Trends in Plant Science

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Review

Ecological Interactions, Environmental Gradients, and Gene Flow in Local Adaptation

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Despite long-standing interest in local adaptation of plants to their biotic and abiotic environment, existing theory, and many case studies, little work to date has addressed within-species evolution of concerted strategies and how these might contrast with patterns across species. Here we consider the interactions between pollinators, herbivores, and resource availability in shaping plant local adaptation, how these interactions impact plant phenotypes and gene flow, and the conditions where multiple traits align along major environmental gradients such as latitude and elevation. Continued work in emerging model systems will benefit from the melding of classic experimental approaches with novel population genetic analyses to reveal patterns and processes in plant local adaptation.

Highlights

Although the study of local adaptation has a long history, recent advances come from integration of experimental field approaches with population genetics.

Given that natural selection and gene flow are two key aspects of local adaptation, abiotic and biotic impacts on reproductive traits are expected to have a strong influence on population divergence.

Natural selection from abiotic factors, enemies, and mutualists combine in a complex, context-dependent manner, and may lead to diverse evolutionary outcomes in local adaptation.

Steeper environmental variation over shorter distances and with greater consistency occurs across locations in elevation versus latitude.

The ability to tease apart the relative effects of selection, distance, and gene flow with emerging methods will shed light on the ecological processes shaping local adaptation.

Past and Current Trends in Local Adaptation

Adaptation of plants to their local environment has been studied by evolutionary ecologists for decades (e.g., [1–3]). Interest in **local adaptation** (see Glossary) stems from an appreciation of functional matches between phenotypic diversity within species and the selective aspects of their biotic and abiotic environments. In classic and extreme cases, populations of plants within meters of each other may exhibit differentiation due to strong natural selection even in the face of **gene flow** [4–6].

Traditional studies explored the extent to which plants are locally adapted by using reciprocal transplants and common gardens [4,7], and through the use of quantitative genetics [8–10]. However, these approaches typically explore polygenic traits that evolved from recent selection, and often measure traits that may only be weakly related to fitness. Accordingly, such traditional approaches alone often fail to identify the key traits responsible for local adaptation [11]. More recent integration of molecular methodologies, including inferences from genomic architecture [11,12] and from modeling the relative contribution of environment and space [13,14], have provided direct insight into the evolutionary processes and genetic basis of local adaptation (Box 1) [11,12,15].

Despite scientific advances and summaries from meta-analyses (see [16] and references therein), adaptive differentiation between populations is still often studied through a single lens, focusing on the evolution of traits due to variation in abiotic conditions (e.g., [17]), antagonistic interactions (e.g., [18]), or mutualisms (e.g., [19]). Yet, the highly integrated nature of plant functions suggests that adaptation is likely to occur in response to multiple selective agents simultaneously. The way in which multiple selective agents interact with geographic distance between populations shapes the evolutionary dynamics of the species through gene flow. The dual nature of gene flow is that it increases genetic diversity and can accordingly foster rapid evolution, but depending on population conditions, may also slow responses to selection due to nonadaptive introgression [14] (Figure 1). Selection and gene flow play a key role in the shared evolutionary history (i.e., nonindependence) of populations, which is often overlooked in comparisons within species (but see [20–22]).

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Research on plant local adaptation has recently been reviewed from the molecular perspective [11,12,15] and in meta-analyses of fitness effects [16], but not from an integrative perspective of ecology and evolution of plant–environment interactions. Thus, here we focus on the interactive nature of ecological and evolutionary processes, and in particular how pollinators, herbivores, and their interaction with abiotic factors, shape plant adaptation. Indeed, local adaptation along widely studied natural gradients such as latitude and elevation are likely the result of combined influences of selection and gene flow impacted by multiple ecological effects.

Herbivory and Pollination

Herbivores and pollinators can both impose selection on **plant defense** [23], phenology [24], apparency, and certain floral characteristics [25–28], and in addition both biotic interactions can drive shifts in **mating system** [27,28]. Therefore, interactions between the effects of herbivores and those of pollinators (hereafter 'herbivore–pollinator interactions') sometimes result in conflicting selection for plant traits (e.g., [28–30]). Although the study of herbivore–pollinator interactions is well established and reviewed [23,26,31,32], their relative impact on local adaptation, primarily through effects on gene flow, are not well understood. In this section we outline mechanisms by which herbivore–pollinator interactions may affect gene flow and selection, thereby impacting **population divergence**.

