Life-history evolution in range-shifting populations

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Abstract. Most evolutionary theory does not deal with populations expanding or contracting in space. Invasive species, climate change, epidemics, and the breakdown of dispersal barriers, however, all create populations in this kind of spatial disequilibrium. Importantly, spatial disequilibrium can have important ecological and evolutionary outcomes. During continuous range expansion, for example, populations on the expanding front experience novel evolutionary pressures because frontal populations are assorted by dispersal ability and have a lower density of conspecifics than do core populations. These conditions favor the evolution of traits that increase rates of dispersal and reproduction. Additionally, lowered density on the expanding front eventually frees populations on the expanding edge from specialist, coevolved enemies, permitting higher investment into traits associated with dispersal and reproduction rather than defense against pathogens. As a result, the process of range expansion drives rapid life-history evolution, and this seems to occur despite ongoing serial founder events that have complex effects on genetic diversity at the expanding front. Traits evolving on the expanding edge are smeared across the landscape as the front moves through, leaving an ephemeral signature of range expansion in the life-history traits of a species across its newly colonized range. Recent studies suggest that such nonequilibrium processes during recent population history may have contributed to many patterns usually ascribed to evolutionary forces acting in populations at spatial equilibrium.

Key words: climate change; contemporary evolution; defense allocation; density dependence; dispersal rate; enemy escape; genotype "smearing"; nonequilibrium processes; range shift; rapid life-history evolution; reproductive rate.

INTRODUCTION

The vast majority of evolutionary theory is predicated on a reasonable simplifying assumption: that populations are at spatial equilibrium. By this, we mean that the habitat available to the population (or metapopulation) does not expand or contract in space. That assumption is often invalid, however. Populations move through space; ranges expand and contract, and dispersal barriers are surmounted (Vermeij 2005). In this review, we argue that such nonequilibrium populations experience different selective forces than do populations in spatial equilibrium, and we suggest that range shift can have profound impacts on the evolution of a species’ life history. These evolutionary forces can cause change in life history over ecological timescales.

Understanding the evolutionary forces at work during range shift is of more than theoretical interest. For example, the rate at which invasive species spread is an important consideration in our attempts to manage their impacts (Travis and Park 2004). Such rates can be radically modified by evolutionary shifts in life history (Holt et al. 2005, Phillips et al. 2008). The rates and correlates of population expansion also affect our understanding of historical biogeography and thus the historical events that have generated current biodiversity (Schoonmaker and Foster 1991, Clark et al. 1998, Davis et al. 2005). Range shifts are also critical to the impact of climate change on biodiversity, because species that can physically track climate change are likely to face a lower impact than those that cannot (Thomas et al. 2004, Mustin et al. 2009). If species’ life histories evolve during climate-induced range shift, then the ramifications for biodiversity conservation may be far-reaching indeed.

Any case of continuous range shift includes two unavoidable aspects: on the edge of the range, an
invading population (1) is assorted by dispersal ability (i.e., only the best dispersers make it to the new range edge each generation), and (2) exhibits a lower-than-normal population density. These outcomes (which we will explain in more detail) have at least three consequences for life-history evolution in the vanguard of invading populations: first, they encourage the evolution of increased dispersal rate; second, they encourage the evolution of increased reproductive rate; and third, they lead to the extirpation of specialist enemies on the invasion front.

**Evolution of Dispersal**

Populations spread through a combination of dispersal and population growth (Fisher 1937, Skellam 1951). Traditionally, models of range advance suggested waves of advance that traveled at constant speed, an assumption at odds with many empirical observations. Theoretical advances in the last 30 years show that accelerating range advance can arise from subtleties in how dispersal and population growth are modeled (Kot et al. 1996, Shigesada and Kawasaki 1997, Hastings et al. 2005), but these models have continued to treat dispersal and population growth as constant through time. Here, we suggest that evolution often may drive changes in these critical parameters during invasion, and thus accelerate range advance.

Dispersal, defined here as displacement between birth and reproduction (Ronce 2007), appears to be a highly labile trait (Roff and Fairbairn 2001, Bowler and Benton 2005, Ronce 2007). Part of this lability stems from the trait’s complexity; dispersal can be achieved actively (in which case, numerous behavioral traits are important; Barton et al. 2009), passively (in which case, numerous morphological traits are important), or both; dispersal also can be condition dependent (Ferriere et al. 2000, Bowler and Benton 2005). Even an apparently simple example, a wind-dispersed seed, will disperse according to its mass, the height from the ground of its release, its buoyancy, the timing of its release, and its tendency to settle. The complex phenotypic determinants of dispersal mean that selection for enhanced rates of dispersal has numerous phenotypic targets.

