

# An evolutionary process that assembles phenotypes through space rather than through time

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**In classical evolutionary theory, traits evolve because they facilitate organismal survival and/or reproduction. We discuss a different type of evolutionary mechanism that relies upon differential dispersal. Traits that enhance rates of dispersal inevitably accumulate at expanding range edges, and assortative mating between fast-dispersing individuals at the invasion front results in an evolutionary increase in dispersal rates in successive generations. This cumulative process (which we dub “spatial sorting”) generates novel phenotypes that are adept at rapid dispersal, irrespective of how the underlying genes affect an organism’s survival or its reproductive success. Although the concept is not original with us, its revolutionary implications for evolutionary theory have been overlooked. A range of biological phenomena (e.g., acceleration of invasion fronts, insular flightlessness, preadaptation) may have evolved via spatial sorting as well as (or rather than) by natural selection, and this evolutionary mechanism warrants further study.**

colonization | evolution | spatial disequilibrium | nonadaptive evolution

In 1859, Charles Darwin proposed a mechanism to explain the process by which organisms become well matched to local conditions. That mechanism was natural selection (1). At its heart lies the concept of differential lifetime reproductive success (LRS). Significant extensions to the paradigm since Darwin’s work—such as multiple levels of selection (2, 3)—all rely upon the basic principle that, through time, some genes leave more copies of themselves than do others (4). Here we describe an additional mechanism whereby traits evolve because genes are differentially successful through space rather than time. This idea is not new; the process was described long ago (5), has been explored in several spatially explicit models of nonequilibrium populations (6–8), and is widely recognized by researchers who work with range-edge dynamics (9). The basis of the idea is that on expanding range edges evolutionary change can arise from differential dispersal rates (spatial sorting) as well as from differential survival or reproductive success. Spatial sorting and classical natural selection both require heritable variation, and both result in deterministic shifts in phenotypic attributes, but the two evolutionary processes rely on fundamentally different mechanisms (spatial filtering versus temporal filtering). Mainstream biology has failed to recognize that evolutionary change can be caused by spatial sorting as well as by conventional natural selection.

## Spatial Sorting

Imagine a species expanding its range into hitherto unoccupied territory and with a genetic basis to variation among individuals in dispersal rates (6–8). For example, continuously distributed variation may occur in dispersal-relevant morphological traits [e.g., seed shape (5), flight musculature and wing size (7, 10), leg length (11), foot size (12)], behavior [movement patterns (13)], and physiology [locomotor endurance (14)]. Alleles that confer the highest rates of dispersal inevitably accumulate at the expanding range edge. The reason is straightforward: If a cohort of individuals all start out (at birth) from a fixed point and move away from that

point consistently, the ones that move quickest will be the only ones at the expanding range edge. Because an organism’s rate of dispersal is influenced by many phenotypic traits, it will be affected by many genes (15). Some of the organisms that disperse fast enough to be at the invasion front are there because of speed, others because of endurance, others because of directional movement, and still others because of lowered investment in processes that tradeoff against dispersal [e.g., immune function (16)].

Those fast-dispersing individuals at the edges of the dispersing front inevitably will breed with each other, because any individuals that disperse slowly or nondirectionally will have been left behind (8). Interbreeding at the fast-moving invasion front thus will produce offspring with higher mean dispersal rates (and hence higher extreme maximum values for dispersal-enhancing traits, given additive genetic variance) than was the case in the parental generation. Successive generations evolve faster and faster dispersal by the collocation of such traits (e.g., genes conferring speed, endurance, and high activity levels) within the same individuals, even without new mutations (17). Such mutations may be readily available, however, because they “surf” expanding range fronts where selection against them is ineffective (18–20). The end result is evolution—the cumulative assembly of a novel phenotype that is adept at dispersal—but without requiring the genes involved to affect an organism’s survival or reproduction (i.e., without the operation of classical natural selection).