Herbivory alters flowering phenology through **phenotypic plasticity**, typically within the same season [25,33,34], potentially facilitating escape from herbivory or future seed predation [26] (e.g., asynchrony between flowering time and herbivore pressure). Importantly, such phenological

Box 1. Combining Classic and Modern Approaches to Understand Local Adaptation

Classic field ecological and modern molecular approaches have only been combined to understand local adaptation in a few emerging model plant systems. In no one system yet have the following questions all been answered: (i) what is the relative importance of biotic versus abiotic drivers of plant local adaptation; (ii) is the case for local adaptation compelling based on fitness effects and phenotypic differentiation beyond what can be explained by shared evolutionary history; and (iii) to what extent are the traits (and genes) under selection multifunctional versus trade-offs in function. The brief case studies and references below are meant as an entryway to the literature.

Pinus spp. (Pinaceae) (Figure IA) have been well studied for local adaptation because of their diversity, importance in forestry, and the impact of the biotic and abiotic environment during postglacial migration and recolonization processes. Traditional Q_{ST}–F_{ST} tests and association genetics were used to detect patterns of population differentiation and adaptations to the environment [22,119,120]. Accounting for evolutionary nonindependence of populations using SNPs revealed patterns of adaptive variation in resistance to herbivory and defense traits driven by a resource availability gradient [55].

Erythranthe guttata (formerly *Mimulus guttatus*, Phrymaceae) (Figure IB) has adapted to diverse environments that drastically vary in the length of growing season and drought stress. Genetic basis of local adaptation to contrasting environments was related to multiple quantitative trait loci (QTLs) for phenology [81,121], and detected by phenotype–genotype associations using SNPs [122]. After controlling for population structure, evidence suggested that increasing herbivore pressure along latitude drives adaptive investment in chemical defenses among populations [82].

The genus *Asclepias* (Apocynaceae) (Figure IC) inhabits diverse habitats and interacts with multiple antagonists and mutualists. Adaptive differentiation between populations was investigated in natural populations and common garden experiments along *Asclepias syriaca* and *Asclepias speciosa* ranges covering latitude and precipitation gradients, while accounting for shared evolutionary history within species [20]. Studies revealed patterns of local adaptation for traits involved in abiotic tolerances and species interactions [50,56], but the primary driver has not been identified and genotype–phenotype linkages have not yet been made.

Boechera stricta (Brassicaceae) (Figure ID) is an herbaceous perennial that has been well studied from the perspective of local adaptation to biotic and abiotic conditions along elevational gradients. In particular, local adaptation occurs in response to natural selection, and is likely favored by antagonistic pleiotropy and conditional neutrality in QTLs [123]. Local adaptation to herbivores emerged due to duplication and further neofunctionalization of defense genes [124], which may be facilitated by plasticity [125], and some evidence using microsatellite markers suggests that adaptation to biotic and abiotic conditions is occurring independently [126].

Glossary

Assortative mating: sexual reproduction between similar phenotypes more frequently than expected by chance.
Gene flow: the degree of interbreeding between individuals within or among populations.
Isolation by distance: increasing population divergence in absence of selection associated with increasing distance between populations, driven by geographically limited gene flow or dispersal.
Isolation by environment: increasing population divergence associated with non-random mating due to selective environmental (abiotic and/or biotic) differences.
Local adaptation: a pattern resulting from natural selection within species whereby individuals have higher fitness in their local environment compared to a distribution of different environments.
Mating system: the relative frequency of selfing versus outcrossing that impacts patterns of gene flow.
Phenotypic plasticity: the ability of a single genotype to produce different phenotypes depending on the environment.
Plant defense: traits that increase plant fitness in the presence compared to absence of enemies. Such traits may provide resistance (less damage), tolerance (reduced fitness impact of enemies), or avoidance (reduced host finding by enemies).
Population divergence: genetically determined phenotypic differences between populations generated by one or many factors, including mutation, selection, heterogeneous gene flow, genetic drift, and founder effects.
Resource availability: abiotic conditions that impact plant functions, including nutrients, water, light, and climate.
Scale-dependent evolution: differences in the expectation of evolutionary outcomes within versus between species.
Standing genetic variation: the extent of allelic variation at loci within a population.
Trade-off: the advantage of a single or multivariate organismal phenotype in one ecological context that is accompanied by a disadvantage in the same or different context.