When habitat is homogenous, natural selection on dispersal is driven by issues such as the avoidance of inbreeding and competition (Hamilton and May 1977, Ferriere et al. 2000, Clabet et al. 2001, Ronce 2007). Where habitat is heterogeneous (on range edges or in dynamic metapopulations, for example), dispersal responds in complex ways to a combination of natural selection and spatial assortment by dispersal ability. In these cases, the dispersal strategy that evolves depends strongly upon the spatial and temporal variation in habitat quality, as well as the cost of dispersal (e.g., McPeek and Holt 1992, Travis and Dytham 1999, Dytham 2009). In the present review, we ignore variance in habitat quality and focus instead on a simpler case in which habitat quality is homogenous and not limiting (and hence, a population is expanding into new suitable habitat). In these situations, where a species is shifting its range, some very clear predictions emerge. In particular, during range expansion we can expect dispersal rates on the advancing front to evolve upward due to spatial selection.

**Spatial selection: a runaway evolutionary process**

Why do we expect dispersal to evolve upward on the expanding front during range advance? The shift is a natural consequence of range expansion and occurs due to a process that we refer to here as “spatial selection” (Fig. 1). Imagine a population where all the individuals disperse, then reproduce, and then die. If this population is placed into a large area of suitable vacant habitat, the population will advance its range as individuals disperse (Fig. 1A). Importantly, the process of dispersal effectively sorts individuals through space by dispersal ability. That is, individuals on the edge of the expanding population front are at that edge simply because they dispersed farther than other individuals in the population: the process of dispersal has spatially assorted the best dispersers in the population and placed them on the expanding front (Fig. 1B). Now, because all the best dispersers are in the same place at the same time, they will tend to breed with each other (the “Olympic Village effect”). Thus, if any component of dispersal ability is heritable in this hypothetical species, the offspring of the individuals on the front will tend to have higher dispersal ability than the offspring of individuals from the core of the population (Fig. 1C). If we imagine this process occurring every generation as the population expands, the process of spatial assortment for dispersal ability behaves like a runaway evolutionary process, continually selecting for increased rates of dispersal on the advancing front.

Density effects interact with this process of spatial assortment. Indeed, the only process that can counteract the Olympic Village effect is an Allee effect, where low-density populations confer lower survival or reproductive rate on their members (Travis and Dytham 2002). In the absence of such an effect, individuals near the advancing front may actually benefit from a low-density environment (i.e., fewer conspecifics in their vicinity) and, as a consequence, leave more offspring. Those offspring will tend to inherit their parent’s high dispersal rates. Thus, in cases where Allee effects are weak relative to the Olympic Village effect, dispersal rates will evolve upward on the expanding front. Several simulation models now show that spatial selection drives the evolution of increased rates of dispersal. All of these models are spatially explicit, individual-based models, but vary in other aspects (Travis and Dytham 2002, Hughes et al. 2007, Phillips et al. 2008; O. J. Burton, J. M. J. Travis, and B. L. Phillips, unpublished manuscript).
Dispersal, however, is only one of the two factors determining the rate of range expansion; the other is the rate of population growth. Increases in the rate of population growth also will accelerate invasion (Holt et al. 2005). As we will explain, we expect evolution to lead to increases in the rate of population growth on the expanding population front.

**Evolution of Traits Increasing Population Growth Rate**

*Density dependence, density independence, and the r–K selection spectrum*

It is a venerable result of life-history theory that, in exponentially growing populations (such as may often be the case at an invasion front), variance in fitness is summarized by variance in individuals’ reproductive rates (MacArthur and Wilson 1967); high reproductive rates are favored in exponentially growing populations. This is simply because individuals that replace themselves more rapidly than others will soon numerically dominate such a population. In contrast, in populations that are density regulated (such as may often be the case at the core of the species’ range), fitness is tied to variance in individuals’ ability to survive and reproduce at high conspecific density (MacArthur and Wilson 1967, Roff 1993); individuals that leave more offspring behind in environments of high conspecific density are favored, so selection maximizes the carrying capacity of the population. For idealized, single life-history stage, discrete-generation organisms (as are found in many ecological and evolutionary models), this notion of changed selection pressures between density-regulated and non-density-regulated populations is encapsulated in the *r–K* selection spectrum.

