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Local Adaptation: Causal Agents of Selection and Adaptive Trait Divergence

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reciprocal transplant experiment, target of selection, agent of selection

Abstract

Divergent selection across the landscape can favor the evolution of local
adaptation in populations experiencing contrasting conditions. Local adaptation is widely observed in a diversity of taxa, yet we have a surprisingly
limited understanding of the mechanisms that give rise to it. For instance,
few have experimentally confirmed the biotic and abiotic variables that
promote local adaptation, and fewer yet have identified the phenotypic
targets of selection that mediate local adaptation. Here, we highlight critical
gaps in our understanding of the process of local adaptation and discuss
insights emerging from in-depth investigations of the agents of selection
that drive local adaptation, the phenotypes they target, and the genetic
basis of these phenotypes. We review historical and contemporary methods
for assessing local adaptation, explore whether local adaptation manifests
differently across life history, and evaluate constraints on local adaptation.

1. INTRODUCTION

Abiotic and biotic conditions vary spatially, which can favor the evolution of local adaptation when populations inhabit disparate environments (Hereford 2009, Kawecki & Ebert 2004, Leimu & Fischer 2008, Savolainen et al. 2007). Indeed, local adaptation has been documented in a diversity of taxonomic groups (Bachmann & Van Buskirk 2021, Campbell-Staton et al. 2017, Dias & Blondel 1996, Lowry & Willis 2010, Nosil & Crespi 2004, Peterson et al. 2014, Pfeifer et al. 2018, Sanford & Worth 2010). Key biotic interactions, such as plant–mycorrhizal associations, also show evidence of local adaptation (Rúa et al. 2016). Furthermore, local adaptation can evolve rapidly, as in the case of the invasive forb *Lythrum salicaria* in its nonnative range in North America (Colautti & Barrett 2013) or the rapid adaptation of the frog *Rana arvalis* to lake acidification in Sweden (Räsänen et al. 2003). Field experiments often reveal that these locally adapted ecotypes have the greatest fitness in their home sites relative to alternative habitats, and local ecotypes typically outperform those from other habitat types, satisfying the home–away and local–foreign criteria for local adaptation (Kawecki & Ebert 2004).

At its core, the study of local adaptation is inherently interdisciplinary, linking ecological factors to evolutionary outcomes and, in rare cases, examining the community- and ecosystem-level consequences of within-species adaptive population divergence (Bassar et al. 2010). Local adaptation can maintain intraspecific genetic variation, leading to species that consist of mosaics of genetically diverged populations adapted to different environments. When gene flow rates across habitat boundaries are negligible, local adaptation can be an initial stage in the process of reproductive isolation and ecological speciation (Lowry 2012). In contrast, when the migration–selection balance tips in the other direction, extensive gene flow can restrict the evolution of local adaptation (Slatkin 1987). While local adaptation is common, it is not ubiquitous (Hereford 2009, Leimu & Fischer 2008), leaving us with the intriguing tasks of investigating the biological processes that constrain local adaptation and determining what factors restrict our power to detect local adaptation.

Here, we highlight critical gaps in our understanding of the process of local adaptation and discuss insights that can emerge from in-depth investigations of the agents of selection that drive adaptive population divergence and the locally adaptive phenotypes they target. In the process, we explore whether local adaptation manifests differently across life history, and we evaluate constraints on local adaptation. We begin by providing a historical perspective in which we discuss long-standing and emerging approaches in the study of local adaptation.

2. HISTORY OF APPROACHES

2.1. Provenance Experiments

In the eighteenth century, European foresters initiated provenance experiments (**Figure 1**) with the goal of generating enough timber to satisfy naval shipbuilding needs (Langlet 1971). The term local adaptation emerged in the forestry literature, although it was used in passing and not clearly defined [e.g., individuals that are "the strongest, best circumstance-suited, for reproduction" (Matthew 1831, pp. 307–8)]. Later provenance trials continued to have an applied focus, seeking to identify accessions of commercially important tree species that would be suitable for silviculture and reforestation efforts; nevertheless, some experiments investigated intraspecific variation to address goals in basic science (e.g., Langlet 1971, Liepe et al. 2016, Risk et al. 2021). In these experiments, foresters collect seeds from multiple populations throughout the range that have been subject to different local selective regimes across their evolutionary histories and then transplant these propagules into multiple experimental gardens, measuring survival, height, and phenology, due to their relevance for timber production and reforestation (**Figure 1**) (Risk et al. 2021, Wang et al. 2010). As early as 1787, foresters noted the importance of the climate for

Local adaptation:
a pattern that occurs when local genotypes have higher fitness than foreign genotypes in at least two contrasting habitats

Ecotype:
a genetically and phenotypically distinct locally adapted genotype that is found in a particular habitat

Migration–selection balance: the balance between gene flow increasing genetic variation and selection decreasing genetic variation by purging maladapted alleles

Provenance experiment:
an experiment that compares the fitness and phenotypes of many accessions that are transplanted into multiple field gardens

Accession:
a propagule collected from a known source population; the term is often used interchangeably with genotype, family, or population and does not imply local adaptation
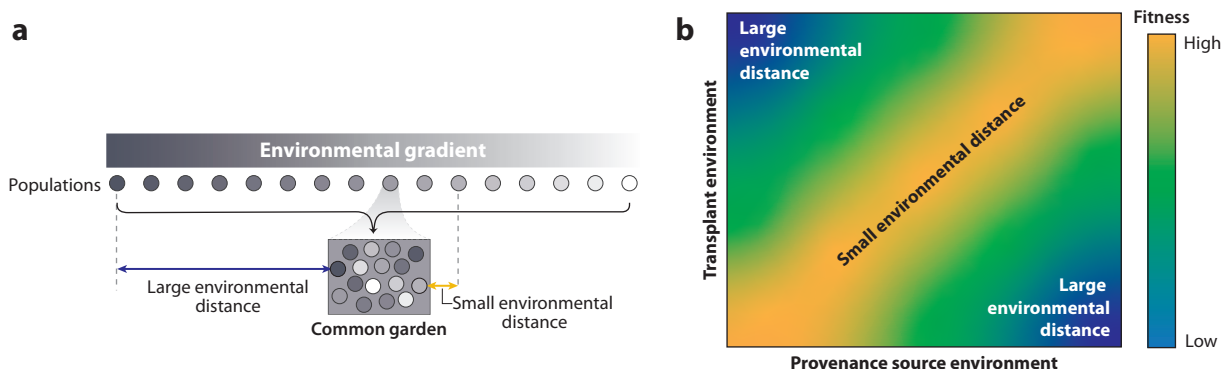
Figure 1

Provenance experiment. (*a*) A hypothetical field experiment in which populations from across an environmental gradient are established in the same common garden. Some populations experience similar environmental conditions to those in their home sites (i.e., environmental distance is small) while others experience very different conditions (i.e., environmental distance is large). Ideally, data from multiple sites could be pooled to generate (*b*) a heat map depicting the relationship between the source environment of provenances and the environments of the transplant sites. This transfer function demonstrates that populations achieve the highest fitness when they experience environmental conditions similar to those of their home site. This pattern is indicative of local adaptation.

tree performance, with trees showing the highest growth rates when the climate of the garden was similar to the climate of origin (Langlet 1971). By the beginning of the twentieth century, other researchers working with tree and herbaceous species demonstrated that high-elevation or high-latitude accessions often flower earlier than their lower-elevation or -latitude counterparts when transplanted into a common garden (Langlet 1971), a pattern that has been corroborated in modern studies (e.g., Kawakami et al. 2011, Wadgymar et al. 2017a). Thus, these early provenance experiments uncovered local adaptation and intraspecific variation in phenology, which likely evolved in response to divergent selection mediated by climatic variation across the range.

