Individual-based modeling of genome evolution in haplodiploid organisms

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Abstract

Ants, bees, wasps, bark beetles, and other species have haploid males and diploid females. Although such haplodiploid species play key ecological roles and are threatened by environmental changes, no general framework exists for simulating their genetic evolution. Here, we use the SLiM simulation environment to build a novel model for individual-based forward simulation of genetic evolution in haplodiploid populations. We compare the fates of adaptive and deleterious mutations and find that selection is more effective in haplodiploid species than in diploid species. Our open-source model will help understand the evolution of sociality and how ecologically important species may adapt to changing environments.

Main text

Approximately 15% of all animal species, including ants, bees, wasps, thrips, and bark beetles, have a haplodiploid sex-determination system: haploid, unfertilized eggs develop into males, while diploid eggs develop into females (Pamilo and Crozier 1981). These haplodiploid species display a huge diversity of morphologies and behaviors. For example, solitary and social bees occupy essential ecological and agricultural roles as pollinators (Potts et al, 2016), and bees and ants are charismatic models for studying social evolution (Hölldobler and Wilson, 1990).

Haplodiploid populations evolve differently from diploid populations (Hedrick and Parker, 1997), yet no flexible, general genome simulation framework incorporates haplodiploidy. Simulations are crucial for understanding how demographic and genomic processes affect haplodiploid evolution, enabling the interpretation of genome-wide analyses of haplodiploid species, testing competing hypotheses regarding their abilities to respond to human-induced environmental changes, and exploring genomic models of social evolution (Bank et al. 2014; Favreau et al 2018; Lopez-Orsorio and Wurm 2020; Colgan et al. 2021).

Here, we present a model for individual-based forward evolution of haplodiploid genomes. Our model is built upon SLiM, a software framework for genomic simulation of populations of individuals (version 3.3; Haller and Messer, 2019). To work around SLiM's assumption that all individuals are diploid, we restrict males to inherit one random chromosome from the recombined genome of a female and give them a NULL second chromosome. We assign a relative fitness of $1 + s$ to male carriers of a mutation with selection coefficient s . The Supplementary Text includes more details. Our model can be extended to consider variation in recombination rates, selection, and complex demographic structures.

We used our model to compare the fates of mutations between haplodiploid populations and diploid populations. We first subjected both types of population to neutral mutations ($s = 0$). As expected from evolution by drift, with a mutation rate of 10^{-8} on a genome of 10^6 loci, 0.01 mutations were fixed per generation in both population types (fig. 1A). Because recessive mutations are fully exposed to selection in haploid males but masked in heterozygote males of diploid populations, we subsequently tested whether selection on recessive mutations is more effective in haplodiploid populations (Avery 1984). This was indeed the case. Advantageous recessive mutations ($s > 0$) fixed at a higher rate in

haplodiploid populations, with stronger effects in simulations with larger selection coefficients (fig. 1B). Similarly, weakly deleterious recessive mutations ($s = -0.0005$ and $s = -0.001$) fixed at a lower rate in haplodiploid populations (fig. 1C). Very few more strongly deleterious mutations ($s = -0.003$ and $s = -0.01$) became fixed in either type of population, likely because selection against such mutations can overpower drift.

In reality, most mutations are neither fully recessive (dominance coefficient $h = 0$, as considered in the simulations described so far) nor fully dominant ($h = 1$). We therefore compared fixation rates of advantageous mutations between population types across a range of dominance coefficients. For simulations of recessive mutations ($h < 0.5$), selection was more effective in haplodiploid populations. However, when mutations were dominant ($h > 0.5$), this pattern was reversed (fig. 1D). This somewhat counterintuitive reversed pattern occurs because haplodiploid populations have fewer chromosomes than diploid populations of the same size ($1.5N$ versus $2N$), so they have fewer mutations entering the population in each generation ($1.5N\mu$ versus $2N\mu$), and thus, fewer mutations that can ultimately become fixed (Charlesworth et al. 2018). If both population types have identical numbers of chromosomes rather than individuals, the main pattern of higher efficacy of selection in haplodiploid should prevail whenever $h < 1$.

Overall, our results agree with predictions and empirical evidence regarding selection on X-linked alleles (Charlesworth et al. 2018), which are inherited in a pattern similar to haplodiploidy. The ability to model haplodiploid evolution has the potential to fill major gaps in the study of the demographic and selective processes that have shaped the evolution of social behaviors and other ecologically important traits in ants, bees, and other haplodiploid species. We hypothesize that higher efficacy of selection against recessive deleterious mutations in haplodiploid species may have facilitated the evolution of long lifespans of ant and bee queens, and that it may reduce the degeneration of supergene regions of suppressed recombination (Stolle et al. 2019, Martinez-Ruiz et al. 2020). Additionally, haplodiploidy may modulate the effects of antagonistic selection between sexes or among colony members (Vicoso and Charlesworth 2009, Eyer et al. 2019). We hope to see our model used in the exploration of such processes, and for understanding how interactions between selection efficacy, population size and migration can affect the abilities of haplodiploid species to adapt to environmental changes (Potts et al. 2016).

FIG. 1. The effect of haplodiploidy on the fixation rate of (A) neutral mutations, (B) advantageous mutations, (C) deleterious mutations, and (D) advantageous mutations with different levels of dominance. Each line represents one simulation run (only 20 shown for each treatment). On each plot, we also show the average difference in the number of fixed mutations between haplodiploid and diploid simulations after 40,000 generations and a burn-in period of 10,000 generations, when statistically significant (Wilcoxon rank sum test, $p < 0.05$; Supplementary Table 1). For each treatment, we ran 200 simulations with populations of 1,000 males and 1,000 females, a genome with 10^6 loci, a mutation rate of 10^{-8} , and a recombination rate of 10^{-6} . For the simulations in A to C, mutations were fully recessive (dominance coefficient $h = 0$) and had a range of selection coefficients (s , as shown); for the simulations in D, mutations had $s = 0.001$ and a range of dominance coefficients (h , as shown).

Supplementary Material

Supplementary data include the SLiM model of haplodiploidy presented here, an explanatory Supplementary Text, and Supplementary Table 1.

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Author Contributions

Conceptualization, YW and RB; Methodology, YW, RB, BCH and RP; Investigation, RP, RB and YW; Writing—Original Draft, YW, RB, and RP; Writing—Review and Editing, YW, RB, BCH, RH and RP; Supervision, YW.

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