Figure I. Emerging Model Plant Systems in Which Local Adaptation Was Investigated Combining Traditional and Modern Molecular Approaches. (A) Maritime pine (*Pinus pinaster*). (B) Monkeyflower (*Erythranthe guttata*). (C) Common milkweed (*Asclepias syriaca*). (D) Drummond's rockcress (*Boechera stricta*). Photo credits: (A) X.L.-G., (B) A. Scharnagl, (C) A.A., and (D) J. Anderson.

shifts may reduce gene flow through temporal isolation [14], and could facilitate subsequent local adaptation even among spatially close populations if the responses are consistent (e.g., [33]). However, opposing plant responses to herbivores and pollinators may result in no net selection on flowering time, thus hampering phenotypic divergence [29,35]. In addition, specific responses to herbivory can also shape floral morphology and scent, altering plant–pollinator interactions [23,35,36]. Such herbivory-induced changes may reduce gene flow through pollinator shifts, or reduction in floral attractiveness [31,33,36]. Conversely, phenotypic divergence may be limited if the diversity and availability of pollinators maintain gene flow despite herbivore-induced plant responses, or if reductions in time spent by visitors do not decrease pollination efficiency [31,36].

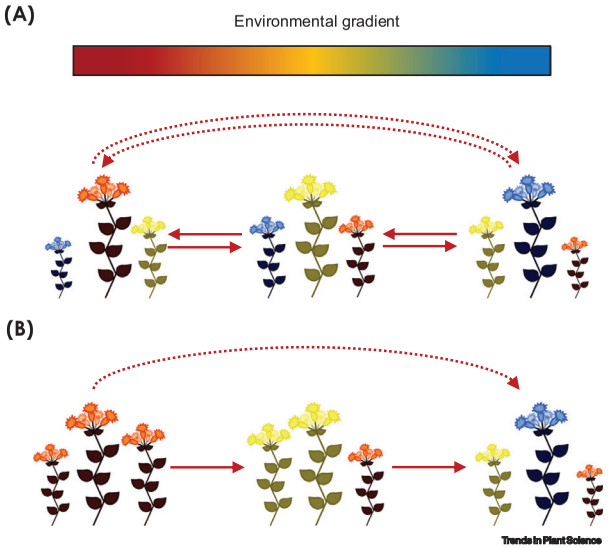

Figure 1. Beneficial and Detrimental Effects of Gene Flow along Environmental Gradients. In these schematic diagrams, the largest plant type (by size) is the locally adapted form along an environmental gradient, whereas smaller plants indicate the ability of foreign types to persist locally. (A) Random gene flow (arrows) between populations tend to homogenize the allelic and genotype frequencies across all populations, contingent on the selection exerted in each environment. The center of the range of a species (i.e., yellow) is expected to harbor the greatest genetic diversity due to admixture from neighboring populations. (B) In the case of directional gene flow, some populations are donors and others are recipients of alleles or genotypes. Directional gene flow can be beneficial when the environment of the recipient population resembles the one of the donor (i.e., cogradient gene flow [14]). In this case, alleles or individuals from the donor can be beneficial for local adaptation of the recipient population. Alternatively, directional gene flow can be maladaptive when the environment of the recipient population is more different than the one of the donor (i.e., counter-gradient gene flow [14]). In this scenario, incoming alleles or individuals from the donor can hamper local adaptation of the recipient population. Gene flow between distant populations (e.g., red vs. blue) may also delay the transference of adaptive alleles to face rapid environmental changes. Although the extent of local adaptation can be assessed by reciprocal transplants, population genetic analyses can inform about the degree of gene flow impacting this adaptation.

These possibilities highlight the importance of considering the larger biotic community of herbivores and pollinators, because depending on how they interact, and the plant responses they induce, evolutionary outcomes may vary substantially [37].

Spatiotemporal consistency in the direction and intensity of herbivore–pollinator interactions may favor genetically fixed traits over phenotypic plasticity, fostering genetic divergence [27,28,38,39]. On the one hand, pollinators can exert specific and consistent directional selection, causing adaptive divergence in plant traits that reinforce interactions with pollinators over generations [27,28,40]. Pollinator-mediated selection is expected to be stronger for traits related to pollination efficiency, since these can directly impact plant fitness [40]. Plant attractiveness can be

maximized by pollinators through a combination of traits (e.g., taller plants, and larger and more fragrant flowers) [27,28], although the selective strength will depend on the composition of the pollinator community [40]. On the other hand, herbivores may negatively impact floral attractiveness to pollinators [23,30], and even disrupt pollinator-mediated responses to selection [28]. Since herbivory often impacts plant fitness through selection of traits less attractive for pollen vectors, or reducing mating opportunities (e.g., mate scarcity, castration), evolutionary transitions from outcrossing to selfing strategies are predicted to ensure reproduction in populations evolving with strong herbivory [23,26,28].