Reciprocal transplant experiments (**Figure 2**) are the gold standard for evaluating local adaptation to discrete habitat types (Johnson et al. 2021). This approach involves transplanting experimental individuals into at least two habitat types with contrasting conditions to test whether local genotypes have a fitness advantage over foreign genotypes and have a home-site advantage (e.g., Kawecki & Ebert 2004, Kim & Donohue 2013). However, many species do not simply inhabit two distinct habitat types. Rather, they have geographic ranges that span environmental gradients, necessitating studies that can investigate the interactions of evolutionary processes, such as divergent selection and gene flow, at small spatial scales (Richardson et al. 2014). Provenance experiments have greater power than reciprocal transplant experiments to inform our understanding of local adaptation across continuous environmental gradients where conditions change gradually, variation in selection is subtle, and rates of gene flow are high. Toward that end, provenance trial experiments have two advantages over reciprocal transplant experiments: (*a*) They include accessions from numerous source populations, typically distributed across latitudinal, longitudinal, or elevational gradients, and (*b*) the accessions are transplanted into numerous field gardens, established broadly across the landscape to capture variation along multiple environmental axes. This approach interrogates the fitness and trait expression of diverse accessions under many field environments, thereby facilitating powerful tests of local adaptation across gradients (Wang et al. 2010). Results often reveal clear local adaptation, with peak fitness for accessions whose climate of origin is similar to the climate of the garden (**Figure 2**) (Wang et al. 2010), although provenance trial experiments can also uncover cases of local maladaptation, in which local accessions

Common garden: an experiment in which organisms are reared in a common environment, either in the field or the lab

Reciprocal transplant experiment: an experiment that compares the fitness of two or more populations reciprocally established in each of their sites of origin
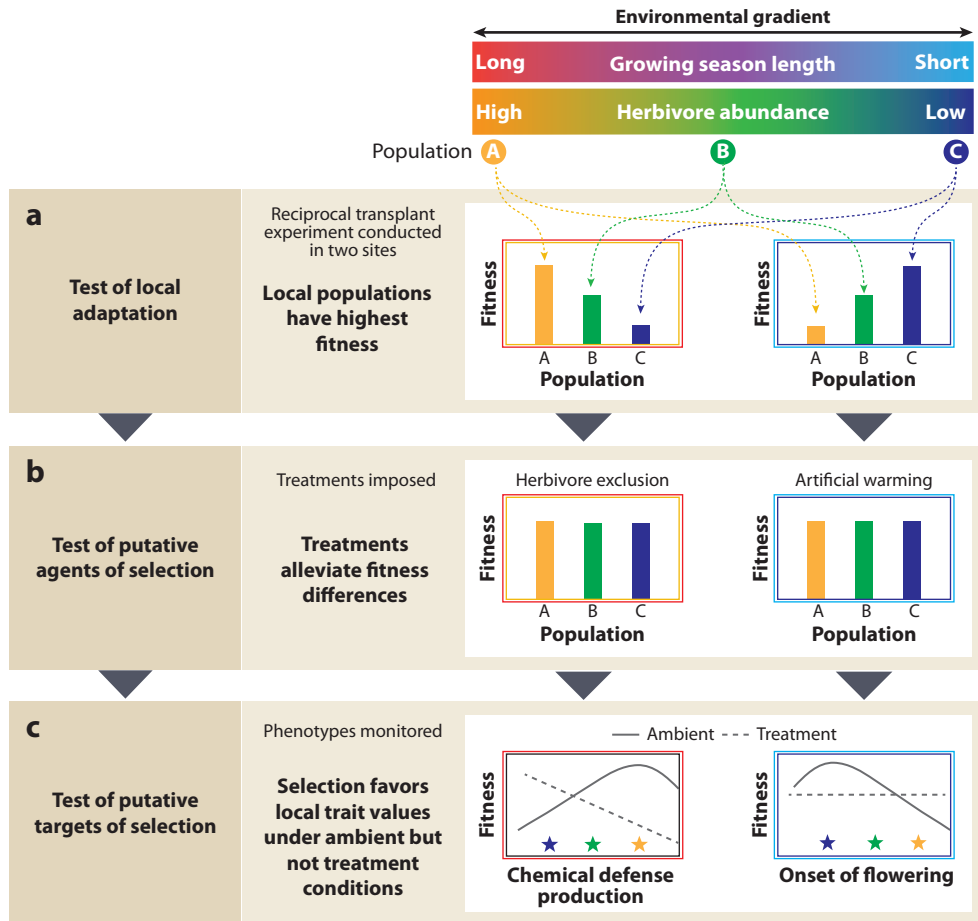
Figure 2

Reciprocal transplant experiment. (*a*) A hypothetical field experiment on a plant species in which three populations (A in yellow, B in green, and C in blue) from across environmental gradients of growing season length and herbivore abundance are reciprocally transplanted into two common gardens. Fitness assays reveal that local populations achieve higher fitness than foreign populations within each common garden, confirming local adaptation. (*b*) Fitness differences among populations in each common garden are alleviated in experimental manipulations, thereby identifying the agents of selection that promote local adaptation in each site. (*c*) Selection analyses reveal the association between putative locally adapted phenotypes and fitness, with the average phenotype of each population depicted by a star. Under ambient conditions (*solid lines*), selection favors local phenotypes in each site, confirming these traits are targets of selection that enable local adaptation. In the absence of herbivory, selection may favor the reduced expression of defenses (*dashed line in left panel*), as allocating resources to defenses when herbivores are not present could incur a cost to other life history functions. Artificial warming treatments could relax selection on flowering time (*dashed line in right panel*). However, if warming coincides with increased herbivore pressure, selection may favor delayed flowering as plants allocate more resources to defense.

do not have the highest fitness (Lu et al. 2016). These cases are, perhaps, the most intriguing because they provide us with the opportunity to examine the evolutionary processes that constrain adaptive population divergence.

Risk and colleagues (2021) compiled a database of traits and climatic variables from 30 provenance trials dating back to the 1950s for seven North American tree species, which is an invaluable resource for evaluating local adaptation in an era of rapid environmental change. Provenance experiments are more expensive to execute than reciprocal transplants because of the increased

numbers of source populations and field gardens spread across the range. Nevertheless, provenance trial experiments with *Arabidopsis thaliana* (Wilczek et al. 2014) and the perennial forb *Boechera stricta* (Anderson & Wadgymar 2020) have shown that climate change has disrupted long-standing patterns of local adaptation across the landscape. Indeed, researchers have leveraged data from large-scale tree provenance trial studies to test the extent to which adaptation could lag behind changing climates and the necessity of assisted migration programs (Aitken et al. 2008). Furthermore, Lovell and colleagues (2021) leveraged this approach to investigate the genomic basis of local adaptation in switchgrass (*Panicum virgatum*). Their elegant large-scale field study also revealed a key role of gene flow in adaptation to northern climates during range expansion caused by the Holocene glacial retreat (Lovell et al. 2021). Future provenance experiments could quantify genotypic variation in climatic tolerances under realistic field environments to generate robust predictions of population persistence during contemporary climate change.

2.2. Common Garden Studies

Until recently (e.g., Wang et al. 2010), the evolutionary and genetics literature mostly neglected to consider the advancements made during several hundred years of provenance studies on local adaptation (Langlet 1971). Within the eco-evolutionary literature, common garden experiments began to address the contributions of genetic variation and plasticity to trait variation a century ago. The plant systematist Turesson (1922) and contemporaries (e.g., Sumner 1926) contemplated the role of the environment in exerting selection on local populations. Turesson's (1922) common garden studies with Swedish plants belonging to ∼20 species demonstrated that many traits had a genetic basis, that species inhabiting similar environments often shared suites of traits, and that traits can vary across populations of the same species originating from different habitat types. These studies inspired Turesson (1922) to coin the term ecotype, which he distinguished from genotype as having evolved through an adaptive response to a specific environment. The modern usage is still consistent with Turesson's definition in strongly connoting a locally adapted genotype within a species (Lowry 2012).