By analogy, imagine a race between rowboats (organisms) crewed by randomly allocated oarsmen (genes). If all boats begin simultaneously and head the same way, the proportion of skilled oarsmen per boat (dispersal-enhancing genes per organism) will be highest among the race leaders. If we stop the race at intervals and interchange oarsmen at random among boats that are close together at that part of the race (i.e., breeding between syntopic individuals), some crews formed by exchanging oarsmen among the fastest-moving boats will contain an even higher proportion of skilled rowers. There will be an increasing spatial assortment of rowing ability (dispersal rate) as the race progresses, because interchange (breeding) at the vanguard produces “offspring” that inherit their parent’s high mean dispersal rate (Fig. 1).

An expanding range edge inevitably imposes a complex mixture of selective forces driven both by classical natural selection and by spatial sorting. For example, the departure of fast-dispersing individuals from the core population means that if we look only within that core area, there appears to be classical natural selection for lower dispersal rates (i.e., the departing individuals do not contribute to future generations and so are genetically dead at that spatial scale of comparison). The critical point is that classical

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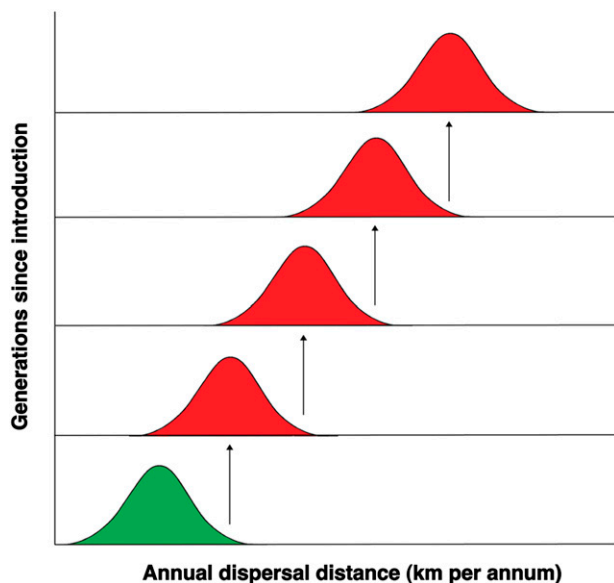
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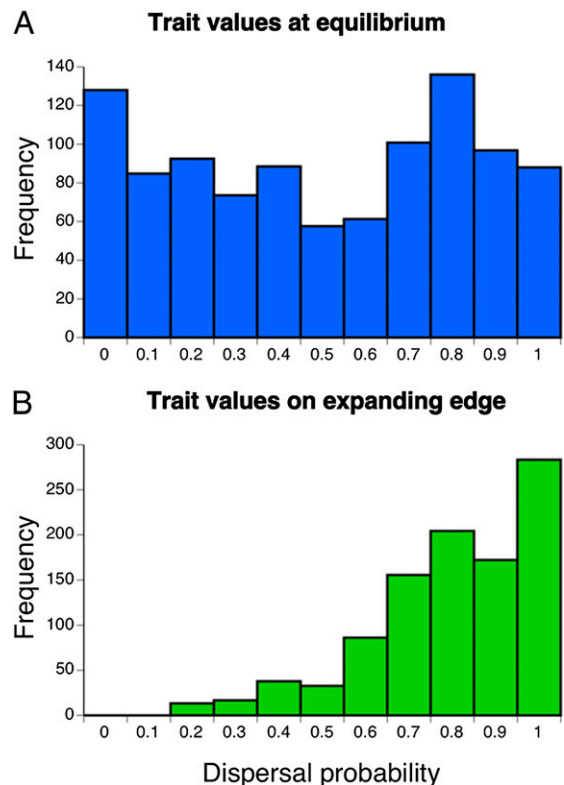


**Fig. 1.** A schematic model of the evolution of increasing dispersal distances (km per annum) in a hypothetical organism that is in the process of range expansion into hitherto unoccupied territory. The initial distribution of dispersal distances through time is given by the green curve (that is, some individuals within the population do not disperse as far as others, and this variation is genetically determined). The progeny of the fastest-dispersing individuals in each generation (shown in red) exhibit a rapid increase in mean values for per-generation dispersal, because assortative mating at the invasion front progressively colocalizes multiple dispersal-enhancing genes (e.g., for speed, endurance, and activity level) within individual organisms. Through the generations, this pressure results in individuals that disperse much faster than any in the original founding population, regardless of any effects of dispersal rate on LRS.

natural selection is not the only driver of evolution in this system; the spatial sorting of genotypes caused by differential dispersal, followed by random mating (at the periphery) will result in significant and predictable evolutionary changes.

