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Digest: Local adaptation at close quarters*

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Although the theory of how gene flow and genetic drift interact with local adaptation is well understood, few empirical studies have examined this process. Hämälä et al. (2018) present evidence that adaptive divergence between populations of *Arabidopsis lyrata* can persist in the face of relatively high levels of gene flow and drift. Maintaining divergence despite gene flow and drift has important implications for understanding adaptive responses of populations in response to human-driven environmental change.

Migration rates and the intensity of genetic drift determine the efficiency of selection and thus the likelihood that locally adaptive differences among populations can arise and persist. In an ideal population, local adaptation should occur most efficiently when selection pressures differ considerably across space, gene flow is low, and population sizes are large enough to make the effects of genetic drift negligible (Fig. 1A). Local adaptation is hindered by high migration rates, which tend to homogenize populations and introduce differently adapted alleles. In small populations, genetic drift becomes stronger than selection and can disrupt adaptation by causing the random fixation and loss of alleles.

The theory underlying how drift, migration, and selection interact is well understood, but few studies have empirically examined the process of local adaptation jointly with gene flow and drift. As such, the demographic conditions that support local adaptation with ongoing gene flow warrant further investigation (Savolainen et al. 2013). Using a combination of reciprocal transplantation, common garden experiments, whole genome sequencing, and demographic analyses, Hämälä et al. (2018) find that locally adaptive divergence among small populations can be maintained in the presence of gene flow.

Studying *Arabidopsis lyrata* populations distributed on altitudinal clines at two Norwegian sites (Jotunheimen and Trollheimen), Hämälä et al. (2018) found evidence that local adaptation in Jotunheimen populations could be maintained despite recent divergence times, ongoing gene flow, and low effective population sizes (Fig. 1B). The researchers also detected adaptive phenotypic variation between habitats in flowering time, a trait that is strongly correlated with fitness in *A. lyrata*. Migration between *A. lyrata* populations was 36 times more likely to occur from alpine to lowland areas than in the opposite direction. These results suggest that adaptation to different selection pressures (toward higher survival in alpine habitats vs increased reproductive output in lowlands) contributes to the preservation of local adaptation in this system. The authors additionally note that greater gene flow toward lower altitudes may be detrimental for these populations given future climate change.

Hämälä et al. chose to sample *A. lyrata* across elevations because they present steep environmental gradients at spatial scales where gene flow could be substantial. Results from such experiments have important implications for understanding local adaptation in general, as well as the effects of climate change on species associated with altitudinal gradients. Steep environmental transitions where strong divergent selection, gene flow, and drift interact are becoming increasingly common, and are important to understand. New steep environmental gradients, particularly human-created gradients such as urban-rural, agricultural, and forest harvest-related transitions, are emerging across the globe (Fig. 1C and D; Kark 2013). Fragmentation associated with rapid environmental change can lead to increased genetic drift by subdividing populations, between which individuals can easily move despite experiencing very different selection pressures (e.g., urbanization; Johnson and Munshi-South 2017). Additionally, the altitudinal dynamics investigated by Hämälä et al.

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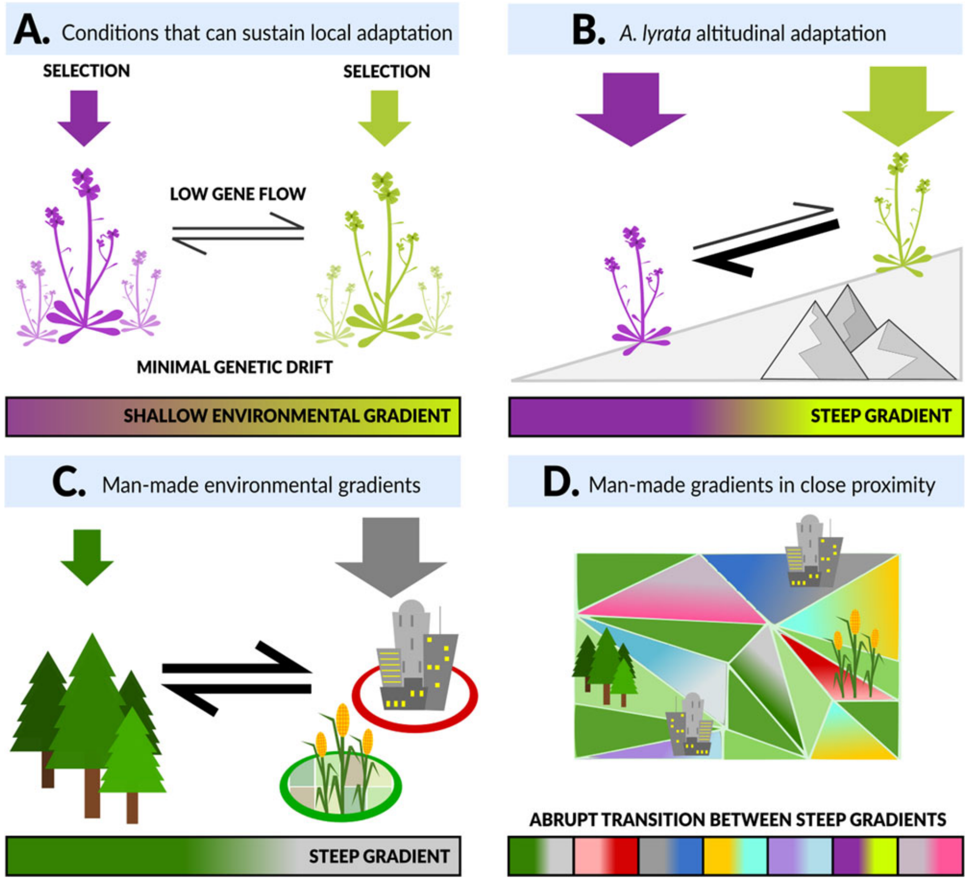

Figure 1. (A) In an ideal population distributed along a shallow gradient, local adaptation is expected to be common because the strength of selection will often overcome the homogenizing effects of gene flow, and drift can be negligible. (B) Hämälä et al. demonstrate that *A. lyrata* populations along a steep altitudinal gradient maintain local adaptive divergence despite high levels of gene flow and low effective population sizes (increased drift). Migration rate was greater from alpine to lowland populations than vice versa. (C) Human-driven habitat change creates new, steep environmental gradients where similar outcomes may be expected. (D) Steep man-made gradients are becoming more common, resulting in abrupt transitions between environments with very different selection pressures.

(2018) appear to be playing out across shallower environmental gradients as a result of considerable range movement by some species in response to climate change (Parmesan 2006). These shifts can bring previously isolated, differently adapted populations into contact, leading to likely important but poorly understood evolutionary consequences (Hoffmann and Sgrò 2011). This study suggests that the strength of human-driven environmental change may sometimes be enough to create and sustain population divergence on man-made scales despite high levels of gene flow and drift-–an important, and possibly overlooked consideration when predicting potential consequences of global change.

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