A lottery model of density-dependent selection

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Abstract

Fitness is typically represented in heavily simplified terms in evolutionary genetics, often using constant selection coefficients

This excludes fundamental ecological factors such as dynamic population size or density-dependence from the most genetically-realistic treatments of evolution, a problem that inspired MacArthur's influential but problematic r/K theory.

Following the spirit of r/K-selection as a general-purpose theory of density-dependent selection

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

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

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

Introduction

MacArthur's r/K scheme [MacArthur, 1962, MacArthur and Wilson, 1967] is famous for its early role in life-history theory [Charlesworth, 1994, Reznick et al., 2002], and for initiating a sizeable literature on density-dependent selection [Christiansen, 2004], which contains some of earliest treatments of the interplay between ecology and evolution [Roughgarden, 1979, Travis et al., 2013]. The central claim of the r/K scheme is that in "crowded populations ... fitness is K" (K will be defined below) [MacArthur and Wilson, 1967, pp. 149]. Remarkably, not only does MacArthur's argument for this claim seem to apply to essentially any population subject to density-regulated growth, the claim is also incompatible with the standard representation of selection in evolutionary biology. Since the general version of the "fitness is K" claim has been somewhat obscured by the widespread use of single-locus variants of the logistic model in the density-dependent selection literature, as well as well as the problems of the r/K life-history literature [Charlesworth, 1994, pp. 265], we briefly review MacArthur's argument before proceeding.

MacArthur considers two types subject to density-dependent population growth described by

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

where f_1 and f_2 are strictly decreasing functions of the population densities n_1 and n_2. Plotting the nullclines $f_1(n_1, n_2) = 0$ and $f_2(n_1, n_2) = 0$, it becomes clear that one type will be excluded unless it is able to grow at greater densities than the other type in some region of (n_1, n_2) space (Fig. 1). The term "K-selection" comes from four "carrying capacities" defined by $f_1(K_{11}, 0) = 0$, $f_1(0, K_{12}) = 0$, $f_2(0, K_{22}) = 0$ and $f_2(K_{21}, 0) = 0$. These K values summarize the nullcline structure provided that the nullclines do not curve too much. Note that only K_{11} and K_{22} are saturation densities analogous to "K" in the logistic model; K_{12} and K_{21} represent the effects of competition between types. For instance, under Lotka-Volterra competition we have $f_1(n_1, n_2) = r_1(1 - \alpha_{11}n_1 - \alpha_{12}n_2)n_1$, where $\alpha_{11} = 1/K_{11}$ measures intra-type competitive effects, and $\alpha_{12} = 1/K_{12}$ measures inter-type competitive effects. In the case of exploitation competition
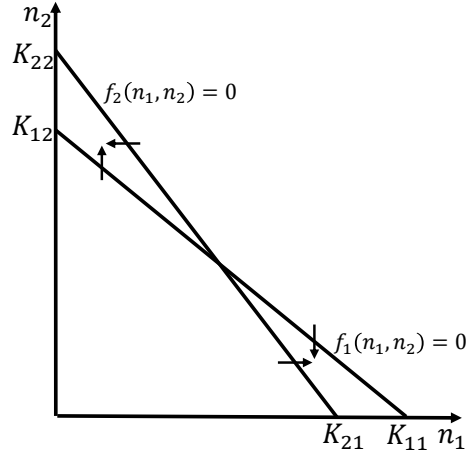
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n_2

K_{22}

$f_2(n_1, n_2) = 0$

K_{12}

$f_1(n_1, n_2) = 0$

K_{21} K_{11} n_1

Figure 1: MacArthur's argument for why "fitness is K" in crowded environments (adapted from [MacArthur and Wilson, 1967, pp. 147]). Arrows show the local direction of the dynamical trajectories of Eq. (1). The nullclines where $f_1(n_1, n_2) = 0$ and $f_2(n_1, n_2) = 0$ need not be linear, but the "carrying capacities" K are then less informative about the nullcline structure. Assuming these nullclines exist, exclusion is certain unless a type's nullcline extends out to greater densities in some region (here the outcome depends on initial condition).

for consumable resources, intra- and inter-type competition are connected via resource use "efficiency", but obviously this need not be true more generally [Case and Gilpin, 1974, Gill, 1974]. Nevertheless, bearing in mind MacArthur's broad use of "K", it seems hard to disagree that "fitness is K" i.e. that selection in crowded populations either favors the ability to keep growing at ever higher densities, or the ability to stop the growth of competitors at lower densities.

By contrast, in the standard "relative fitness" representation of selection, each type is assigned a selection coefficient describing the change in its relative proportion over time (e.g. [Barton et al., 2007, pp. 468]), with no consideration of population density. While this can describe selection in an uncrowded, expanding population, most commonly (e.g. in the Wright-Fisher model) it is assumed that total population density N is fixed. In the latter case, the population is crowded in the sense that one type must displace another to grow. Selection happens along a line defined by $n_1 + n_2 = N$ and population density is otherwise irrelevant. Given this inconsistency with the r/K scheme, the constant-N, shifting-frequency picture of selection does not seem compatible with the extremely broad variety of absolute population growth dynamics represented by Eq. (1).