Sumner (e.g., 1926) used the common garden approach to examine trait variation in *Peromyscus* mice, revealing a strong genetic basis to body size and coloration patterns. During this research, Sumner (1929) observed that correlated characteristics could evolve in parallel, foreshadowing research into the processes through which agents of selection shape the evolution of correlated suites of traits (Brodie 1992). In studies of wild populations, Sumner (1926) noted the clear congruence between the coat pigmentation patterns of *Peromyscus polionotus* and soil substrate color in Florida through Alabama. At first, he attributed this phenotypic variation to climatic differences (Sumner 1926), but he later recognized the potential role of camouflage (Sumner 1929). Subsequent manipulative experiments identified predation as the primary agent of selection in *P. polionotus* (Vignieri et al. 2010). Similarly, a field exclosure revealed that selection favors cryptic pigmentation in *Peromyscus maniculatus* (Barrett et al. 2019), likely due to visually hunting predators (Linnen et al. 2013).

Sumner's (1926) work built the foundation for an extensive contemporary literature that explores clinal variation in and selection on coat coloration, behavior, and other traits, as well as the genetic underpinnings of the phenotypes that mediate local adaptation (Barrett et al. 2019, Linnen et al. 2013). Indeed, Huxley (1938, p. 219) introduced the cline, as a "gradation in measurable characters," citing Sumner's research on *Peromyscus*. Common garden studies with diverse genomes can be instrumental in formulating testable hypotheses about the agents of selection driving local adaptation and the traits subject to divergent selection. For example, in a laboratory experiment, Campbell-Staton and colleagues (2017) found that cold tolerance increased with

latitude in *Anolis carolinensis* populations from Texas through Oklahoma, enabling sophisticated genomic analyses of evolutionary responses to a severe winter storm in the region. Field studies that examine fitness along with phenotypes can evaluate the magnitude of genetic clines and examine the adaptive nature of those clines (Wadgymar et al. 2017a).

2.3. Reciprocal Transplant Experiments

Shortly after Turesson's (1922) and Sumner's (1926) initial contributions, Clausen, Keck, and Hiesey (1941) set the stage for decades of eco-evolutionary research through their pioneering reciprocal transplant experiment. This notable collaboration originated in earlier work by the plant taxonomist Harvey Hall, who established a reciprocal transplant experiment in 1926 at three elevations across the Sierra Nevada mountains in California (30 m, 1400 m, and 3050 m above sea level), with the aim of addressing questions at the intersection of ecology, genetics, taxonomy, and evolution (Hagen 1993). After Hall's unexpected death in 1932, his group—Jans Clausen, David Keck, and William Hiesey—expanded the scope of the research, eventually making critical, yet underappreciated, contributions to the modern evolutionary synthesis (Núñez-Farfán & Schlichting 2001).

Clausen and colleagues (1941) collected trait and fitness data from approximately 50 species transplanted into the three field gardens, examining evolutionary processes operating within and among species. They generated lasting insights into the process of local adaptation primarily through their intensive studies characterizing fitness and traits in yarrow (*Achillea*) (Clausen et al. 1948) and their work on the genetics of adaptation using hybrid lines derived from crosses of low-elevation and alpine ecotypes of sticky cinquefoil (*Potentilla glandulosa*) (Clausen & Hiesey 1958). These studies documented pronounced ecotypic differentiation, genetic divergence in functional traits, phenotypic plasticity, and genotype-by-environment interactions in trait expression. Clausen et al. (1941) highlighted the importance of climatic factors as agents of selection, noting the congruence between their results and Turesson's (1925) findings of local adaptation to climate. Their body of research formed a solid foundation for modern investigations of the agents of selection underlying local adaptation, the evolution of genetically correlated suites of complex traits, the genetic basis of local adaptation, and the role of plasticity in local adaptation.

After Clausen and colleagues began disseminating their results, reciprocal transplant and common garden studies demonstrated local adaptation to edaphic conditions, photoperiod, climate, and other factors, primarily in plant systems (e.g., Bocher 1949, Bradshaw 1960, Vaartaja 1959). Several studies before 1975 also evaluated adaptive population divergence in laboratory experiments with animals, documenting genetic clines in morphology in *Drosophila* (Stalker & Carson 1948) and in developmental rates in amphibians (Ruibal 1955). Continued fieldwork in *Peromyscus* species shed light on the influence of gene flow on local adaptation (Blair 1950) and predator-mediated selection on coat coloration (Dice 1949). These studies focused on experimentally tractable species that could be manipulated in the field or lab and showed a continued bias toward North American and European terrestrial ecosystems. Although reciprocal transplant experiments are feasible for many sessile marine invertebrates (Sanford & Kelly 2011), studies of these species are conspicuously missing from the early local adaptation literature (e.g., Segal 1956).

2.4. Building an Inclusive Field

The published historical literature on local adaptation is dominated by Western, white, and male voices. Our understanding of local adaptation is severely limited because of the deliberate exclusion of scholars with diverse racial, cultural, geographic, linguistic, socioeconomic, and gender

backgrounds. Additionally, the dismissal or suppression of traditional ecological knowledge has precluded us from learning how organisms adapt to their environment from the stewards who observed and protected them long before the fields of ecology and evolution were established. We call for the active removal of barriers to inclusion for scientists from historically excluded groups, including recognizing diverse expertise and skills, increasing the accessibility of resources, and promoting equity in opportunities (Berhe et al. 2021, Massey et al. 2021, Sidik 2022).

2.5. Modern Approaches

The contemporary literature documents local adaptation across numerous taxonomic groups. Field experiments continue to enable sophisticated tests of (*a*) the extent of local adaptation; (*b*) the phenotypic traits involved; (*c*) the agents of selection underlying local adaptation, when field experiments are paired with environmental manipulations; (*d*) the processes that constrain local adaptation; and (*e*) the effects of anthropogenic change on local adaptation. Furthermore, complementary field experiments and genomic analyses can illuminate the genetic and genomic basis of local adaptation and facilitate predictions about adaptive responses to global change (Johnson et al. 2021, VanWallendael et al. 2022, Wadgymar et al. 2017b). Even in the absence of reciprocal transplant experiments, local adaptation can be inferred through examining whether population divergence in functional traits (Q_{ST}) in common gardens exceeds divergence in putatively neutral molecular markers (F_{ST}). Karhunen et al. (2014) extended this framework by linking trait expression measured in common gardens to environmental and genetic variation, enabling them to examine whether populations inhabiting comparable conditions are more similar than expected based on relatedness.

Reciprocal transplant approaches and field gardens can be difficult to execute effectively for mobile or long-lived species, perhaps due to logistical constraints (see the sidebar titled Logistical and Safety Constraints), which could be why many published local adaptation studies still focus on plants (Briscoe Runquist et al. 2020, Hargreaves et al. 2020, Johnson et al. 2021). Alternative approaches have been developed to evaluate local adaptation at the levels of the whole organism (Manzanedo et al. 2019) and the genome (Berg & Coop 2014). In species that deposit annual rings, growth rates of individuals can be contrasted across years that vary in climate to examine the extent of local adaptation to the average local climate and to investigate the climatic factors involved, without laborious field experiments (Manzanedo et al. 2019). This approach, however, would not be successful if local adaptation is driven by nonclimatic factors. Studies of highly mobile species, such as fish, can provide models for how to infer local adaptation in the absence of reciprocal transplant experiments. For instance, Peterson et al. (2014) examined the effect of gene flow on local adaptation by genotyping sockeye salmon, *Oncorhynchus nerka*, from wild populations, revealing that individuals that dispersed to alternative habitats had reduced fecundity. Combining approaches allows us to interrogate the underlying processes that contribute to local adaptation in a diversity of taxa.

