Microgeographic adaptation and the spatial scale of evolution

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Local adaptation has been a major focus of evolutionary ecologists working across diverse systems for decades. However, little of this research has explored variation at microgeographic scales because it has often been assumed that high rates of gene flow will prevent adaptive divergence at fine spatial scales. Here, we establish a quantitative definition of microgeographic adaptation based on Wright's dispersal neighborhood that standardizes dispersal abilities, enabling this measure to be compared across species. We use this definition to evaluate growing evidence of evolutionary divergence at fine spatial scales. We identify the main mechanisms known to facilitate this adaptation and highlight illustrative examples of microgeographic evolution in nature. Collectively, this evidence requires that we revisit our understanding of the spatial scale of adaptation and consider how microgeographic adaptation and its driving mechanisms can fundamentally alter ecological and evolutionary dynamics in nature.

The spatial scale of local adaptation

Understanding the adaptive evolution of populations in response to environmental variation constitutes a foundational research program for evolutionary ecologists working across diverse systems [1,2]. Local adaptation occurs when a population evolves traits that support higher fitness in its home environment relative to populations from foreign environments [3,4]. Most research on local adaptation has focused on adaptations that evolve across distances that, despite the 'local' moniker, often extend tens to hundreds of kilometers [5–7]. These distances often exceed both the environmental grain (the spatial scale of environmental variation) and the distances moved by focal organisms or their propagules. Theory shows that local adaptation can occur when selection exceeds the homogenizing effect of gene flow [8–11] (Box 1), a prediction supported by empirical evidence [12,13]. Yet, when designing their research, most biologists have assumed that high gene flow at small spatial scales would overwhelm local selection and prevent adaptive divergence (see Glossary). As a result, research has not sufficiently challenged the presumption that adaptation only occurs at coarse spatial scales [14].

The number of studies investigating evolutionary divergence at small spatial scales has increased in recent years, and the accumulating evidence requires that we revisit our understanding the spatial scale of adaptation. The term 'microgeographic' has long been used to describe patterns of divergence at fine spatial scales [15,16]. Mounting evidence suggests that microgeographic divergence is more widespread than is commonly appreciated and occurs across a wide range of species and geographic contexts [17–21]. Here we use the term 'microgeographic divergence' to refer to trait differences across fine spatial scales and microgeographic adaptation when these trait differences confer increased fitness in their native sites. We examine the support for microgeographic divergence and adaptation occurring in nature and identify its underlying mechanisms. We also examine how microgeographic adaptation can alter fundamental processes in ecology and evolution, and conclude with a roadmap for future research.

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Glossary

Adaptive divergence: the evolution of differences between populations as a result of adaptation to different environmental conditions and divergent natural selection.

Dispersal: the displacement of offspring away from their parents or natal site of origin.

Dispersal neighborhood: the geographic area within which individuals and genes regularly move and interact; estimated as two standard deviations of the dispersal distribution of a population.

Divergent selection: variation in natural selection resulting in different alleles being favored in different habitats or populations.

Effective gene flow: the movement and establishment of novel genes that are not currently present in the recipient population.

Gene flow: the exchange of genes and alleles between populations that subsequently contributes to the future gene pool of the recipient population; a result of successful reproduction by migrants.

Genetic drift: stochastic changes in allele frequencies across generations due to random sampling effects of parental genotypes.

Local adaptation: the evolution of traits in a population that results in higher fitness of native individuals in the home environment relative to individuals from foreign populations, regardless of spatial scale.

Maladaptation: the phenotypic deviation of a population or organism from the optimal adaptive peak within a particular environment.

Microgeographic adaptation: local adaptation of a population occurring within the dispersal neighborhood of the focal organism.

Microgeographic divergence: differences in trait distributions between samples of individuals within the same dispersal neighborhood. Unlike microgeographic adaptation, this term makes no presumption about the adaptive value of the trait divergence.

Selective barriers: natural selection that impedes the colonization of migrants and reduces their fitness in the recipient population.

Box 1. The theory behind adaptation in the face of gene flow

Consider two populations *i* and *j*, with allele frequencies p_i and p_j, respectively, that exchange migrants at rate *m* (complete mixing occurs when *m* = 0.5, where half the individuals switch populations every generation). In population *i*, following immigration the allele frequency becomes $p_i(m) = (1-m)p_i + mp_j$, and so p_i will always approach p_j (and vice versa if migration is symmetrical). Haldane [90] presented the first model of the balance between migration and selection, yielding the widely cited prediction that divergence will occur when the strength of divergent selection *s* exceeds the migration rate *m*. This is an approximation rather than an exact cut-off. It is more precise to recognize that some small divergence is likely to occur for most migration scenarios. The question is how much: a locally favored allele will reach an equilibrium frequency shown in Equation I [91]:

$$\hat{p}_i = 1 - \frac{1}{s_i}[m(1 - p_j)] \qquad [I]$$

but this result requires several limiting assumptions, such as weak selection and migration. The exact magnitude of divergence with migration–selection balance depends on many factors, including the genetic variance–covariance matrix, the relative strength of selection and migration, the timing of selection and dispersal within each generation (e.g., see Equations 7 and 8 of [11]), details of the underlying trait genetics (e.g., single-locus, multi-locus additive, dominant, or linkage among loci), and asymmetries in these parameters across populations. Asymmetries in habitat quality and population size, in particular, can influence divergence, where strong source–sink dynamics leading to directionally biased dispersal can hinder local adaptation in a recipient sink population (or comparatively small population) facing antagonistic selection [92,93]. Importantly, the high levels of migration anticipated at small spatial scales indicate that gene flow must be lower or selection stronger than expected (Figure I).

The above results rest on the widely held assumption that all genotypes are equally likely to migrate. In the context of Equation I above, the focal population *i* receives some fraction of immigrants *m* with allele frequencies equal to the donor population (p_j). However, genotypes can differ in their dispersal rate. In particular, in a population inhabiting a spatially heterogeneous habitat, some individuals will be more fit in particular microhabitats. Random dispersal will tend to introduce mismatches between genotype and habitat, such that selection should favor the evolution of either matching habitat choice (genotypes avoiding low fitness habitats),

natal habitat imprinting, or philopatry (reduced dispersal) [94,95]. The evolution of such habitat preferences can increase equilibrium divergence between populations, and steepen clines [95,96].
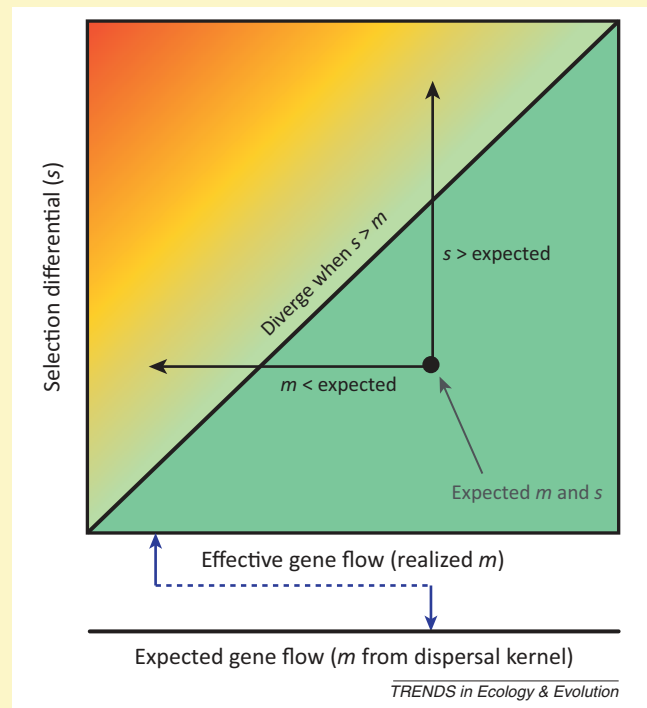

Figure I. High levels of dispersal and gene flow are expected at fine spatial scales. The diagonal line in this simple illustration represents equal strengths of divergent selection and migration (*m* = *s*). Negligible divergence is expected below this line in the area indicated in green. Above this line, increasing trait divergence will occur because selection exceeds gene flow, as indicated by the gradient from green to red. Microgeographic divergence depends on some combination of stronger divergent selection (*s*) and lower gene flow (*m*) than originally expected. For instance, a focal population (black dot) might experience some observed selection differential (*s*), with some dispersal capacity (*m*), leading to little expected divergence. Greater than expected divergence is possible if selection is stronger than expected (vertical arrow) or effective gene flow is less than expected from dispersal patterns (horizontal arrow).

