dots, x_G} \frac{c_i x_i}{\sum_j c_j x_j} p_1(x_1) \dots p_G(x_G). \quad (1)$$

In addition to propagule birth and competition, occupied territories become unoccupied due  
 102 to mortality. For the vast majority of this manuscript we assume that mortality only occurs  
 in adults, and at a constant, genotype-specific per-capita rate  $d_i$ , so that the overall change in

genotype abundances is

$$\Delta n_i(t) = \Delta_+ n_i(t) - d_i n_i(t). \quad (2)$$

105 We will introduce a different mortality model when we consider the effects of disturbances (Section ??), which will also affect competing juveniles.

Note that the competitive ability coefficients  $c_i$  represent a strictly relative aspect of fitness in  
108 the sense that they only influence population size  $N$  indirectly by changing genotype frequencies; that may in turn change the population mean birth and death rates. This can be seen by summing Eq. (2) over genotypes to get the change in population size  $N$ ,

$$\Delta N = U(1 - e^{-L}) - \sum_i d_i n_i, \quad (3)$$

111 which is independent of  $c_i$  (here  $L = \sum_j l_j$  is the overall propagule density).

## Results

### Mean Field Approximation

114 Eq. (2) gives little intuition about the dynamics of density-dependent lottery competition, since (1) involves an expectation over the random dispersal distributions  $p_i$ , which depend on how the  $n_i$  change over time. We now evaluate this expectation using a “mean field” approximation; the  
117 intuition behind this approximation is as follows.

If the unoccupied territories are saturated with propagules from every genotype ( $l_i \gg 1$  for all genotypes), the fluctuations in the  $x_i$  are small compared to their means  $l_i$  (since the  $x_i$  are  
120 Poisson distributed), and so the composition of propagules in a territory will only rarely differ appreciably from the mean composition  $l_1, l_2, \dots, l_G$ . Consequently, we can replace  $x_i$  with  $l_i$  in Eq. (1). This gives the classic lottery model (Chesson and Warner, 1981),

$$\Delta_+ n_i(t) = U(t) \frac{c_i m_i}{\sum_j c_j m_j} = b_i n_i \frac{1}{L} \frac{c_i}{\bar{c}}, \quad (4)$$

123 where  $\bar{c} = \sum_j c_j m_j / M$  is the mean propagule competitive ability for a randomly selected propagule ( $M = \sum_j m_j$  is the total number of propagules).

However, in general the  $l_i$  are not all large, and the  $x_i$  cannot simply be replaced by their  
 126 means in Eq. (1). Indeed, Eq. (4) is nonsensical if  $l_i$  is sufficiently small: genotype  $i$  can win at  
 most  $m_i$  territories, yet Eq. (4) demands a fraction  $c_i m_i / \sum_j c_j m_j$  of the unoccupied territories  $U$ ,  
 no matter how large  $U$  is. The source of this pathological behavior when  $l_i \ll 1$  is that  $x_i = 1$  in  
 129 the few territories where  $i$  propagules do land, and so  $i$ 's growth comes entirely from territories  
 which deviate appreciably from the mean.

Our mean field approximation is similar to the high- $l_i$  approximation leading to Eq. (4)  
 132 in that we replace the  $x_i$  with appropriate mean values. The key distinction is that territories  
 with a single propagule from the focal genotype, which are critical at low densities, are handled  
 separately. In place of the requirement of  $l_i \gg 1$  for all  $i$ , our approximation only requires  
 135 that there are no large discrepancies in competitive ability (discussed further below). We obtain  
 (details in Appendix B)

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

where

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

138 and

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

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  
 141 unoccupied territories; these territories are won without contest. The second term,  $R_i c_i/\bar{c}$  repre-  
 sents competitive victories when the  $i$  genotype is a rare invader in a high density population:  
 from Eq. (6),  $R_i \rightarrow 0$  when the  $i$  genotype is abundant ( $l_i \gg 1$ ), or other genotypes are collectively  
 144 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  
 the overall propagule density  $L$  and the relative propagule frequencies  $l_i/L$ . If  $l_i \gg 1$  for all  
 147 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 for each genotype.

Fig. 1 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 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 enough (Fig. 1b). 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. 1d).

