

In hybrid populations, genes from barred salamanders had the greatest representation in permanent bodies of water like cattle ponds and were less frequent in *vernal pools*, the natural habitat of California tiger salamanders. Human habitat modification (creation of numerous permanent bodies of water in grassland habitats) may be promoting the fitness of hybrids. To date, we do not know whether hybridization compromises the ability of native salamanders to persist in ephemeral vernal pools.

CAN EVOLUTION BY NATIVES PROVIDE RESILIENCE FOR INVADED NATIVE COMMUNITIES?

While many introduced species appear to have few dramatic effects, some pathological invasions clearly have huge impacts on ecosystem function and the persistence of natives. The ability of natives to evolve to lessen those impacts is important to conservation strategies. Adaptations such as the reduced gape size in snakes described above or resistance to introduced pathogens may allow native populations to persist and may even eventually compensate for the adverse effects of invaders. The native Amakihi bird in Hawai'i was forced to retreat to higher-altitude forests after the invasion of avian malaria; as resistance to malaria has evolved in Amakihi populations, they have been able to recolonize some lower-elevation forests.

Much of the ability to adapt will depend on extant genetic variation, population size, gene flow, and mutation rates. Conservation strategies that preserve genetic variation in native populations by conserving large populations and promoting gene flow in increasingly fragmented landscapes may provide genetic variation on which selection can act to ameliorate negative impacts of invaders.

SEE ALSO THE FOLLOWING ARTICLES

Climate Change / Evolution of Invasive Populations / Hybridization and Introgression / Lag Times

FURTHER READING

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EVOLUTION OF INVASIVE POPULATIONS

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Evolutionary mechanisms that operate at multiple stages of invasions (e.g., transport, introduction, establishment) could profoundly affect the invasive success of populations. Evolution within the native range shapes the intrinsic properties of populations (e.g., plasticity, evolvability) in a manner that would dictate their response to novel environments. Confronted with a sudden introduction into a novel range, a rapid evolutionary response is often essential for survival. Continued selection might be necessary following establishment, as traits that are beneficial during early stages of colonization would often differ from those that favor continued range expansion or long-term persistence. While much progress has been made in characterizing the process of evolution during invasions, more study is needed to understand the evolutionary forces that lead to populations with a greater propensity to invade.

BACKGROUND

Invasive populations experience abrupt and often dramatic ecological shifts on contemporary time scales, allowing observation of ongoing evolutionary changes in wild populations. In contrast to natural range expansions, which typically involve incremental geographic shifts, invasive populations are frequently transported across vast geographical distances that can span continents. These invasions often entail movement into novel habitats, at times with acute changes in abiotic (e.g., temperature, salinity) and biotic (e.g., competitors, predators, food) conditions. Thus, it is unsurprising that only a tiny fraction of introduced species become successful as invaders.

The evolution of invasive populations was first raised as a focal point of discussion by C.H. Waddington through a 1964 symposium, which resulted in the classic volume *The Genetics of Colonizing Species*, edited by Baker

and Stebbins (1965). Waddington argued that recent and sudden transplantation of invasive species make them valuable models for studying constraints on adaptive evolution. He was interested in understanding limits to selection response and constraints on rapid phenotypic evolution, particularly in populations under acute stress, and the genetic consequences that would result. Waddington was also concerned with how phenotypic plasticity and natural selection might interact to produce an evolutionary response. For instance, environmental stress might induce a plastic response where an extreme phenotype is expressed. This extreme phenotype could then be subjected to selection and become fixed in the population. Waddington argued that the prevalence of this process, which he termed genetic assimilation, could be tested in the wild using invasive populations.

After a multi-decadal hiatus, interest in the evolution of invasive populations resurged in the 1990s. The advent of polymerase chain reaction (PCR) and advances in DNA sequencing allowed the proliferation of phylogeographic studies that reconstructed geographic pathways and evolutionary histories of invasions. Concurrently, application of quantitative genetic approaches uncovered patterns of phenotypic evolution associated with invasion events. At present, a few research programs are probing specific genetic mechanisms underlying adaptive evolution during invasions (see next sections). Epigenetic changes might play an important role in facilitating invasions, but explorations of such mechanisms are only in their infancy.