The application of *r* and *K* selection to real organisms (such as are found in nature) is controversial, however. This controversy has involved the assignation of particular traits to *r*-selected or *K*-selected life histories (Pianka 1970), and the discovery that mortality rates that vary with life-history stage can produce complex selection scenarios that are not adequately explained by the *r–K* spectrum (Reznick et al. 2002). Nonetheless, *r* and *K* selection remains as a powerful theoretical concept (Roff 1993), primarily because it neatly captures the idea that optimal life-history strategies differ between density-regulated and non-density-regulated populations: it is this idea that we refer to in our use of *r* and *K* selection here. The difficulty lies in applying this straightforward theoretical result to complex life histories, where, for example, reproductive rate depends upon survival at different ages, age at first reproduction, number of offspring, variation in number of offspring with age, and age at last reproduction, by claiming that a shift in a single trait, e.g., number of offspring at a given age, accurately measures a shift in reproductive rate. All else being equal, an increase in the number of offspring will increase the reproductive rate, but often (particularly in comparative studies across species) all else is not equal; the number of offspring may increase, but another trait (e.g., survival) may decrease. These practical complexities have seriously muddied the water around the theoretical concept of *r* and *K* selection. Nonetheless, life-history theory clearly shows that optimal life-history strategies differ between density-regulated and non-density-regulated populations. In-
deed, a shift from density-dependent to density-independent regulation on an invasion front, and the selection that follows from this shift, may help to explain the acceleration of species invasions.

By definition, on an expanding population front, the density of conspecifics grades from something near carrying capacity to zero (Fig. 2). One fundamental implication of this density gradient is that individuals on the newly colonized edge of the range probably will experience exponential population growth. Individuals farther back into the core of the range, however, will probably experience density-regulated population growth (Brook and Bradshaw 2006). Thus, an invasion front can be thought of as a steep gradient between $r$-selective and $K$-selective environments. Critically, this shift in environments is experienced within a single species over a relatively narrow cline. Thus, more correctly, invasion front individuals face an $r$-selective environment relative to the individuals within the core of the range. As the population expands through space, the invasion front always represents an environment with low conspecific density and thus consistently provides a place where population growth is unfettered by density regulation. Therefore, even in species with irruptive population dynamics, the front will tend to be more consistently $r$ selective than the range core. On the expanding edge of a population, life-history strategies with high reproductive rates will be favored.

Given that the expanding range edge also must be made up of the best dispersers in the population, we can see that range expansion selects for a population of highly dispersive individuals with high reproductive rates (O. J. Burton, J. M. J. Travis, and B. L. Phillips, unpublished manuscript). If we remember that the rate at which a population expands is a function of dispersal and population growth rate, then we can see that the process of range expansion causes selection on the very traits that drive that expansion. Evolution will cause accelerating range advance.

**Trait Smearing and Empirical Patterns**

Given that the invasion front is the seed for all later populations that arise in the areas it passes over, genotypes on the invasion front will tend to be “smeared” over the landscape (Fisher 1937, Klopfstein et al. 2006, Excoffier and Ray 2008, McInerny et al. 2009). This smearing effect can even lead to maladaptive genes being widespread behind the invasion front (Travis et al. 2007, Burton and Travis 2008). Considerable time may be needed for natural selection to remove maladapted genes following the passing of the invasion front, particularly if there is little or no variation at that locus (in which case mutation or immigration has to boost diversity before selection can operate; Excoffier and Ray 2008). Insofar as they have a genetic basis, phenotypes at the invasion front also will be smeared across the landscape. Evolution occurring on the invasion front thus can leave an ephemeral signature of range advance in the variation of life-history traits across the invasion history (Travis and Dytham 2002, Phillips et al. 2008).

The signature of range advance is ephemeral because natural selection behind the expanding front will act to optimize the phenotype for the new conditions of (local) spatial equilibrium. Thus, trait values that evolve on the expanding front will be less fit, following colonization of an area, than trait values that evolve in the population core. Fitness is, however, relative to local phenotypes, so the rate at which trait values decay back to equilibrium values will depend upon the rate at which mutation and immigration can provide the variance on which selection can act. Nonetheless, some time after the population stops expanding, the signature of range advance will have completely decayed.

Because traits are smeared across the landscape during invasion, comparisons between frontal and successively older populations of an ongoing invasion should yield clines in life-history traits that reflect the differing selective forces operating on the invasion front vs. at spatial equilibrium (behind the front).
LIFE-HISTORY EVOLUTION AND RANGE SHIFT

SELECTION ON TRAITS AFFECTING DISPERSAL AND REPRODUCTIVE RATES

Unless we can measure intergenerational dispersal or the rate of population growth (which is always difficult, and usually impossible), we will be forced to examine these life-history parameters using data on the distributions of phenotypic traits. In such cases (e.g., where we measure wing length as a surrogate for dispersal, or fecundity as a surrogate for reproductive rate), we are forced to assume that all else is equal. This assumption is risky when comparisons are made across species, because such comparisons are muddied by differences in habitat and geographic range as well as greater time to a common ancestor, so major restructuring of life history is possible. The “all else is equal assumption” is, however, presumably less risky within a single species and over the short timescales within which evolution can act on life-history traits during an invasion. With these caveats, we now turn to empirical observations of shifts in traits associated with dispersal and reproductive rates during range expansion.