In fact, one step in MacArthur's argument considerably narrows its scope: assuming that the nullclines of f_1 and f_2 exist at all. The strength of this assumption is clear if we note that essence of the dichotomy underlying the r/K scheme is between interaction-dependent selection and interaction-independent selection. That is, selective shifts in frequency are a result of differences in absolute growth rates, but these differences can arise in two logically distinct ways: 1) some types expand more rapidly the absence of interactions between individuals or 2) some types are superior in their interactions with other types. Population density is a key factor controlling whether individuals interact, thereby setting the relative contributions of these forms of selection. But there are obviously important forms of interaction that are not expressible in terms of slanted density isoclines. For instance, contests for territory and mates are predominantly relative. MacArthur's argument starts with assumptions about how selection depends on density, and then tries to make sense of what this says about the evolution of competitive traits such as "efficiency" of consumable resource consumption. The study of density-dependent selection should start from a description of the interactions between types, and then analyze how the effects of those interactions vary with density.

in a simplified, territorial model of growth, dispersal and competition.

We revisit the classic lottery model of Chesson and Warner [1981], which has two features that make it well suited for this role, but one critical flaw that we rectify here.

The first feature is that the lottery representation of competition is particularly concise. Mature individuals ("adults") each require their own territory, whereas newborn individuals ("propagules") disperse to, and subsequently compete for, territories made available by the death of adults. Territorial contest among propagules leaves a single victorious adult per territory, the victor chosen at random from the propagules present, with probabilities weighted by a coefficient for each type representing competitive ability, akin to a lottery [Sale, 1977].

The second feature is the close connection between the lottery model and one of the foundational models of population genetics, the Wright-Fisher model of genetic drift, which we discuss further below.

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The critical flaw of the classic lottery model is that it breaks down at low densities (few propagules dispersing to each territory), precluding density-dependent behaviour. Our first task is to analytically extend the classic lottery model to correctly account for low density behavior (sections "Model" and "Mean field approximation").

Taking an example inspired by recent studies of rapid, seasonal evolution in *Drosophila* [Bergland et al., 2014], we discuss how environmental fluctuations might stabilize polymorphisms when population density is cyclical.

Model

We assume that reproductively mature individuals ("adults") each require their own territory to survive and reproduce (Fig. 2). All territories are identical, and the total number of territories is T. Time t advances in discrete iterations, each representing the time from birth to reproductive maturity. In iteration t, the number of adults of the i'th 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 $U(t) = T - N(t)$.

We assume that the n_i and T are large enough that stochastic fluctuations in the n_i ("drift") can be ignored. We derive deterministic equations for the expected change in the n_i over time, leaving the evaluation of drift for future work. This is an excellent approximation when the n_i are all large. However, we also do not evaluate the initial stochastic behaviour of adaptive mutant lineages while they are at low abundance. When considering new mutations, we therefore restrict our attention to begin with the earliest (lowest n_i) deterministic behavior of mutant lineages (the transition to deterministic growth occurs at an abundance n_i of order equal to their inverse expected absolute growth rate; Uecker and Hermisson 2011).

Each iteration, adults produce new offspring ("propagules"), m_i of which disperse to unoccupied territories. We assume that adults cannot be ousted from their territories, so that m_i only includes propagules landing on unoccupied territories. Propagules disperse at random over the unoccupied territories, regardless of distance from their parents, and independently of each
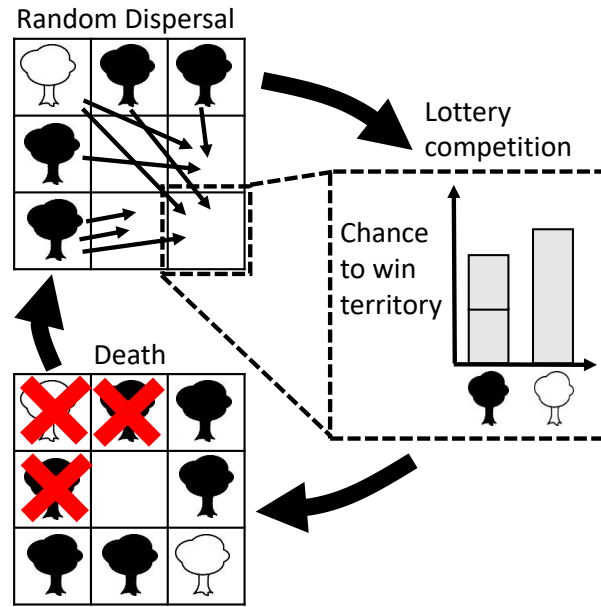
Figure 2: Each iteration of our model has three elements. First, propagules are produced by adults and dispersed at random (only propagules landing on unoccupied territories are shown). Lottery competition then occurs in each unoccupied territory (only illustrated in one territory). Each genotype has a probability proportional to $c_i x_i$ of securing a given territory, where c_i measures competitive ability and x_i is the number of propagules that disperse there. In the illustrated territory, the black genotype disperses more propagules but is a poorer competitor. Territories are then made available by adult mortality (red crosses).

other. There is no interaction between propagules (e.g. avoidance of territories crowded with propagules). Loss of propagules during dispersal is subsumed into m_i.