Although many questions raised by Waddington have remained largely unresolved and are current topics of active research, it has become widely recognized that evolutionary processes and genetic attributes of invasive populations can be important for their success in becoming established in a novel range. While extrinsic factors (e.g., transport vectors, dispersal barriers, resources, enemies) impose challenges and opportunities for invading populations, intrinsic properties of the organisms and populations dictate their response to the extrinsic factors, through mechanisms such as phenotypic plasticity or evolutionary adaptation.

Invasions are dynamic processes, with multiple stages of progression (i.e., transport, introduction, establishment, spread, stabilization, etc.) at which evolutionary mechanisms could impact invasive success. Prior to invasions, evolutionary forces within the native range could select for properties that make some populations more likely to invade than others, or more likely to invade specific habitat types. During the early stages of

colonization, selection could act on traits that promote dispersal or enable survival in the invaded range. In addition, demographic processes might result in population bottlenecks or admixture during invasions, affecting the nature of genetic variance available for selection in the invading population. Following establishment, selection might act on traits that influence ongoing range expansion and long-term persistence in the novel range. Alternatively, evolution might occur as a mere byproduct of relaxed selection in the invaded range, due to removal of selective forces that were formerly important in the native range, or from changes in evolutionary tradeoffs in the novel range. Some evolutionary mechanisms that are important at various stages of the invasion process are described briefly below, although these mechanisms might not operate exclusively at any given stage.

EVOLUTION WITHIN THE NATIVE RANGE

The evolutionary history of populations within their native ranges would influence their capacity and propensity to become invasive. Selection regimes in the native range would mold the response of populations to novel conditions, as selective forces would determine levels of plasticity, physiological tolerance, genetic variation, and other intrinsic properties of the population. For example, fluctuating selection might lead to the evolution of generalist strategies (e.g., broad tolerance or plasticity) or to enhanced evolvability, depending on the period of fluctuations relative to generation time. Nonselective evolutionary forces might also be important, as demographic processes in the native range, such as population bottlenecks and population expansions, could affect levels of genetic variation across the genome.

Invasive species commonly span a broad array of habitats within their native ranges, such that populations are exposed to a diversity of selection regimes. Such diverse selection regimes would lead to the evolution of populations that vary in their intrinsic capacities to invade. Phylogeographic studies are revealing a great deal of population genetic structure and large genetic divergences among invasive populations across their native ranges. Indeed, such studies are increasingly showing that certain populations might be more able to invade habitat boundaries than others, and that these populations tend to arise from particular lineages or from particular habitat types within their native ranges. For example, two genetically distinct clades of the copepod *Eurytemora affinis* cooccur in the St. Lawrence estuarine system, but populations from only one of the clades have invaded freshwater

habitats, while the other clade has remained restricted to its native distribution.

Conditions in the native range would preadapt populations for similar habitat types in the invaded range, such that the invasion between similar habitats would essentially be that of habitat matching. In such cases where niche evolution is absent during invasions, the geographic distribution in the native range could be used to predict the potential range of an invasive species in its invaded range. However, accurate prediction requires information on the fundamental niche of an invasive species, which encompasses the full range of environmental conditions (biotic and abiotic) that the organism could inhabit. But most current methods of niche modeling capture the realized niche, which includes only the range where organisms are actually found. Environmental factors, such as competition and predation, could limit species distribution in the native range, such that the realized niche is smaller than the fundamental niche. Thus, species might have broader tolerances than those reflected in their native distribution, and the limits of such distribution data would hinder the predictive power of niche modeling.

Lineages that arose in certain environments would be preadapted to invading the conditions in which they evolved. For example, the plant family Poaceae (i.e., grasses) is overrepresented as both agricultural weeds and natural area invaders, relative to what would be expected based on estimated rates of introduction. Climate change of the mid-Miocene (approximately 6–8.5 million years ago) toward drier conditions led to the diversification of Poaceae and the prevalence of grass-dominated ecosystems. An evolutionary history in savannah environments is likely to have preadapted members of Poaceae to colonize human-impacted and deforested environments, as grasses tend to thrive under denuded, desiccated, and disturbed conditions. For instance, wind pollination by grasses (such that they do not depend on insect pollinators in the novel range) is a feature that aids in colonizing new and disturbed environments.

