Coexistence of sexually antagonistic alleles

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1 Abstract

Sexually antagonistic selection (SAS) occurs when the selection in the traits or loci differs between the sexes. This sexual conflict offers the opportunity for maintaining polymorphism in a population, but it often results in the eventual fixation of the fitter allele. However, the effects of SAS have generally been studied under strong simplifying assumptions, such as constant populations and homogeneous environments, which could considerably change the expected outcomes of SAS. Thus, in this study, we examined how fluctuations in selection and population sizes contributed to the coexistence of sexually antagonistic alleles by adopting an ecological framework that allowed us to examine evolutionary dynamics through the same lens as the coexistence of competing species. We performed simulations of alleles invading a population while allowing selection and populations sizes to fluctuate over time. Then, we quantified coexistence outcomes and the relative contribution of each type of fluctuation to each alleles' invasion growth rate. Our results showed that environmental fluctuations can dramatically increase the expected genetic variation under SAS. The positive contribution of fluctuations, however, depended on the sex and allele where invasion occurred. This study contributes to the growing body of work that shows the importance of non-constant environments on the maintenance of genetic diversity.

2   Introduction

The question of how genetic variation is maintained despite the effects of selection and drift is central within evolutionary biology (Walsh & Lynch, 2018). Classical explanations include overdominance (heterozygote advantage) or frequency-dependent selection (Hedrick, 2007), but in the modern era of genomic data, all patterns of variation that exceed the expected variation under neutrality tend to be categorized broadly as balancing selection, regardless of the evolutionary mechanism (Mitchell-Olds *et al.*, 2007). In species with separate sexes, balancing selection can arise due to sexually antagonistic selection (Connallon & Clark, 2014), which occurs when the direction of natural selection on traits or loci differs between the sexes (Lande, 1980; Arnqvist & Rowe, 2013).

Sexually antagonistic selection can maintain polymorphisms of otherwise disadvantageous alleles in a population (Gavrilets, 2014), which in turn can result in phenotypically distinct sexes that express different morphological, physiological, and behavioral traits (Mori *et al.*, 2017; Connallon & Hall, 2018). Nonetheless, the extent to which sexually antagonistic selection can maintain polymorphism in a population is thought to be limited (Connallon & Clark, 2012). This is because theoretical studies have found that the necessary parameter conditions that give rise to balancing selection are often highly restrictive (Kidwell *et al.*, 1977; Pamilo, 1979; Hedrick, 1999; Curtsinger *et al.*, 1994; Patten *et al.*, 2010; Jordan & Charlesworth, 2012). Importantly, the effect of sexually antagonistic selection generally has been studied under strong simplifying assumptions such as constant population sizes and homogeneous environments (Kidwell *et al.*, 1977; Pamilo, 1979; Immler

et al., 2012; Jordan & Charlesworth, 2012). Studies that have explored the effect of sexually antagonistic selection with more realistic assumptions, such as temporal fluctuations in selection (Connallon *et al.*, 2018) or demographic fluctuations (Connallon & Clark, 2012) have found that polymorphism can be maintained in a much wider set of conditions than classical studies predict. These results suggest that environmental fluctuations are essential to fully understand the effects of sexually antagonistic selection.

The contribution of environmental fluctuations to genetic diversity remains a debated issue in evolutionary biology. Classic theoretical models predict that temporal fluctuations in environmental conditions are unlikely to maintain a genetic polymorphism in haploid populations (Dempster, 1955; Hedrick, 1974; 1986). However, other studies have found that fluctuating selection can maintain genetic variance when populations experience density dependence (Dean, 2005), on sex-linked traits (Reinhold, 2000), or in populations where generations overlap (Ellner & Hairston Jr, 1994; Ellner & Sasaki, 1996). Similarly, temporal changes in population sizes have been shown to mitigate the effect of genetic drift in small populations (Pemberton *et al.*, 1996) and in annual plant systems (Nunney, 2002). Importantly, progress requires more than just identifying if environmental fluctuations can maintain genetic diversity in a population, but to quantify how exactly they contribute to its maintenance (Ellner *et al.*, 2016).

Temporal variability in the environment has been shown to promote diversity maintenance in ecological contexts (Levins, 1979; Armstrong & McGehee, 1980; Chesson, 2000a; Barabás *et al.*, 2018). Note that from an ecological perspective, polymorphism of sexually antagonistic alleles is equivalent to the coexistence of species, and the fixation of either

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one of the alleles in a population is equivalent to competitive exclusion. Allelic poly-morphism, thus, can be examined through the same lens as the coexistence of competing species. (Ellner & Hairston Jr, 1994; Ellner & Sasaki, 1996; Dean, 2005; Schreiber, 2010). The benefit of analyzing evolutionary dynamics through this lens is that the main theo-retical framework used to examine how competing species coexist, often called Modern Coexistence Theory (Chesson, 2000b; 1994; Barabás *et al.*, 2018), allows the quantifica-tion of how environmental fluctuations contribute to coexistence. Despite that the use of Modern Coexistence Theory often requires complex mathematical analysis of the mod-els describing the systems dynamics and restrictive assumptions to make them tractable (Barabás *et al.*, 2018), recent computation approaches allow the quantification of the rel-ative importance of environmental fluctuations to coexistence using simulations (Ellner *et al.*, 2016; 2019; Shoemaker *et al.*, 2020).

Here, we seek to explicitly apply recent advances in Modern Coexistence Theory to the question of how polymorphism is maintained under sexually antagonistic selection. We examined how fluctuations in selection values, fluctuations in population sizes, and their interactions can further or hinder polymorphism. In particular, we examined i) Can fluctuations in population sizes and selection values allow sexually antagonistic alleles to coexist when differences in their fitness would typically not allow them to? and ii) What are the relative contributions of different types of fluctuations that allow two sexu-ally antagonistic alleles to be maintained in a population? Our study provides the tools to analyze evolutionary dynamics from a novel perspective and contributes to answer-ing long-lasting questions regarding the effect of non-constant environments on genetic

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90   diversity.

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