In general, m_i will increase with n_i, and will 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]. In section "Cyclical birth and death rates" we evaluate Eq. (5) numerically using this functional form for m_i, with b_i assumed to be constant.

In "Invasion of rare genotypes and coexistence", we assume the simpler form $m_i = b_i n_i$, with constant b_i, meaning that all propagules land on unoccupied territories (a form of directed dispersal). This simplifies the mathematics without affecting the results of those sections, which only depend on the low-frequency invasion behavior of Eq. (5). 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. We assume that x_i follows a Poisson distribution $p_i(x_i) = l_i^{x_i} e^{-l_i} / x_i!$, where $l_i = m_i/U$ is the mean territorial propagule density. This is approximation becomes exact when the n_i are large enough that drift in n_i can be ignored (Appendix A).

When multiple propagules land on the same territory, the victor is determined by lottery competition: genotype i wins a territory with probability $c_i x_i / \sum_j c_j x_j$, where c_i is a constant representing relative competitive ability (Fig. 2).

In the classic lottery model [Chesson and Warner, 1981], unoccupied territories are assumed to be saturated with propagules from every genotype $l_i \gg 1$. From the law of large numbers, the composition of propagules in each territory will then not deviate appreciably from the mean composition $l_1, l_2, \ldots, l_G$ (G is the number of 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 $\Delta_+ n_1, \Delta_+ n_2, \ldots, \Delta_+ n_G$ follow a multinomial distribution with U trials and success probabilities $\frac{c_1 l_1}{\sum_j c_j l_j}, \frac{c_2 l_2}{\sum_j c_j l_j}, \ldots, \frac{c_G l_G}{\sum_j c_j l_j}$, respectively. 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

$$\Delta_+ n_i(t) = \frac{c_i l_i}{\sum_j c_j l_j} U(t) = b_i n_i \frac{1}{L} \frac{c_i}{\bar{c}}, \tag{2}$$

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 $w_i = b_i c_i$. Thus, 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 evaluate selection at different densities (after appropriate extensions are made), in an otherwise very similar model to the canonical Wright-Fisher. We therefore expect that drift in realized values of n_i in our extended lottery model should be similar to that in the Wright-Fisher model, but we leave this for future work.

In our extension of the classic lottery model, we do not restrict ourselves to high propagule densities. Eq. (2) is nonsensical if even a single type has low propagule density ($l_i \ll 1$): genotype i can win at most m_i territories, yet Eq. (2) 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 some small fraction of a propagule as would be implied

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by small l_i in the classic lottery model. In other words, deviations from the mean propagule composition $l_1, l_2, \ldots, l_G$ are important at low density.

We expect that a fraction $p_1(x_1) \ldots p_G(x_G)$ of the U unoccupied territories will have the propagule composition $x_1, \ldots, x_G$. Genotype i is expected to win $c_i x_i / \sum_j c_j x_j$ of these. Ignoring fluctuations about these two expectations (due to our no-drift, large T, large n_i approximation), genotype i's territorial acquisition is given by

$$\Delta_+ n_i(t) = U(t) \sum_{x_1, \ldots, x_G} \frac{c_i x_i}{\sum_j c_j x_j} p_1(x_1) \ldots p_G(x_G), \tag{3}$$

in our extended lottery model, where the sum only includes territories with at least one propagule present. Note that unlike the classic lottery model, not all unoccupied territories are claimed each iteration, since under Poisson dispersal a fraction e^{-L} remain unoccupied.

We assume that mortality only occurs in adults (Fig. 2; setting aside the juvenile deaths implicit in territorial contest), and at a constant, genotype-specific per-capita rate $0 \le d_i \le 1$, so that the overall change in genotype abundances is

$$\Delta n_i(t) = \Delta_+ n_i(t) - d_i n_i(t). \tag{4}$$

Results

Mean Field Approximation

Eq. (3) involves an expectation over the time-dependent dispersal distributions p_i, and is thus too complicated to give intuition about the dynamics of density-dependent lottery competition. We now evaluate this expectation using a "mean field" approximation.

Similarly to the high-l_i approximation of classic lottery model, we replace the x_i with appropriate mean values, although we cannot simply replace x_i with l_i. For a genotype with low propagule density $l_i \ll 1$, we have $x_i = 1$ in the territories where its propagules land, and so its

growth comes entirely from territories which deviate appreciably from l_i. To account for this, we separate Eq. (3) into $x_i = 1$ and $x_i > 1$ parts. Our more general mean field approximation only requires that there are no large discrepancies in competitive ability (i.e. we do not have $c_i/c_j \gg 1$ for any two genotypes). We obtain (details in Appendix B)

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

where

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

and

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

To supplement our analytical mean field derivation, we did numerical simulations of our exact our density-dependent lottery model, and verified that Eq. (5) is a good approximation (Appendix B). Thus, Eq. (5) describes how type abundances change over time in a lottery model where population density can itself vary with time.