Populations that experience human-altered environments (e.g., agricultural fields, reservoirs, pavement) in their native range could become preadapted for invading similar habitats. For example, the corn root worm *Diabrotica virgifera virgifera* is adapted to infesting cultivated maize and has evolved resistance to a wide variety of insecticides and cultural control practices such as crop rotation. Some agricultural weeds have evolved crop mimicry to evade eradication. A striking example is the barnyard grass *Echinochloa crus-galli* var. *oryzicola*, which

resembles rice when hand-weeding (and morphological identification) is used for control. Reservoirs appear to provide havens for many aquatic invaders, as they possess properties that would tend to inhibit native freshwater species, such as high ionic load, eutrophic conditions, and high levels of disturbance. As the planet becomes increasingly blanketed by such human-impacted environments, effectively homogenizing habitats throughout the globe, invasive populations will increasingly adapt to such conditions.

More generally, it has been hypothesized by Di Castri (1989) and others that habitats characterized by disturbance or fluctuating conditions would tend to promote the evolution of populations that have a greater capacity to invade novel environments. Empirical observations appear to support this hypothesis. For example, brackish-water habitats that lie at the interface between marine water and freshwater typically exhibit fluctuating conditions across multiple spatial and temporal scales. Such brackish-water habitats have disproportionately given rise to invasive populations, including those that invade freshwater. In particular, the brackish Black and Caspian Sea basin has spawned many species invading freshwater habitats of Europe and North America. Such species include zebra mussels, quagga mussels, the fishhook waterflea *Cercopagis pengoi*, and many gammarid amphipods, such as *Corophium curvispinum*. An evolutionary history of fluctuating conditions in the Black and Caspian Sea basin has likely selected for lineages that have a tendency to become invasive. In another example, a variety of ant species invading North America from South America, such as the Argentine ant *Linepithema humile* and the fire ant *Solenopsis invicta*, show high levels of genetic differentiation across their native ranges. However, invasive populations appear to have originated from only a subset of their native range, from regions characterized by large-scale disturbances in the form of regular flooding. Whether the observed bias in sources of invasions is indeed due to the selection regime of the native habitat, or alternatively to the availability of transport vectors, warrants further investigation.

Habitats prone to disturbance or fluctuating conditions might promote the evolution of traits that confer invasive success. Theoretical studies indicate that fluctuating conditions might lead to the evolution of two distinct types of attributes that could increase the potential of populations to invade novel habitats. In environments where fluctuations are very rapid, occurring within an organism's lifespan, generalist strategies that allow the organisms to grow and persist under disturbed conditions are likely to