3. AGENTS OF LOCAL ADAPTATION

Multiple abiotic and biotic factors can exert selection on natural populations and interact to produce synergistic or antagonistic patterns of selection on the phenotypes they target (**Figure 1**). Agents of selection that consistently vary in magnitude or frequency across space can promote local adaptation. These agents of local adaptation influence metapopulation dynamics, range limits, speciation, and restoration efforts (DiVittorio et al. 2020, Hufford & Mazer 2012, Rice & Knapp 2008). Despite the prevalence of local adaptation, identifying agents of local adaptation operating in nature remains a daunting task. Observational studies can help detect plausible agents of local

LOGISTICAL AND SAFETY CONSTRAINTS

There are a number of logistical and safety constraints to conducting field experiments exploring local adaptation, relevant agents of selection, and locally adapted phenotypes:

- Experimental design
  - ☐ Low sample sizes, sometimes due to unanticipated events like drought, flood, or wildfire, can reduce statistical power.
  - ☐ Limited study duration, which can reduce the likelihood that the experiment captures lifetime fitness, that individuals experience the key drivers of local adaptation, and that targets of selection are monitored in pertinent years.
  - ☐ Experimental manipulations needed to confirm relevant agents of selection are costly or not feasible.
  - ☐ Important biotic interactions can be altered or oversimplified by experimental protocols (e.g., if plots are weeded or otherwise altered, plants are transplanted in monocultures, or common gardens are conducted exclusively in a laboratory or greenhouse).
  - ☐ Studies are unable to tease apart the contributions of genes, plasticity, and transgenerational plasticity on offspring performance if they do not homogenize parental environmental effects by rearing individuals for at least one generation in a greenhouse or laboratory before transplanting multiple individuals per accession into field sites.
  - ☐ Coordination and standardization of experimental design and data collection in transplant gardens across large spatial extents can be arduous.
  - ☐ Local adaptation may be most relevant at group, family, or community levels of organization (e.g., in microbial systems or those that function in aggregations).

- Personal safety and site security
  - ☐ Hazards, threats, racism, misogyny, religious discrimination, and homo- and transphobia can hinder or prevent researchers—particularly those from groups historically excluded from science, technology, engineering, and mathematics—from safely conducting research in some places. Additionally, sexual harassment and inappropriate behavior can be prevalent in some research programs or field sites.
  - ☐ The security of field sites could be hard to maintain (e.g., vandalism, habitat destruction, animals that damage experimental gardens).
  - ☐ Reliable access to field sites can be limited (e.g., natural disasters, road closures, funding cuts, public health concerns).

- Challenges of some focal species
  - ☐ Highly mobile or long-lived species can be difficult to monitor or transplant in the field.
  - ☐ The choice of fitness component can bias the results, including when nonrandom mortality events early in life are unaccounted for (the invisible fraction).
  - ☐ Obtaining permits and permissions can take a substantial amount of time, and it may not be possible to collect certain species or transplant individuals into desired locations.
  - ☐ Reciprocal transplants and common gardens in the field could introduce nonlocal genotypes (and possibly pests or diseases) that could spread into local ecosystems.

- Sociology of science
  - ☐ Investigations of local adaptation are undervalued by funding agencies, journal editors, and reviewers because they are perceived as addressing well-understood processes and lacking cutting-edge methods.
  - ☐ Funding to support the personnel needed for large-scale reciprocal transplant experiments or provenance trials is not trivial.

adaptation by identifying the relevant suites of conditions that covary across the landscape. Once the set of potential factors is reasonably narrowed, laboratory experiments can isolate the effects of specific treatments on fitness and traits. For example, Clausen et al. (1948) complemented their field transplant experiments of *Achillea* clones with manipulations of light and temperature under controlled conditions, thereby identifying climatic agents of selection. However, putative agents of local adaptation should be confirmed using manipulative field experiments, as controlled environments are often poor proxies of natural conditions (e.g., Kellermann et al. 2015).

Manipulative field experiments are vital for disentangling the contributions of various abiotic and biotic factors to local adaptation. For example, in locally adapted populations of the grass species *Festuca lenensis*, a precipitation addition experiment minimized differences in survival between local and foreign populations at an arid high-elevation site but not at the wetter low-elevation site, demonstrating that agents of local adaptation can differ across the range (Liancourt et al. 2013). Additionally, interspecific competition amplified local adaptation for two species of bunchgrass (*Elymus glaucus* and *Nassella pulchra*), whereas the removal of competitors favored foreign genotypes at one site (Rice & Knapp 2008). Further studies on *N. pulchra* determined that local adaptation is maintained by grazing pressures, but this effect is detectable only in some years (Hufford & Mazer 2012). These studies illustrate how abiotic and biotic agents of selection can act in cumulative, dynamic, and context-dependent ways and emphasize the value of conducting long-term field experiments across multiple sites.

Ethical, logistical, or practical concerns often preclude manipulative field studies of animals, fungi, and microbes (see the sidebar titled Logistical and Safety Constraints); however, several comprehensive studies explore agents of local adaptation in well-established animal systems. Experimental ponds with three-spined sticklebacks (*Gasterosteus aculeatus*) demonstrated that competition and predation promote character divergence (Rundle et al. 2003, Schluter 1994) and could have contributed to repeated parallel adaptive evolution across populations (Miller et al. 2019). Similarly, predation and competition impose selection on guppies (*Poecilia reticulata*) and promote population divergence in life history, behavior, morphology, and physiology (Reznick & Travis 2019). We know less about local adaptation in the sea than on land (Sasaki et al. 2021). Nevertheless, Sanford & Worth (2010) conducted an elegant reciprocal transplant experiment with the predatory snail *Nucella canaliculata*, which inhabits coastal regions in western North America. Californian ecotypes have a greater capacity to drill through the thick shells of the local mussel (*Mytilus californianus*) than do ecotypes from Oregon, where the preferred prey (*Mytilus trossulus* and *Balanus glandula*) are more common; reciprocal transplants into caged experimental mussel beds confirmed local adaptation in *N. canaliculata* to prey abundance. Thus, biotic interactions can strongly influence the evolution of ecotypic divergence.

Plant–microbial interactions strongly affect plant population and community dynamics (David et al. 2019, Rudgers et al. 2020), and microbial communities can vary substantially across the landscape (Benning & Moeller 2021). Recently, researchers have begun to interrogate the extent to which microbial communities could act as agents of selection (Wagner et al. 2014), promoting or restricting local adaptation in plant populations. For instance, a greenhouse experiment with Douglas fir (*Pseudotsuga menziesii* var. *glauca*) accessions from diverse source populations revealed local adaptation to climate, edaphic conditions, and ectomycorrhizal fungi (Pickles et al. 2015). However, local adaptation to soil microbial communities is not ubiquitous. For example, Benning & Moeller (2021) transplanted the wildflower *Clarkia xantiana* ssp. *xantiana* into sites within the center of the range, at the range edge, and beyond its current range and exposed experimental individuals to variation in the soil microbial community; they complemented this field study with a greenhouse experiment. They found limited evidence for local adaptation to soil communities within the range; however, novel soil microbial communities outside of the current distribution

can both increase and decrease plant fitness via escape from pathogens and reductions in mutualists, respectively (Benning & Moeller 2021). Under drought stress, these biotic interactions had a negligible effect on plant fitness, but plant–soil microbe interactions had a greater effect when abiotic conditions were benign (Benning & Moeller 2021). Disentangling the contributions of microbes from abiotic agents of selection remains challenging, especially in ecologically relevant settings in the field. Yet, such studies could generate novel insights into plant population persistence and species range limits under climate change (Afkhami et al. 2014, Rudgers et al. 2020).

We know less about local adaptation in microbes themselves owing to the difficulties of conducting manipulations in the field (Kraemer & Boynton 2017). For systems like these that are less experimentally tractable, a combination of approaches can yield evidence about the agents of local adaptation (Kraemer & Boynton 2017). For example, in a reciprocal transplant experiment in a laboratory, isolates of the bacteria *Bacillus mycoides* grew best in medium derived from their home soils, suggesting soil properties act as agents of local adaptation (Belotte et al. 2003). Moreover, samples were systematically taken from every 10-m² subdivision of a hectare of old growth forest, enabling the authors to estimate the spatial extent of local adaptation as 6.1 m.

Similar creative approaches have yielded important insights into the process of local adaptation in other highly mobile species. For instance, following a controlled experiment that explored behavioral responses of the amphipod *Gammarus pulex* to predator cues (Åbjörnsson et al. 2000), a second experiment found that individuals from ponds with predators had greater antipredatory behavior and survival when exposed to predatory fish or fish cues relative to individuals from ponds without predators (Åbjörnsson et al. 2004). This effect was also observed in lab-reared offspring, demonstrating that behavioral responses to predation are inherited and suggesting populations are locally adapted to predation regimes. In the frog *Rana temporaria*, reciprocal transplants documented local adaptation to elevation, and a laboratory experiment demonstrated no effect of the adult overwintering period on offspring performance, suggesting that populations have adapted locally to selective agents other than winter duration (Bachmann & Van Buskirk 2021). Thus, complementary field and laboratory methods can reveal likely agents of local adaptation.