An extensive literature has identified a wide range of circumstances under which we would expect to see evolved increases in dispersal ability at an expanding range edge. To our knowledge, however, all these analyses have dealt with an amalgam of spatial sorting and classical natural selection; for example, individuals at the invasion vanguard may have higher LRS because of reduced competition from conspecifics (6, 21) or because local populations have high rates of extinction and all surviving populations are founded by former migrants (22, 23), or because dispersal reduces competition among kin (24). Clearly, classical natural selection often favors dispersal-enhancing phenotypes in non-equilibrium systems. However, even if these classical selective forces on dispersal-enhancing traits are absent (i.e., faster dispersal does not increase the number of genes coding for dispersal-enhancing traits in subsequent generations), spatial assortment alone can generate the evolution of a highly dispersive phenotype by cumulative directional change.

To test this proposition, we need to exclude any advantage to faster dispersers in terms of LRS. In previous models, population growth has been dictated by local density dependence, and thus the evolution of increased dispersal on the invasion front (where densities are lower) may have been driven by classical natural selection processes rather than by spatial sorting. We constructed an individual-based coupled map lattice model to exclude conventional natural selection (i.e., an organism's genotype has no effect on its LRS). The lattice model shows that spatial sorting alone can generate evolutionary change (Fig. 2 and *SI Text*). This



**Fig. 2.** Change in gene frequencies arising through spatial sorting alone (rather than by orthodox natural selection for higher LRS) during the process of range expansion. In this model system, dispersal probability and LRS (number of offspring) are uncorrelated. (A) A sample of 1,000 individuals from this population after 500 generations in an equilibrium space reveals no net selection on dispersal probability. (B) After 100 generations of range expansion, a sample of 1,000 individuals from the invasion front reveals markedly different gene frequencies, with highly dispersive genes at high frequency despite their lack of impact on LRS.

sorting process clearly results in evolution [a net directional change over many generations (25)] but does not arise from classical natural selection in that traits evolve in a predictable direction despite never conferring any benefit in survival or reproduction to the organisms that exhibit them.

The simplicity of this process (cumulative spatial assortment of dispersal-enhancing genes) means that spatial sorting will operate at expanding range edges unless the system lacks additive genetic variation for traits that influence dispersal rate. Such a lack is unlikely: Additive genetic variation for such traits is common (26). Whether spatial sorting is significant is a more difficult question to answer; for example, its effects on invasion rate might be trivial relative to classical natural selection. To answer this question, we will need detailed data on selective factors at invasion fronts.

### Evidence for Spatial Sorting

If selection at an invasion front favors faster dispersal (via spatial assortment and/or classical natural-selection advantages), we expect such fronts to be dominated by unusually fast-dispersing individuals. Several systems show this pattern. For example, wing-dimorphic crickets exhibit more large-winged individuals at the expanding front (10); wind-dispersed seeds in lodgepole pines have a higher ratio of wing to seed mass on the expanding front (5); range-expanding populations of butterflies have more strongly developed flight muscles and wing aspect ratios (7); and ants have higher proportions of dispersing females in invasion-front pop-

ulations (27). The most detailed studies, however, involve the cane toad (*Rhinella marina*) in tropical Australia. The toad invasion front has accelerated dramatically through its 75-y history (11, 28) because of a three- to 10-fold increase in the daily dispersal rate of invasion-front toads (8, 13). The accelerated dispersal reflects changes in morphology [longer-legged toads are overrepresented at the invasion front (11)], behavior [frontal toads move more often, move further per move, and follow straighter paths (8, 13)], and physiology [greater endurance (14)]. This spectacular phenotypic divergence has a genetic basis, as evidenced by significant heritability of dispersal rates (29).