Differences in selection exerted by herbivore–pollinator interactions are expected to be large between populations due to the interactive effects of distance and the composition of the biotic community, but also due to the direction and intensity of such selection, even at finer scales [4,30]. Given the general opposing effects of herbivores and pollinators on fitness-related plant traits, these selective pressures may push diverged populations towards a single optimum phenotype (i.e., stabilizing selection). Alternatively, opposing selection by herbivores and pollinators may foster evolutionary divergence (i.e., divergent selection) even with minor changes within plant populations, which can cause larger differences between populations [23,25,39,41]. For instance, an extensive study of 69 populations of bird's-eye primrose (*Primula farinosa*) found that variation in the intensity of herbivores and pollinators facilitated population divergence [39]. Greater selection exerted by vertebrate herbivores fostered the evolution of populations with smaller plant sizes, shorter-scaped morphs, and cryptic flowers, each as an adaptation to herbivore avoidance; selection by pollinators favored populations with taller plants, longer-scaped morphs, and prominent flowers as an adaptation to increase reproductive success through floral attractiveness [39]. Thus, the tremendous variation in the selective landscape by the community of herbivores and pollinators may lead to a complex mosaic of evolutionary outcomes to shape plant local adaptation [30,42], which can be exacerbated when the distance travelled by pollinators is limited [43,44].

We therefore expect that pollinators select for more attractive phenotypes through **assortative mating** driven by the community of pollen vectors [27,30], whereas herbivores may indirectly favor selfing to ensure plant reproductive success when outcrossing processes are impaired [26,45,46]. Although it seems clear that the interactions between herbivores and pollinators contribute to local adaptation, the relative importance of either group over the other is still under debate ([40] vs. [47]). When differentiated populations are studied, experimental manipulations of herbivores and pollinators and subsequent measures of natural selection would be particularly informative.

Abiotic–Biotic Interactions

It is well-established that biotic and abiotic conditions interact to shape plant adaptation. Variation in light, temperature, soil characteristics, and precipitation, often modify **resource availability** and biotic interactions, representing excellent natural tests of interactive selective agents, often through changes in resource allocation to different plant functions (e.g., growth [48], reproduction [49], or defense [50]) (Figure 2). Over the past 60 years, a large effort has been made to understand the ecological and evolutionary patterns of variation in plant growth and defense (reviewed in [51]). One of the most prominent postulates, the resource availability hypothesis (RAH), predicts that evolutionary patterns of allocation to growth and defense between plant species are contingent on resource availability [52]. The RAH predicts that in resource-rich sites, fast-growing and less-defended species are favored because of the lower cost of replacing tissues eaten by herbivores. Conversely, plants in resource-poor environments grow more slowly and allocate more resource to defenses because of higher costs of replacing tissue lost by herbivores. Past work addressed the RAH within species as well, but the expected pattern was often not found