Comparing Eq. (5) to Eq. (2), the classic lottery per-propagule success rate $c_i/\bar{c}L$ has been replaced by three separate terms. The first, e^{-L}, accounts for propagules which land alone on unoccupied territories; these territories are won without contest. The second, $R_i c_i/\bar{c}$ represents competitive victories when the i genotype is a rare invader in a high density population: from Eq. (6), $R_i \to 0$ 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: $A_i \to 0$ 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 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 $A_i \to 1/L$).

Coexistence in constant and cyclical environments

In the previous section we only considered how b, c and d should respond to selection in Grime's environmental extremes, based on invasion fitness. Here we further explore the low frequency behavior of Eq. (5) to determine which types can coexist in a constant environment, and then consider the full time-dependent behaviour of Eq. (5) in a cyclical environment.

In a constant environment, stable coexistence is possible in our extended lottery model. A b-specialist i and c-specialist j ($b_i > b_j$, $c_j > c_i$) can co-exist because then propagule density L is frequency-dependent, and so is the importance of competitive ability (Appendix D). This is a version of the classic competition-colonization trade-off [Levins and Culver, 1971, Tilman, 1994]; the competitor (c-specialist) leaves many territories unoccupied (low L) due to its poor colonization ability (low b), which the colonizer (b-specialist) can then exploit. A similar situation holds for coexistence between high-c and low-d specialists; a "competition-longevity" trade-off [Tilman, 1994]. These forms of co-existence require density dependence (being mediated by L), and are not present in the classic lottery model. Coexistence is not possible between b- and d-specialists in a constant environment (Appendix D).

Now suppose that birth and death rates vary periodically with amplitude sufficent to cause large changes in population density. This example 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. Along with this seasonal population density cycle, hundreds of polymorphisms exhibit frequency cycles that are in phase with the seasons [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 en-

vironments 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 that promote coexistence in fluctuating environments [Messer et al., 2016]. The first is the classic version of the storage effect, which occurs when part of the population is protected from selection (due to overlapping generations in the lottery model; Chesson and Warner 1981). The second is the bounded population size effect of Yi and Dean [2013], which occurs when each environmental cycle involves growth from low to high density, with the time spent growing each cycle dependent on the fitness of the types present.

Fig. 3a-c 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 due to a combination of the storage and bounded density effects (recall that stable coexistence between b and d specialists was not possible in a constant environment).

The classic lottery model (Eq. 1) fails to give co-existence for these parameters because expansion to carrying capacity occurs immediately at the start of the summer (Fig. 3d-f). As a result, coexistence requires that the winter survivor's b must be about 5 times smaller than required when we properly account for the growth in the abundance of each type using Eq. (5) (keeping the other parameters the same; Fig. 3g-i). Previous models of the promotion of genetic variation via the storage effect [Ellner and Hairston Jr, 1994] similarly assume that the total number of offspring per iteration is constant, and would produce a similar error.
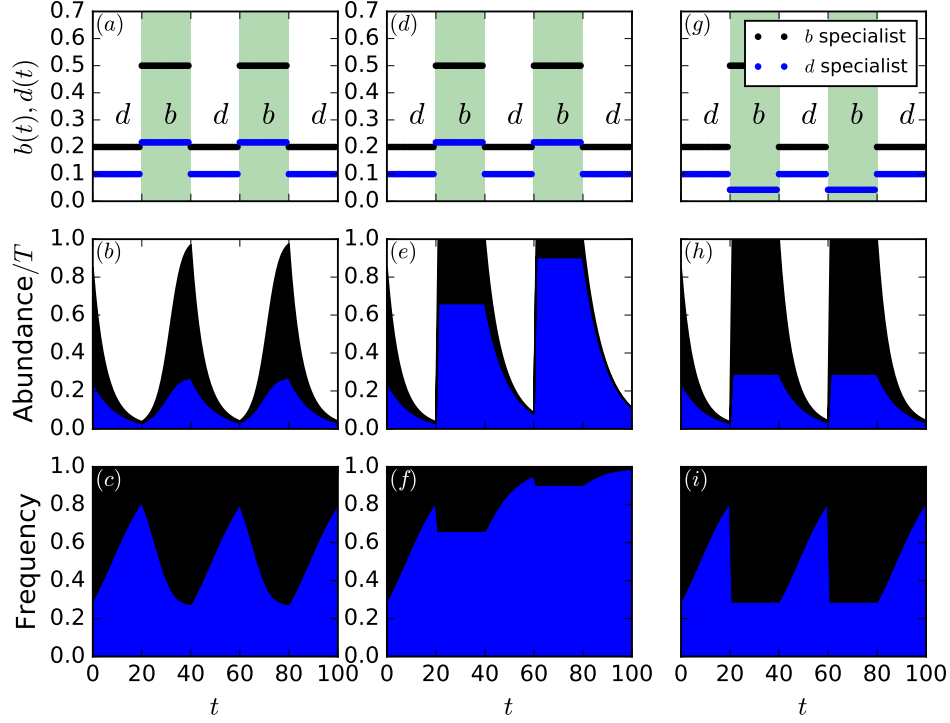
Figure 3: Stable coexistence between b and d specialists in a fluctuating environment requires a much greater b advantage in the classic lottery model compared to our density-dependent extension of it when population density is seasonally cyclical. (a) Birth and death rates seasonally alternate being 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 ($b = 0.217$, $d = 0.1$) (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. (d-f) Same as (a-c) for the classic lottery model; the types no longer coexist. (g-i) Same as (d-f) where now $b = 0.0421$ for the d specialist and the types coexist. For illustration, the propagule abundances are assumed to have the form $m_i = b_i(1 - N/T)n_i$, reflecting non-directed dispersal.