How can we distinguish between the effects of classical natural selection and spatial sorting? Both hypotheses predict that invasion fronts often will accelerate and be dominated by fast-dispersing individuals. The simplest prediction to test involves expanding range fronts in which faster dispersal has not been favored by classical natural selection. Under those (possibly rare) conditions, we would predict LRS to be uncorrelated or negatively correlated with dispersal rate. For example, faster dispersers might experience higher mortality, or feed less, or grow more slowly, or reproduce less often. Such correlations at an invasion front [but not necessarily in a metapopulation system (23)] would be inconsistent with conventional natural selection as an explanation for accelerating expansion rate, leaving spatial sorting as the only likely cause for accelerating rates of invasion.

We do not have enough data to test this proposition. Even in the most intensively studied invasion-front system [cane toads in Australia (11, 13, 14)], the fitness consequences of variation in dispersal rate remain unclear. However, the effects of dispersal rate on viability often are negative in this system: The locomotor traits that enhance dispersal rate also cause spinal injuries (30, 31), and highly dispersive toads suffer higher mortality (8). These patterns suggest spatial sorting rather than classical natural selection is at work, but further studies of natural selection on rates of dispersal in invasion-front populations are needed.

### What Phenotypic Traits Can Be Affected by Spatial Sorting?

Spatial sorting could favor the elaboration of any trait that enhances an organism's ability to disperse, not just locomotor structures or physiological traits as described above. For example, some taxa are transported by attaching themselves to other species (e.g., burrs, ticks), or in the digestive tract [e.g., seeds and fruits (32)], or in vehicles [stowaways in cars and boats (33–35)]. Spatial sorting also may favor bold, risk-taking behaviors (36) or individuals that readily handle the stress of intense physical activity and novel environments. Our first human ancestors to cross the oceans and invade new lands probably were highly non-random in dispersal-relevant traits as well as in behavioral flexibility and within-group cooperation (5, 37). Indeed, selection for rapid dispersal at the invasion front may explain the rapid spread of modern humans through Europe and North America and the large body sizes of those early dispersers (37, 38). In other taxa, selection for rapid rates of range expansion might affect traits such as social responsiveness (39) or high levels of aggression, as in killer bees (40) and birds (41).

Any parasite that infects a range-expanding host taxon will itself be subject to spatial sorting (42). Candidate traits involve duration of attachment to the range-expanding host (e.g., gut passage time of internal parasites) and life-history shifts that increase the probability of finding new hosts (which probably are at low densities on the invasion front). Virulence also should be under selection: Because parasites that cause only minor illness impede host dispersal less than parasites that debilitate the host, we expect the evolution of lowered virulence in parasites near the invasion front (42). Some of the loss of native-range parasites in introduced species may be due to this process (42).

Spatial sorting offers a possible alternative explanation for many other biological phenomena. For example, imagine a spe-

cies that expands its range by dispersing from the mainland to numerous islands and exhibits strong phenotypic similarities between organisms on different islands even though they were founded by separate dispersal events from the mainland. The Darwinian view would attribute that similarity to convergent adaptation to island conditions, but spatial sorting could generate the same pattern (5, 12, 43, 44). That is, individuals from island populations resemble each other not because they have experienced similar selective forces in their insular homes but because of similar winnowing for dispersal-enhancing phenotypes in the process of reaching those islands. Similarly, specific phenotypic traits that facilitate success during the transport phase could be overrepresented in founding populations of translocated species (15).