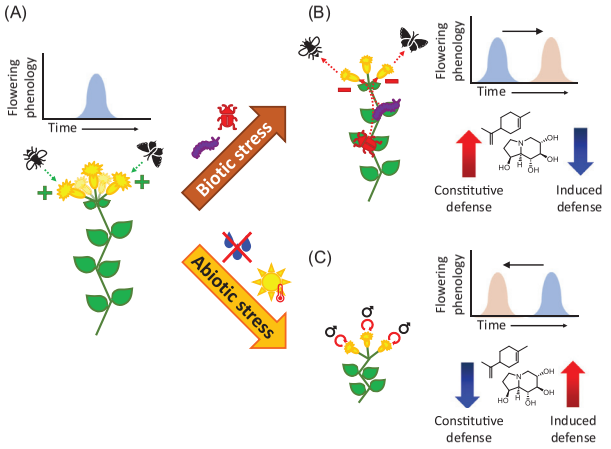

Figure 2. A Simplified Schematic of the Impacts of Abiotic and Biotic Factors on Local Adaptation for Plant Growth, Reproduction, and Defense. (A) Optimal conditions of resource availability and growing season length may foster local adaptation towards greater allocation to growth and reproductive traits within a species. (B) Greater lifespan and plant apparency may increase biotic pressure and persistence of enemy populations over time, favoring the evolution of constitutive defenses over induced defenses. However, enemies may foster delayed flowering to avoid herbivory, and also reduced plant attractiveness to pollinators through chemical or physical changes in reproductive traits. Alternatively, (C) abiotic stress typically favors smaller sizes because of lower resource availability, and early flowering due to shorter growing seasons. Reduced plant apparency and lifespan may decrease incidence and host finding by enemies, favoring resource-saving defensive strategies, like induced defenses. In addition, harsher environments may foster self-fertilization due to reduced life span, mate density, and pollinator availability. As discussed in the main text, abiotic and biotic stresses may be environmentally coupled, and likewise plant traits may be coupled through genetic correlations as well.

(e.g., [53–56]). This is likely because of inherent differences in habitats, communities of enemy associates, and genetic exchange between populations compared to that between species (i.e., **scale-dependent evolution**) [57,58]. In addition, patterns of relative allocation to plant reproduction and plant–pollinator interactions within species have not been well studied in the context of adaptation to resource availability. In the next paragraphs we review and discuss how abiotic–biotic interactions impact trait evolution and shape plant local adaptation.

Warmer, wetter, and longer growing seasons may promote plant local adaptation towards simultaneous allocation to growth and defense within species, a pattern not predicted by the RAH [50,55,59,60]. Larger plant size is expected from those environments due to greater resource acquisition by individuals, and also due to interactions with competitors through shade-avoidance responses or niche partitioning [48,61–63]. In such cases, because larger plants are often associated with increased risk of biotic attack, greater investment in plant resistance mechanisms may be favored [41,55,57,61], although contingent on plant life-history strategy and population conditions (Figure 2) [41,54,61,64]. For example, greater plant apparency and lifespan may facilitate persistence of enemies over time, favoring evolution of constitutive plant defenses over induced

strategies [54,55,61]. Alternatively, plant populations suffering from strong herbivore damage (e.g., mammalian grazers) may evolve compensatory growth (i.e., tolerance) [61] or less apparent plant morphologies for herbivores (i.e., avoidance) [41], due to lower costs compared to investment in resistance.

In some cases, abiotic and biotic factors may exert selective pressures favoring the evolution of specific plant traits that simultaneously cope with multiple stresses. For example, plant trichomes (i.e., leaf hairs) are primarily associated with abiotic stress, modulating heat balance, and reducing UV damage [65,66], but also function in resistance to herbivory [67,68]. Similarly, phenolic compounds are diverse and widespread plant secondary metabolites involved in resistance to both abiotic and biotic stresses [53,69,70]. Thus, local adaptation in plants can be facilitated by the evolution of multifunctional traits to different selective pressures. For instance, Buckley *et al.* [71] found that *Arabis alpina* plants showed higher trichome density at low- and high-elevations compared to mid-elevation, suggesting local adaptation to greater biotic pressure and abiotic stress often found at low- and high-elevations, respectively (see [72]). Nevertheless, under the same selective regime, two or more traits that share a resource (e.g., nitrogen) may display different relationships, depending on resource availability. For example, growth-defense relationships are expected to be positive due to greater competition and enemy pressure in resource rich sites [50,55], but may also be negative (i.e., a **trade-off**) because of physiological constraints in resource-limited environments [57,73].

Despite recent progress in understanding patterns of growth and defense along resource gradients (see reviews in [57,58,61,72]), predictions regarding relative allocation to reproduction itself, and impacts on plant–pollinator interactions have not been widely considered. This is likely an indirect consequence of past work focusing primarily on life-history comparisons between species, where reproductive traits are highly variable [74], but less relevant to local adaptation. Nonetheless, reproductive traits should be strongly impacted during local adaptation within species, where costs of reproduction are experienced, pollinator availability may be variable, and phenology may change along resource gradients. For example, evolution of smaller plant sizes and shorter lifespan due to harsher conditions may foster greater relative allocation to reproductive biomass [49,75]. This is because larger plant sizes and perennial life-history strategies, often linked to high resource habitats, must balance the investment between vegetative growth and reproduction. In addition, harsher environments may increase the cost of reproduction directly through reduced plant fecundity and survival [76], but also indirectly through reduced mate density and pollinators [77,78]. In such cases, evolution of selfing-related traits may be favored to ensure reproduction. For instance, shifts from larger and heterostylous flowers to smaller and homostylous ones were associated with reduced pollinator availability with increasing environmental harshness in *Primula oreodoxa*, favoring transitions from outcrossing to selfing [79]. Finally, shorter growing seasons may favor the evolution of early flowering to escape future stresses (i.e., summer droughts) [80,81] (Figure 2C).