Several recent meta-analyses have explored how, when, and where agents of selection affect local adaptation. In a meta-analysis including field and greenhouse studies that manipulated at least one biotic factor in combination with at least one abiotic factor, there was weak evidence that biotic factors have a larger effect on local adaptation in animals, while abiotic factors were more influential in plants (Briscoe Runquist et al. 2020). Biotic interactions increased the magnitude of local adaptation across taxa in one meta-analysis (Briscoe Runquist et al. 2020) but not another (Hargreaves et al. 2020). Biotic effects were stronger at lower latitudes whereas abiotic effects were stronger at higher latitudes (Briscoe Runquist et al. 2020). To examine how the probability of local adaptation varies geographically, Hargreaves et al. (2020) assigned a binary score to studies, indicating whether local adaptation occurred (i.e., local fitness exceeded foreign fitness) or not. They found that there was a marginally higher probability of local adaptation in unmanipulated control conditions in the tropics and under treatments that alleviated biotic pressures in temperate zones. Thus, temperate plants could potentially be less locally adapted to the biotic community than tropical plants.

The most striking finding of these meta-analyses was how few studies have tested or detected agents of local adaptation. For instance, Hargreaves et al. (2020) identified 13 field studies wherein the experimental manipulation of a biotic factor altered the expression of local adaptation. In those cases, local adaptation emerged under unmanipulated conditions, but the fitness of foreign populations exceeded that of local populations in treatments that reduced a biotic interaction. We interpret this finding to indicate that these studies manipulated a relevant agent of local adaptation. Six additional cases displayed the opposite pattern, with the fitness of local populations

exceeding that of foreign transplants only when a biotic interaction was manipulated; we suggest these studies identified an agent of selection that is impeding local adaptation. Given the dearth of investigations, we call for a renewed focus on reciprocal transplant studies that manipulate putative agents of local adaptation, especially for exploring anthropogenic drivers of local adaptation, biotic interactions, nontemperate biomes, and organisms other than plants.

4. LOCALLY ADAPTED PHENOTYPES

Natural selection simultaneously operates on complex suites of phenotypes, including morphological, life history, physiological, behavioral, and biochemical traits. For any given population, many traits collectively contribute to local adaptation (Clausen et al. 1941), and the specific targets of selection can differ across the range (Núñez-Farfán & Schlichting 2005). Furthermore, geographic variation in conditions could lead to the evolution of genetically correlated trait combinations, such as variation in life history strategies and sexually selected traits in guppies in response to predator abundance (Rodd & Reznick 1997). To evaluate the role of ecological factors in generating or maintaining genetic variation within and among populations, researchers need to identify the heritable traits subject to selection and test whether selection favors the multidimensional traits expressed by local ecotypes.

Investigating the targets of selection that mediate local adaptation can test whether similar sets of phenotypes give rise to local adaptation across species, identify factors that limit local adaptation, and predict scenarios in which environmental change could disrupt local adaptation. Genetic constraints (e.g., pleiotropy, linkage), limited genetic variation, or gene flow from phenotypically divergent populations could all prevent local populations from expressing optimal trait values for their home sites (Orr 2000, Slatkin 1987). Increasingly accurate fine-scale climate change projections enable predictions about expected shifts in the strength of many abiotic factors (e.g., Gauthier et al. 2021). Coupled with knowledge of the phenotypes targeted by these agents of local adaptation (**Figure 1**), we can form hypotheses about expected shifts in trait distributions, species interactions, and geographic ranges. Similarly, familiarity with the locally adapted phenotypes of a declining population can help conservation practitioners select suitable propagules to bolster population growth (Aitken & Whitlock 2013).

In their foundational work, Clausen & Hiesey (1958) examined targets of selection by calculating a composite phenotypic index for 12 traits measured on *Potentilla glandulosa* hybrid lines transplanted into their common gardens and monitored for 9–13 years. The *P. glandulosa* lines with suites of traits more similar to the local parent had greater survival in the parental environment. By linking a metric of trait variation to fitness, Clausen & Hiesey (1958) evaluated selection decades before Lande & Arnold (1983) described how multivariate selection can be quantified from regressions of relativized fitness on traits. Using data from Clausen & Hiesey (1958), Núñez-Farfán & Schlichting (2005) discovered that the magnitude and direction of selection on traits varied geographically. For example, stabilizing selection operated on flowering time at the low-elevation site, directional selection favored delayed flowering at the high-elevation site, and there was no evidence for selection on this trait at mid-range elevations. Studies that analyze selection in the context of field experiments can evaluate the extent to which local genotypes express phenotypes that enhance fitness in their home sites by exposing a broad range of phenotypes to selection in one or more sites. This task can be accomplished by transplanting accessions sourced from multiple locations across the range into common gardens. For instance, selection favored the phenotypes of resident *Impatiens pallida* ecotypes in floodplain and hillside transplant sites (Bennington & McGraw 1995). Alternatively, researchers can generate mapping populations by crossing two (or more) lines, as transgressive segregation often leads to a wider range of trait values than that

expressed by the parents (Clausen & Hiesey 1958). Using the F2 generation of the annual herb *Datura stramonium* derived from crosses between two populations that vary in their level of defenses, a reciprocal transplant experiment demonstrated that selection favored the alkaloid that conferred resistance to the local herbivores in each site (De-la-Cruz et al. 2020). Studies seldomly identify locally adapted phenotypes, perhaps because targeted phenotypes shift through time and ontogeny. Nevertheless, integrating fitness and trait data from field gardens can identify locally adapted phenotypes and test how selection differs across environments.

When paired with field experiments, controlled experiments allow us to develop compelling hypotheses about relevant targets of selection. This approach demonstrated that urban populations of the acorn ant *Temnothorax curvispinosus* have simultaneously evolved the ability to withstand high temperatures and lost their tolerance of cool temperatures compared to rural populations (Diamond et al. 2017), indicating that divergent selection on thermal tolerance may have contributed to local adaptation in these populations (Martin et al. 2021). Another intriguing system is the blister beetle, *Meloe franciscanus*, whose larvae form aggregations, emit chemical signals that mimic the sex pheromones of female bees of the genus *Habropoda*, attach to any male bees attracted to the signal, transfer to the bodies of female bees after copulation, and feed on provisions and bee eggs once transported to the female's nest (Saul-Gershenz & Millar 2006). A transplant experiment in two field sites including local and foreign aggregations revealed that male bees of each species are most attracted to the pheromones emitted from sympatric aggregations of the blister beetle. When considering male bee attraction as a proxy for parasite fitness, this work suggests that divergent selection on chemical signaling and reproductive behaviors contributes to local adaptation of *M. franciscanus* to its native host.

The selection analyses we have described are inherently correlative. In contrast, experimental manipulations of traits can establish causal relationships between phenotypic variation and fitness. Data on putative targets of selection can guide research efforts. For instance, data from Sumner's (1929) work on *Peromyscus* mice suggested coat coloration could be a target of predator-mediated selection. Indeed, studies with painted plasticine models of *P. polionotus* showed strong selection for crypsis in natural habitats (Vignieri et al. 2010). Field studies often detect strong selection on phenology (e.g., Austen et al. 2017), suggesting that phenological traits could be good targets for experimental manipulations. By staggering planting dates, Austen & Weis (2015) generated cohorts of *Brassica rapa* individuals that flowered at different times, breaking the correlation between age at flowering and date at flowering and testing the direct fitness effects of flowering time. Trait manipulations have rarely been conducted in locally adapted systems to test whether selection favors the trait value of resident ecotypes, and many traits of interest are not amenable to experimental manipulation. Nevertheless, these manipulations enable powerful tests of the magnitude of divergent selection on specific phenotypes in different environments, which illuminate how these traits contribute to local adaptation and could point to the putative agent of selection.