Discussion

It is interesting to compare the predictions of the extended lottery model with earlier approaches, such as the r/K scheme, where $r = b - d$ is the maximal, low-density growth rate [Pianka, 1972]. 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 predictions of an r/K trade-off, empirical studies have shown that maximal growth rate at low density and the high density at which saturation occurs (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 positive 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 a tradeoff between r and the competitive aspect of K. 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 "α-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 α (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 (the total number of territories occupied per iteration is $\Delta_+ N = U(1 - e^{-L})$, which does not depend directly on the c_i). 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

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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- strategists on the other.

K-selection in the narrow logistic sense of selection for a greater environmental carrying capacity for given r, sometimes referred to as "efficiency" [MacArthur and 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 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. We leave these complications for future work.

Nevertheless, it is interesting to note that ruderals, which are typically thought of as high fecundity dispersers (b-specialists), may also be strongly d-selected, which while unintuitive, is consistent with our findings. An effective way to reduce d in the face of unavoidable physical destruction is to shorten the time to reproductive maturity — short life cycles are a characteristically ruderal trait. Moreover, a recent hierarchical cluster analysis of coral traits did find a distinct "ruderal" cluster, but high fecundity was not its distinguishing feature. Rather, ruderals used brood- (as opposed to broadcast-) spawning, which could plausibly be a mechanism for improving propagule survivorship in disturbed environments [Darling et al., 2012].

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

territorial acquisition effectively coincide, and in principle resource competition could be represented by a competitive ability c (or conversely, c should be derivable from resource competition). The situation is more complicated if the resources are well-mixed, since, in general, resource levels then need to be explicitly tracked. It seems plausible that explicit resource tracking may not be necessary when the focus is on the evolution of similar genotypes that use identical resources rather than the stable co-existence of widely differing species with different resource preferences [Ram et al., 2016]. We are not aware of any attempts to delineate conditions under which explicit resource tracking is unnecessary even if it is assumed that community structure is ultimately determined by competition for consumable resources. More work is needed connecting resource competition models to the density-dependent selection literature, since most of the former has to date been focused on narrower issues of the role of competition at low resource availability and in the absence of direct interactions between organisms at the same trophic level [Aerts, 1999, Davis et al., 1998, Tilman, 2007].

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

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

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

References

Rien Aerts. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, 50(330):29–37, 1999.

NK Arenbaev. Asymptotic behavior of the multinomial distribution. *Theory of Probability & Its Applications*, 21(4):805–810, 1977.

NH Barton, DEG Briggs, JA Eisen, DB Goldstein, and NH Patel. *Evolution*. NY: Cold Spring Harbor Laboratory Press, 2007.

Alan O. Bergland, Emily L. Behrman, Katherine R. O'Brien, Paul S. Schmidt, and Dmitri A. Petrov. Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in drosophila. *PLOS Genetics*, 10(11):1–19, 11 2014. doi: 10.1371/journal.pgen.1004775.

Benjamin M. Bolker and Stephen W. Pacala. Spatial moment equations for plant competition:

Understanding spatial strategies and the advantages of short dispersal. *The American Naturalist*, 153(6):575–602, 1999. doi: 10.1086/303199.

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

Ted J Case and Michael E Gilpin. Interference competition and niche theory. *Proceedings of the National Academy of Sciences*, 71(8):3073–3077, 1974.

Brian Charlesworth. *Evolution in age-structured populations*, volume 2. Cambridge University Press Cambridge, 1994.

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

F Christiansen. Density dependent selection. In *Evolution of Population Biology: Modern Synthesis*, pages 139–155. Cambridge University Press, 2004.

Emily S. Darling, Lorenzo Alvarez-Filip, Thomas A. Oliver, Timothy R. McClanahan, and Isabelle M. Côté. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, 15(12):1378–1386, 2012. ISSN 1461-0248. doi: 10.1111/j.1461-0248.2012.01861.x. URL http://dx.doi.org/10.1111/j.1461-0248.2012.01861.x.

Mark A Davis, Keith J Wrage, and Peter B Reich. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology*, 86(4):652–661, 1998.

Everett Ross Dempster. Maintenance of genetic heterogeneity. *Cold Spring Harb Symp Quant Biol*, 20:25–31, 1955.

Michael M. Desai and Daniel S. Fisher. Beneficial mutation–selection balance and the effect of linkage on positive selection. *Genetics*, 176(3):1759–1798, 2007. doi: 10.1534/genetics.106.067678.

Stephen Ellner and Nelson G Hairston Jr. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *The American Naturalist*, 143(3):403–417, 1994.

Warren J Ewens. *Mathematical Population Genetics 1: Theoretical Introduction*. Springer Science & Business Media, 2004.