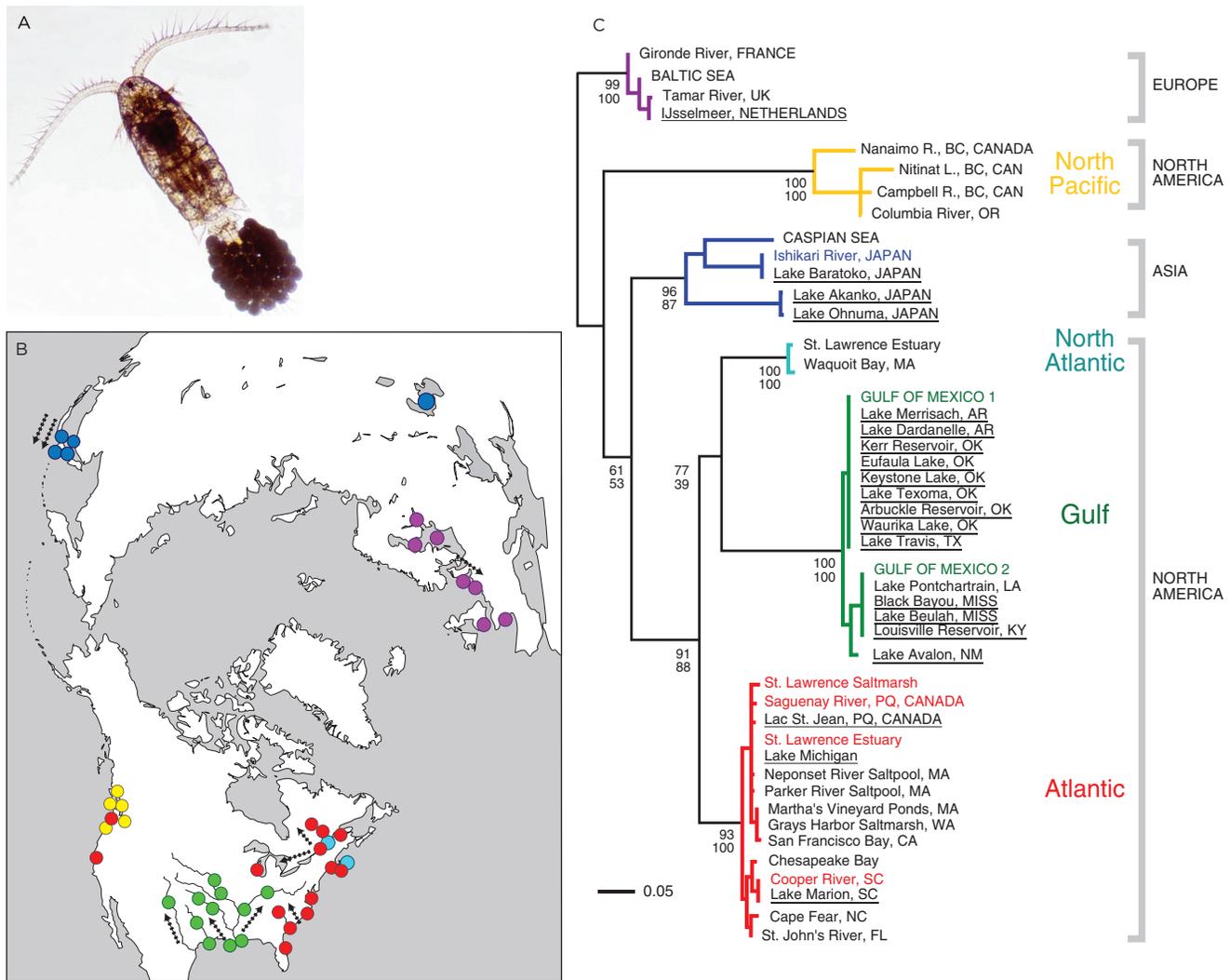


FIGURE 1 (A) The invasive copepod *Eurytemora affinis*. (Photograph by the author). (B) Geographic pathways of invasions (arrows) by the copepod *E. affinis* from saline sources into freshwater habitats, revealed using a phylogeographic analysis. (C) Phylogeny of *E. affinis* populations, showing saline source (colored) and freshwater invading populations (underlined). Many of the invaded freshwater sites are recently constructed reservoirs. Phylogeny used consensus sequences of haplotypes for each population. The invasions occurred primarily within the past 70 years or so, through human-mediated transport.

evolve. Generalist strategies might include life history and demographic traits that facilitate escape from harsh conditions or promote rapid population growth, broad tolerance, or phenotypic plasticity. Alternatively, environmental fluctuations over a slightly longer time scale, across a few generations, might select for increased evolvability, resulting in organisms with increased capacity to adapt rapidly to changing conditions. Theoretical models and empirical studies indicate that temporally fluctuating selection across generations could act to promote evolvability by increasing the propensity to produce adaptive variants (i.e., by increasing mutational variability or the recombination rate), or by promoting the maintenance of standing genetic variance for quantitative traits in a population.