We predict simultaneous investment in plant competitive ability and resistance through greater growth and stronger herbivore pressure in resource-rich environments, at the expense of lower relative allocation to reproduction. Conversely, growth-defense tradeoffs will likely emerge in harsher sites due to physiological constraints and different selective pressures (e.g., less persistent herbivory), and greater relative investment in reproduction is predicted due to shorter lifespan.

Local Adaptation to Environmental Gradients

Latitude and elevation have been extensively studied in recent decades because they constitute reasonable proxies for suites of changing environmental conditions, and have important

evolutionary implications for plant local adaptation (e.g., [21,53,82,83]). Lower latitudes and elevations are often associated with longer growing seasons that typically foster the evolution of larger plant size, delayed phenology, and greater fecundity compared to shorter growing seasons [76,84,85]. Natural selection on these growth-phenology strategies can lead to a temporal barrier in gene flow, facilitating local adaptation of populations via assortative mating [25,86]. Latitudinal and elevational gradients have additionally been investigated as drivers of anti-herbivore defense evolution, with higher investment in plant defense predicted at lower latitudes [18,87,88] and elevations [72,89,90] due to stronger antagonistic interactions in these locations. Although evolution of defense mechanisms may not hamper gene flow between populations, the strength and type of antagonistic biotic interactions may differentially favor plant resistance phenotypes, fostering local adaptation of better defended populations where enemy pressure is higher [50,91].

In the vast literature addressing the evolutionary implications of gradients in latitude and elevation, previous studies have reported mixed evidence in relation to the expected pattern between the gradient and traits of interest. For instance, several studies found limited covariation between flowering time and latitude or elevation [92,93]. Moreover, studies that have explored intraspecific variation in plant defenses across latitudes sometimes showed unclear (e.g., [94,95]) or opposing trends (i.e., plant defense increases as latitude increases) from the expected patterns (e.g., [53,56,82]). Recent studies within species found greater investment in plant defense as elevation increases, which was contrary to expectations [96–98]. These inconsistencies can be due to differences in covariation between the trait of interest *in situ* versus covariation with source latitude in a common environment, especially in trait phenology [85,99]. In addition, some plant traits are often assumed as 'defensive' without testing their functional association with herbivores. Herbivore pressure may depend on the abiotic gradient *per se*, and also on the direction of expansion of plant populations from the center of the species' range, where the main herbivores are expected to concentrate. Sources of controversy surrounding the evolution of plant traits across latitude and elevation have received much attention between species (see recent reviews [72,100,101]). Less attention has been paid, however, to the ecological and evolutionary implications of geography and environmental gradients together in shaping plant local adaptation within species [62].

As a means to reconcile previous evidence and predict how patterns of local adaptation emerge, we first suggest that relationships between selective factors and environmental gradients differ between latitude and elevation. Increasing elevation is typically and consistently associated with lower temperatures, shorter season length, greater exposure to sunlight and wind, and increased environmental seasonality [49,72,91,102]. Conversely, environmental factors are more diffuse and less continuous across latitudes than across elevations, and only a few coarse grained variables consistently follow latitudinal trends (e.g., photoperiod and temperature) [85,103]. Hence, plant traits are expected to integrate more across elevation, due to greater consistency of multiple axes of environmental variation as well as their direction of selection, than across latitude (Figure 3, Key Figure). In addition, since environmental differences between elevation and latitude occur at different spatial scales (short vs. long distances, respectively), it is expected that gradients in elevation show steeper environmental variation per unit distance compared to latitude, potentially exerting stronger selection to overcome the homogenizing effects of gene flow. Therefore more persistent and stronger environmental pressures similarly across different elevations may facilitate the emergence of parallel patterns of local adaptation that follow the line of elevation, in comparison with latitude (Figure 3).