### Invasion of rare genotypes and coexistence

To determine how  $b$ ,  $c$  and  $d$  will evolve in a population where those traits 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  $\Delta n_i = 0$ , and so Eq. (5) gives

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

Now suppose that a new genotype  $j$ , which is initially rare, appears in the population. Then  $A_j \ll 1$ ,  $l_j \ll L$  and  $\bar{c} \approx c_i$ , and so, from Eq. (5),  $n_j$  will increase if

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

Combining Eqs. (8) and (9), it is easily verified that if  $j$  is superior in one trait, but otherwise identical to  $i$ , it will invade. Moreover,  $j$  will eventually exclude  $i$ , since it is strictly superior. However, stable coexistence is possible between genotypes that are superior in different traits. To illustrate, suppose that  $j$  is better at securing territories ( $c_j > c_i$ ), that  $i$  is better at producing propagules ( $b_i > b_j$ ), 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”). It is not hard

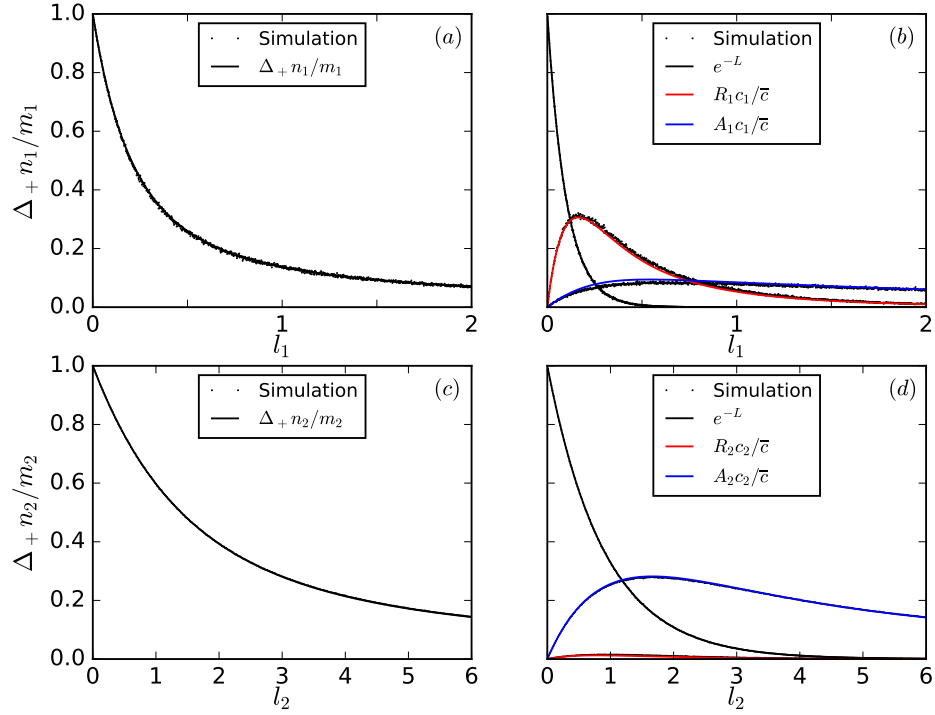


Figure 1: The change in genotype abundances in a density dependent lottery model is closely approximated by Eq. (5).  $\Delta_+ n_i / m_i$  from Eq. (5) (and its separate components) are shown, along with direct simulations of random dispersal and lottery competition over one iteration over a range of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

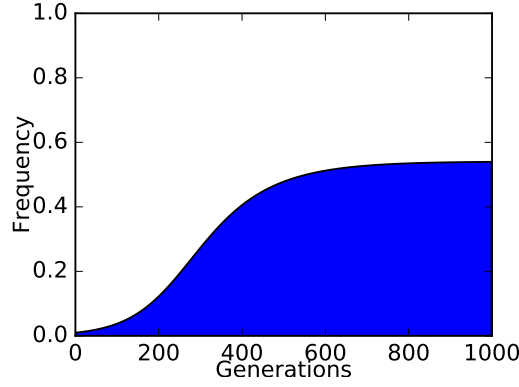


Figure 2: Coexistence between  $b$  ( $c_i = 1$ ,  $b_i = 1$ ) and  $c$  ( $c_j = 2$ ,  $b_j = 0.7$ ) specialists, where  $d_i = d_j = 0.3$ . Vertical axis shows frequency of the  $c$ -specialist predicted by Eq. (5).

to show that this is possible, since 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), 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  $c_j$  is large enough. Intuitively, the mechanism for coexistence is that territorial contests are important in an  $i$ -dominated population (high  $L$ ), ensuring that the  $c$ -specialist  $j$  is not excluded, yet territorial contests are irrelevant in a  $j$ -dominated population (low  $L$ ), ensuring that the  $b$ -specialist  $i$  is not excluded. Fig. 2 shows an example of this coexistence between  $b$  and  $c$  specialists.

