

Revisiting classic clines in *Drosophila melanogaster* in the age of genomics

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Adaptation to spatially varying environments has been studied for decades, but advances in sequencing technology are now enabling researchers to investigate the landscape of genetic variation underlying this adaptation genome wide. In this review we highlight some of the decades-long research on local adaptation in *Drosophila melanogaster* from well-studied clines in North America and Australia. We explore the evidence for parallel adaptation and identify commonalities in the genes responding to clinal selection across continents as well as discussing instances where patterns differ among clines. We also investigate recent studies utilizing whole-genome data to identify clines in *D. melanogaster* and several other systems. Although connecting segregating genomic variation to variation in phenotypes and fitness remains challenging, clinal genomics is poised to increase our understanding of local adaptation and the selective pressures that drive the extensive phenotypic diversity observed in nature.

The clinal genomic framework

Despite vast phenotypic and genetic diversity in the tree of life, species often appear precisely adapted to their local environment, suggesting strong selection for DNA variants that underlie local adaptation. Evolutionary biologists have long sought to connect this genetic variation to variation in phenotypes and fitness within natural populations. One fruitful approach has been to sample individuals along geographic transects – such as latitude, longitude, or altitude – that vary predictably in abiotic (e.g., temperature, precipitation, UV radiation) and biotic (e.g., species biodiversity, levels of competition) conditions. Evaluation of variation along such transects enables the identification of clines, broadly defined as a predictable geographic gradient in a measurable genotypic (e.g., allozyme or allele frequencies) or phenotypic (e.g., body size, thermal tolerance) character [1]. Two types of clines – those situated along discrete environments and those along continuous environments

– have been historically evaluated theoretically and empirically (Box 1).

Sampling along clines provides unique benefits and can potentially attenuate some of the confounding effects of demography that may be difficult to control for when sampling populations from patchy landscapes. For example, gene flow should be more predictable along clines, thus making it easier to identify adaptive from nonadaptive differentiation [2]. Clines are often predictable and replicable to a degree that variation sampled from patchy landscapes is not; for example, a cline along a coastal latitudinal transect can potentially be replicated on multiple continents. Such patterns of differentiation repeated among clines provide evidence of parallel adaptation. Finally, properties of a cline – such as the width, slope, and shape – can also inform inferences about underlying demographic and selective forces [1–5].

Although adaptation to spatially varying selection has been evaluated for decades using phenotypic data and genetic data from a small number of candidate loci, the recent abundance of whole-genome data provides an opportunity to discover novel causative variants beyond those previously identified by candidate gene studies. Moreover, the discovery of novel clines allows researchers to ask fundamental questions about natural selection and the genetic basis of adaptation. What are the genomic targets of spatially varying selection and how do they facilitate adaptation to the local environment? What are the molecular mechanisms underlying local adaptation? How widely distributed across the genome are loci with alleles under clinal selection and what does this imply about the genetic basis of adaptive traits? As homologous characters may exhibit parallel responses to similar underlying selection pressures, how often does adaptation occur in parallel – within and between species – among clines? Here we highlight some of the decades-long research on local adaptation in *D. melanogaster* from a group of particularly well-studied clines in North America and Australia. We explore the evidence for parallel adaptation and identify commonalities in the genes responding to clinal selection among continents. We also highlight cases where patterns are not repeatable among clines. Finally, we explore recent studies utilizing whole-genome data that have just begun to identify the targets of selection along clines in *D. melanogaster* and in other species.

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Box 1. Genetic models underlying discrete- and continuous-environment clines

Two major types of clinal pattern have historically been studied in natural populations: clines where two discrete environments meet in a tension zone (or sometimes a hybrid zone) and clines where populations are locally adapted along a continuous environment (Figure 1). Clines in tension zones are often sharp, narrow, and centered on an ecotone – the transition between two biomes. The exact shape of discrete-environment clines is determined by a balance between selection against maladapted alleles – due to either intrinsic or extrinsic incompatibilities in the tension zone – and dispersal distance [3,4,128]. Individuals in the tension zone should therefore have lower fitness relative to their ‘pure’ counterparts in the tails of the cline. Discrete-environment clines have been well studied both theoretically [4,5,128–130] and empirically, with some of the best examples coming from studies of three-spined sticklebacks [131,132], mice [133,134], *Heliconius* butterflies [135,136], and fire-bellied toads [4,5]. The genetic model underlying discrete-environment clines can be contrasted with that of continuous-environment clines – clines arising due to adaptation to continuously varying local environments – which are the primary

focus of this review. Relative to discrete-environment clines, continuous-environment clines are found in a single species where populations are connected by high levels of gene flow. In contrast to the stepped fitness function of discrete-environment clines, fitness optima of continuous-environment clines gradually shift with the environmental gradient, and selection favors locally adapted alleles at all positions along the geographic transect. While continuous-environment clines are often broader than their discrete-environment counterparts, their shape should parallel changes in the environment, leading to sharp clines under certain environmental conditions. In continuous-environment clines, causative variants are expected to closely track their environmental selection pressures while clines of neutral variants should not. Despite these expectations, distinguishing causal variants from background noise remains a challenge. The underlying genetic model of continuous-environment clines suggests that these clinal variants will have a quantitative genetic basis. Whether all variants underlying such quantitative traits will track the environmental gradient equally well remains an outstanding theoretical and empirical question.