These evolutionary expectations stem from previous evidence repeatedly reported in multiple plant traits and in different species (e.g., [71,72,90,91,103]). For example, greater divergence in

Key Figure

Expectations of Patterns for Local Adaptation along Gradients in Latitude and Elevation

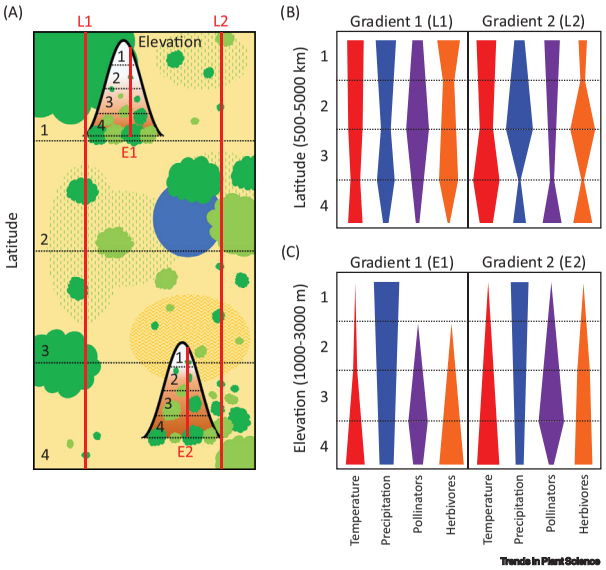

Figure 3. We predict that patterns of local adaptation differ between latitude and elevation because of differences in environmental variation per unit distance, and how consistently selective factors covary within each gradient. (A) Landscape scheme representing environmental heterogeneity along latitude and elevation. Green patches represent plant populations, contingent on resource availability in the local environment, which shapes plant traits and interactions with herbivores and pollinators. Broken horizontal lines separate numbered transects of environmental variation within the gradient, and red vertical lines represent different locations along the latitudinal (L1, L2) and elevational gradients (E1, E2). (B,C) Predictions of how the multiple axes of environmental variation vary in intensity (width of the colored shapes) and how well that variation is aligned (similar trends across transects) along latitude (B) and elevation (C), respectively. Patterns of local adaptation are expected to follow the gradient in elevation more than that in latitude due to: (i) greater environmental variation per unit distance in elevation versus latitude (note average distance range used in studies for both gradients on the *y*-axis); (ii) multiple axes of environmental variation are more similar and persistent across transects in elevation than in latitude; and (iii) gradients in elevation are expected to be more consistent between locations than in latitude.

flowering time is expected across elevations due to greater environmental variation per unit distance than across latitudes [103,104]. Similarly, greater differences in temperature, rainfall, and growing season length across elevational versus latitudinal gradients, may have stronger impacts on host availability for plant enemies, fostering local adaptation in defense strategies as herbivore pressure declines with elevation [71,72,90,91]. We predict that covarying environmental axes

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exerting persistent selection will be more frequent across elevational gradients, which may foster the emergence of locally adapted syndromes (i.e., convergent suites of covarying traits in response to selection) among populations of different species [89,105–107]. For instance, environmental harshness in populations from high elevations consistently fosters smaller plant size and lower constitutive defense (due to reduced herbivory) in multiple species (e.g., [71,89,91]). Finally, given the directionality and the higher environmental variation per unit distance, positive covariation between environment and plant responses (i.e., cogradient plasticity) is expected as an adaptation to steep changes in elevational gradients [104,108]. These patterns contrast with those across latitudinal gradients, which do not often follow a strict line along latitude (Figure 3) [16]. In other words, greater environmental heterogeneity (i.e., precipitation, habitat type, etc.) blurs the more consistent pattern of variables such as day length and temperature, making local adaptation along a latitudinal gradient more diffuse and less likely to be parallel among different transects or species.