Jay M Fitzsimmons, Sijmen E Schoustra, Jeremy T Kerr, and Rees Kassen. Population consequences of mutational events: effects of antibiotic resistance on the r/k trade-off. *Evolutionary Ecology*, 24(1):227–236, 2010.

Philip J Gerrish and Richard E Lenski. The fate of competing beneficial mutations in an asexual population. *Genetica*, 102:127–144, 1998.

Douglas E Gill. Intrinsic rate of increase, saturation density, and competitive ability. ii. the evolution of competitive ability. *American Naturalist*, 108:103–116, 1974.

A Jan Hendriks, Johanna LM Maas-Diepeveen, Evelyn HW Heugens, and Nico M van Straalen. Meta-analysis of intrinsic rates of increase and carrying capacity of populations affected by toxic and other stressors. *Environmental Toxicology and Chemistry*, 24(9):2267–2277, 2005.

Amitabh Joshi, NG Prasad, and Mallikarjun Shakarad. K-selection, α-selection, effectiveness, and tolerance in competition: density-dependent selection revisited. *Journal of Genetics*, 80(2):63–75, 2001.

Vladimir Alexandrovitch Kostitzin. *Mathematical biology*. George G. Harrap And Company Ltd.; London, 1939.

Eizi Kuno. Some strange properties of the logistic equation defined with r and K: Inherent defects or artifacts? *Researches on Population Ecology*, 33(1):33–39, 1991.

Richard Levins and David Culver. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences*, 68(6):1246–1248, 1971.

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Leo S Luckinbill. r and k selection in experimental populations of escherichia coli. *Science (New York, NY)*, 202(4373):1201–1203, 1978.

Leo S Luckinbill. Selection and the r/k continuum in experimental populations of protozoa. *American Naturalist*, pages 427–437, 1979.

Robert H MacArthur. Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences*, 48(11):1893–1897, 1962.

Robert H MacArthur and Edward O Wilson. *Theory of Island Biogeography*. Princeton University Press, 1967.

Philipp W Messer, Stephen P Ellner, and Nelson G Hairston. Can population genetics adapt to rapid evolution? *Trends in Genetics*, 32(7):408–418, 2016.

Eric R. Pianka. On r- and K-Selection. *The American Naturalist*, 104(940):592–597, 1970. ISSN 00030147, 15375323. URL http://www.jstor.org/stable/2459020.

Eric R. Pianka. r and K selection or b and d selection? *The American Naturalist*, 106(951):581–588, 1972. ISSN 00030147, 15375323. URL http://www.jstor.org/stable/2459721.

Yoav Ram, Eynat Dellus-Gur, Maayan Bibi, Uri Obolski, Judith Berman, and Lilach Hadany. Predicting microbial relative growth in a mixed culture from growth curve data. *bioRxiv 10.1101/022640*, 2016.

David Reznick, Michael J. Bryant, and Farrah Bashey. r- and k-selection revisited: The role of population regulation in life-history evolution. *Ecology*, 83(6):1509–1520, 2002. ISSN 1939-9170. doi: 10.1890/0012-9658(2002)083[1509:RAKSRT]2.0.CO;2. URL http://dx.doi.org/10.1890/0012-9658(2002)083[1509:RAKSRT]2.0.CO;2.

Jonathan Roughgarden. Theory of population genetics and evolutionary ecology: an introduction. 1979.

Peter F. Sale. Maintenance of high diversity in coral reef fish communities. *The American Naturalist*, 111(978):337–359, 1977.

A. Shmida and S. Ellner. Coexistence of plant species with similar niches. *Vegetatio*, 58(1):29–55, 1984. ISSN 00423106.

Hannes Svardal, Claus Rueffler, and Joachim Hermisson. A general condition for adaptive genetic polymorphism in temporally and spatially heterogeneous environments. *Theoretical Population Biology*, 99:76 – 97, 2015. ISSN 0040-5809. doi: http://dx.doi.org/10.1016/j.tpb.2014.11.002.

D Tilman. Resource competition and plant traits: a response to craine et al. 2005. *Journal of Ecology*, 95(2):231–234, 2007. ISSN 1365-2745. doi: 10.1111/j.1365-2745.2007.01201.x. URL http://dx.doi.org/10.1111/j.1365-2745.2007.01201.x.

David Tilman. *Resource competition and community structure*. Princeton University Press, 1982.

David Tilman. Competition and biodiversity in spatially structured habitats. *Ecology*, 75(1):2–16, 1994.

Joseph Travis, Jeff Leips, and F. Helen Rodd. Evolution in population parameters: Density-dependent selection or density-dependent fitness? *The American Naturalist*, 181(S1):S9–S20, 2013. doi: 10.1086/669970.

Hildegard Uecker and Joachim Hermisson. On the fixation process of a beneficial mutation in a variable environment. *Genetics*, 188(4):915–930, 2011.

Xiao Yi and Antony M Dean. Bounded population sizes, fluctuating selection and the tempo and mode of coexistence. *Proceedings of the National Academy of Sciences*, 110(42):16945–16950, 2013.