Phenotypic plasticity is sometimes envisioned as an alternative strategy for coping with environmental variation relative to local adaptation, because individuals can express the phenotypes best suited to the conditions that they experience. This capacity to shift phenotypes in response to the environment can enhance the fitness of individuals that confront predictable temporal variation in conditions and enable their offspring to establish and thrive in nonparental habitat types when propagule dispersal exceeds the spatial scale of environmental variation (Palacio-López et al. 2015). Ecotypes can differ in plasticity if their local habitats vary in the degree of environmental heterogeneity. For example, serpentine ecotypes of the invasive annual plant *Erodium cicutarium* exhibit greater adaptive plasticity than do canalized nonserpentine ecotypes, likely because serpentine patches have more microenvironmental variation than do nonserpentine habitats (Baythavong 2011). A recent meta-analysis identified only 34 reciprocal transplant experiments in

plants in which plasticity could be calculated for at least two traits (Radersma et al. 2020). This meta-analysis found that plasticity across environments typically corresponds with trait divergence between source populations grown in their home sites and concluded that plasticity could be a precursor to local adaptation (Radersma et al. 2020). Nevertheless, few studies quantify ecotypic divergence in plasticity or test whether plasticity confers a fitness advantage within (and not across) disparate habitats to examine whether selection on plasticity operates differently across the landscape. Reciprocal transplant studies that measure fitness and functional traits could clarify the role of plasticity in local adaptation.

5. GENETIC BASIS OF LOCAL ADAPTATION

More than half a century ago Clausen & Hiesey (1958) began to document the polygenic nature of the complex traits associated with local adaptation in *Potentilla*. Since then, emerging technologies have enabled researchers to address critical questions about the genetics of local adaptation. Specific loci underlying local adaptation can be detected through association mapping of fitness or fitness-related traits (e.g., Barrett et al. 2019) and population genomic scans, either for increased divergence between populations or for associations with environmental variables (e.g., Forester et al. 2018). Here, we examine scenarios in which studies of local adaptation could benefit from genetic information and highlight situations where genetic information is not helpful.

Local adaptation can arise through genetic trade-offs, in which a local allele has a fitness advantage in its home site and a disadvantage elsewhere, satisfying both the home vs. away and local vs. foreign definitions of organismal local adaptation (Kawecki & Ebert 2004). Since the local allele confers the greatest fitness, these genetic trade-offs can maintain local adaptation, even when gene flow continuously introduces foreign alleles (Hall et al. 2010). In systems in which gene flow across habitats is low, local adaptation can evolve when a local allele augments fitness in its home site relative to foreign alleles but is not costly in other locales, but this conditional neutrality occurs only if loci differ in which parental allele is conditionally advantageous. For example, a reciprocal transplant experiment in *Boechera stricta* using recombinant inbred lines found that at some quantitative trait loci (QTLs), the Montana allele had the greatest fitness in Montana and incurred no cost in Colorado, and at other QTLs, the Colorado allele was conditionally advantageous in its home site (Anderson et al. 2014). If gene flow is spatially extensive, then the conditionally advantageous allele will spread across populations, eliminating the alternative allele(s) and leading to the evolution of a nonlocally adapted generalist (Hall et al. 2010). Nevertheless, researchers have documented conditional neutrality in both selfing species (Anderson et al. 2014, Oakley et al. 2014, Postma & Ågren 2016) and outcrossers (Hall et al. 2010). Given the complex polygenic nature of fitness, both conditional neutrality and genetic trade-offs could contribute to local adaptation (Anderson et al. 2014, Oakley et al. 2014). At any given locus, conditional neutrality and genetic trade-offs are mutually exclusive, but at the genome level, both can be—and likely are—operating.

The relative importance of trade-offs and conditional neutrality is a special example of general questions about pleiotropy. Pleiotropic loci could be constrained in their response to selection since mutations at these loci may be unlikely to increase fitness in multiple traits (Orr 2000). In contrast, pleiotropy could facilitate responses to selection if alleles have effects that consistently increase fitness across phenotypes (e.g., Lovell et al. 2013). Ellis et al. (2021) recently investigated pleiotropy in QTLs associated with local adaptation and found that the effects of a given allele consistently increased or decreased fitness across phenotypes, suggesting that pleiotropy can facilitate adaptation. However, theory predicts that local adaptation is often based in clusters of large-effect alleles, especially if there is migration between locally adapted populations (Yeaman 2022). Distinguishing between pleiotropy and linkage between multiple causal loci requires careful genetic analyses.

Genetic trade-off: a genetic correlation that produces a trade-off between fitness in two environments, two fitness components, or two functional traits

Conditional neutrality: an allele confers a fitness advantage in its site of origin but incurs no fitness cost elsewhere

Quantitative trait loci (QTLs): regions of the genome statistically associated with phenotypic variation in a continuous trait

Identifying the causal loci associated with locally adaptive phenotypes sheds light on the genetic mechanisms involved in local adaptation. Regulatory changes (Studer et al. 2011), loss of function alleles (Monroe et al. 2018), copy number variants (Nelson et al. 2019), transposable elements (Niu et al. 2019), and chromosomal inversions (Lowry & Willis 2010) can all contribute to adaptive phenotypic variation. Certain selective agents could be more likely to favor specific types of alleles. For example, loss of function alleles may be especially important for floral color transitions (Rausher 2008). Since the genetic architecture of phenotypic differentiation shapes the likelihood that ecotypic divergence persists (Yeaman 2022), determining the genetic mechanisms of local adaptation is important for fully understanding adaptive processes.

Using polygenic scores, genomic studies can predict locally adaptive trait values in individuals that have been genotyped but not phenotyped. These polygenic scores summarize allele frequencies across multiple loci associated with a trait and have practical uses in breeding and medicine. Evolutionary biologists have leveraged these scores to test for local adaptation in populations that are not amenable to field experiments (Berg & Coop 2014). However, subtle biases in estimating effect sizes of associated loci can lead to false positive signatures of local adaptation (e.g., Josephs et al. 2019). Indeed, many genomic approaches are stymied when traits have a complex genetic basis because traits can diverge between populations without dramatic allele frequency differentiation, hindering our ability to identify loci underlying adaptation. If much of adaptation is polygenic, we risk biasing our view of adaptation by focusing on the few cases of adaptation that involve alleles of large effect.

6. FITNESS COMPONENTS THAT EXHIBIT LOCAL ADAPTATION

Fitness is fundamental to the study of local adaptation. However, definitions of fitness are famously variable; Stearns (1976, p. 4) described fitness as "something everyone understands but no one can define precisely." Most commonly, fitness is conceptualized as the expected intrinsic rate of increase of an individual or, if population growth is stable, its lifetime reproductive success (McGraw & Caswell 1996). Both measures reflect the cumulative effects of performance across the life cycle. As lifetime fitness can be difficult to quantify empirically, studies of local adaptation in long-lived organisms often focus on early fitness components. Many transplant experiments begin with juveniles (e.g., seedlings) and miss the contributions of earlier or later life stages (Donohue et al. 2010). For mobile animals, local adaptation estimates rely almost entirely on survival rates from mark-recapture studies (Fraser et al. 2011). Much of our understanding of local adaptation is based on these partial fitness measures.

Various fitness components contribute to local adaptation, from juvenile establishment to survival, growth, and reproduction, and the choice of fitness component remains a major consideration. Patterns consistent with local adaptation for a single fitness component are often interpreted as evidence for local adaptation overall, whereas studies that find unclear patterns or maladaptation for a single fitness component are often interpreted as potentially missing local adaptation operating through other fitness measures. In a comprehensive meta-analysis, Hereford (2009) found that local adaptation across reciprocal transplant experiments was strongest when measured with composite fecundity and viability fitness measures, intermediate when measured solely by fecundity, and weakest when measured solely by viability.

Life history theory provides an important context for studies of local adaptation, as not all fitness components contribute equally to lifetime fitness. Crone (2001) suggested that, for a broad swath of taxa, viability better reflects selection and local adaptation than fecundity because variation in survival often exerts larger effects on overall fitness, particularly for iteroparous species. Similarly, life stages vary in their relative contributions to overall fitness, with the reproductive

value of individuals increasing up to the age of reproduction, then decreasing at a rate determined by adult mortality. Thus, a small change in adult survival could be more important for overall fitness than larger changes in either fecundity or juvenile performance; this is one potential explanation for consistently smaller effect sizes for local adaptation when measured with viability (Hereford 2009).