Traits associated with dispersal

Empirical results demonstrating evolved increase in dispersal on expanding range fronts are beginning to accumulate. The process of spatial assortment by dispersal ability is nicely illustrated by Glanville fritillary butterflies on the Åland islands, where recently colonized environments are dominated by highly dispersive individuals (Hanski et al. 2002, 2004). Spatial assortment by dispersal ability also occurs in Australian cane toads, where the first individuals to colonize an area tend to be the individuals with the longest legs (and thus, the greatest dispersal ability; Phillips et al. 2006). Under spatial selection, we expect evolved shifts in dispersal across a species’ invasive range. Increasingly, such shifts are being documented. In North America, for example, lodgepole pines expanded their range northward following the last glaciation; the northernmost populations are less than 100 years old. Recently colonized populations have lighter seeds with a larger wing size:seed mass ratio, indicating increased dispersal ability on the invasion front (Cwynar and MacDonald 1987). In Australia, cane toads on an accelerating invasion front show similarly clear evidence of increased dispersal ability, via changes in morphology (leg length) as well as behavior (frontal toads move more often, move farther when they do move, and follow straighter paths: (Phillips et al. 2006, 2008, Alford et al. 2009). In Britain, crickets expanding their range show evolved increases in wing length and flight stamina on the expanding front (Simmons and Thomas 2004). Also in Britain, butterflies expanding northward because of climate change exhibit evolved shifts toward larger wings and flight muscles (Hughes et al. 2007). As we look further into the possibility of rapid evolution of dispersal-relevant traits during range advance, many more examples are likely to emerge.

Traits associated with reproductive rate

Reproductive rate will be increased by an increase in fecundity or a decrease in the age at first reproduction (Cole 1954, Lewontin 1965). In perennial species, reproductive rate also can be increased by a lengthening of the reproductive period, or by a decrease in the peak reproductive age, although a decrease in the age at first reproduction remains the most efficient way of increasing the reproductive rate (Lewontin 1965). Generally though, having more offspring, and/or having them earlier (if all else remains the same) will increase the individual’s reproductive rate. Intriguingly, these life-history traits often differ between native populations and invasive populations within a single species (“home-and-away comparisons”). In pine trees (genus Pinus), for example, invasive populations have shorter generation times and smaller (more dispersive) seeds (Rejmánek and Richardson 1996). In a common garden, purple loosestrife from its invasive range in North America grows more rapidly (and so presumably reaches maturity earlier) than does purple loosestrife from its native range (Blossey and Notzold 1995). In fact, with a few notable exceptions (Willis et al. 2000, van Kleunen and Schmid 2003, Maron et al. 2004), plants from invaded areas tend to grow faster, grow larger, and/or set more seed, than do conspecifics from the native range (Keane and Crawley 2002, Bossdorf et al. 2005, Colautti et al. 2006).

Such patterns often have been interpreted in the light of the “enemy release” hypothesis; that is, invaders escape their coevolved enemies (e.g., predators, parasites), and so can invest more into growth and reproduction instead of defense. Although “enemy release” is usually attributed to accidents of transport and introduction to new lands (often, an invader’s natural enemies are not transported with it), non-equilibrial models suggest that the same phenomenon can also arise within the invaded range as an outcome of rapid range expansion. Similarly, many of the differences observed between populations in native vs. invaded ranges may have evolved in the invaded range during the process of range expansion, rather than reflecting the nonrandom nature of successful establishment (“propagule bias,” Colautti et al. 2006, Blackburn et al. 2009), or evolution occurring at spatial equilibrium (Blossey and Notzold 1995). In support of this possibility, several recent studies have reported evolved shifts in life history within the invaded range. For example, when grown in a common garden, Chinese tallow trees from their invaded range grow faster and mature earlier than do those from their native range. That pattern is potentially consistent with enemy release (optimality) or propagule bias. Within their invaded range, however, tallow trees from recently colonized areas also grow faster and mature earlier in a common garden than do trees from older populations in the invaded range (Siemann and Rogers 2001). That second pattern cannot be attributed to propagule bias, and
instead must reflect processes at work in the invaded range; presumably, evolution occurring on the invasion front. Similarly, in their invasive Australian range, cane toads from recently colonized areas grow faster than do toads from older, long-established populations, even when raised under identical conditions (Phillips 2009). Glanville Fritillaries in recently colonized environments tend not only to be highly dispersive, but also to invest more in reproduction (Hanski et al. 2006, Saastamoinen 2007). Few studies to date have looked for such changes in life history traits of introduced species across their invasive range (Gaston 2009). We expect a rapid increase in such studies, and hence in insights into this process, in the years ahead. Importantly, such studies will need to pay careful attention to the invasion history of the organism in its invaded range. It may be that many of the exceptions (species that do not show a shift in life history in home-and-away comparisons) may, given our new understanding, simply reflect samples taken from an inappropriate part of the invaded range.

