The overall aim of our manuscript is to develop a simplified, general purpose model of density-dependent selection for use in genetically explicit, time-resolved models of evolution. This was precisely MacArthur's initial motivation for his influential r/K scheme, a fact now largely forgotten. Yet, fifty years later, population genetics still treats fitness in heavily simplified terms, usually with constant selection coefficients for the change in relative type frequencies over time, omitting even the most of basic ecological factors like population density.

In the last twenty years, the eco-evolutionary literature has flourished, particularly with the rise of adaptive dynamics. Yet the more ecologically-grounded treatments of fitness in “eco-evo” are typically specific to particular traits and ecological scenarios, and are focused on the invasion of rare types (“invasion fitness”). The demands of evolutionary genetics are more specific, in that we wish to make inferences and predictions about how allele frequencies change over time, but also more general, in that they are not restricted to particular traits or ecological circumstances. As such, we hope that our overall aim will appeal to a wide range of readers working on the interface between ecology and evolutionary biology.

The heart of our manuscript is a new model of density-dependent selection, which is derived by generalizing the classic lottery model of co-existence in fluctuating environments to make it density dependent. Apart from simply making the lottery model more general, this also introduces a form of stable co-existence which was not present in the original version, and which should be of interest to readers working on co-existence. The lottery model is also closely related to the canonical Wright-Fisher model of population genetics, a connection that we spell out in detail, and so the density-dependent generalization should be of interest to population geneticists.

We use our generalized lottery model to explore the role of selection in shaping trait evolution under Grime’s famous triad of environmental extremes. We view this as a sort of “sanity check” on the density-dependent lottery model, but it is also presents a step towards a mathematical formulation of Grime’s verbal scheme. Readers from a trait classification or plant ecology background may find this interesting.

Finally, we consider the time-dependent behavior of our model in a scenario with great contemporary interest: seasonally fluctuating selection coupled to large fluctuations in population density. This is inspired by the natural ecology of drosophilid fruit flies, a central model organism of genetics. We show how fluctuating selection promotes co-existence, with density dependence playing a critical role.

This submission is related to a previous submission that was rejected by the American Naturalist, “Density-dependent selection in evolutionary genetics: a lottery model of Grime’s triangle” (manuscript number 57532). Our new submission differs in three major ways from the previous one, to the point where we believe it should be considered a fresh submission:

1. A new results section has been added which emphasizes the time-dependent behavior of our model and co-existence under seasonally variable conditions, inspired by contemporary *Drosophila* work. The central reason for prior rejection was that we had not yet used our model for anything, and hence the manuscript contained no real “results”. This submission contains such results.
2. The amount of material and emphasis devoted to Grime’s triangle, which was the primary emphasis of the previous submission, has been dramatically reduced. The title has been changed to reflect this.
3. The time that we do spend on Grime’s triangle is now restricted to a discussion of how selection may operate to drive trait evolution in each environmental extreme, in isolation from physiological constraints.

Given the scope of these changes, we believe that our manuscript amounts to submission of a new paper, based on the same mathematical kernel but using it for different ends, not a resubmission of the previously rejected version. Nevertheless, for convenience we have attached a response (regular font) to the previous round of reviews (italics) below.

Suggested associate editors:

Mark Vellend

Stephen R. Proulx

Charles F. Baer

Benjamin Bolker (competition colonization; Bolker and Pacala)

Michael G. Neubert (math-ey. Some stuff on density dependence. Works on invasions)

Robin E. Snyder (math-ey, fluctuating environments, storage effect type stuff)

This work was financially supported by the National Science Foundation (DEB-1348262).

*MS #57532  
  
Senior editor comments:*  
*Verbal theory can be unsatisfying and I was interested to read about your work adapting the lottery model to accommodate competition among genotypes as a means of formalizing Grime’s ideas relating CSR trait syndromes to specific selective environments. Along with the reviewers and Dr. Vellend, I am enthusiastic about the goals of providing a mathematical foundation to support Grimes verbal model and I found your approach potentially promising.*

This is no longer our primary goal in the new submission. See points 1-3.

*However after reading the paper, I felt that the effort stopped short of demonstrating what new insight could be gained from the formalization you offer. Both reviewers converged on a similar conclusion that although your approach can recapitulate aspects of Grimes ideas, the inferences you draw from it are not novel or surprising and are, in any case, based primarily on verbal arguments, making the model seem superfluous. The reviewers also identified problems with the structure of some components of the model and took issue with the biological realism of some assumptions.*

See points 1 and 2.