Appendix A: Poisson approximation

For simplicity of presentation, we have assumed a Poisson distribution for the x_i as our model of dispersal. Strictly speaking, the total number of i propagules $\sum x_i$ (summed over unoccupied

territories) is then no longer a constant m_i, but fluctuates between generations for a given mean m_i, which is more biologically realistic. Nevertheless, since we do not consider the random fluctuations in type abundances here, and for ease of comparison with the classic lottery model, we ignore the fluctuations in m_i. Instead we focus, on Poisson fluctuations in propagule composition in each territory.

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

Appendix B: Derivation of growth equation

We separate the right hand side of Eq. (3) 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

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

Competition when rare

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

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

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

Our "mean field" approximation is to replace x_j with its mean in the last term in Eq. (9),

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

Below we justify this replacement by arguing that the standard deviation $\sigma_{\tilde{p}}(\sum_{j \neq i} c_j x_j)$ (with respect to $\tilde{p}$), is much smaller than $\langle \sum_{j \neq i} c_j x_j \rangle_{\tilde{p}}$.

We first calculate $\langle x_j \rangle_{\tilde{p}}$. Let $X = \sum_j x_j$ denote the total number of propagules in a territory and $\mathbf{x}_i = (x_1, \ldots, x_{i-1}, x_{i+1} \ldots, x_G)$ denote the vector of non-focal abundances, so that $p(\mathbf{x}_i) =$

$p_1(x_1)\ldots p_{i-1}(x_{i-1})p_{i+1}(x_{i+1})\ldots p_G(x_G)$. Then, $\tilde{p}$ can be written as

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

and so

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

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

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

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

The exact analysis of the fluctuations in $\sum_{j \neq i} c_j x_j$ is complicated because the x_j are not independent with respect to $\tilde{p}$. These fluctuations are part of the "drift" in type abundances which we leave for future work. Here we use the following approximation to give some insight into the magnitude of these fluctuations and also the nature of the correlations between the x_j. We replace $\tilde{p}$ with $\tilde{q}$, defined as the $\mathbf{x}_i$ Poisson dispersal probabilities conditional on $X_i \geq 1$ (which are independent). The distinction between $\tilde{p}$ with $\tilde{q}$ will be discussed further below. The $\tilde{q}$ approximation

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

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

and

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

where $C = 1 - e^{-(L - l_i)}$ and $j \neq k$.

The exact distribution $\tilde{p}$ assumes that exactly one of the propagules present in a given site after dispersal belongs to the focal type, whereas $\tilde{q}$ assumes that there is a focal propagule present before non-focal dispersal commences. As a result, $\tilde{q}$ predicts that the mean propagule density is greater than L (in sites with only one focal propagule is present) when the focal type is rare and the propagule density is high. This is erroneous, because the mean number of propagules in every site is L by definition. Specifically, if $L - l_i \approx L \gg 1$, then the mean propagule density predicted by $\tilde{q}$ is approximately $L + 1$. The discrepancy causes rare invaders to have an intrinsic rarity disadvantage (territorial contests under $\tilde{q}$ are more intense than they should be). In contrast, Eq. (13) correctly predicts that there are on average $\sum_{j \neq i} \langle x_j \rangle_{\tilde{p}} \approx L - 1$ nonfocal propagules because $\tilde{p}$ accounts for potentially large negative covariances between the x_j "after dispersal". By neglecting the latter covariences, $\tilde{q}$ overestimates the fluctuations in $\sum_{j \neq i} c_j x_j$; thus $\tilde{q}$ gives an upper bound on the fluctuations. The discrepancy between $\tilde{q}$ and $\tilde{p}$ will be largest

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

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

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

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

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

Suppose that the c_j are all of similar magnitude (their ratios are of order one). Then Eq. (17) is $\ll 1$ for the case when $L - l_i \ll 1$ (due to the factor of $C^{1/2}$), and also for the case when at least some of the nonfocal propagule densities are large $l_j \gg 1$ (since it is then of order $1/\sqrt{L - l_i}$). The worst case scenario occurs when $L - l_i$ is of order one. Then Eq. (17) gives a relative error of approximately 50%, which from our earlier discussion we know to be a substantial overestimate when L is of order 1. Our numerical results (Fig. 4) confirm that the relative errors are indeed small.

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

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

$$\Delta_r n_i \approx m_i R_i \frac{c_i}{\bar{c}}, \tag{18}$$

where R_i is defined in Eq. (6).

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Competition when abundant

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

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

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

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

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,

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

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

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

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

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

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

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

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

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

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

$$\Delta_a n_i = m_i A_i \frac{c_i}{\bar{c}}, \tag{25}$$

where A_i is defined in Eq. (7).

Comparison with simulations

Fig. 4 shows that Eq. (5) and its components closely approximate our density-dependent lottery model over a wide range of propagule densities (the latter is evaluated by direct simulations of uniform random dispersal and lottery competition). Two genotypes are present, one of which 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. 4b). 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. 4d). Fig. 3 also shows the breakdown of the classic lottery model at low propagule densities.

Appendix C: Mutant invasion and coexistence in a constant environment

Here we evaluate the initial growth or decline of mutants in a population with a single resident type, which is in equilibrium. To determine whether coexistence is possible, we check for "mutual invasion", that is, we check that type j will invade an i-dominated population, but type i will also invade a j-dominated population.