**TRADE-OFFS**

Both models and data suggest that, during continuous range expansion, selection drives the evolution of increased dispersal and reproductive rate. Whether or not individuals in invasive populations can evolve to become more highly dispersive, rapidly growing, and highly fecund (relative to conspecifics in older populations) depends on the nature of trade-offs between traits (O. J. Burton, J. M. J. Travis, and B. L. Phillips, unpublished manuscript). If dispersal trades off directly against the traits determining reproductive rates (as it does in many theoretical models to date), then both of these attributes cannot increase at the same time. Given the complexity of dispersal and reproductive rate, however, it seems unlikely that these two attributes directly trade off against each other. The complex phenotypic determinants of dispersal and reproductive rate provide many selective targets, generating a vast number of possible trade-off relationships. As a simple example, if dispersal is determined entirely by three traits (e.g., seed mass, wing size, and release height), and reproductive rate is determined entirely by three traits (e.g., growth rate, size at maturity, and seed number), then there are nine possible trade-offs between traits determining dispersal and population growth. What are the chances that all of these trade-offs are negative? If some of them are neutral, or even positive (e.g., perhaps there is no relationship between seed mass and size at maturity), then both dispersal and reproductive rates may increase simultaneously under the selective forces experienced at the expanding range edge.

Alternatively, dispersal and reproductive traits may trade off against other traits unrelated to dispersal and reproduction. In particular, dispersal and reproductive rates may trade off against traits that are important in equilibrium populations; traits that increase fitness in times and places of high conspecific density. In such a case, traits associated with dispersal and reproduction may be able to increase at the expense of traits that are not tied to fitness in the invasion vanguard (e.g., traits associated with defense against enemies).

**ESCAPE FROM ENEMIES DURING INVASION**

Introduced species often have fewer parasites and pathogens in their invasive range than in their native range (Mitchell and Power 2003, Torchin et al. 2003, Perkins et al. 2008). This phenomenon is driven primarily by founder events: typically only a few individuals are transported to the introduced range and these few individuals are, by chance, unlikely to harbor all the parasites and pathogens that attack the species in its native range. Thus, as a general rule, individual invaders will need to invest less in defenses against natural, coevolved enemies than had been true in their native range (Muller-Scharer et al. 2004). This well-understood pattern is often invoked to explain the success of invasive species (Blossey and Notzold 1995, Keane and Crawley 2002, Colautti et al. 2004). Less appreciated, however, is the ongoing nature of the founder effect leading to escape from enemies. Following colonization, as a population expands through space, the vanguard population undergoes a founder event every generation (few individuals make up the expanding edge; Klopfstein et al. 2006). Thus, in each generation, as the population expands, there is a high probability that parasites and pathogens will not be present on the invasion front (Fig. 2, unless parasites disperse independently from, and farther than, their hosts; Hilker et al. 2005). When parasite transmission is density dependent, this serial founder effect is compounded by low transmission rates at low host densities on the invasion front. Thus, over multiple generations of expansion, even high-prevalence pathogens and parasites will be left behind (Phillips et al. 2010). Thus, invasive species not only start with fewer coevolved enemies, but also, once range advance begins, on the expanding front they may lose even the few coevolved parasites that they brought with them from the native range. Similarly, native species spreading their range through climatic shift may lose their coevolved enemies on the expanding population front.

The recently discovered phenomenon of ongoing enemy escape during invasion has now been demonstrated in two different spatially explicit models (Moorcroft et al. 2006, Phillips et al. 2010). Recently the effect has been empirically demonstrated in butterflies expanding northward due to climate change in Britain (Menendez et al. 2008), and in introduced cane toads in Australia (Phillips et al. 2010). In these cases, parasite richness and/or prevalence was lower on the expanding front.