Since selection is strongest for reproductive life stages and weakens progressively with age (Haldane 1941), we could predict that local adaptation would also be strongest for these life stages. Indeed, Cotto & Ronce (2014) showed that older life stages accumulate increasing variance in fitness and greater lags in local adaptation, particularly when antagonistic pleiotropy influences fitness across life stages. Nevertheless, few studies have explicitly tested the magnitude of local adaptation across life stages. Rice & Knapp (2008) showed that local adaptation was expressed most strongly for adult reproduction and seed germination for two perennial bunchgrasses. Similarly, in a meta-analysis, Hargreaves et al. (2020) found some evidence that biotic interactions contributed to local adaptation for adult reproduction but not emergence or viability. Overall, the role of senescence (i.e., weakening selection acting on later life stages) remains an important yet understudied factor in local adaptation (Cotto & Ronce 2014).

Local adaptation can involve trade-offs between different fitness components. For example, Trinidadian guppies (*Poecilia reticulata*) have adapted to pools with high versus low predation pressure by evolving divergent life history strategies (Rodd & Reznick 1997). Guppies from high-predation environments experience significant extrinsic adult mortality and have evolved a life history strategy with faster growth and greater reproductive investment relative to low-predation guppies (Reznick et al. 1990). Similarly, local adaptation of white clover (*Trifolium repens*) across a latitudinal gradient is driven by antagonistic pleiotropy for QTLs related to early flowering and reduced adult survival in southern populations versus delayed reproduction and high adult survival in northern populations (Wright et al. 2021). Studies based on limited fitness components may fail to detect local adaptation if one ecotype always has higher survival or lower fecundity. Fitness trade-offs can exacerbate local maladaptation driven by rapid environmental change, though this may be detectable only by examining the full suite of affected fitness components (Cotto et al. 2019). Additionally, life history divergence can alter the patterns of selection acting on traits (Cotto et al. 2019). For example, drought shifted the direction of selection on flowering time in *Mimulus guttatus* in part by decreasing the importance of reproductive life stages for overall population growth (DeMarche et al. 2020). Thus, integrative fitness measures are key for accurately measuring local adaptation. When portions of the life cycle are experimentally intractable, the choice of particular fitness components needs careful justification based on a species' life history.

Statistical approaches have been developed to allow robust hypothesis testing of local adaptation while leveraging data across multiple fitness components. The Aster statistical framework allows data on recruitment, survival, and reproduction, modeled with distinct statistical distributions, to be integrated into lifetime performance (Shaw et al. 2008). For example, local genotypes of *Arabidopsis lyrata* exhibit greater fecundity at low-elevation sites and greater survival at high-elevation sites, with the overall pattern of fitness estimated by Aster models demonstrating local adaptation (Hämälä et al. 2018). Similarly, several studies have used demographic modeling methods to test for local adaptation (e.g., Anderson & Wadgymar 2020, DeMarche et al. 2016). For example, Waser & Price (1985) used demographic models to integrate data on survivorship and fecundity to demonstrate fine-scale local adaptation of the perennial herb *Delphinium nelsonii*. Demographic models offer a promising—and virtually untapped—approach for testing local adaptation due to their ability to integrate across fitness components while explicitly modeling genotype-by-environment interactions, environmental drivers, and the hierarchical nature of data.

Antagonistic pleiotropy: a gene benefits fitness in one life stage or environment and decreases fitness in a different life stage or environment

Demographic model: a statistical model that integrates survival, growth, or fecundity data to model population growth and other demographic processes

7. CONSTRAINTS ON THE EVOLUTION OF LOCAL ADAPTATION

7.1. Migration–Selection Balance

Gene flow across habitat boundaries could introduce maladapted alleles into local populations, shifting average phenotypes away from local optima and restricting the evolution of local adaptation (Slatkin 1987). Conversely, gene flow could spread advantageous alleles across populations or increase genetic variation, facilitating adaptive evolution (Slatkin 1987). Ultimately, the evolutionary consequences of gene flow depend on the magnitude of disruptive selection across environments relative to the degree and directionality of interhabitat gene flow. Studies often make inferences about the migration–selection balance by genotyping individuals from disparate populations to model the rate and spatial extent of gene flow and conducting complementary experiments to ascertain the level of local adaptation (Nosil & Crespi 2004). Alternatively, in some systems, researchers can contrast levels of local adaptation within a species across regions with variable levels of interhabitat gene flow (Fitzpatrick et al. 2015, Hendry & Taylor 2004). If the extent of local adaptation is greater when gene flow is negligible, then gene flow likely constrains adaptive differentiation. For instance, in the stick insect *Timema cristinae*, two locally adapted ecotypes are best camouflaged on distinct host plant species, and predator-mediated selection drives heritable morphological divergence (Bolnick & Nosil 2007). Local maladaptation can emerge when host plant species are in close enough proximity for individuals to disperse to the alternate plant species. Additionally, observational studies show that the locally maladapted morph occurs more frequently early in life history soon after dispersal, indicating that selection favors the locally adapted morph across ontogeny (Bolnick & Nosil 2007).

Gene flow does not universally constrain adaptive population divergence. Instead, divergent selection across habitats can be strong enough to counterbalance gene flow (Westram et al. 2018). For instance, deer mice (*Peromyscus maniculatus*) show clear ecotypic divergence in coat coloration, although ecotypes do not differ in other morphological characters (Pfeifer et al. 2018). Genome-wide association studies and demographic models found low population differentiation genome wide, suggestive of high levels of gene flow across populations, except at the *Agouti* locus, which encodes a protein influencing pigmentation (Pfeifer et al. 2018). This result points to a strong role of selection favoring cryptic coloration patterns, notwithstanding homogenizing gene flow.

The advent of genomic studies has revealed the striking prevalence of introgression in shaping adaptive responses to selection. For example, introgressed alleles have been linked to adaptation to high elevation in humans and maize (Huerta-Sánchez et al. 2014, Barnes et al. 2022) and local adaptation to climate in switchgrass (Lovell et al. 2021). Thus, gene flow can facilitate adaptation to new conditions, and related species likely evolve similar solutions to the agents of selection they confront. Under environmental change, gene flow could potentially hasten adaptive responses to novel selection by introgressing alleles for thermal or drought tolerance from low-elevation or equatorial populations into populations in upslope elevations or poleward latitudes (e.g., Bontrager & Angert 2019).

7.2. Demographic Source–Sink Dynamics

Populations can occur in habitats that differ in resource availability, such that mean fitness is substantially higher in one habitat type than another (Kawecki 2008, Pulliam 1988, Stanton & Galen 1997). Similarly, habitat types can differ in frequency across the landscape, such that more individuals of a species reside in the common habitat. Unequal population sizes can lead to asymmetric migration from populations in the higher quality or more frequent (source) habitat into populations in the lower quality or less frequent (sink) habitat, restricting adaptation to the sink environment (Holt & Gaines 1992, Kawecki 2008). In extreme cases, this asymmetrical migration

can maintain populations in black-hole sinks where local populations would otherwise go extinct (Kawecki 2008, Pulliam 1988). However, even when small populations are self-sustaining, theory predicts that traits favorable in the source environment evolve at the cost of adaptations to the marginal habitat because a much larger proportion of the overall population occupies source habitats (Holt & Gaines 1992, Kawecki 2008), leading to specialization to the productive source environment and local maladaptation to the sink environment.