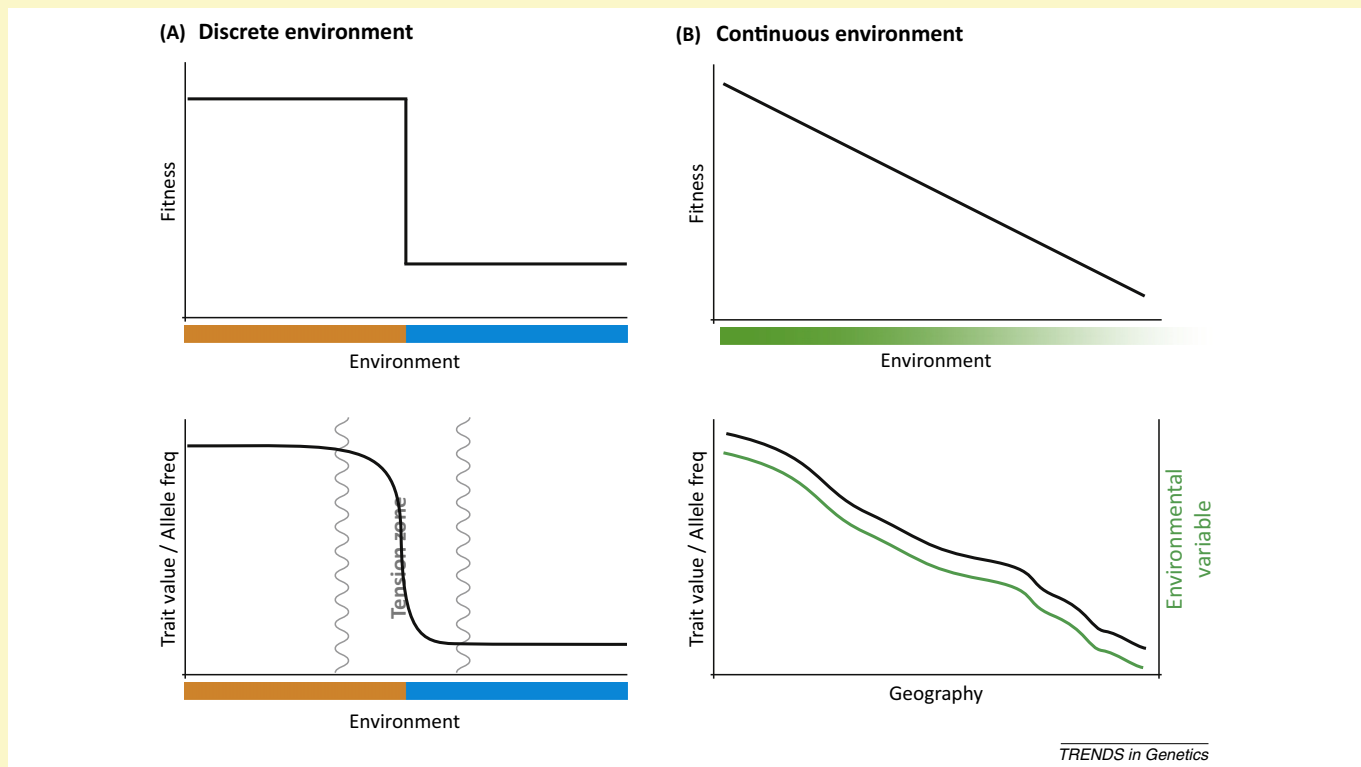


Figure 1. A simplified fitness landscape contrasting discrete- and continuous-environment clines, as well as their expected shapes. **(A)** In discrete-environment clines, the fitness landscape (top: pattern shown for the orange population; blue population would be a mirror image) is often represented by a step function with two fitness optima, where alleles from one species are selected against as they introgress away from their home population. Consequently, the slope of the resulting trait/allele frequency cline (bottom) is relatively shallow in the tails and transitions sharply through the tension zone, although the exact shape is dependent on the strength of selection and dispersal distance. **(B)** The fitness landscape of a continuous-environment cline (top: pattern shown for leftmost population) represents a shifting fitness optimum along a continuous-environmental gradient. The resulting trait/allele frequency cline (bottom: black line) may be less steep than a discrete-environment cline and should closely track the environmental selection pressure (green line).

Phenotypic, genetic, and genomic variation in *D. melanogaster* clines

Expansion of D. melanogaster out of equatorial Africa
Decades of careful study has made *D. melanogaster* the most extensively explored system for elucidating phenotypic, genetic, and genomic divergence among natural populations. Genetic data suggest that *D. melanogaster* expanded out of its native range in equatorial Africa into Eurasia approximately 10 000–20 000 years ago and that

this expansion was associated with a severe population bottleneck [6]. Changes in climatic conditions during the late Pleistocene period are likely to have facilitated migration out of Africa [7,8], but adaptation to numerous ecological factors that vary with latitude has been required in the derived high-latitude populations that now extend as far north as Finland (64°N) and as far south as Tasmania (43°S) [9]. More recently, *D. melanogaster* invaded North America and Australia, and was first collected within only

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