Defining the scale of microgeographic adaptation

As early as the 1940s, Carl Epling and Theodosius Dobzhansky used 'microgeographic races' to describe divergent groups of the desert annual plant *Linanthus parryae* [22]. Subsequently, Robert Selander used the term 'microgeographic variation' to describe genetic divergence in house mice (*Mus musculus*) situated in adjacent barns [23]. Ehrlich and Raven [15] cited Selander's work as evidence for widespread fine-scaled differentiation in nature in their classic paper arguing that the local population was the most important evolutionary unit. Since then, evolutionary biologists have used the term 'microgeographic adaptation' to describe local adaptation at small, albeit inconsistent, spatial scales. The 'microgeographic' designation has been applied to genotypic and phenotypic differences observed across distances ranging from 25 m [16] to 40 km [7]. Thus, despite more than 70 years of use, the term 'microgeographic' lacks a clear quantitative definition, which limits its value for comparisons among species and systems.

For microgeographic adaptation to be applied consistently across species, we need to define a spatial extent

that is scaled to the dispersal ability of each species. Here we define 'microgeographic' relative to the dispersal neighborhood, an idea first derived by Sewall Wright to describe the geographic area within which movement of individuals regularly occurs. Specifically, the dispersal neighborhood represents all of the individuals located within a radius extending two standard deviations from the mean of the dispersal kernel of a species [8,24] (Box 2). Hence, microgeographic adaptation is defined as a special case of local adaptation occurring at the fine spatial scales at which populations should experience high gene flow based on the expected levels of dispersal.

Recognizing that evolutionary divergence occurs across a continuum of spatial scales, we propose a metric of adaptive divergence across space that serves as a spatial analog to measures of evolutionary rate [25]. This metric, the '*wright*', indicates the phenotypic difference between populations relative to the number of species-specific dispersal neighborhoods separating these populations (Box 2). The units of the *wright* are the number of trait standard deviations separating two samples per dispersal

Box 2. Estimating the standardized spatial scale of divergence and adaptation

To enable comparisons among species and systems, the spatial scale of adaptation should be normalized by the dispersal capacity of a species. We define microgeographic adaptation as adaptive divergence occurring within Sewall Wright's dispersal neighborhood, which defines the area where dispersal is frequent enough to prevent genetic drift. This concept and the details below are easily extended to any form of trait divergence across space, adaptive or otherwise.

The dispersal neighborhood for individuals distributed in two dimensions is based on the area under the distribution of dispersal distances and frequencies for that species or population (i.e., the dispersal kernel). The neighborhood is the area of a circle with a radius extending two standard deviations (2σ) from the center of the kernel (Figure I). Assuming a bivariate normal distribution, this area incorporates 86.5% of dispersal events (95% for linearly distributed organisms). Microgeographic adaptation occurs if two groups of individuals (e.g., populations) sampled from less than one neighborhood radius apart have adaptively diverged (Figure I). Adaptation between sites that are farther than one neighborhood apart would be considered 'local' but not microgeographic adaptation.

Many species exhibit leptokurtic dispersal distributions characterized by more short- and long-distance dispersers than assumed by the normal distribution [97]. Calculating a leptokurtic neighborhood size requires a correction factor k (Equation I):

$$A_{genetic\ neighborhood} = k\pi\sigma^2 \qquad [I]$$

where k depends on the degree of kurtosis [8,27]. $k = 4$ for normally distributed dispersal. Increasing leptokurtosis generates lower k values and smaller neighborhoods due to the increased observations near the center of the kernel [27]. Considering discrete population patches, the migration rate (m) can also be estimated by integrating the probability distribution of the kernel over the area of the recipient patch at its geographic location under the kernel (Figure I). The population mixing parameter Nm can be calculated if effective size N_e is known.

So far, we have suggested a rule of thumb for defining microgeographic adaptation. However, adaptation occurs across a spatial continuum, and is often a matter of degree rather than simply presence or absence. Therefore, we define the '*wright*', a metric of divergence across space that is directly analogous to the previously defined *haldane*, a metric of divergence through time [25] (Equation II):

$$w = \frac{|x_1 - x_2|}{ds_p} \qquad [II]$$

where x_1 and x_2 represent the means of the genetically determined traits of populations 1 and 2, standardized by the pooled standard deviation (s_p) of those trait values across populations, and d is the distance in number of dispersal neighborhoods separating the two populations. When $d \leq 1$ and $|x_1 - x_2|$ is significantly greater than zero, microgeographic adaptation is indicated. The *wright* standardizes divergence relative to the dispersal of the organism, allowing comparisons among species with different dispersal abilities. For continuously distributed samples, the numerator could instead be the slope of trait values per unit geographic distance divided by the number of dispersal neighborhoods per geographic distance. This metric is consistent with the *wright* if trait divergence is linearly related to distance; otherwise generalized additive models or similar techniques might better estimate nonlinear relationships. We can also amend this formulation to create a second metric using Euclidean distance in the denominator, providing a measure of divergence per unit absolute distance, analogous to the *darwin* for absolute time. For appropriate transformations of data, see [25].
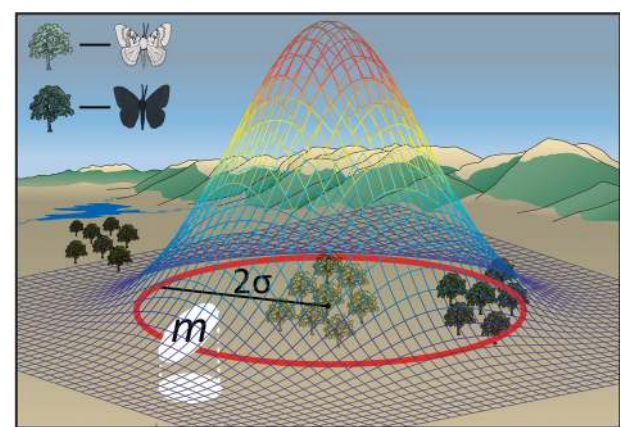
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Figure I. Hypothetical dispersal kernel for a moth species overlaid onto a landscape with three clusters of suitable forest habitats. This moth has two distinct color morphs, each experiencing higher fitness on the trees that more closely match their color and provide better camouflage (upper left). The red ring inside the kernel delineates the dispersal neighborhood boundary proposed by Wright, with a radius of two standard deviations (2σ) of the dispersal distribution. Microgeographic adaptation occurs when two populations located less than one neighborhood radius apart adaptively diverge (e.g., the dark and light moths diverge between the two forests under the kernel). Divergence between sites outside of the neighborhood would be considered 'local', but not microgeographic adaptation (e.g., between the light center forest and the far left group of dark trees). To accommodate the island model of habitat patches, the migration rate (m) can be estimated from the kernel by integrating the distribution over the area of the recipient patch on the landscape (the white circle and corresponding area on the dispersal kernel surface).

neighborhood. By defining divergence in terms of a dispersal neighborhood instead of Euclidean geographic distance, we can compare the differentiation between organisms with radically different dispersal capabilities. Once significant divergence is found, researchers interested in local adaptation must then determine whether the observed divergence is adaptive and heritable, typically through transplant and common garden experiments.

Wright's neighborhood has a long history of theoretical development and application in population genetics and represents a common evolutionary distance scaled to dispersal [8,26,27]. The dispersal neighborhood was originally derived for populations where individuals are continuously distributed on the landscape. Using the dispersal kernel and information about the recipient population, the dispersal neighborhood proposed here can also be extended to the island model of discrete populations and the Nm metric of dispersal and gene flow (Box 2). For our purposes, the

dispersal neighborhood represents the expected neighborhood size defined by dispersal capacity rather than what might be realized by gene flow. We use 'dispersal' to define the displacement of offspring away from parents, and 'gene flow' to define the movement of genes among populations that subsequently contributes to the future gene pool of the recipient population. As we show later, multiple mechanisms can decrease realized gene flow below that expected based on dispersal ability alone. Any mechanism that reduces the flow of maladapted genes relative to expectations based on dispersal capacity can promote microgeographic adaptations.

Empirical support for microgeographic adaptation

Increasingly, researchers are finding evidence for microgeographic adaptation that occurs within a dispersal neighborhood and across a wide range of taxa and selective environments, including toxin tolerance in plants [28],

morphological traits in land snails [16], and thermal tolerance in fish [18]. For example, despite a dispersal neighborhood estimated to be greater than 1 km, wood frog (*Rana sylvatica*) populations separated by as little as tens of meters show divergent development rate, morphology, and behavior in response to tree canopy cover [29,30]. In the apple maggot (*Rhagoletis pomonella*), adaptation to different hosts and their fruiting phenology has led to assortative mating based on host choice and sympatric divergence between host-specific races at fine scales [31]. Other examples thought to show microgeographic evolution include isopod pigmentation in response to vegetation [32], life-history variation in Trinidadian guppies corresponding with predation [33], fungal pathogen resistance in narrowleaf plantain [34], and sympatric divergence in crater lake cichlid fishes [35]. Box 3 highlights three illustrative examples of microgeographic adaptation in greater detail.