A similar argument applies for coexistence between high- $c$  and low- $d$  specialists; again coexistence occurs because the importance of territorial contests declines along with propagule density  $L$  as the  $c$ -specialist increases in frequency. Coexistence is technically possible between  $b$ - and  $d$ -specialists which exactly satisfy  $b_i/d_i = b_j/d_j$  (this follows from the fact that all propagules have the same probability of success when  $c_i = c_j$  i.e.  $A_i + R_i = A_j + R_j$ ). However, this coexistence scenario is not biologically relevant, since the tiniest deviation from  $b_i/d_i = b_j/d_j$  will lead to the eventual exclusion of the genotype with greater  $b_i/d_i$ .

186 If the rare genotype  $j$  arises due to mutation, then it's initial low-density behavior is more complicated than the above invasion analysis suggests. The mutant lineage starts with one individual  $n_j = 1$ , and remains at low abundance for many generations after its initial appearance. 189 During this period, the mutant abundance  $n_j$  will behave stochastically, and the deterministic equations (1) and (5) do not apply (Section ). However, if  $n_j$  becomes large enough, its behavior will become effectively deterministic, and governed by Eq. (5). For mutants with fitness greater 192 than the population mean fitness, this process is known as "establishment", and occurs when  $n_j$  is of order  $1/s$ , where  $s$  is the mutant's fitness advantage relative to the mean (Desai and Fisher, 2007). Here we do not consider the initial stochastic behavior of novel mutants, and have 195 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 starts when  $n_j \ll N$ .

## 198 **Primary strategies and Grime's triangle**

We now discuss which changes in the traits  $b, c$  and  $d$  will be most favored under different environmental conditions. Of particular interest are Grime's "disturbance", "stress" and "ideal" 201 environmental archetypes. To proceed, we need to map these verbal archetypes to quantitative parameter regimes in our model.

The ideal environmental archetype is characterized by the near-absence of stress and distur- 204 bance. Consequently,  $d_i \ll 1$ , whereas  $b_i$  is potentially much larger than 1. From Eq. (3), the equilibrium value of  $L$  only depends on the ratio of birth and death rates. For one genotype,  $L/(1 - e^{-L}) = b_i/d_i$ , and so the propagule density is high  $L \approx b_i/d_i \gg 1$ . Moreover, since 207  $L = b_i N/(N - K)$  by definition, population density is also high  $N/K \approx 1$ . Thus, territorial contests are decisively important.

The disturbance archetype is characterized by unavoidably high extrinsic mortality caused by 210 physical destruction. Disturbances do not only affect adults as in Eq. (2), but also juveniles in the process of territorial contest. These juvenile deaths can be represented as a fractional reduction

in the number of territories secured. To illustrate, we assume that the disturbance is equally  
 213 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. Then, the disturbance archetype is characterized by  $d_i$  being  
 close to 1 for all genotypes (almost all adults and juveniles are killed each iteration). The single  
 216 genotype equilibrium then gives  $L \approx 2(1 - d_i/[(1 - d_i)b_i])$ , where  $b_i$  must be exceptionally large  
 to ensure population persistence, and we have  $L \ll 1$  and  $N/K \ll 1$ . The terms proportional to  
 $c_i/\bar{c}$  in Eq. (5) are then negligible, and  $\Delta_+n_i$  depends primarily on  $b_i$ .