Intriguingly, spatial sorting also might generate distinctive phenotypes at the lower end of the dispersal-rate continuum by favoring lower, not higher, dispersal rates (45). This situation could be the exact opposite of the one described in the previous paragraph. Imagine an island population with genetically based individual variation in dispersal ability (say, variation in wing length). All individuals with large wings can disperse to high-quality habitat on the nearby mainland and achieve higher LRS by doing so. Because small-winged individuals cannot leave the island, they have lower LRS and are the only ones left behind in the ancestral patch. Over time, interbreeding of small-winged individuals on the ancestral patch could generate a novel phenotype, by colocalizing many alleles that prevent normal development of the wings. This model predicts the evolution of flightlessness on islands without positing any LRS advantage for the trait. Ever since Darwin, reduced dispersal rates in island organisms have been attributed to LRS differentials; that is, dispersing individuals die because they cannot find new habitat patches (43, 46). Spatial sorting offers an alternative explanation, simpler than the Darwinian hypothesis: Insular flightlessness can evolve regardless of whether dispersing individuals have higher or lower LRS than their sedentary conspecifics (46).

Another classical topic in evolutionary theory is preadaptation as an explanation for complex traits that (*i*) enhance the bearer's current LRS but (*ii*) differ so much from the ancestral condition that they would require multiple sequential changes to exhibit their current form, and (*iii*) for which it is difficult to imagine functional advantages (i.e., enhanced LRS) for the intermediate stages. Wings are clearly useful for birds, but what use is half a wing (47)? Possible solutions to this puzzle include gradually accumulating functional advantages (e.g., vertebrate visual systems) or shifts in function [e.g., feathers evolve for thermoregulation and then are co-opted for locomotion (47)]. Spatial sorting offers another solution, because it can construct complex arrays of phenotypic traits, in novel combinations, without requiring the modifications to enhance LRS. This process might amplify the phenotypic variation upon which conventional natural selection can operate, allowing lineages to cross adaptive valleys between fitness peaks (48).

### Overview

Both spatial sorting and classical natural selection require heritable variation, but the two evolutionary processes differ in the mechanism causing trait evolution (spatial versus temporal filtering). The assumptions underlying spatial sorting are simple and realistic, and the process itself has been recognized for decades (5). Nonetheless, it has not been widely understood that spatial sorting differs from classical natural selection in not requiring differential LRS and thus does not constitute natural selection as that process currently is defined. There are at least two potential solutions to this nomenclatural problem:

- i*) Expand our definition of “natural selection” to include processes driven by spatial as well as temporal filtering.

Classical natural selection and spatial sorting thus would be viewed as subsets of natural selection (the former based on differentials in survival and/or reproductive success through time, and the latter on differentials in dispersal rate through space). We would have to envisage selection working on variance among individuals in dispersal-enhancing traits as well as on mating ability, fertilizing ability, fertility, fecundity, and/or survivorship (25). Because all the other measures have their effect via LRS, but dispersal-driven selection does not, combining categories in this way would conceal an important difference.

- ii) Retain the current definition of “natural selection” (25), and treat spatial sorting as a different (additional) type of evolutionary process. This option avoids potentially confusing implications of the term “selection” (which implies differential LRS to most evolutionary biologists) and identifies spatial sorting as fundamentally different from the processes that Charles Darwin described. Under this terminology, deterministic evolutionary change can occur via either of two processes—not only through natural selection (as currently understood) but also through spatial sorting. This option is the one we advocate.

Spatial sorting operates on a more limited set of traits (those that affect dispersal rate or ability) and within a more restricted set of conditions (range edges) than does classical natural selection. Nonetheless, the possibility that some traits have evolved via “mating betwixt the quickest” rather than “survival of the fittest” warrants further attention (15). In a nonequilibrium world where many taxa are changing their distributions because of anthropogenic challenges, the evolutionary forces operating on the edges of expanding populations deserve careful study. Many species exhibit strong metapopulation structure, with frequent local extinctions followed by recolonizations (49), and each of those recolonization events provides an opportunity for spatial sorting to mold phenotypic attributes. Spatial sorting may prove to be classical natural selection’s shy younger sibling, not as important as Darwinian processes but nonetheless capable of shaping biological diversity by a process so far largely neglected. Determining whether cumulative spatial assortment has played a significant role in biological evolution is an exciting challenge both for modelers and for empiricists.

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