Invasive populations do eventually accumulate enemies in their introduced range (e.g., Carroll and Boyd 1992, Perkins et al. 2008). Sometimes these enemies make instantaneous shifts to the invasive species, but
more often some time elapses before enemies can host-switch effectively. Given this common lag time in host switching, vanguard populations of invaders also may be relatively free of non-coevolved enemies. Vanguard populations may have arrived so recently that local enemies have had no time to effect host-switching. Thus, on the invasion front, an invader will only experience impact from the most generalist of enemies: those that can host-switch instantaneously. One clear implication of these patterns is that, on an expanding population front, resources normally invested in defense against coevolved or specialized enemies can now be redirected to dispersal and reproduction.

The Evolution of Defenses Against Enemies

If vanguard populations of a range-expanding species are free of coevolved and specialized enemies, and are under strong selection for increased rates of dispersal and reproduction, we expect to see evolved shifts in defenses against enemies. General defenses will still be important, as the invader will encounter generalist enemies as it invades new areas (Muller-Scharer et al. 2004). In contrast, specific defenses (those tailored to deal with coevolved and specialized enemies) will no longer be under strong maximizing selection. Thus, evolved shifts in defenses may occur as a consequence of trade-offs between defense capacity vs. traits associated with dispersal and reproduction. Strong directional selection on dispersal and reproductive rates may create strong directional selection against enemy defenses if any trade-offs exist, and the release from coevolved enemies in the population vanguard allows lowered investment in these defenses to evolve.

Dispersal and reproductive rates are complex traits, and the same can be said of traits associated with defense against enemies. In motile animals, these defenses will be manifest as predator avoidance/escape strategies (Edmunds 1974), and in the immune system. In plants and sessile animals, these defenses will be manifest as physical and chemical defenses. Very few studies examine shifts in these traits within the invasive range, but numerous studies have examined shifts in defenses between native and invasive ranges (home-and-away comparisons). Although these studies are often unclear about exactly where invasive range samples came from in relation to the spread history, we note that, more often than not, these studies find changed investment in defenses in the invaded range (Keane and Crawley 2002, Lee and Klasing 2004). Again, we point out that these changes can occur during range expansion and be left behind as an ephemeral signature of that range expansion. Evolutionary change occurring as a consequence of mechanisms acting in equilibrium populations (i.e., natural selection at spatial equilibrium) is then overlaid on this trait landscape. Thus, differences between invaded and native ranges occur first as a consequence of founder and establishment biases (“propagule bias”: introduced populations are not a random sample of the native population Colautti et al. 2006, Blackburn et al. 2009), second as a consequence of range advance (evolution in nonequilibrium populations), and then last as a consequence of standard evolutionary processes (at spatial equilibrium). Differences between native and invaded ranges can be due to any one or all of these processes, so such comparisons necessarily are fraught with ambiguity. Nonetheless, these home-and-away studies make up the bulk of our information to date. What changes in defense do we observe between native and introduced ranges?

Plants

We can arbitrarily divide plant chemical defenses into two categories: quantitative and qualitative (Stamp 2003). This division is artificial and will not capture the full variation in plant defenses, but is a useful didactic distinction. Qualitative defenses are toxins (e.g., alkaloids and glycosides); they tend to be cheap to produce and effective against broad suites of enemies (Muller-Scharer et al. 2004). Qualitative toxins tend to be less effective against specialized, coevolved, enemies (which can evolve numerous coping mechanisms, and may even use the qualitative toxins to identify their host; Muller-Scharer et al. 2004). The other major type of plant chemical defenses, quantitative defenses, act by decreasing the plant’s nutritional value: either by decreasing digestibility (e.g., via high lignin content), or nutrient availability (e.g., via high tannin content; Stamp 2003). As a gross generalization, quantitative defenses are costly, because they are composed of large molecules that need to be at high concentrations to be effective (Stamp 2003). Similarly, quantitative toxins tend to be constitutive defenses (i.e., they are always present), whereas qualitative defenses can be either constitutive or inducible following attack (Strauss et al. 2002). Quantitative defenses are useful against specialist herbivores because they constrain the nutrient uptake (and thus growth and reproduction) of the herbivore. Thus, as a plant expands its range and leaves specialist enemies behind, we expect to see decreased quantitative defenses, and may or may not see increased qualitative defense (Muller-Scharer et al. 2004, Lankau 2007). We may also expect a shift toward inducible defenses (which elicit costs only after being induced), as opposed to constitutive defenses (which incur a constant cost).