Mechanisms promoting microgeographic adaptation

Microgeographic adaptation is particularly interesting because it occurs despite a high potential for mixing within a dispersal neighborhood, making it unlikely that neutral processes can generate appreciable variation at this scale.

Box 3. Examples of microgeographic adaptation in nature

Example 1: edaphic adaptations in plants
One of the classic examples of evolutionary adaptation comes from the recent evolution of tolerance to toxic metals in plants, either in serpentine soils or following anthropogenic contamination, such as mine tailings. For instance, as one moves from contaminated mine tailings onto normal adjacent soil, grass flowering phenology and metal tolerance diverge over less than 20 m (Figure I; [28,98]). Such short clines are striking given that the grass *Anthoxanthum odoratum* is wind pollinated; thus, gene flow in the form of pollen dispersal can readily occur across the cline boundary. The steep cline is apparently maintained by strong divergent selection and partial reproductive isolation between metal-tolerant and intolerant grasses.

Example 2: cryptic coloration in the peppered moth
In pre-industrial England, peppered moth (*Biston betularia*) populations were dominated by a light-colored phenotype providing camouflage on lichen-covered trees. Concurrent with coal-powered industrialization, naturalists documented a rapid increase in the frequency of the black *carbonaria* morph in and around manufacturing areas (Figure II). Coined 'industrial melanism', the dark phenotype blended well with soot-covered trees, and increased from no observations before 1848 to nearly 98% frequency in 1895 in at least one population. Experiments by Kettlewell, and later Majerus, showed that this shift in phenotypic frequency was caused by strong selection from visual predators [99]. Regulation of air pollution over the past 50 years has reduced soot deposition, and the frequency of each color phenotype has since reverted, leaving the dark *carbonaria* morph in rapid decline [86]. Complementing the temporal shifts, spatial variation in industrial emissions created local adaption of populations across short distances on the landscape. Mark–recapture, genetics, and modeling studies indicate that peppered moths have broad dispersal neighborhoods (54-km wide) and that microgeographic adaptation resulted from intense selective barriers created by visual predators [86,99].

Example 3: depth clines in threespine stickleback
Threespine stickleback (*Gasterosteus aculeatus*) males build small nests and court females to induce them to lay eggs in the nest, after which the male guards the nest. Given that males are closely associated with their nest throughout the breeding season, one can unambiguously match males (and their traits) to particular microhabitat features, such as nest depth, substrate, or distance to protective cover. Within single lake populations (e.g., not the well-known benthic–limnetic species pairs), nests typically range from 0.5 to 2.5 m deep. Surprisingly, male body size, trophic morphology, and diet vary predictably across this narrow range of nest depths (Figure III; [100]). Nests at different depths are often only a few meters apart horizontally, well within the daily cruising range of individual fish.
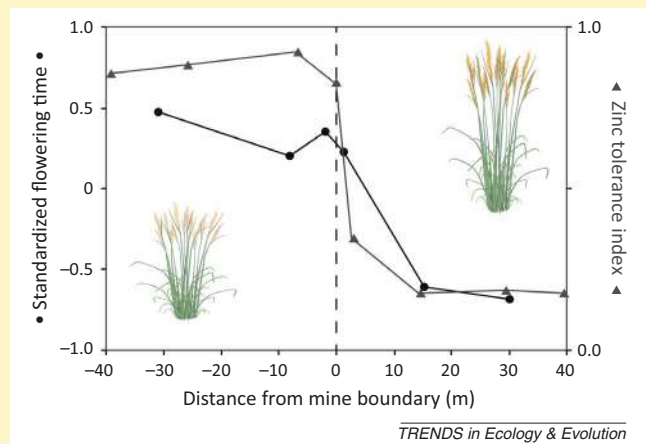

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Figure I. *Anthoxanthum odoratum* is a wind-dispersed grass that grows continuously within and beyond the boundaries of a mine contaminated with high levels of zinc and lead in northern Wales, UK. The focus of intense study since the 1960s, this population of *A. odoratum* shows clear divergence of several phenotypic traits spanning an area less than 50 m on either side of the mine boundary (represented by zero on the x-axis; negative distances are samples from within the mine boundary). Common garden experiments found dramatic differences in flowering time (7–8 days), zinc tolerance levels (four times higher tolerance within mine boundary), and plant height (plants 50% taller outside of mine) between plants on either side of the mine boundary. Adapted from [28,98].
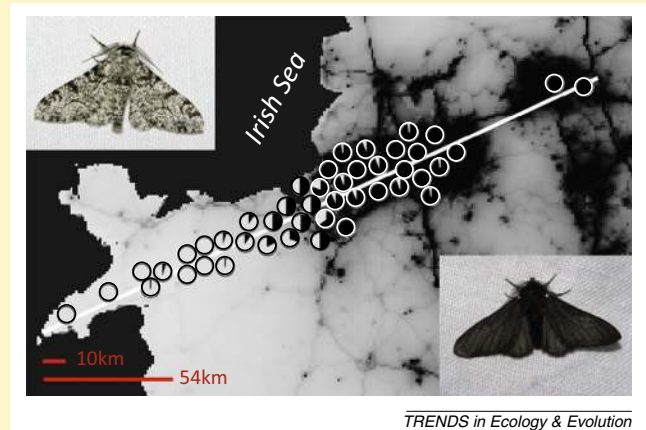

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Figure II. The peppered moth, *Biston betularia*, has two distinct color morphs, a light morph and a dark morph that dramatically increased in frequency after the industrialization of the 1800s. The frequencies of each morph were estimated between 1964 and 1975 along a 230-km transect across north Wales and northwest England. The map shows this area, with the color representing the level of emissions (a proxy for urbanization; black areas are heavily urban). Circles represent the proportion of moths sampled at a site that were either light (white) or dark (black), and are offset from the transect line for clarity. The 54-km scale bar represents the diameter of the dispersal neighborhood estimated from maximum likelihood. Adapted from [86]; inset photos by O. Leillinger.
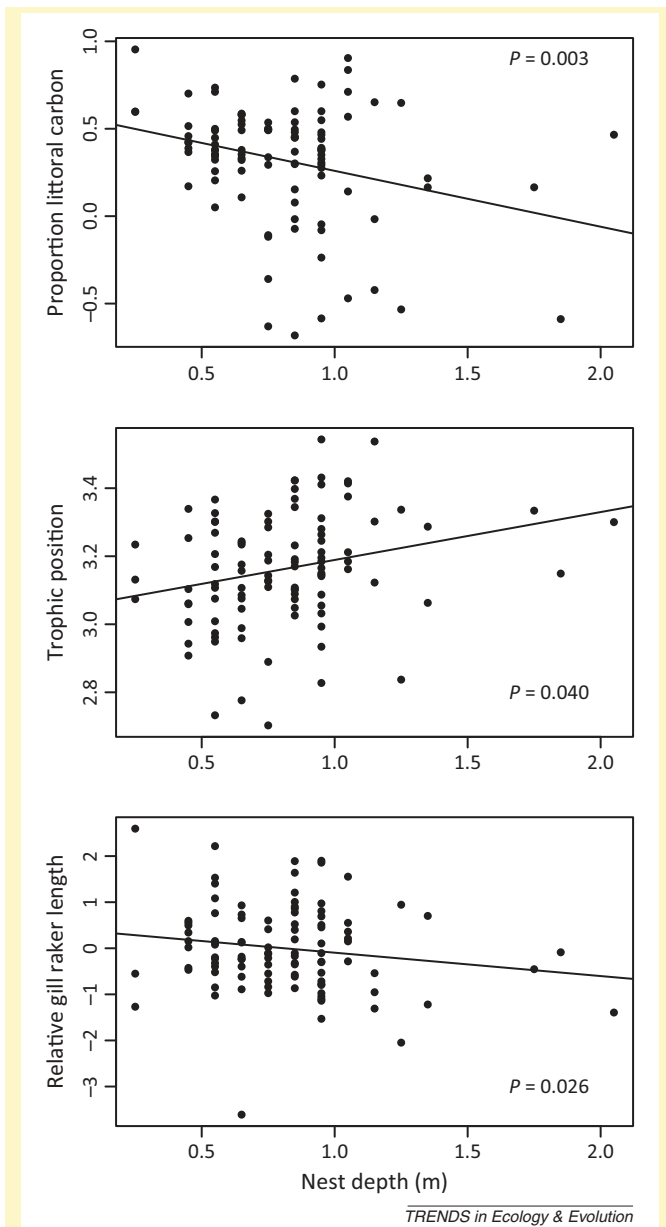
Figure III. The diet and morphology of male threespine stickleback, *Gasterosteus aculeatus*, are correlated with nest depth within a single population. Diet was measured using carbon and nitrogen stable isotope ratios, converted into measures of the proportion littoral carbon and trophic position. Morphology was measured as size-adjusted gill raker length (residuals on body mass). Importantly, fish were sampled near the start of the breeding season; thus, there should have been insufficient time for isotopic turnover and phenotypic plasticity to generate these correlations. Instead, it appears that the diet and morphology of individuals influence the choice of nest depths. The adaptive value of these clines remains uncertain, because we lack estimates of fitness for individuals that match or deviate from this trend. However, it is known that the focal traits have a heritable basis. Data from [100].

