

# Maintenance of genetic diversity through plant–herbivore interactions

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Identifying the factors governing the maintenance of genetic variation is a central challenge in evolutionary biology. New genomic data, methods and conceptual advances provide increasing evidence that balancing selection, mediated by antagonistic species interactions, maintains genome-wide functionally important genetic variation within species and natural populations. Because diverse interactions between plants and herbivorous insects dominate terrestrial communities, they provide excellent systems to address this hypothesis. Population genomic studies of *Arabidopsis thaliana* and its relatives suggest spatial variation in herbivory maintains adaptive genetic variation controlling defense phenotypes, both within and among populations. Conversely, inter-species variation in plant defenses promotes adaptive genetic variation in herbivores. Emerging genomic model herbivores of *Arabidopsis* could illuminate how genetic variation in herbivores and plants interact simultaneously.

## Addresses

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## Introduction

Understanding the maintenance of genetic variation within species and populations is a fundamental goal in evolutionary biology. Balancing selection, a suite of adaptive evolutionary processes that maintain greater genetic or phenotypic diversity in a population or species than expected under a neutral evolutionary model, was once regarded as the primary force maintaining functional genetic variation. However, until recently, a paucity of genomic signatures of balancing selection suggested that polymorphisms maintained by balancing selection may be rare [1]. Advances in population genomics (e.g. [2]) and in linking genotype to fitness in nature (e.g. [3]) have

provided new support for widespread balancing selection acting on genes underlying ecologically important traits.

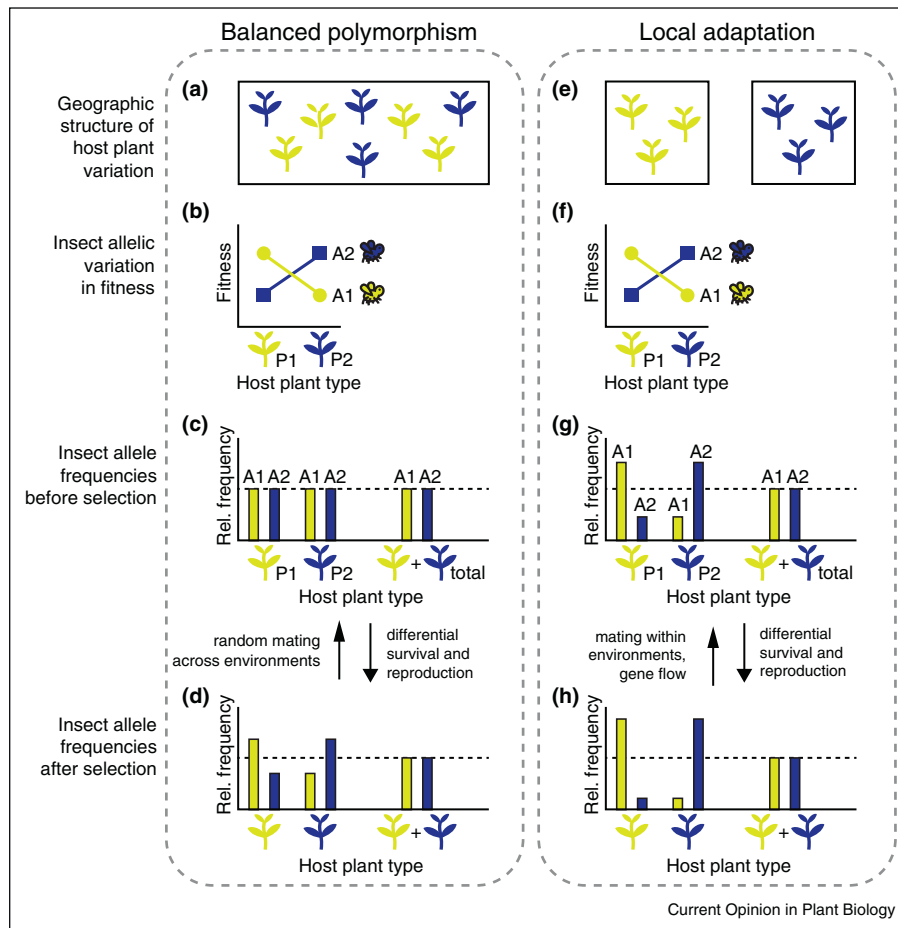
Despite the ecological ubiquity of plant–herbivore interactions, the extent to which they maintain genetic variation in plants and insects is not well understood. Here, we highlight empirical examples and theoretical predictions related to how plant–herbivore interactions could maintain genetic variation through balancing selection. Non-exclusive forms of balancing selection include fitness advantages for heterozygotes, frequency dependent selection favoring rare alleles, and antagonistic selection across temporally and spatially variable environments (reviewed in [1,4]). We focus on the role of spatially varying selection (SVS) because of its rich theoretical framework and testability with modern genomic resources. We suggest major questions that future studies might address, and highlight experimental techniques and genetically enabled model systems well suited to answer these questions.