219 The stress archetype is more ambiguous, and has been the subject of an extensive debate  
 in the plant ecology literature (the “Grime-Tilman” debate; Aerts 1999). Stressful environments  
 severely restrict growth and reproduction, so that  $b_i \ll 1$  Grime (1974, 1977). Mutations which  
 222 appreciably improve  $b_i$  will be either non-existent or extremely unlikely, so  $b_i$  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  $b_i/d_i \approx 1$  in our  
 225 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 stressful environments simply have a lower carrying capacity  
 228 (Taylor et al., 1990); in our model, this means a greater per-individual territorial requirement  
 represented by a lower  $K$  for a given amount of space. In particular, it is argued that when stress  
 is induced by a scarcity of consumable resources, competition for those resources would likely  
 231 be intense. Thus,  $b_i$  need not be particularly close to  $d_i$ , but contests for consumable resources at  
 the juvenile phase would kill off most propagules before adulthood. In other words, the stressed  
 population is a high density population where competition is important (Taylor et al., 1990) (that  
 234 is, high density relative to  $K$ , not relative to ideal conditions).

The mapping of environmental archetypes to our model parameters is summarized in the first  
 two rows of Fig. 3. Also shown is the approximate dependence of  $\Delta_+n_i$  on  $b_i$  and  $c_i$  for each  
 237 archetype (third row). These can be used infer the expected direction of evolution for the traits  
 $b, c$  and  $d$  (fourth row) as follows.

	Ideal	Disturbance*	Stress (G)	Stress (K)
Parameter-	$d \ll 1$	$d \approx 1$	$b \ll 1$	$b \ll 1$
regime	$b/d \gg 1$	$b/d \gg 1$	$b \approx d$	$b > d$
Density $N/K$	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 3: The realization of Grime’s environmental archetypes in our model, as well as the low- $K$  variant of the stress archetype. Shown are the mapping to our parameters of each archetype, 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 disturbance archetype, with  $\Delta_+ n_i$  replaced by  $(1 - d_i)\Delta_+ n_i$  in Eq. (2).

As noted in the previous section, if beneficial mutations establish (i.e survive the low-abundance stochastic regime), they will proceed to grow deterministically according to Eq. (5). The probability of establishment 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 confer an appreciable benefit, subject to the constraints imposed by the environment.

For example, in Grime’s version of the stress archetype,  $L$  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, by definition of the stress archetype,  $b$  is constrained to be small. Thus, while some rare mutations may produce small improvements in  $b$ , it is much more likely that mutations will arise that lower  $d$ , making this the expected direction of evolutionary change for Grime’s stress archetype.

Following Grime’s original argument for a triangular scheme (Grime, 1977), Fig. 4 represents each environmental archetype schematically as a vertex on a triangular space defined by

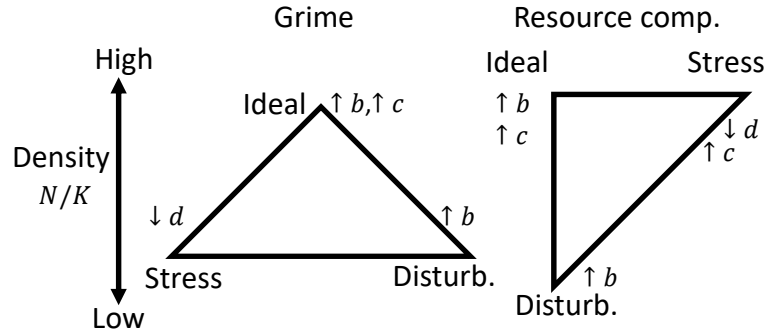


Figure 4: The realization of Grime’s triangle in our model. Schematic representation of the triangular space bounded by the low/high extremes of stress/disturbance. The low- $K$  interpretation of stress is also shown. The vertices of the triangles correspond to environmental archetypes. Selection favors different traits at each vertex, leading to different trait clusters.

perpendicular stress and disturbance axes. The ideal archetype lies at the origin (no stress or disturbance), while the stress and disturbance archetypes 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 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 and the starting assumption of our model is site-occupancy .