Hypotheses on the role of disturbance or fluctuating conditions in promoting the evolution of invasive populations require further testing. In order to make definitive inferences, future studies would need to compare the invasive success of multiple populations from lineages that originate from fluctuating versus more constant habitats, preferably within a phylogenetic context. In general, studying the evolutionary history of invasive populations in their native ranges would provide insights into conditions that lead to the propensity to invade. The evolutionary history in the native range would dictate the types of habitats that populations could colonize without requiring niche evolution, while simultaneously influencing the capacity of these populations to extend their ranges into novel habitats.

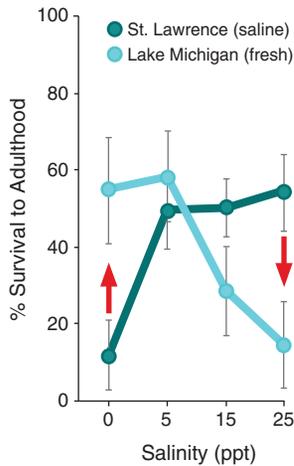


FIGURE 2 Evolutionary shifts in salinity tolerance following invasions. Common-garden experiments revealed heritable shifts in salinity tolerance between saline ancestral (St. Lawrence) and freshwater invading (Lake Michigan) populations (Fig. 1, Atlantic clade). Graph shows percentage (%) survival to adulthood \pm SE for eight full-sib clutches split across four salinities.

EVOLUTION DURING INITIAL STAGES OF INVASIONS

When a population is confronted with a sudden introduction into a novel range, a rapid evolutionary response is often essential for survival. Empirical studies are showing that evolutionary changes during the process of invasions can be extremely rapid. Transport to a new location itself could select for survival during transit, while range expansion in the invaded range could select for dispersal capacity. Challenges imposed by biotic and abiotic factors in the novel range could induce rapid phenotypic evolution to enable survival in new niches in the invaded range.

A number of empirical studies demonstrate rapid phenotypic evolution in response to acute environmental shifts during invasions. For example, many species have invaded the North American Great Lakes from more saline habitats. In the case of the copepod *Eurytemora affinis* (Fig. 1), invasions from estuaries into the Great Lakes and other freshwater habitats have been accompanied by increases in freshwater tolerance and evolutionary shifts in ion regulatory functions (Fig. 2). In another case, the Eurasian barnyard grass *Echinochloa crus-galli* (Poaceae) recently extended its range into colder climates (Quebec, Canada) from southern regions of North America. This grass has a C₄ photosynthetic system, which confines this and many other species to warmer geographical regions. Relative to the southern population, the northern population has elevated specific activity for several oxygen-scavenging enzymes and greater catalytic efficiency for one enzyme tested. Also, plants often show latitudinal clines in flowering time to modulate the length of their growing season. For instance, evolution of reproductive timing, toward earlier flowering time, was critical for northern range expansion by the North American annual cocklebur (*Xanthium strumarium*, Asteraceae).

Adequate genetic variation within a population is necessary for adaptive evolution to occur. Given the rapid time scale of invasions, selection on standing genetic variation is likely to be more prevalent than selection from new mutations. Theoretical studies suggest that when populations move into a new niche, early stages of adaptation might rely more on selection on standing variation from the source habitat than on new mutations in the new “sink” habitat. Fluctuating environments in the native range could provide the conditions under which standing genetic variation would be available for selection in the source population (see previous section).

Invasions from multiple sources are resulting in the unprecedented mixing of genetically distinct populations, providing additional sources of genetic variation. For example, admixture among populations from multiple independent invasions of the brown Anole lizard (*Anolis sagrei*) in Florida has resulted in invasive populations with increased genetic variation. Hybridization is also occurring between invasive and native species, and between invasive and agricultural crop species, including genetically modified organisms (GMOs). Recombination among multiple invading populations or species could result in increased genetic variance, generation of novel phenotypes, transgressive segregation, and reduction in genetic load. Hybridization between different species, such as allopolyploid hybridization, leads to alterations in genomic architecture and also results in fixed heterosis in cases where populations can no longer reproduce sexually. Many of the most damaging invasive plant populations are the products of allopolyploid hybridization, and in many cases, such populations contain hybrid lines from multiple independent hybridization events. Thus, admixture or hybridization among invasive populations or species could profoundly affect the levels and types of genetic variation available for selection and impact the evolutionary responses of invading populations.