## Why should plant–herbivore interactions maintain genetic diversity?

Host–pathogen interactions are among the most important selective forces known to maintain genetic variation in both hosts [5–7] and pathogens [8], and SVS plays a key role in this process. For example, geographic variation in pathogen communities may be the strongest selective force maintaining non-neutral genetic variation across human populations [6]. Spatial variation in plant and herbivore populations and communities is likely to produce a similar effect. SVS may be particularly important for herbivores, as plants comprise a large fraction of an herbivore’s environment and may be more important than abiotic factors in determining herbivore fitness [9].

Under SVS, selective advantages or disadvantages of alleles at a locus differ between environments that individuals of a species occupy (Figure 1b,f; Supplementary Table 1). A simple model of populations inhabiting multiple environments, connected by varying levels of gene flow, forms the foundation of theoretical models of polymorphism maintenance within populations [1,10] and among locally adapted populations and host races [11,12]. Figure 1 illustrates an application of this model to plant–herbivore interactions: spatial variation in a plant defensive trait (e.g. [13]) — which may arise through complex biotic interactions, abiotic interactions, or

Figure 1



Two simplified models for spatially varying selection (SVS) due to spatial heterogeneity in host plant characteristics. Two alleles ('A1' and 'A2') in an herbivorous insect have opposing effects on insect fitness on two host plant types ('P1' and 'P2'), which may represent plant genotypes or species that differ in a defensive trait. When a single insect population feeds on both sympatric host types (a), the two alleles can be maintained at intermediate frequency within the population (c, d). When host plant types are spatially separated so that insect gene flow between host types is low (e), allele frequencies will diverge between populations feeding on each host type, and the two allele polymorphism will be maintained at the species level (g, h) by migration-selection balance [12]. Both novel mutations and standing genetic variation can be driven by SVS to the intermediate frequencies depicted in the figure. The two models presented above are simplified extremes of situations in nature, which can fall along a continuum of high (right column) versus low (left column) host plant segregation with insect gene flow among host types.

genetic drift — is expected to maintain genetic variation within or among insect populations.

Levene [10] first demonstrated mathematically that SVS can maintain multiple alleles at stable equilibrium frequencies in a single, randomly mating population. Subsequent studies revealed that when gene flow across environments is low, maintenance of polymorphism becomes more favorable [1,10,14]. Further, when the costs of host resistance and enemy virulence vary between environments [15], global polymorphisms in interacting host and enemy genes are even more likely; for plants, geographically variable components of the environment can alter the cost of defense [16]. A final important insight is that the maintenance of polymorphism is more favorable as environment-specific fitness

advantages or disadvantages of an allele increase [10,17]. Thus, alleles maintained by SVS are likely to have large phenotypic effects and contribute a disproportionately large amount to fitness [17,18]. These predictions are consistent with the finding that traits under biotic selection are controlled by loci with larger effects than traits under abiotic selection in plants [19].

### Do herbivores maintain genetic variation in plants?

Population genomic analyses, enabled by whole-genome resequencing of natural *Arabidopsis thaliana* (*Arabidopsis*) accessions ([20], <http://www.1001genomes.org/>), suggest abundant adaptive variation exists for defense-related traits. Loci underlying defense-related traits [21] are highly differentiated between populations compared to

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