In disturbed environments, we predict evolution for higher  $b$  and lower  $d$ , but not higher  $c$ . Higher  $b$  means higher fecundity, but not necessarily mass propagule production:  $b$  represents only those propagules which successfully develop into juveniles in unoccupied territories. This is broadly consistent with the ruderal primary strategy. Plant ruderals devote a large proportion

of their productivity to seed production Grime (1977), whereas the analogous “opportunistic” strategists in fishes have large intrinsic growth rates (Winemiller and Rose, 1992). In corals, a distinguishing feature of the ruderal cluster is brood spawning (rather than broadcast spawning). This corresponds to higher parental investment and lower overall propagule production, but potentially also higher  $b$  at low densities, since broadcast spawners are vulnerable to a powerful Allee effect at the egg fertilization stage (Knowlton, 2001). Lower  $d$  could be achieved by improved individual resistance to physical destruction, but it is hard to reduce mortality in the face of severe disturbances. Given this constraint, shortening the time to reproductive maturity (the iteration time in our model) is an effective way of reducing the chance of death per iteration  $d$ . An exceptionally short life cycle is probably the most defining characteristic of ruderals (Darling et al., 2012; Grime, 1977; Winemiller and Rose, 1992).

In stressful environments, we predict evolution for lower  $d$ , and also for higher  $c$  in the low- $K$  interpretation of the stress archetype. Lowering  $d$  is obviously essential when  $b \ll 1$ , and stress 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 resource 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 low- $K$  interpretation).

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 is rapidly outgrowing and “shading out” competitors; not surprisingly, rapid individual growth is a defining feature of the competitor trait cluster (Darling et al., 2012; Grime, 1977). Evolution for higher  $b$  under high-density, competitive conditions may seem counter-intuitive. Neither particularly high nor low  $b$  have been associated with the competitor strategy in plants and corals. However, for fishes, the analogous “periodic” strategy is characterized by enormous brood sizes as well as rapid development (Winemiller et al., 2015; Winemiller and Rose, 1992), suggesting a strategy of ensuring that many propagules



actually end up contesting areas favorable for development (higher  $b$ ). The evolution of  $b$  in ideal  
297 environments will be discussed further in the Discussion.

## Discussion

Unlike Grime's classic ternary plot for observed traits (Grime, 1974), our realization of Grime's  
300 triangle (Fig. 4) refers only to the direction of trait evolution. We have made no appeal to, or  
attempted to explain, trade-offs between the traits relevant for success in different environmental  
archetypes. Unlike a ternary plot representing constraints between traits, our triangle reflects the  
303 underlying limits of survival under combined stress and disturbance.

given that  $b$  is closely related to the low-density reproductive rate  $r = b - d$ , and the opposite  
outcome is expected in MacArthur's  $r/K$  dichotomy (MacArthur, 1962).

306 Apart from the prediction of evolution for higher  $b$  in ideal environments,

The model developed here is a density-dependent generalization of the classic lottery model  
(Results section).

309 Our model differs from both Grime's C/S/R and MacArthur's  $r/K$  schemes in the role of the  
propagule production rate  $b$ , a measure of intrinsic fecundity closely related to the growth rate  
at low densities  $r = b - d$ . In both of those schemes, the essential feature of life at high densities  
312 is competition. This is less in the  $r/K$  scheme, which does not explicitly it is better to have a  
contributes just as much to

In the Introduction, we noted that the  $r$ - $K$  dichotomy is not consistent with "K-selection" (i.e.  
315 selection at high densities) for growth ability traits.

Specifically, positive correlations between measures of  $r$  and  $K$  are common, both between  
species and strains (Fitzsimmons et al., 2010; Hendriks et al., 2005; Kuno, 1991; Luckinbill, 1979),  
318 and as a result of experimental evolution (Luckinbill, 1978, 1979)). From the perspective of our  
model, this correlation is not at all surprising;

$r$ - $K$  correlation, meaning of K selection

Actual K selection  
Significance of stage structure  
caveats: large c discrepancy

## References

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* 50:29–37.

Allan, J. D. 1976. Life history patterns in zooplankton. *The American Naturalist* 110:165–180.

Boyce, M. S. 1984. Restitution of r-and k-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics* 15:427–447.

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences* 71:3073–3077.

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

Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. McClanahan, and I. M. Côté. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.

Desai, M. M., and D. S. Fisher. 2007. Beneficial mutation–selection balance and the effect of linkage on positive selection. *Genetics* 176:1759–1798.

Ewens, W. J. 2012. *Mathematical Population Genetics 1: Theoretical Introduction*, vol. 27. Springer Science & Business Media.

Fitzsimmons, J. M., S. E. Schoustra, J. T. Kerr, and R. Kassen. 2010. Population consequences of mutational events: effects of antibiotic resistance on the r/k trade-off. *Evolutionary ecology* 24:227–236.