Microgeographic adaptation requires any process that increases selection strength or reduces maladaptive gene flow relative to dispersal ability. We highlight seven mechanisms that either initiate or amplify adaptive divergence at microgeographic scales: (i) strong natural selection; (ii) landscape barriers; (iii) spatially autocorrelated selection regimes; (iv) habitat choice; (v) selective barriers against migrants; (vi) evolutionary monopolization effects; and (vii) sexual selection against migrants. Initiating mechanisms not only introduce divergence between

previously undifferentiated groups, but can also subsequently continue to cause further divergence. By contrast, given some level of preexisting genetic divergence, amplifying mechanisms can exaggerate initial differences. Although strong selection can affect populations at any stage, we organize our discussion based on the order in which these mechanisms occur during the arrival, establishment, and reproduction of migrants (Figure 1). Although we highlight each mechanism separately, in nature these mechanisms often act in concert to promote microgeographic evolution [36].

Mechanisms capable of initiating divergence
Mechanism (i): strong natural selection
Strong natural selection is perhaps the most appreciated mechanism for initiating and sustaining microgeographic adaptive divergence. Strong selection that brings the mean phenotype of a population closer to a locally optimal phenotype (i.e., conveying the highest fitness) can overcome the high gene flow expected at fine spatial scales (Box 1). A review of the magnitude of selection gradients seen in nature suggests that strong selection is rare [37]. However, if most of these measurements come from populations that are already well adapted, then selection would appear weaker than if it was measured on a wider range of phenotypic variation. Indeed, data from transplant experiments suggest that natural selection is often strong, particularly against migrants [see mechanism (v)] [1]. Given the mixed evidence for strong selection in nature, other mechanisms might be required to allow microgeographic adaptation, especially those that reduce gene flow.

Mechanism (ii): landscape barriers
Microgeographic adaptation can occur when landscape barriers, such as rivers [38], highways [39], and unsuitable vegetation cover [40], restrict gene flow between populations. When landscape barriers occur within the dispersal neighborhood of an organism, they can facilitate microgeographic adaptation. For example, waterfalls and rapids on Trinidadian streams block the upstream movement of guppies [33], and within these restricted distances guppies have evolved different life-history traits in response to divergent selection [41]. Given the widespread evidence for landscape filtering of gene flow, population geneticists have developed a suite of methods that quantify how landscape features alter gene flow [42,43].

Mechanism (III): spatially autocorrelated natural selection
Even if migrating individuals arrive, they may not carry alleles that are maladapted to the local environment. Effective gene flow is defined as the establishment of novel genes or alleles in a recipient population [15], and it depends on the distribution of selection on the landscape. Selective environments are often nonrandomly distributed in clumps or along clines, leading to positive spatial autocorrelation [44]. Autocorrelated selection can support microgeographic adaptation between two populations if each population receives less maladaptive gene flow from antagonistic selection regimes compared with randomly distributed selective environments [44,45]. For example,
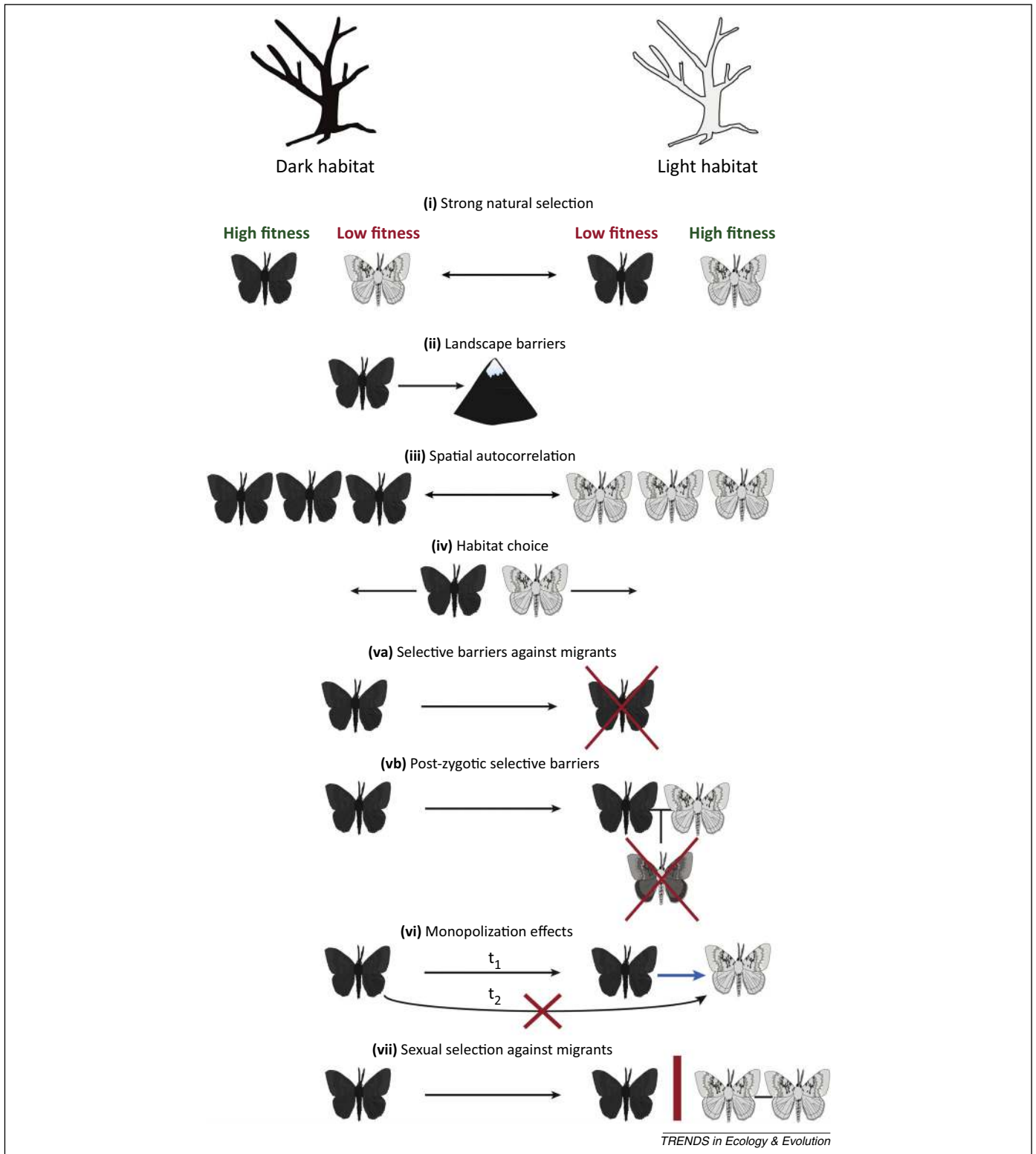
Dark habitat

Light habitat

(i) Strong natural selection

High fitness   **Low fitness**   **Low fitness**   **High fitness**

(ii) Landscape barriers

(iii) Spatial autocorrelation

(iv) Habitat choice

(va) Selective barriers against migrants

(vb) Post-zygotic selective barriers

(vi) Monopolization effects

t_1

t_2

(vii) Sexual selection against migrants

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Figure 1. Conceptual diagram depicting seven mechanisms contributing to microgeographic adaptation. Moths have heritable polygenic variation in color. A moth with coloration that matches the dominant tree trunk color in a region has greater fitness because predators cannot easily detect it and prey on it. Microgeographic adaptation can occur when: (i) strong selection differences between habitats lead to divergence in optimal coloration; (ii) landscape barriers to dispersal prevent movement of maladapted dark morphs into the white-barked tree habitat; (iii) most trees in a region are light colored and, therefore, most migrants are adapted to light bark color; (iv) the two morphs sample and choose the matching colored habitat; (va) strong selection prevents maladapted dark morphs from colonizing; (vb) strong selection impedes the success of migrant offspring via mortality or reduced fitness; (vi) the dark morph colonizes, adapts to light-colored bark, and then prevents further colonization by other morphs by monopolizing resources; and (vii) after colonization, the black morph cannot mate because of sexual selection against migrants.

imagine multiple populations of cryptically colored moths distributed across an equal number of dark and light environments. If environments are randomly distributed, then half the gene flow into a dark population should be maladaptive immigration from light populations. However, if dark environments are clustered, then >50% of genes will come from dark populations. These pre-adapted genes will facilitate adaptation assuming that they are compatible with local genes. Pre-adapted genes can also increase local additive genetic variance and allow for the regional evolution of favorable alleles [46]. Fine-scale adaptations are common in empirical studies performed along abrupt ecotones [28,47], and a recent meta-analysis found that microgeographic adaption often occurred in natural populations exposed to spatially autocorrelated selection [44]. Microgeographic adaptation is less likely for populations experiencing a rare selection environment, where a population located in a clump of opposing selection will receive higher effective (and maladaptive) gene flow. Theory is needed to determine the general circumstances under which the spatial distribution of selection affects adaptive divergence.