Gene flow from nearby populations is largely thought to have disruptive effects on local adaptation [13,14]. However, the degree of gene flow is expected to differ between elevation and latitude, given their different environmental variability and spatial scales, and their impacts on plant traits and species interactions. On the one hand, population divergence across latitude, despite its shallower environmental variation, may occur because of more limited gene flow between more distant populations [22,109] compared to elevation. In other words, **isolation by distance** (IBD) is a pattern generated by limited gene flow that may indicate local adaptation of populations [14], evolving independently across a mosaic of environments even if weakly related to latitude. Alternatively, population divergence across elevations may proceed because of stronger environmental selection that overcomes the effects of gene flow over short distances [110,111] in comparison to latitude. This greater biotic and abiotic variation per unit distance across elevations may lead to patterns of local adaptation through **isolation by environment** (IBE) more so than by IBD [13,14]. Additionally, gene flow may be a double-edged sword. Gene flow, which increases genetic diversity, may allow for a stronger response to selection due to greater **standing genetic variation** on which selection may act [112], which can be especially important at range edges [113,114]. Thus, local adaptation may be facilitated by gene flow between populations facing environmental changes in similar directions. For example, gene flow from warmer populations may have contributed adaptive genetic variation to populations experiencing climate warming [113], especially across elevations. Conversely, although local adaptation can be facilitated via IBD across latitudes, distance between remote populations may also delay the transfer of beneficial alleles [113,114]. The emergence of locally adapted phenotypes and opportunities to rapidly evolve will depend on the intensity and direction of environmental selection, and the balance between the benefits of gene flow (i.e., introgression of adaptive alleles from neighboring populations, genetic rescue [14]) versus any detrimental effects (i.e., gene swamping, introgression of maladaptive genes [14]) (Figure 1).

Despite the well studied context-dependent effects of gene flow in local adaptation, many empirical studies that have explored patterns of trait variation along environmental gradients, within species, often assumed populations as evolutionary independent entities (e.g., [54,56,96,115]). This contrasts with studies conducting comparisons across species, in which the need to account for shared evolutionary ancestry using phylogenetic independent contrasts is widely recognized [116]. Given the complexity of evolutionary processes connecting populations across environmental gradients (including gene flow and shared ancestry), emerging approaches from population genetics and molecular ecology (reviewed in [11–13,15]) have been controlling for nonindependence of populations [117], especially when inferring patterns of local adaptation (Box 1). Indeed, although modern population genetics is continuously advancing, novel

approaches are still needed to unravel the relative importance of spatial variation, gene flow, drift, and environmental selection within species [15]. Since not all phenotypic variation is due to adaptive processes related to environmental heterogeneity across populations [118], disentangling the nuances underlying trait evolution can only be achieved by merging advances from ecological, evolutionary, and molecular disciplines [20–22].

Concluding Remarks

Studies are needed that further explore how the abiotic environment, antagonists, and mutualists interact to drive selection, gene flow, and ultimately the ensemble of trait evolution (see Outstanding Questions). Despite the effort invested in exploring patterns of adaptation along latitudinal and altitudinal gradients between species, comparatively less is known about patterns of local adaptation within species. Variation in reproductive traits and patterns of gene flow are expected to have strong implications for local adaptation, and must be considered (Figure 1). Although we have tried-and-true methodologies to study local adaptation, emerging methods (especially integrating organismal ecology and population genetics) are rapidly advancing progress, particularly in our ability to separate various processes, including gene flow, selection, and genetic drift. Plant local adaptation involves complex selective (and often conflicting) pressures by herbivores and pollinators, shaped by the effects of resource availability on plant traits and function (Figure 2). Investigating the extent to which interactions between mutualists, antagonists, and resource availability aligns with environmental gradients, such as latitude and elevation, will shed light on how complex organismal adaptations emerge (Figure 3). Because gradients are not all equivalent, and species themselves have varying life histories, a predictive framework for plant local adaptation will necessarily require incorporating these nuances.

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Declaration of Interests

No interests are declared.

Outstanding Questions

To what extent is altitude a stronger driver of local adaptation to multiple environmental axes compared to latitude for the same species?

How does variation in herbivore or pollinator communities impact gene flow between populations?

What is the relative importance of pollen versus seed dispersal for gene flow and how do each independently and together impact local adaptation?

Do patterns of local adaptation (i.e., environment–phenotype matches) of a broadly distributed species along a geographical gradient, mirror patterns among closely related species that turn over across the same gradient?

What is the relative importance of different environmental drivers in the evolution of multifunctional traits?

How do plant mating systems impact local adaptation and vice versa?

To what extent are features of genetic architecture, such as genetic correlations, a cause or a consequence of local adaptation?

Does life-history variation (e.g., size, phenology) impact patterns of plant local adaptation?

Does phenotypic plasticity facilitate (or limit) local adaptation?

Are plants more or less likely to show patterns of local adaptation when they are associated primarily with generalized versus specialized biotic interactions?

To what extent do plants locally adapt to multiple enemies independently (e.g., root, shoot, and seed herbivores)?

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Declaration of Interests

No interests are declared.

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