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

345 Grime, J. P. 1974. Vegetation classification by reference to strategies. *Nature* 250:26–31.

———. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American naturalist* pages 1169–1194.

348 ———. 1988. *Plant Evolutionary Biology*, chap. The C-S-R model of primary plant strategies — origins, implications and tests, pages 371–393. Springer Netherlands, Dordrecht.

Hendriks, A. J., J. L. Maas-Diepeveen, E. H. Heugens, and N. M. van Straalen. 2005. Meta-analysis  
351 of intrinsic rates of increase and carrying capacity of populations affected by toxic and other stressors. *Environmental toxicology and chemistry* 24:2267–2277.

Joshi, A., N. Prasad, and M. Shakarad. 2001. K-selection,  $\alpha$ -selection, effectiveness, and tolerance  
354 in competition: density-dependent selection revisited. *Journal of genetics* 80:63–75.

Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* 98:5419–5425.

357 Kuno, E. 1991. Some strange properties of the logistic equation defined withr andk: Inherent defects or artifacts? *Researches on population ecology* 33:33–39.

Luckinbill, L. S. 1978. r and k selection in experimental populations of escherichia coli. *Science*  
360 (New York, NY) 202:1201–1203.

———. 1979. Selection and the r/k continuum in experimental populations of protozoa. *Ameri-  
can Naturalist* pages 427–437.

363 MacArthur, R. H. 1962. Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences* 48:1893–1897.

Pianka, E. R. 1970. On r- and K-Selection. *The American Naturalist* 104:592–597.

- 366 Reznick, D., M. J. Bryant, and F. Bashey. 2002. r- and k-selection revisited: The role of population regulation in life-history evolution. *Ecology* 83:1509–1520.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:337–365.
- 369 Stearns, S. C. 1977. The evolution of life history traits: A critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* 8:145–171.
- 372 Taylor, D. R., L. W. Aarssen, and C. Loehle. 1990. On the relationship between r/k selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* pages 239–250.
- 375 Tilman, D. 2007. Resource competition and plant traits: a response to craine et al. 2005. *Journal of Ecology* 95:231–234.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let  
378 the concept of trait be functional! *Oikos* 116:882–892.
- Winemiller, K. O., D. B. Fitzgerald, L. M. Bower, and E. R. Pianka. 2015. Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters* 18:737–751.
- 381 Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in north american fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196–2218.

## 384 **Appendix A: Poisson approximation**

The propagule numbers  $x_i$  in different territories are not independent random variables. To determine the dispersal outcomes in all unoccupied territories exactly, we would need to proceed  
387 territory-by-territory as follows. In the first territory we evaluate,  $x_i$  drawn from a binomial

distribution with  $m_i$  trials and success probability  $1/U$ . In the second,  $x_i$  is drawn from a binomial distribution with  $m_i - x$  trials and success probability  $1/(U - 1)$ , where  $x$  is the number of propagules that landed in the first territory. And so on.

For sufficiently large  $K$ , holding  $n_i/K$  fixed, the Poisson limit theorem implies that the binomial distributions for  $x_i$  at each successive stage of this procedure are all closely approximated by a Poisson distribution with mean  $l_i$ , where we have used the fact that large  $K$  implies large  $U$  except in the biologically uninteresting case that there is vanishing population turnover  $d_i \sim 1/K$ .

Under the Poisson approximation, the total number of genotype  $i$  propagules  $\sum x_i$  (summed over unoccupied territories) will deviate about its mean value  $m_i$ . Since the coefficient of variation of  $\sum x_i$  is proportional to  $1/\sqrt{m_i}$ , these deviations are negligible unless  $m_i$  is very small (say of order 100 or less).

## Appendix B: Derivation of growth equation

We separate the right hand side of Eq. (1) into three components  $\Delta_+ n_i = \Delta_u n_i + \Delta_r n_i + \Delta_d n_i$  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  $p$ ; for instance  $p(x_1, \dots, x_G) = p_1(x_1) \dots p_G(x_G)$  and  $p(x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_G) = p_1(x_1) \dots p_{i-1}(x_{i-1}) p_{i+1}(x_{i+1}) \dots p_G(x_G)$ . 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

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

## Competition when rare

411 The second component,  $\Delta_r n_i$ , accounts for territories where a single focal genotype propagule is present along with at least one non-focal propagule ( $r$  stands for “rare”) i.e.  $x_i = 1$  and  $\sum_{j \neq i} x_j \geq 1$ . The number of territories where this occurs is  $Up_i(1)P(\sum_{j \neq i} x_j \geq 1) = b_i n_i e^{-l_i} (1 - e^{-(L-l_i)})$ .