Mechanism (iv): habitat selection

Theory often assumes that migrants carry a random sample of regional alleles [14]. However, there is increasing recognition that genotypes can differ in dispersal ability or habitat preference [48,49]. When genotypes redistribute nonrandomly in space, fine-scale population differentiation can arise quickly and be facilitated rather than impeded by gene flow [50]. If this spatial segregation involves matching phenotypes to habitats conferring higher fitness, microgeographic adaptation can result. Such spatial segregation is only feasible within the typical dispersal range of individuals because individuals must sample alternate habitats and choose the one conferring high fitness. Habitat selection offers some of the greatest potential for promoting microgeographic adaptation.

The most dramatic examples of adaptive divergence via habitat choice might occur in host races of phytophagous insects, where different genotypes segregate onto different host plant species, leading to genetic divergence, local adaptation, and perhaps speciation [51]. For example, different color morphs of the Wrangler grasshopper settle on colored substrates that match their camouflage [52]. Habitat preferences also occur in vertebrates: different phenotypes of threespine stickleback preferentially disperse into lake or stream habitats, promoting their divergence [53]. The resulting genetic clines can occur as little as a few meters upstream from a lake, despite the capacity of sticklebacks to disperse hundreds of meters in a few days [53].

Amplifying mechanisms that require some prior divergence

Mechanism (v): selective barriers against migrants

Selective barriers are defined as selection that reduces the fitness of migrants before their alleles are incorporated into the recipient gene pool [15]. This decreased fitness can reduce the stream of maladapted migrant genes expected

at microgeographic scales and thereby facilitate adaptation. Selective barriers occur when selection decreases the colonization or success of migrant phenotypes either en route to or within a habitat. For instance, deep-bodied salmon trying to migrate upstream become stranded and die, such that stream-breeding populations are genetically more shallow-bodied than downstream lake-breeding populations [54]. Within habitats, Nosil [55] showed that predators reduced by 15% the fitness of stick insects that had migrated from alternative host plant species. These insects had evolved cryptic morphologies on their original host, which made them more conspicuous to predators on the new host.

Beyond increasing mortality, selective barriers can decrease the mating success [see mechanism (vii) below] and fecundity of migrants. For example, if a resident and migrant successfully mate, they might encounter postzygotic impediments if they produce unviable offspring or intermediate phenotypes with low fitness in that local environment [56]. Thus, selection can further decrease maladaptive gene flow, which exaggerates spatial and reproductive isolation and thereby supports microgeographic adaptation.

Selective barriers can be identified by transplant experiments and observations of neutral divergence. Hereford [1] reviewed transplant experiments and found, on average, 45% higher fitness for the resident population compared with foreign populations, suggesting the operation of contemporary selective barriers. However, these results cannot indicate if selective barriers initiated the original adaptive differences or reinforced nascent divergence. Also, most populations in this review were separated by distances that exceeded microgeographic scales. Thus, we still do not know how commonly strong selective barriers operate at fine scales. Neutral genetic patterns can also uncover the role of selective barriers. 'Isolation by Adaptation' is a pattern that occurs when neutral genetic markers correlate with local selection rather than with landscape distance [20,57–59]. For instance, Richter-Boix *et al.* [59] found that moor frogs differed in larval life-history traits that were correlated with environmental characteristics and neutral genetic variation, but not geographic distance.

Mechanism (vi): evolutionary monopolization effects

De Meester and colleagues [60] proposed the monopolization hypothesis to explain an evolution-mediated priority effect, whereby adaptation by early colonists creates a selective barrier against future maladaptive gene flow. With sufficient time and additive genetic variation, the first colonists to a patch adapt to the local environment, and this initial divergence facilitates rapid population growth. Through a numerical advantage and by exploiting resources, resident genotypes limit the inflow of comparatively poorly adapted subsequent immigrants and thus initiate a positive feedback between adaptive divergence and reduced gene flow [58,60]. For example, *Daphnia magna* originating from ponds in the UK were allowed to adapt to experimentally elevated temperatures for *c.* 34 generations. These recently adapted UK clones then dominated over clones added to the experiment from France that would have dominated had they arrived concurrently

because they were pre-adapted to the warmer conditions [61]. Hence, adaptation can provide an advantage to early colonists in their interactions with future immigrants. We currently do not know how much preexisting adaptive divergence is necessary to facilitate this positive feedback at microgeographic scales. Therefore, further theoretical and empirical development is needed.

Mechanism (vii): sexual selection against migrants
If maladapted individuals arrive in a population and survive, they still might not contribute to the local gene pool if residents avoid mating with them. Sexual selection is a specific type of selective barrier mediated through mating opportunities, which can act on phenotypic differences produced due to dispersal (e.g., poor body condition of arriving migrants), plastic responses to source environments, or genetic divergence. These phenotypic differences can reduce the mating success of immigrants if: (i) immigrants are poorly adapted and females prefer well-adapted local males; (ii) local females are less likely to recognize the mating signals of immigrants; or (iii) populations experience divergent preferences for mate advertisements. The first option requires prior divergence in adaptive traits, the second requires differences in male signals, and the third requires prior divergence in male signals and female preferences. Consequently, these processes are more likely to amplify preexisting divergence, rather than initiate microgeographic divergence from an initially well-mixed population. Similarly, positive assortative mating within each population could produce discrimination against phenotypically dissimilar immigrants [62]. However, this is not likely to be an effective source of complete reproductive isolation between populations except in the most extreme cases of population divergence or assortment [63].

Adaptive differentiation via mate choice occurs most readily when traits under divergent natural selection also affect mate choice [64] either via pleiotropy or genetic linkage. These 'magic traits' reduce gene flow concurrent with adaptive divergence and thus can reinforce initial divergence even with significant gene flow [65]. Nonmagic traits can also play a role. For instance, outbreeding avoidance occurs when local individuals avoid mating with genetically divergent migrants. Although inbreeding avoidance is well appreciated [66], many species also avoid outbreeding, including frigatebirds, salamanders, cichlid fishes, and self-pollinating plants [66–69]; thus, this preference might commonly support microgeographic adaptation.

Broader ecological and evolutionary implications
Historically, evolutionary biologists searched for local adaptation across the broader geographic scales where gene flow was limited and finding local adaptation was more certain. Recent studies suggest that microgeographic adaptation occurs more commonly than once expected. We anticipate that an increased research focus will uncover additional examples. This broader scope for adaptation will affect how we think about the maintenance of genetic and species diversity, importance of eco-evolutionary dynamics, and the application of evolution to conservation biology and human health at fine spatial scales [70–74].

If microgeographic adaptation is widespread, small-scale environmental variation could help explain the maintenance of functionally relevant genetic diversity [1]. The potential for widespread microgeographic adaptation also suggests that more genetic diversity with functional relevance exists in nature than is currently appreciated. This greater genetic variation could buffer species against future changes by storing adaptive genes. For instance, a few populations exposed to hot microclimates might supply the adaptive alleles that promote more widespread adaptation to warming temperatures. Given microgeographic adaptation, conservation biologists will need to focus at even smaller scales to locate and preserve the full range of unique evolutionary histories and capacities to persist under future environmental conditions [75].

Ecologists increasingly recognize that evolutionary changes might affect ecological patterns and dynamics [74,76,77]. Most eco-evolutionary studies evaluate the effect of evolution on populations separated by coarser scales. Yet, ecologists often seek to explain patterns of community structure at more localized spatial scales, where neighboring populations are well connected by dispersal (e.g., in a metacommunity; [78]). If evolutionary divergence can alter community dynamics across the same spatial scales at which ecologists have traditionally understood them, then the need to synthesize ecology and evolution becomes that much more compelling (Figure 2). For instance, microgeographic adaptation in salamander populations was shown to buffer top-down effects of local predators on community diversity [79]. In such a case, ecologists could draw the wrong conclusions because cryptic evolutionary dynamics operate in the background to weaken or exaggerate ecological dynamics ([80]; Figure 2).