*There was also a sense that that the introduction of the paper makes a number of bold claims that are not fulfilled, adding to a sense of disappointment in the extent to which the work supports a significant advance.*

We agree with this critique and the new Introduction refers more concretely to the problems of evolutionary genetics that are our primary impetus.

*Aspects of the modeling could be defended or altered in a revision, but ultimately the paper did not make convincing argument for its utility. I agree with Dr. Vellend that your efforts here could be a promising start towards theory that can make sense of empirical data on sets of covarying traits, but it has not yet progressed to a point where it would appeal to a broad audience. Thus I also agree with his recommendation to decline the paper.*

Our main aim is not to make sense of empirical trait data, although we can see how our previous submission was misleading in that respect. The data that we expect it to one day help to analyze, after the construction of an appropriate inferential framework, is timecourse data on allele frequencies and population densities. In the current submission, our main aim is to incorporate ecology into the treatment of fitness in evolutionary genetics.   
  
  
*xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx  
ASSOCIATE EDITOR'S (MARK VELLEND) RECOMMENDATION*  
  
*This paper develops a version of the widely-used lottery model for ecological community dynamics, modified to allow for small propagule numbers, with the aim of mathematically reproducing Grime’s CSR scheme for plant strategies.*

This is no longer our primary Aim (see points 1-3).

*I think the goal of connecting formal theory to influential qualitative heuristics is laudable, and many of the model results are intuitively appealing.  My mathematical abilities do not allow me to evaluate the details of the model, but two expert reviewers in this area have carefully reviewed the manuscript.  Unfortunately, their opinions are consistent in not feeling that the paper makes a sufficiently novel and important conceptual advance to justify publication in the American Naturalist.  For example, some of the key conclusions don’t require a complex mathematical model at all, such as invasion from rare being more likely if mutant has high fecundity, lower mortality or high competitive ability.*

The complexity of the model is needed when the full time course of type frequencies or abundances is of central interest, as is the case in evolutionary genetics. It is needed for the new Figure 4 that is the central result of the new manuscript (point 1).

*There was also a strong sense that the link between the model itself and the CSR scheme is somewhat unclear, with the verbal argument only loosely related to the model.  I found myself in agreement with these critiques.*

See points 1 and 2.

*Personally, I have always been drawn to the heuristic of Grime’s triangle, but I do think it’s overstated to start from the premise that “different species can be divided into a small number of distinct trait clusters”.  Stress tolerance, disturbance tolerance, and competitive ability do indeed appear to be important axes of trait variation among plants, but they relate in complex multivariate ways to measurable traits, with little evidence for clusters in trait space, at least as far as I know.*

We agree that this claim was overstated given the age and thus statistical techniques used in most of these citations. However, we now give more specifics about the study of Darling et al. (Evaluating life-history strategies of coral reefs from species traits, Ecology Letters, 2012), which applies modern statistical methods (hierarchical cluster analysis) and does indeed find distinct trait clusters, at least for corals.

*Efforts to use mathematical models to make sense of the empirical data like these are important, and hopefully this study might be the beginning of more pronounced advances in this direction.*

As discussed above in the response to the Senior Editor, our long-term aim was and is to make sense of allele frequency data, not empirical trait data, although we can see how our previous submission was misleading in that respect.  
  
*Reviewer #1:   
  
This manuscript presents a model of lottery competition, modified to allow for potentially small numbers of propagules reaching each available territory; the model is then interpreted in the light of Grime's triangle, that identifies different types of strategies (competitors, stress tolerators, ruderals) corresponding to different adaptation to stress and/or disturbance.*   
  
*The different parts of the paper are somewhat disconnected;*

The new version has a new structure. Some mathematical details have been moved from the main text into two new Appendices C and D.

*first, the model is presented and analyzed; then comes an invasion analysis, the conclusions of which do not really differ from what is obtained with a classical lottery model (a mutant fares better if it has a lower death rate / higher fecundity / higher competitive ability);*

Much of this invasion analysis material has either been removed, or relegated to Appendix C. Note, however, that invasion analysis in the classic lottery is dubious because the classic lottery model breaks down at low density for any type, and by definition an invading type is at low density.

*finally, connections are made with the different types of strategies described in Grime's triangle, and illustrations are given for large but also vague clades of organisms (fishes, corals, plants). But no part appears essential to the other ones.*

See points 2-3 re Grime’s triangle. These “illustrations” have been removed.