414 Thus

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

where  $\langle \rangle_{\tilde{p}}$  denotes the expectation with respect to  $\tilde{p}$ , and  $\tilde{p}$  is the probability distribution of nonfocal propagaule abundances  $x_j$  *after* dispersal, in those territories where exactly one focal propagule, and at least one non-focal propagule, landed.

We now show that, with respect to  $\tilde{p}$ , the standard deviation in  $\sum_{j \neq i} c_j x_j$ ,  $\sigma(\sum_{j \neq i} c_j x_j)$ , is much smaller than its mean  $\langle \sum_{j \neq i} c_j x_j \rangle_{\tilde{p}}$ . Then  $x_j$  can be replaced by its mean in the last term in Eq. (12),

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

which will give us Eq. (6).

The exact expression for  $\langle x_j \rangle_{\tilde{p}}$  is somewhat complicated. Letting  $k$  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,  $\tilde{p}$  can be written as

$$\begin{aligned} \tilde{p}(\mathbf{x}_i) &= p(\mathbf{x}_i | k \geq 2, x_i = 1), \\ &= \frac{P(k \geq 2 | \mathbf{x}_i, x_i = 1) p(\mathbf{x}_i | x_i = 1)}{P(k \geq 2)}, \\ &= \frac{p(\mathbf{x}_i | x_i = 1)}{1 - (1 + L)e^{-L}}, \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{k=2}^{\infty} P(k) p(\mathbf{x}_i | \sum_{j \neq i} x_j = k - 1), \\ &= \frac{1}{1 - (1 + L)e^{-L}} \sum_{k=2}^{\infty} \frac{P(k) \delta_{k-1}^{\sum_{j \neq i} x_j}}{P(\sum_{j \neq i} x_j = k - 1)} p(\mathbf{x}_i), \\ &= \frac{Le^{-l_i}}{1 - (1 + L)e^{-L}} \sum_{k=1}^{\infty} \left( \frac{L}{L - l_i} \right)^k \frac{\delta_k^{\sum_{j \neq i} x_j}}{k + 1} p(\mathbf{x}_i), \end{aligned} \quad (14)$$

where  $\delta_k^{\sum_{j \neq i} x_j} = 1$  if  $\sum_{j \neq i} x_j = k$ , and equals zero otherwise. Then, since

$$\begin{aligned} \sum_{\mathbf{x}_i} \delta_k^{\sum_{j \neq i} x_j} p(\mathbf{x}_i) x_j &= \frac{l_j}{L - l_j} k P(\sum_{j \neq i} x_j = k) \\ &= l_j P(\sum_{j \neq i} x_j = k - 1), \end{aligned} \quad (15)$$

after some algebra we obtain,

$$\langle x_j \rangle_{\tilde{p}} = \frac{l_j}{1 - (1 + L)e^{-L}} \frac{L - 1 + e^{-L}}{L - l_i}. \quad (16)$$

423 To calculate the relative fluctuations in  $\sum_{j \neq i} c_j x_j$ , we use the following approximation, which gives considerably simpler expressions for the means, variances and covariances of the  $x_j$  compared with the exact expressions using  $\tilde{p}$ . Rather than evaluating the situation in each territory  
426 after dispersal as above, we let  $\tilde{p}$  instead be the  $\mathbf{x}_i$  dispersal probabilities in a territory where one focal propagule is assumed to be present, conditional on  $\sum_{j \neq i} x_j > 1$ . This gives  $\langle x_j \rangle_{\tilde{p}} = l_j / C$ ,

$$\sigma^2(x_j) = \frac{l_j^2}{C} \left(1 - \frac{1}{C}\right) + \frac{l_j}{C}, \quad (17)$$

and

$$\sigma(x_j, x_k) = \frac{l_j l_k}{C} \left(1 - \frac{1}{C}\right), \quad (18)$$

429 where  $C = 1 - e^{-(L-l_i)}$  (note the difference from Eq. (16) for  $\langle x_j \rangle_{\tilde{p}}$ ). Then, since

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

and  $1/C > 1$ , we have

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

Without loss of generality, we restrict attention to the case that the total nonfocal density  $L - l_i$   
432 is of order 1 or larger (otherwise  $\Delta_r n_i$  does not contribute significantly to  $\Delta_+ n_i$  because  $\Delta_r n_i$  is proportional to  $C = 1 - e^{-(L-l_i)}$ ).