Microgeographic adaptations might frequently evolve across the abrupt selection mosaics created by human land use and pollution. Some of our best examples of microgeographic adaptation originate from moths adapting to industrialization and plants adapting to toxic mine tailings (Box 3). Fine-scale evolution could generate more resilience in the face of human disturbance than is currently recognized and even prevent extinctions through evolutionary rescue [81,82]. Microgeographic adaptations could also affect direct human interactions with other species. For instance, prey species might evolve localized responses to spatially variable harvesting techniques of plants and animals [83], requiring a smaller spatial scale of management. Agricultural organisms might evolve resistance to pests or herbicides at fine scales [84]. Human pathogens could also evolve in response to locally prevalent pesticides, antibiotics, or levels of resistance in human populations [71]. Overall, microgeographic adaptation forces applied biologists to consider a finer scale of management than is typically examined.

A roadmap for studying the spatial scale of adaptation
Our review of microgeographic adaptation highlights the opportunities for a deepened understanding of evolution in nature, which will emerge from a closer consideration of spatial scale in the study of selection and movement. Equally, we emphasize the serious limitations in understanding microgeographic adaptation imposed by the
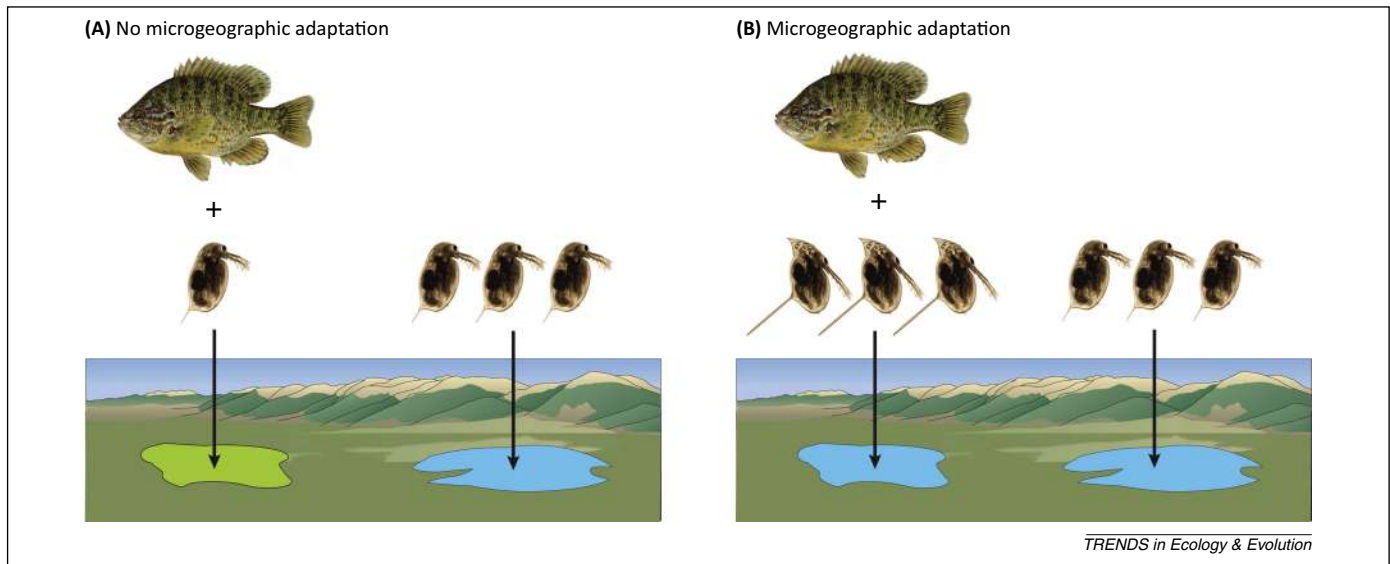
Figure 2. Microgeographic adaptation could influence fine-scale ecological patterns through eco-evolutionary processes. In this example, a generalist fish predator consumes zooplankton, which in turn consumes phytoplankton in this common aquatic food chain. Dense zooplankton can reduce phytoplankton and create a clear-water phase in lakes that otherwise would enter a green-water phase dominated by photosynthetic phytoplankton. Fish can reduce zooplankton numbers to produce the green-water phase through a trophic cascade of indirect consumptive effects. In **(A)**, we assume no microgeographic adaptation, and observations of nearby lakes with and without fish confirm the importance of fish in determining phytoplankton density. In **(B)**, we assume that the zooplankton can evolve helmets and spines that protect them from fish, which then switch to other prey species. These adaptations are common in zooplankton and enable them to maintain high densities in the face of fish predation and control phytoplankton regardless of fish presence. Not considering microgeographic adaptation would incorrectly lead to the conclusion that fish have minor effects on aquatic food chains in local lakes. Fish strongly affect food chains, but this effect is mediated by cryptic evolutionary dynamics rather than through the commonly assumed ecological pathways.

lack of data available to evaluate its generality. We can cite examples, but we are far from being able to characterize typical scales over which we can expect microgeographic adaptation to occur, or to enumerate the causes underlying observed examples. We believe that creating a standard definition will catalyze the collection of needed information. The techniques to study natural selection and estimate movement patterns and gene flow are well developed (Box 4) [3,85]. However, few researchers have combined these methods with an eye toward

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Box 4. Evaluating microgeographic adaptation in nature

The prospect of microgeographic adaptation creates the opportunity for novel insights into the scale of adaptation in nature. Here we highlight two compelling questions that will facilitate our understanding, and offer approaches to answering them. Progress will be made by integrating standard methods with less commonly used approaches, such as the introduction and tracking of maladapted genotypes.

What is the lower spatial boundary of adaptive divergence?
A lack of data at fine scales means that we know little regarding this lower boundary.
- Measuring the spatial distribution of phenotypes and selection across the landscape provides the context needed to evaluate the scale of divergence, selection variation, and autocorrelation [44].
- Common garden experiments provide evidence that observed phenotypic differences have a genetic basis and can identify the role of experimental selective factors [3].
- Reciprocal transplant experiments between populations measure fitness differences in both the home and foreign environments and quantify local adaptation *in situ* [3,4].
- Estimating dispersal and gene flow in tandem and comparing their relative magnitudes can uncover the relative scale of divergence and discern among potential mechanisms.
- Measuring adaptive divergence across sharp gradients in selection (e.g., ecotones; [28,47]) is an efficient way to determine the minimum scale of adaptation (Figure I in Box 3).

What mechanisms promote microgeographic adaptation?
The unexpected nature of microgeographic adaptation usually arises from overestimates of disruptive gene flow. We currently have limited

data to assess the role of the seven highlighted mechanisms that can reduce gene flow (Figure 1, main text), and the following approaches, combined with the methods above, will provide such data.
- Landscape genetics methods can identify landscape barriers to gene flow [42,43].
- Behavioral trials are used to evaluate habitat choice [49].
- Tracking phenotypes and genotypes *in situ* enables researchers to estimate selection over time and the relative fitness of residents and migrants. Changes in migrant representation can reveal the timing and strength of selection.
- Introducing 'migrants' and tracking their fate provides invaluable information on the suite of mechanisms driving divergence. Do migrants die soon after introduction? Is their mating success similar to residents? How fit are their offspring [101]?
- Experimentally manipulating the selective environments will enable researchers to track changes in dispersal patterns and shifts in fitness between populations experiencing altered selection.
- Identifying the genes under selection uncovers the molecular underpinnings of adaptive divergence and allows for more efficient tracking of maladapted individuals and selection at the genic level [102].

Investigating local adaptation at fines scales requires additional considerations beyond those applied at broader scales. For example, the degree of trait divergence is expected to become small, and thus large samples sizes will be needed to detect significant differences. Given that the scale of adaptation will not usually be known in advance, study designs should include multiple sampling points collected within and beyond the dispersal kernel (e.g., geometrically scaled sampling). Lastly, examining adaptation in replicated populations and landscapes can suggest the generality of observed patterns.

understanding the minimum spatial scale of adaptive differentiation [28,86].

This dearth of studies at small scales highlights a need for evolutionary biologists to examine more closely the role of spatial scale in driving evolution across a wider range of scales. The ecological literature has had a comprehensive focus on scale for the past two decades [87–89]. By contrast, spatial scale, as opposed to temporal scale, has received less attention in discussions of major themes for evolutionary biology, the contentious topic of the geography of speciation notwithstanding. This distinction in research agendas might partially explain why phenotypic patterns at very small spatial scales are almost reflexively described as ecological phenomena. We view an emerging interest in microgeographic adaptation as a useful entry point for a larger evaluation of spatial scale in evolution, as well as its relation to ecological responses occurring in the same landscapes. We suspect that we will find that many patterns previously attributed exclusively to plasticity and other nominated ecological mechanisms will originate in part from fine-scale evolution.