*Take for instance Figure 4 (a table). The modified lottery model allows the consideration of cases with low density; in this case competitive ability does not matter, so there is no selection for changes in competitive ability. There is not really a need for a detailed model to reach this verbal conclusion... What Figure (/table) 4 also shows is that a parameter that is constrained does not evolve  
(e.g., Ideal column, d has to be <<1, it cannot change). Again, there is no need for a complicated model to obtain this result...*

In the new manuscript, we set aside the issue of physiological constraints and only consider the role of selection (point 3). As noted above, this section is now just to explore the basic behavior of our model under Grime’s environmental extremes as a sort of sanity check. Where the detailed model is really needed is for the time-dependent dynamics in the new Figure 4.   
  
*Considering the different parts separately:  
  
The model is a modified lottery model; in the lottery model, there is a large number of propagules competing for each territory; here, this number can be small.*   
  
*- The distribution of numbers of propagules of a given type are said to be given by a product of independent Poisson distributions (Appendix A, line 605). There needs to be a better justification for this claim given how the model is constructed; the Poisson limit theorem deals with binomial distribution, not a multinomial. Also, the conditions under which this is a valid approximation could be clearer (see e.g. Deheuvels & Pfeifer 1988, "Poisson approximations of multinomial distributions and point processes")  
  
On the other hand, it would not be too unrealistic to directly assume a Poisson distribution as suggested lines 608-213.*

To simplify the presentation of the model, we now first assume a Poisson and then point out its connection to random sampling. We have added a reference to the mathematical literature on the limiting distributions of multinomials (Arenbaev, 1977).   
  
*- The decomposition presented in eq. (5) is useful in that it helps understand the consequences of different levels of propagule density. However, eq. (5) in the main text is presented as if the decomposition was obtained after lines of calculations, while it is assumed from the start (Appendix B). This should be clearer.*

This has been clarified.

*It is not really clear what eqs (6) and (7) bring to the study, because they are not much interpreted (except to say when the terms vanish).*

These complete the equation. No numerical computation (eg as presented in the Figure 4 timecourse) is possible without them.  
  
*- Details of the simulations are missing. What is the underlying model? (multinomial or Poisson?) What is the value of T? How many replicates are there?*

Fixed.  
  
*The invasion analysis is not a proper invasion analysis, as hinted at around line 267.*

It is not clear what a “proper” invasion analysis is supposed to be. Our invasion analysis, now relegated to Appendix C, is the standard analysis of deterministic growth or decline from low frequencies, such as used for “invasion fitness” in adaptive dynamics.

*In spite of the decomposition presented in eq. (5), the model remains rather complicated, hindering the presentation of unexpected results. There is no need for a complicated model to conclude that, all else being equal, a mutant with higher fecundity or lower death rate or higher competitive ability will invade (lines 239-246).*

This material has been removed. The interesting aspects of our more complicated equation are now brought out more clearly when we consider its co-existence properties, and its time-dependent behavior, which is much more pertinent to evolutionary genetics applications.   
  
  
*Finally, as mentioned above, the discussion of different strategies of Grime's triangle can totally be done verbally. There does not seem to be any point that required the modified lottery model to be made.*

See point 1.  
  
*The empirical examples given at the end of the Results section are too vague to be relevant.*

Removed.  
  
*Other comments  
lines 120-122 Presenting/discussing a potential feature that is actually not used may confuse the reader.*

Logistic propagule production is now used in the fluctuating population density example of Figure 4, to illustrate that we are not particularly committed to the assumption of constant b, it is simply a convenience when analyzing mutant invasion.

*Line 131: "held fixed" is confusing because n\_i changes with time.*

Fixed  
  
*Figure 2: the figure looks like there is isolation by distance (only two black trees send propagules to the bottom right-hand cell), while this does not seem to be the case in the model.*

Fixed  
  
*Line 189 No I think it is already long enough*

We are unsure what the reviewer is referring to, and it is in any case likely obsolete given our extensive changes. The “Model” section has been shortened.   
  
*Line 317 Where does this 1% figure come from?*

The typical size of beneficial mutations is not important and this material has been removed.  
  
*Line 411-412 It could be useful to expand on this.*

The effects of clonal interference would take us too far from the main flow of the discussion.  
  
*Line 456-461 Sorry, but no, this is not a model that could be described as lying on the "understudied evolution-only end of the spectrum". What is the justification for such a claim? Then the comment on adaptive dynamics (AD) being on the ecology side of the spectrum does not make much sense either; AD is a framework, not a model: you can use AD techniques to describe evolution in this modified lottery model.* *Figure 6 is unnecessary, many of the check-marks are very debatable.*

Figure 6, and the associated text, has been removed.    
  