Solving for equilibrium when i is the resident ($\Delta n_i = 0$), we have $R_i = 0$, $\bar{c} = c_i$, $A_i = (1 - (1 + L)e^{-L})/L$, and Eq. (5) becomes
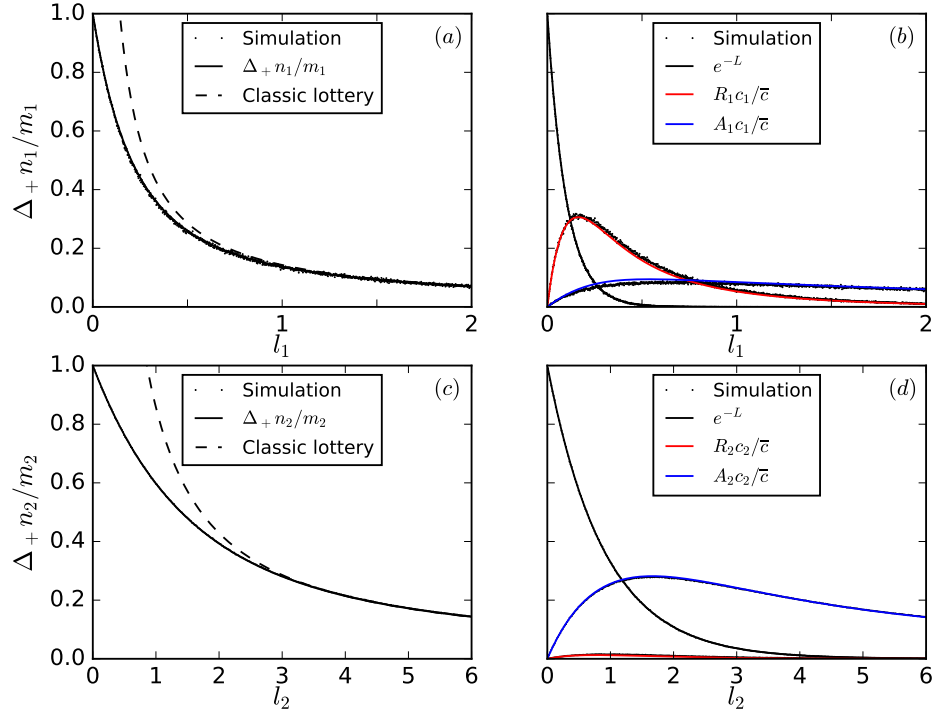
$$b_i(1 - e^{-L})/L - d_i = 0. \tag{26}$$

Figure 4: 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 (U is varied between 5×10^3 and 10^6 with $m_1 = 10^4$ and $m_2 = 9 \times 10^4$). Two genotypes are present. (a) and (b) show the low-frequency genotype with c-advantage ($c_1 = 1.5$), (c) and (d) show the high-frequency predominant genotype ($c_2 = 1$). 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 breakdown of the classic lottery model.

554   This implies $L \approx b_i/d_i$ if $b_i/d_i \gg 1$ and $L \ll 1$ if $b_i/d_i \approx 1$.

555   Now suppose that a novel mutant j, which is initially rare, appears in the population. Then

556   $A_j/R_j \ll 0$, $l_j \approx 0$ and $\bar{c} \approx c_i$, and so, from Eq. (5), the mutant lineage's fitness is

$$\Delta n_j/n_j \approx b_j \left(e^{-L} + R_j \frac{c_j}{c_i} \right) - d_j \qquad (27)$$

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

558   We consider the case of coexistence between a b-specialist i and a c-specialist j ($b_i > b_j$, $c_j > c_i$

559   and $d_i = d_j$). Suppose that b_i is so large that $L \gg 1$ when i is dominant, and b_j is so small that $L \ll$

560   1 when j is dominant. Then, when j is dominant, we have $\Delta n_i/n_i = b_i - d_i = b_i - d_j = b_i - b_j > 0$.

561   When i is dominant, Eq. (**??**) applies, where Eq. (26) implies $d_j = d_i = b_i(1 - e^{-L})/L \approx b_i/L$, and

562   so

$$\Delta n_j/n_j \approx \frac{b_j}{L} \frac{c_j}{c_i} - \frac{b_i}{L}. \qquad (28)$$

563   Therefore, coexistence occurs if c_j/c_i is sufficiently large. The analogous argument for d- and

564   c-specialists ($d_i < d_j$ with $L \gg 1$ when i dominates, $L \ll 1$ when j dominates, and $b_i = b_j$) gives

565   $\Delta n_j/n_j \approx d_i \frac{c_j}{c_i} - d_j$, which again implies coexistence if c_j/c_i is sufficiently large.

566   For b-and d-specialists ($c_i = c_j$), we have $\Delta n_j/n_j \approx b_j d_i/b_i - d_j$ when i dominates and

567   $\Delta n_i/n_i \approx b_i d_j/b_j - d_i$ when j dominates. Thus, either i or j grows when rare, but not both,

568   and stable coexistence is not possible in a constant environment.