To be more specific, even the most ardent skeptics of the notion of microgeographic adaptation will agree that, for a given study system, there is some minimum scale over which adaptive differentiation is likely to occur. What is that scale? This is the paramount question in the study of microgeographic adaptation. An alternative approach is to estimate the minimum scale at which a given degree of adaptive differentiation is possible. To make such a determination, the researcher must identify the degree of differentiation known to have biologically relevant effects. Once more data are available and we can identify a lower spatial boundary for adaptive divergence, then we can debate whether the observed scales are 'micro'. Much as the debates about rates of rapid evolution that emerged during the 1990s were quelled by data, we expect that the same will occur once we can assess quantitative patterns amassed over numerous systems.

To accomplish this transition will require an ambitious set of both observational and experimental studies integrated and applied at a finer spatial scale than is typical (detailed in Box 4). On the observational front, we need to systematically sample patterns of phenotypic variation concurrently with estimates of movement patterns and gene flow. A specific goal should be to identify the scale of neighborhoods across which phenotypes and genes vary and how those scales relate to observed patterns of movement. Only by sampling at finer spatial scales than we suspect divergence will occur will we detect or discount microgeographic variation. Beyond observational studies, an experimental approach is required to estimate the adaptive significance of observed trait divergence and identify the mechanisms promoting adaptive divergence at fine scales. Multiple approaches, ranging from common garden experiments to more novel methods such as long-term introductions and tracking of maladapted genotypes must be integrated to identify the mechanisms and genomic underpinnings of microgeographic divergence (Box 4).

Much research remains to be done before we understand when and where we should expect to see microgeographic adaptation. This work will require integrating theory,

experiments, and observations with the common goal of determining the spatial scale of adaptation. Abundant opportunities exist for novel manipulations of the environmental grain of selection, dispersal, and genetic composition of populations in the wild to reveal how evolution works at fine scales. The payoff will be a robust understanding of spatial evolutionary patterns and the processes creating them. The time has come for an expansion into new frontiers of spatial evolutionary research. Our understanding has now advanced to the point where we cannot assume that evolution is something that only happens at great distances. We can no longer neglect the possibility of adaptive evolution at small spatial scales or its consequences for ecological and evolutionary processes.

References

1 Hereford, J. (2009) A quantitative survey of local adaptation and fitness trade-offs. *Am. Nat.* 173, 579–588

2 Conover, D.O. *et al.* (2009) The covariance between genetic and environmental influences across ecological gradients: reassessing the evolutionary significance of countergradient and cogradient variation. *Ann. N. Y. Acad. Sci.* 1168, 100–129

3 Kawecki, T.J. and Ebert, D. (2004) Conceptual issues in local adaptation. *Ecol. Lett.* 7, 1225–1241

4 Blanquart, F. *et al.* (2013) A practical guide to measuring local adaptation. *Ecol. Lett.* 16, 1195–1205

5 Clausen, J. *et al.* (1940) *Experimental Studies on the Nature of Species. I. Effects of Varied Environments on Western North American Plants*, Carnegie Institute of Washington, Publishers No. 520

6 Laugen, A.T. *et al.* (2003) Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates: evidence for local adaptation. *J. Evol. Biol.* 16, 996–1005

7 Stelkens, R.B. *et al.* (2012) Genetic and phenotypic population divergence on a microgeographic scale in brown trout. *Mol. Ecol.* 21, 2896–2915

8 Wright, S. (1969) *Evolution and the Genetics of Populations, Volume 2: The Theory of Gene Frequencies*, University of Chicago Press

9 Felsenstein, J. (1976) The theoretical population genetics of variable selection and migration. *Annu. Rev. Genet.* 10, 253–280

10 Garcia-Ramos, G. and Kirkpatrick, M. (1997) Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51, 21–28

11 Hendry, A.P. *et al.* (2001) Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* 55, 459–466

12 Hendry, A.P. *et al.* (2002) Adaptive divergence and the balance between selection and gene flow: lake and stream stickleback in the misty system. *Evolution* 56, 1199–1216

13 Nosil, P. and Crespi, B.J. (2004) Does gene flow constrain adaptive divergence or vice versa? A test using ecomorphology and sexual isolation in *Timema cristinae* walking-sticks. *Evolution* 58, 102–112

14 Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends Ecol. Evol.* 17, 183–189

15 Ehrlich, P.R. and Raven, P.H. (1969) Differentiation of populations. *Science* 165, 1228–1232

16 Selander, R.K. and Kaufman, D.W. (1975) Genetic structure of populations of brown snail (*Helix aspersa*). I. Microgeographic variation. *Evolution* 29, 385–401

17 Steiner, K.C. and Berrang, P.C. (1990) Microgeographic adaptation to temperature in pitch pine progenies. *Am. Midl. Nat.* 123, 292–300

18 Kavanagh, K.D. *et al.* (2010) Contemporary temperature-driven divergence in a Nordic freshwater fish under conditions commonly thought to hinder adaptation. *BMC Evol. Biol.* 10, 350

19 Willi, Y. and Hoffmann, A.A. (2012) Microgeographic adaptation linked to forest fragmentation and habitat quality in the tropical fruit fly *Drosophila birchii*. *Oikos* 121, 1627–1637

20 Richardson, J.L. and Urban, M.C. (2013) Strong selection barriers explain microgeographic adaptation in wild salamander populations. *Evolution* 67, 1729–1740

21 Krueger-Hadfield, S.A. *et al.* (2013) Intergametophytic selfing and microgeographic genetic structure shape populations of the intertidal red seaweed *Chondrus crispus*. *Mol. Ecol.* 22, 3242–3260

22 Epling, C. and Dobzhansky, T. (1942) Genetics of natural populations. VI. Microgeographic races in *Linanthus parryae*. *Genetics* 27, 317–332

23 Selander, R.K. (1968) Behavior and genetic variation in wild populations. In *Annual Meeting of the AAAS*. Dallas, Texas

24 Wright, S. (1946) Isolation by distance under diverse systems of mating. *Genetics* 31, 39–59

25 Hendry, A.P. and Kinnison, M.T. (1999) Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53, 1637–1653

26 Wright, S. (1943) Isolation by distance. *Genetics* 28, 114–138

27 Crawford, T.J. (1984) What is a population? In *Evolutionary Ecology: The 23rd Symposium of the British Ecological Society, Leeds 1982* (Shorrocks, B., ed.), pp. 135–174, Blackwell Scientific

28 Antonovics, J. (2006) Evolution in closely adjacent plant populations X: long-term persistence of prereproductive isolation at a mine boundary. *Heredity* 97, 33–37

29 Relyea, R.A. (2002) Local population differences in phenotypic plasticity: predator-induced changes in wood frog tadpoles. *Ecol. Monogr.* 72, 77–93

30 Skelly, D.K. (2004) Microgeographic countergradient variation in the wood frog, *Rana sylvatica*. *Evolution* 58, 160–165

31 Filchak, K.E. *et al.* (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* 407, 739–742

32 Hargeby, A. *et al.* (2004) Habitat-specific pigmentation in a freshwater isopod: adaptive evolution over a small spatiotemporal scale. *Evolution* 58, 81–94

33 Reznick, D.N. and Endler, J.A. (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 36, 160–177

34 Laine, A-L. (2006) Evolution of host resistance: looking for coevolutionary hotspots at small spatial scales. *Proc. Biol. Sci.* 273, 267–273

35 Elmer, K.R. *et al.* (2009) Color assortative mating contributes to sympatric divergence of neotropical cichlid fish. *Evolution* 63, 2750–2757

36 Via, S. (2009) Natural selection in action during speciation. *Proc. Natl. Acad. Sci. U.S.A.* 106 (Suppl.), 9939–9946

37 Kingsolver, J.G. *et al.* (2001) The strength of phenotypic selection in natural populations. *Am. Nat.* 157, 245–261

38 Richardson, J.L. (2012) Divergent landscape effects on population connectivity in two co-occurring amphibian species. *Mol. Ecol.* 21, 4437–4451

39 Riley, S.P.D. *et al.* (2006) FAST-TRACK: a southern California freeway is a physical and social barrier to gene flow in carnivores. *Mol. Ecol.* 15, 1733–1741

40 Wang, I.J. *et al.* (2009) Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (*Ambystoma californiense*). *Mol. Ecol.* 18, 1365–1374