  
*Reviewer #2:   
  
This paper is an attempt to recover the traits associated with the CSR strategies of Grime as the result of evolution in a lottery model.*  
*The first part of the paper (pp 6-15) develops a lottery model with finite fecundity and hence Poisson-distributed number of propagules competing for a site. As it turns out later, the details of the model are not too important, but let me give a few comments anyway: The model assumes directed dispersal (line 124), which is less suitable for plants (a prime example for the Grime classification), but easier technically; line 126 claims that this does not matter.*

The model can deal with either directed or nondirected dispersal. Different parts of the new manuscript explore both of these cases, which are now better signposted.

*Given the broad scope the paper intends to address, the model is rather simplistic. Yet the model presents a technical challenge: the sum in equation (2) over the possible numbers of competitors is an infinite sum. In Appendix B, the authors derive the analytic approximation given in eqs (5)-(7), which can very nicely simplify and speed up the analysis of stochastic lottery models, so that the approximation could be useful for other related models as well.*

To comfort readers concerned with the scope of the “simplistic” lottery model, in the new manuscript we place greater emphasis on the close connection between the lottery model and the equally simplistic Wright-Fisher model, a cornerstone of population genetics.

*I have several problems with the derivation in Appendix B (see below), and therefore I was surprised to see a very good match with simulations in Figure 3. I have checked the approximation against my own numerics, and indeed it is very good; but this does not excuse the problems in its derivation.*

We believe that the derivation is sound: see detailed comments below.  
  
*From page 15 onwards, the authors infer the evolution of fecundity (b), mortality (d) and competitive ability (c) in ideal/disturbed/stressful environments as in Grime's triangle. The summary table in Figure 4 is based on a verbal argument. The only link to the preceding model seems to be that in low-density environments, competitive ability is unimportant - which is immediately obvious and generalizes way beyond the concrete model. The verbal argument of this main part is weak. Essentially, it says that b and c should increase whereas d should decrease (as it is obvious), except when c is unimportant (density is low), or when d cannot decrease further (presumably this is why it is not expected to evolve in the ideal environment, although doubling a lifetime is good even if it's already long), or when b cannot increase by definition (this is how the authors define a stressful environment). We do not need any model to be able to say this much. Life-history trade-offs are intentionally missing from the argument.*

Made irrelevant by points 1 and 2.

*Moreover, equating disturbance to a constant high mortality is doubtful,*

Our justification for this choice has been expanded (Lines 220-228).

*and the definition of a stressful environment is also problematic so that the authors use actually two different definitions in Figure 4.*

As described in the text, this is a long running debate in the literature which has not been resolved. In principle both scenarios could be possible (setting aside the plant specifics of the Grime-Tilman debate). Hence, we include both for comparison.  
 *I doubt that Grime's triangle is a good way to gain a deeper understanding of the diversity of life history strategies, and the present model does not add any significant new element to it.*

Made irrelevant by points 1 and 2.

*The Discussion relies heavily on pre-2000 references. The authors summarize related approaches in Figure 6; details of this table might be disputed, but my point here is that almost every entry goes back to the 1970's or earlier.*

The relevant Discussion has been greatly shortened, and the table has been removed.   
  
*Appendix B  
  
- lines 653-654, the authors have not shown that the neglected covariances would "significantly reduce" the variance  
- line 672, the Poisson probability of 2 or more propagules can be of order 1 when also the probability of no propagule is of order 1, therefore p(x\_i=0) is not negligible  
- line 677, it does not follow from l\_i being of order 1 that the rhs of (27) is much less than 1*

The derivation of the mean field approximation has been rewritten to clarify these points. We now emphasize that a thorough analysis of the variances and covariances is not possible with fully addressing the issue of drift in our model, which is beyond the scope of this manuscript.  
  
*- this does not affect the approximation but wrong: line 637-, the x\_j's are strictly independent of x\_i. If the focal genotype is rare, then in a site that harbours a propagule of the focal genotype, there are on average L nonfocal propagules, not L-1. L is the unconditional mean propagule number, but once we have conditioned on having a focal propagule, the conditional mean number is L+1.*  
The explanation of this subtle issue has been expanded in Appendix B. The issue revolves around what we mean by “harboring a propagule”. As the reviewer notes, if we assume that a propagule is already present, the propagule density is biased. But this is an incorrect representation of the dispersal process – by definition, the mean propagule density is L. This seemingly minor bias leads to a pathological rarity disadvantage. The correct procedure is to condition on knowing that one of the propagules present after dispersal has a specific genotype.