Presumably, all defenses are costly, although these costs may range from undetectably small to quite obvious, depending on the defensive trait being examined. Importantly, these costs are often expressed via direct trade-offs with growth and reproduction (Strauss et al. 2006). Thus, on the expanding range edge of range-shifting plants, we might expect evolved increases in dispersal and reproductive rates, which, in turn, drive decreases in costly defenses (usually quantitative defenses directed against specialist enemies). Lowered quantitative defenses, in turn, may encourage greater investment in less costly, inducible defenses (usually
qualitative defenses, to maintain protection against generalist enemies). Empirical results comparing invasive and native populations support this idea (Müller-Scharer et al. 2004). First, plants from invasive populations often show higher growth rates than plants from the native range (Keane and Crawley 2002, Joshi and Vrieling 2005). Second, these higher growth rates often are associated with reduced quantitative defenses (Siemann and Rogers 2001, Müller-Scharer et al. 2004). Last, plants from introduced populations tend to be better adapted to generalist herbivores than are those from native populations (Schierenbeck et al. 1994, Joshi and Vrieling 2005, Engelkes et al. 2008, Cano et al. 2009). Unfortunately, to our knowledge, there are no studies examining defensive traits across an invasive range. Given that defensive traits are likely to evolve during range advance, this is a serious gap in our understanding of the evolutionary dynamics of range shift.

**Animals**

Animals can exhibit behavioral or morphological adaptations to avoid or escape enemies, and these traits are likely to be under selection during range advance. Because these traits vary from species to species, we confine ourselves to discussion of a defense trait common to most animals: the immune system. The immune system is somewhat more complex than plant defenses, but some parallels can be found. Lee and Klasing (2004) suggest that when animals are confronted with fewer, less specialized enemies, costly innate immune defenses (i.e., systemic inflammation) should be down-regulated. This rapid-response immune defense is not necessary, they argue, when facing attack by a non-coevolved pathogen, and may, in fact, cause damaging overreaction to a pathogen that is incapable of infecting its novel host anyway. When facing non-coevolved pathogens, a heightened humoral response (i.e., that driven primarily by antibodies) may be adequate. Humoral responses are slower but (they argue) less costly, and can “remember” pathogens (such that a repeat exposure will generate a more rapid response). Therefore, Lee and Klasing (2004) suggest that species with a low systemic inflammatory response but a high humoral response will make better invaders. Invertebrates (which lack humoral immunity) can become better invaders simply by down-regulating their innate responses.

As with our discussion of plant defenses, these generalities are a gross simplification of reality. Indeed, the distinction between innate and humoral immunity is somewhat artificial (much like the distinction between quantitative and qualitative defenses in plants), but remains a useful didactic device (Murphy et al. 2008). Additionally, the costs of the immune system are poorly understood. For example, it could equally be argued that maintenance and activation of the humoral system is costly (massive cell proliferation and maintenance), and that innate responses (although costly when activated) are cheaper, in the long term, than humoral immunity, particularly when serious immune challenges are rare. Given that humoral immunity is also mediated by the innate arm of the immune system, and that humoral immunity is the derived state, presumably having evolved to deal with an increased evolutionary discrepancy between long-lived organisms and their short-lived pathogens, an argument could be mounted for the down-regulation of humoral immunity in response to life-history evolution and enemy release during range expansion. Similarly, innate immunity might be sufficient to deal with nonspecialist enemies (although systemic inflammation would still be costly, and may be down-regulated independently of the rest of the innate system), reducing selection for the maintenance of humoral immunity in vanguard populations. These predictions are in partial opposition to those of Lee and Klasing (2004).

Although improving steadily, our understanding of plant and animal defenses and their various costs (as measured by trade-offs with dispersal and reproductive rate) is poor. Hence, it is difficult to predict the evolution of defensive traits during range expansion. Nonetheless, when taken on a case-by-case basis, we expect negative selection on an expanding population edge against defensive traits that carry reproductive or dispersal costs, and that are tailored toward specialist enemies. To our knowledge, no studies have compared aspects of the immune system over the course of an invasion. However, Möller and Cassey (2004) show an increase in T-cell-mediated immunity associated with invasion success in birds, and Lee et al. (2005) show lowered inflammatory response in an invasive species when compared with a noninvasive congener. Martin et al. (2007) show that immune systems are geared toward low-cost generic defenses in short-lived, high-growth species of *Peromyscus* mouse more than in long-lived, slow-growing congeners. Given the clear importance of shifts in the immune system for understanding the process of biological control, as well as the long-term outcomes of range shift on native species shifting their range through climate change, this avenue of study merits further investigation.