41 Torres Dowdall, J. *et al.* (2012) Fine-scale local adaptation in life histories along a continuous environmental gradient in Trinidadian guppies. *Funct. Ecol.* 26, 616–627

42 Manel, S. *et al.* (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* 18, 189–197

43 Balkenhol, N. *et al.* (2009) Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography* 32, 818–830

44 Urban, M.C. (2011) The evolution of species interactions across natural landscapes. *Ecol. Lett.* 14, 723–732

45 Endler, J.A. (1973) Gene flow and population differentiation. *Science* 179, 243–250

46 Morjan, C.L. and Rieseberg, L.H. (2004) How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. *Mol. Ecol.* 13, 1341–1356

47 Rosenblum, E.B. (2006) Convergent evolution and divergent selection: lizards at the White Sands ecotone. *Am. Nat.* 167, 1–15

48 Rice, W.R. (1984) Disruptive selection on habitat preference and the evolution of reproductive isolation: a simulation study. *Evolution* 38, 1251–1260

49 Edelaar, P. *et al.* (2008) Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62, 2462–2472

50 Bolnick, D.I. and Otto, S.P. (2013) The magnitude of local adaptation under genotype-dependent dispersal. *Ecol. Evol.* 3, 4722–4735

51 Drès, M. and Mallet, J. (2002) Host races in plant-feeding insects and their importance in sympatric speciation. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 357, 471–492

52 Cox, G.W. and Cox, D.G. (1974) Substrate color matching in the grasshopper *Circotettix rabula*. *Gt. Basin Nat.* 34, 60–70

53 Bolnick, D.I. *et al.* (2009) Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution* 63, 2004–2016

54 Lin, J. *et al.* (2008) Fine-scale differentiation between sockeye salmon ecotypes and the effect of phenotype on straying. *Heredity* 101, 341–350

55 Nosil, P. (2004) Reproductive isolation caused by visual predation on migrants between divergent environments. *Proc. R. Soc. B* 271, 1521–1528

56 Via, S. *et al.* (2000) Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. *Evolution* 54, 1626–1637

57 Nosil, P. *et al.* (2008) Heterogeneous genomic differentiation between walking-stick ecotypes: 'Isolation by adaptation' and multiple roles for divergent selection. *Evolution* 62, 316–336

58 Orsini, L. *et al.* (2013) The role of selection in driving landscape genomic structure of the waterflea *Daphnia magna*. *Mol. Ecol.* 22, 583–601

59 Richter-Boix, A. *et al.* (2013) Fine-grained adaptive divergence in an amphibian: genetic basis of phenotypic divergence and the role of nonrandom gene flow in restricting effective migration among wetlands. *Mol. Ecol.* 22, 1322–1340

60 De Meester, L. *et al.* (2002) The Monopolization Hypothesis and the dispersal–gene flow paradox in aquatic organisms. *Acta Oecologica* 23, 121–135

61 Van Doorslaer, W. *et al.* (2009) Local adaptation to higher temperatures reduces immigration success of genotypes from a warmer region in the water flea *Daphnia*. *Global Change Biol.* 15, 3046–3055

62 Jiang, Y. *et al.* (2013) Assortative mating in animals. *Am. Nat.* 181, E125–E138

63 Bolnick, D.I. and Kirkpatrick, M. (2012) The relationship between intraspecific assortative mating and reproductive isolation between divergent populations. *Curr. Zool.* 58, 484–492

64 Thibert-Plante, X. and Gavrilets, S. (2013) Evolution of mate choice and the so-called magic traits in ecological speciation. *Ecol. Lett.* 16, 1004–1013

65 Servedio, M.R. *et al.* (2011) Magic traits in speciation: 'magic' but not rare? *Trends Ecol. Evol.* 26, 389–397

66 Szulkin, M. *et al.* (2013) Inbreeding avoidance, tolerance, or preference in animals? *Trends Ecol. Evol.* 28, 205–211

67 Cohen, L.B. and Dearborn, D.C. (2004) Great frigatebirds, *Fregata minor*, choose mates that are genetically similar. *Anim. Behav.* 68, 1229–1236

68 Chandler, C.H. and Zamudio, K.R. (2008) Reproductive success by large, closely related males facilitated by sperm storage in an aggregate breeding amphibian. *Mol. Ecol.* 17, 1564–1576

69 Wright, S.I. *et al.* (2013) Evolutionary consequences of self-fertilization in plants. *Proc. Biol. Sci.* 280, 20130133 http://dx.doi.org/10.1098/rspb.2013.0133

70 Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science* 236, 787–792

71 Thompson, J.N. (1999) The evolution of species interactions. *Science* 284, 2116–2118

72 Stockwell, C.A. *et al.* (2003) Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* 18, 94–101

73 Ricklefs, R.E. (2010) Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proc. Natl. Acad. Sci. U.S.A.* 107, 1265–1272

74 Schoener, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331, 426–429

75 Fraser, D.J. and Bernatchez, L. (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol. Ecol.* 10, 2741–2752

76 Post, D.M. and Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the

ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. Lond. B* 364, 1629–1640

77 Ellner, S.P. *et al.* (2011) Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol. Lett.* 14, 603–614

78 Holyoak, M. *et al.* (2005) Metacommunities: a framework for large-scale community ecology. In *Metacommunites* (Holyoak, M. *et al.*, eds), pp. 1–32, University of Chicago Press

79 Urban, M.C. (2013) Evolution mediates the effects of apex predation on aquatic food webs. *Proc. R. Soc. B: Biol. Sci.* 280, 20130859 http://dx.doi.org/10.1098/rspb.2013.0859

80 Yoshida, T. *et al.* (2007) Cryptic population dynamics: rapid evolution masks trophic interactions. *PLoS Biol.* 5, e235

81 Gomulkiewicz, R. and Holt, R.D. (1995) When does evolution by natural selection prevent extinction. *Evolution* 49, 201–207

82 Bell, G. and Gonzalez, A. (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* 12, 942–948

83 Darimont, C.T. *et al.* (2009) Human predators outpace other agents of trait change in the wild. *Proc. Natl. Acad. Sci. U.S.A.* 106, 952–954

84 Thrall, P.H. *et al.* (2011) Evolution in agriculture: the application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. *Evol. Appl.* 4, 200–215

85 Clobert, J. *et al.* (2012) *Dispersal Ecology and Evolution*, Oxford University Press

86 Saccheri, I.J. *et al.* (2008) Selection and gene flow on a diminishing cline of melanic peppered moths. *Proc. Natl. Acad. Sci. U.S.A.* 105, 16212–16217

87 Levin, S.A. (1992) The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73, 1943

88 Kareiva, P. (1994) Space: the final frontier for ecological theory. *Ecology* 75, 1

89 Chave, J. (2013) The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecol. Lett.* 16, 4–16

90 Haldane, J.B.S. (1930) A mathematical theory of natural and artificial selection. (Part VI Isolation) *Math. Proc. Camb. Philos. Soc.* 26, 220–230

91 Wright, S. (1931) Evolution in Mendelian populations. *Genetics* 16, 97–159

92 Kawecki, T.J. and Holt, R.D. (2002) Evolutionary consequences of asymmetric dispersal rates. *Am. Nat.* 160, 333–347

93 Anderson, J.T. and Geber, M.A. (2010) Demographic source-sink dynamics restrict local adaptation in Elliott's blueberry (*Vaccinium elliottii*). *Evolution* 64, 370–384

94 Ravigné, V. *et al.* (2009) Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *Am. Nat.* 174, E141–E169

95 Armsworth, P.R. (2009) Conditional dispersal, clines, and the evolution of dispersiveness. *Theor. Ecol.* 2, 105–117

96 Armsworth, P.R. and Roughgarden, J.E. (2008) The structure of clines with fitness-dependent dispersal. *Am. Nat.* 172, 648–657

97 Clark, J.S. *et al.* (1998) Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *Bioscience* 48, 13–24

98 Antonovics, J. and Bradshaw, A.D. (1970) Evolution in closely adjacent plant populations VIII. Clinal patterns at a mine boundary. *Heredity* 25, 349–362

99 Cook, L.M. *et al.* (2012) Selective bird predation on the peppered moth: the last experiment of Michael Majerus. *Biol. Lett.* 8, 609–612

100 Snowberg, L.K. and Bolnick, D.I. (2012) Partitioning the effects of spatial isolation, nest habitat, and individual diet in causing assortative mating within a population of threespine stickleback. *Evolution* 66, 3582–3594

101 Barrett, R.D.H. *et al.* (2008) Natural selection on a major armor gene in threespine stickleback. *Science* 322, 255–257

102 Stinchcombe, J.R. and Hoekstra, H.E. (2008) Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity* 100, 158–170