When at least some of the nonfocal propagule densities are large  $l_j \gg 1$ , then the RHS of  
435 Eq. (20) is  $\ll 1$ , as desired. This is also the case if none of the nonfocal genotype densities

are large and the  $c_j$  are all of similar magnitude (their ratios are of order one); the worst case scenario occurs when  $(L - l_i) \sim O(1)$ , in which case the negative covariances (Eq. (18)) which  
 438 were neglected in the RHS of Eq. (20) significantly reduce the overall variance  $\sigma^2(\sum_{j \neq i} c_j x_j)$ .

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, if  $c_j l_j \gg c_k l_k$  ( $j, k \neq i, j \neq k$ ) and  $l_j \ll 1$  (i.e. in the presence of a rare,  
 441 extremely strong competitor), then we cannot make the replacement Eq. (13).

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

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

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

#### 444 **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. (12), we have

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

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

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

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

Following a similar procedure as for  $\Delta_r n_i$ , where the vector of propagule abundances is denoted



$\mathbf{x}$ , we have

$$\begin{aligned}
\langle x_j \rangle_{\hat{p}} &= \sum_{\mathbf{x}} x_j p(\mathbf{x} | x_i \geq 2) \\
&= \sum_k P(k | x_i \geq 2) \sum_{x_i} \sum_{\mathbf{x}_i} x_j p(\mathbf{x}_i | \sum_{j \neq i} x_j = k - x_i) p(x_i | x_i \geq 2, k) \\
&= \sum_k P(k | x_i \geq 2) \sum_{x_i} \frac{l_j(k - x_i)}{L - l_j} p(x_i | x_i \geq 2, k) \\
&= \frac{l_j}{L - l_j} \left( L \frac{1 - e^{-L}}{1 - (1 + L)e^{-L}} - l_j \frac{1 - e^{-l_j}}{1 - (1 + l_j)e^{-l_j}} \right)
\end{aligned} \tag{24}$$

for  $j \neq i$ , and

$$\langle x_i \rangle_{\hat{p}} = l_i \frac{1 - e^{-l_i}}{1 - (1 + l_i)e^{-l_i}}. \tag{25}$$

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 the  $\mathbf{x}$  dispersal probabilities in a territory where at least two focal propagule is assumed to be present. All covariances are now zero, so that  $\sigma^2(\sum c_j x_j) = \sum c_j^2 \sigma^2(x_j)$ , where  $\sigma^2(x_j) = l_j$  for  $j \neq i$ . The expression for  $\sigma^2(x_i)$  is more complicated. We assume  $p(x_i = 0) \approx 0$  without loss of generality (since otherwise  $D \gg 1$  and  $\Delta n_a$  is negligible). Then

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

where  $D = 1 - (1 + l_i)e^{-l_i}$ , analogous to Eq. (17), and

$$\frac{\sigma(\sum c_j x_j)}{\langle \sum c_j x_j \rangle} \approx \frac{\left( \sum_{j \neq i} c_j^2 l_j + c_i^2 \sigma^2(x_i) \right)^{1/2}}{\sum_{j \neq i} c_j l_j + c_i l_i / D}. \tag{27}$$

Similarly to Eq. (20), the RHS of (27) will not be  $\ll 1$  if there is a nonfocal genotype  $j$  with  $l_j \ll 1$  and  $c_j l_j \gg c_k l_k$  for  $j, k \neq i, j \neq k$ . When this is not the case, then since  $l_i$  must be of order 1 or larger for  $\Delta_a n$  to make an appreciable contribution to  $\Delta_+ n_i$ , the RHS of Eq. (27) is  $\ll 1$  as desired.

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

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \tag{28}$$

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