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.