Demographic source–sink dynamics restrict local adaptation of *Vaccinium elliottii* in bottomland forests of the southeastern U.S., as evidenced by asymmetric gene flow from robust upland populations to less abundant bottomland populations in conjunction with elevated fitness of individuals from both habitat types in upland relative to bottomland gardens (Anderson et al. 2021). Despite divergent selection for different functional trait values in the two habitat types (Anderson et al. 2021), the genetic response to selection is biased toward traits that are advantageous in upland forests, consistent with expectations (e.g., Holt & Gaines 1992). The Eurasian blue tit, *Cyanistes caeruleus*, exemplifies a system in which variation in the frequency of habitats constrains local adaptation (Charmantier et al. 2016, Dias & Blondel 1996). This species inhabits mainland and island environments, which differ in the frequency of deciduous versus evergreen forests. In each region, bird population densities and reproductive success are highest in the more prevalent habitat, and reproductive phenology is maladaptive in the infrequent habitat (Dias & Blondel 1996). Source habitat differs across regions, indicating that this species has the capacity to adapt to both forest types. Nevertheless, local adaptation evolves in response to the predominant direction of selection in each region, and source–sink dynamics constrain adaptation to the infrequent habitat type (Charmantier et al. 2016, Dias & Blondel 1996).

We call for contemporary empirical studies to consider how variation in population size and asymmetrical migration could influence the evolution of local adaptation. Such work requires explicit quantification of population size and population growth rates along with gene flow rates and directionalities. Long-term studies should account for temporal variation in environmental conditions, which could alter meta-population dynamics in source–sink systems. Comparative studies that examine the habitat affiliations of closely related species could illuminate whether species subject to source–sink dynamics could be in the process of expanding into previously unoccupied habitats. Furthermore, anthropogenic stresses can exacerbate, or create, source–sink dynamics (e.g., Newby et al. 2013). Conservation programs that neglect source–sink dynamics may inadvertently focus on maladapted sink populations. Such efforts may fail to effectively preserve a species of interest if source populations—and corridors enabling immigration from those source populations—are not also protected.

7.3. Rapid Environmental Change

Increasing rates of climate change and habitat fragmentation have dramatically altered natural selection since researchers first began investigating local adaptation (Etterson 2004, Radchuk et al. 2019). Rapid environmental change can weaken or disrupt local adaptation. Indeed, several recent transplant experiments that were conducted under anomalously warm conditions have found that genotypes from historically warmer areas outperform local genotypes, suggesting that climate change could induce local maladaptation (Anderson & Wadgymar 2020, Kooyers et al. 2019, Wilczek et al. 2014). For instance, Wilczek et al. (2014) planted 241 ecotypes of *Arabidopsis thaliana* in a series of common gardens spanning a climate gradient in its native European range. Genotypes from historically warmer climates had greater fitness than local genotypes in all sites, suggesting that recent warming may have shifted adaptive optima across the range. We emphasize the need to shift the focus away from local adaptation under equilibrium conditions. By revisiting the reciprocal transplant experiment of Clausen et al. (1941, 1948), and Turesson's (1922, 1925)

common gardens, modern researchers could examine local adaptation under environmental change in some of the original focal plants, and opportunities to work with *Potentilla* and *Achillea* seem particularly promising (e.g., Ramsey 2011). Such studies could document shifts in the adaptive landscape and test whether the fitness of low-elevation accessions now exceeds that of local accessions in high-elevation locations. Herbarium records were made annually as part of the original experiments (Clausen et al. 1941). If seeds were collected and are still viable, contemporary scholars could attempt resurrection studies to investigate evolutionary responses to climate change. Even if such experiments are not possible, reanalyzing historical data may generate new findings (Núñez-Farfán & Schlichting 2005).

Even if a transplant experiment reveals greater fitness of local than foreign populations, local populations could still be maladapted if mean fitness is below levels of demographic replacement (Brady et al. 2019). Adaptation can rescue declining, maladapted populations from extinction by restoring stable or positive population growth, a process known as evolutionary rescue (Gomulkiewicz & Holt 1995). Concordant with theory, laboratory microcosms suggest that evolutionary rescue is most likely when the starting population size is large, the degree of initial maladaptation is low, the standing genetic variation is high, and the rate of environmental change is gradual (Carlson et al. 2014). Nonetheless, evolutionary rescue has seldom been studied in nature, likely due to limited demographic information, an inability to pinpoint a single environmental effect on abundance, and complicating factors such as dispersal and density dependence.

We know little about the extent to which evolution can rescue populations from extreme climatic events. By combining resurrection approaches (e.g., Wooliver et al. 2020) with long-term demographic data, future studies could examine whether populations that exhibit higher magnitudes of trait evolution have more buffered vital rates and greater intrinsic rates of increase than populations that show little evolutionary change. Further, estimates of additive genetic variance for fitness in ancestral populations would enable predictions about the rate of adaptation under novel climates (Kulbaba et al. 2019). To date, individual studies have focused on pieces of this puzzle. For instance, in *Mimulus cardinalis*, resurrection studies have revealed rates of trait evolution in response to contemporary climate change (Anstett et al. 2021), and long-term demographic studies have examined changes in vital rates and population growth rates (Sheth & Angert 2018), but experiments have not yet connected trait evolution with changes in fitness. Similarly, in the perennial herb *Boechera stricta*, estimates of additive genetic variance for fitness (Bemmels & Anderson 2019) and demographic rates (Anderson & Wadgymar 2020) exist, but rates of evolutionary responses to climate change have not been estimated via resurrection studies. Resurrection experiments in the field could quantify additive genetic variances for fitness and rates of trait and fitness evolution from one generation to the next within one study system, enabling powerful tests of evolutionary rescue.

The genetic basis of local adaptation is likely to influence population persistence under new conditions. If genetic trade-offs underlie local adaptation and local alleles no longer confer fitness advantages in new environments, average fitness in local populations will decline. Assisted migration (Aitken & Whitlock 2013) could be necessary to enable population persistence. In contrast, under conditional neutrality, local populations could even expand if previously neutral alleles become beneficial in new conditions. It is crucial to understand the aspects of the environment that are changing, along with the agents of selection that drove historical local adaptation. For example, in species that have adapted to nonclimatic agents of selection (e.g., serpentine versus nonserpentine soils), the genetic basis of local adaptation might not be pertinent to predictions of biological responses to climate change, as the axes of environmental change do not align with the historical agents of local adaptation (e.g., variation in edaphic conditions). However, in species that display strong local adaptation to climate, genetic trade-offs could reduce the fitness of local

alleles as temperatures warm and precipitation patterns shift. In contrast, conditional neutrality could stabilize these populations if previously neutral alleles confer higher fitness under new climates. Additionally, recent methods have integrated data about the genetic basis of local adaptation and within-population genetic variation to predict the amount of genetic change a locally adapted population needs to adapt to a new phenotypic optimum and identify populations at risk of extinction (Fitzpatrick & Keller 2015). Fitzpatrick et al. (2021) recently validated the predictions from these models, but they also found that using putatively adaptive loci to make predictions did not outperform using randomly chosen loci.

8. CONCLUSION

Evidence abounds for ecotypic divergence and local adaptation. We suspect this robust literature has generated a false sense of understanding of the mechanisms that give rise to local adaptation. To assess the processes that influence the evolution of local adaptation, we call for multi-year, multi-site field experiments that use accessions from multiple populations that evolved in regions with divergent conditions. By transplanting individuals into diverse natural communities, rather than monocultures, and manipulating abiotic or biotic factors, researchers can detect the agent(s) and targets of local adaptation in ecologically relevant settings. Additionally, selection analyses in field experiments, or manipulations of traits, are crucial to test whether selection favors the phenotypes expressed by local ecotypes. We ask that funding agencies recognize the scientific, economic, and conservation value of elucidating the factors that contribute to local adaptation and appreciate the time and resources needed to address hypotheses concerning dynamic processes in a field setting. For instance, the Carnegie Institute supported Clausen and coworkers' project for decades. This reciprocal transplant experiment is unparalleled in scope, both in terms of the duration (but see Bennington et al. 2012, Germino et al. 2019, and provenance trials such as Wang et al. 2010) and the number of focal species. Furthermore, it yielded perspectives about local adaptation that would not have been possible without sustained research funding. In addition, we encourage researchers to test theoretical predictions of the conditions that hinder or facilitate local adaptation with field, laboratory, and genomic studies and to collaborate with Indigenous scholars, communities local to the work being conducted, and scientists in applied fields to expand the scope and impact of their work.

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