**Conclusion**

One clear implication from our emerging understanding of evolution on expanding range edges is that we need to be very careful about how we design studies investigating the evolution of invasive species. Many studies have compared traits between native and invaded ranges (home-and-away comparisons), but patterns at this level are a consequence of three evolutionary phases.

First, the introduction and establishment phase will determine the genotypes available in the invaded range (Blackburn et al. 2009). Where multiple introductions occur, a hybrid population with heightened genetic
diversity may be the starting point (Kolbe et al. 2004). Alternatively, if there is a single introduction, lowered genetic diversity may be the starting point. In either case, the founder event of introduction and the demographic process of establishment means that the genotypes and phenotypes available in the introduced range are unlikely to be representative of those in the invaded range (Blackburn and Duncan 2001, Simons 2003, Colautti et al. 2006, Blackburn et al. 2009). Thus, differences between invaded and native ranges can emerge instantaneously at this juncture.

The second evolutionary phase, spatial disequilibrium, occurs following introduction, during range expansion. This is the phase we have talked about extensively in this paper, defined by two processes: spatial assortment by dispersal ability and lowered conspecific density on the invasion front. These two unavoidable consequences of range expansion lead to predictable evolutionary pressures in the vanguard population, and this vanguard population smears these evolved traits across the landscape, leaving an ephemeral signature of range expansion in the organism’s traits across its invasive range.

The last evolutionary phase occurring in species introductions is that with which we are most familiar: evolution by natural selection in populations at spatial equilibrium. Many of the studies documenting shifts in life history in invasive species have made evolutionary arguments based on evolution at spatial equilibrium. For example, the “evolution of increased competitive ability” hypothesis argues that invasive species will have fewer enemies in their introduced range, so the balance of any trade-off between competitive ability and defense will be tipped in favor of competitive ability (Blossey and Notzold 1995). This may be true, but if the species becomes invasive and spreads its range following introduction, the process of range expansion drives selection for increased reproductive rate on the invasion front, and this process will leave an ephemeral signature through the invasive population. Rates of population growth and dispersal are likely to be highest on the expanding edge of the invasive range and lowest at the core. Ideally, we should not attempt to test equilibrium hypotheses without first understanding the effect of nonequilibrium dynamics on the traits we are examining. Comparison of life-history traits between invasive and native populations (“home-and-away”) is a common research design, but rarely is attention paid to the location of the samples within the invasive range. We suggest that an understanding of variation within the invasive range is critical before sensible comparisons can be made with the native range.

In species that are shifting (or that have recently shifted) their range as a consequence of climate change, we expect to see two distinct evolutionary phases (rather than the three of invasive species): spatial disequilibrium, followed by spatial equilibrium. In 1987, Cwynar and MacDonald showed that lodgepole pines expanding northward since the last glaciation showed clear patterns associated with evolution under spatial disequilibrium. At the recently expanding population edge, seed morphology indicated heightened dispersal rates relative to trees from older populations. If we were not aware that this species had recently shifted its range, we may have come up with an (erroneous) explanation for this pattern based on evolution at spatial equilibrium. This example shows the critical importance of understanding population history before investigating the evolution of life-history traits using population comparisons.

An interesting outcome of evolution on expanding range edges is that life-history traits on expanding range edges are selected toward values that increase the rate of spread. Thus, lags in spread rate and accelerated spread (different sides of the same coin) are explicable through rapid evolution. Evolutionarily accelerated range shift may be the most appropriate null expectation, rather than constant rates of range expansion. Models of range spread that do not incorporate evolved shifts in life history are simpler, but must be carefully parameterized to give accelerated spread, and do not generate the many testable hypotheses emerging from the framework that we present here. In particular, our prediction that both dispersal and traits associated with reproductive rate are maximized during range advance begs the obvious question of trade-offs and thus suggests selective forces behind the evolution of defense mechanisms in range-shifting taxa. Previous hypotheses erected to explain shifts in life history between invaded and native ranges focus purely on equilibrium theory, and so cannot point to selective forces driving these shifts; instead, they rely on optimality arguments.

Evolution on expanding range edges is only now being understood as a potent force in the evolution of life histories. Hence, there is massive scope for empirical and theoretical work to investigate this process. Although we can make reasonably clear predictions about the shifts in life history that should occur during range expansion, the interaction between these selective processes and the effects of serial foundering and Allee effects will be a challenging future problem. Acknowledging the critical role of rapid life-history evolution during range shift not only will clarify observed empirical patterns (such as shifts in life history between invaded and native ranges), but also will clarify the process of range expansion. At a time of high concern over invasive species and the biodiversity impacts of climate change, a focus on the evolution of life histories during range advance may have important outcomes.

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