Aside from adaptive shifts, genetic drift during invasions could alter the nature of genetic variation within invading populations. For instance, reduction in population size during invasions could result in reduced allelic diversity and shifts in allele frequencies in the invading relative to source populations (i.e., a population bottleneck). The magnitude of this effect would depend on the size of the founding population, the extent and duration of the population bottleneck, the rate of population expansion following introduction, and the levels of ongoing migration from other populations. Literature surveys reveal a relatively modest loss of genetic variation following invasions. Recent surveys of animal, plant, and

fungal taxa found a mean loss of heterozygosity of only around 18 percent. Rapid expansion in population size would mitigate effects of a population bottleneck and loss of genetic diversity. Conversely, loss of genetic diversity might potentially be more severe for populations that experience a long lag period prior to population expansion (see next section) as a result of a protracted population bottleneck.

Genetic drift acting on functional loci could also influence invasive success. For example, loss of genetic diversity in invading populations of ants could affect self-recognition systems, with profound consequences for invasive success. Genetic variation at loci affecting conspecific or colony mate recognition influences colony formation and size in many species of ants, and such colony structure affects the expansion of invasive ants into novel territory. For instance, the Argentine ant *Linepithema humile* typically reacts aggressively toward conspecifics that are genetically distinct in their native ranges. However, loss of genetic diversity during invasions has resulted in reduced aggression in the invaded range, as genetically proximate individuals tend to accept one another as colony mates. This loss of genetic diversity has led to the formation of massive supercolonies that have established hegemony over native ant species throughout their invaded ranges.

Invasive populations are regarded as useful models for studying rapid evolution, as invasions are events that occur on observable ecological time scales. The study of early phases of invasions could offer valuable insights into mechanisms of incipient evolution and limits to rapid evolution in response to acute stress. Waddington was particularly interested in adaptation under conditions of stress, and his questions regarding the prevalence of genetic assimilation remain unresolved. In addition, it would be worth exploring the extent to which invasive populations undergo selection at genomic sites with epigenetic modifications, as epigenetic mechanisms could provide a genetically labile source of heritable variation, enabling a rapid evolutionary response.

EVOLUTION FOLLOWING ESTABLISHMENT

Following the initial stages of introduction, evolutionary forces that continue acting on invading populations would influence the rate and extent of their spread and impact their long-term persistence. In many cases, continued selection might be necessary following establishment, as traits that are beneficial during early stages of colonization would often differ from those that favor continued range expansion or persistence in the long term. Also, compensatory evolution might occur in response

to initial evolutionary changes. On the other hand, evolutionary changes might occur simply as a byproduct of relaxed selection due to the absence of selective forces present in the native range. In addition, genetic correlations between traits could shift under new environmental conditions, in some cases reflecting changes in evolutionary constraints and tradeoffs.

Selective forces that act on invading populations are likely to change over progressive stages of invasions. Traits that confer an advantage during initial stages of an invasion would tend to be those that favor rapid individual and population growth. In such cases, selfing, asexual reproduction, and allocation of resources toward growth and reproduction would be favored. In contrast, once a population becomes established, selection might favor traits that are beneficial for responding to biotic or abiotic stressors in the novel environment. In such cases, asexual reproduction or selfing might become less favored, as recombination would increase genetic variance and enhance the efficiency of selection.

Several studies have documented the formation of clines following invasions, corresponding to environmental gradients within the invaded range. These clines appear to have arisen from selection on standing genetic variation in the invaded range. For several species of *Drosophila*, chromosomal inversions are associated with temperature adaptation. Latitudinal clines in chromosomal inversion frequencies have been recapitulated during independent colonizations to resemble those of the native range. A larger than expected number of genes showing differential expression in response to temperature and candidate genes for thermal tolerance were found localized within the inverted segments. For *Drosophila subobscura*, a cline of increased wing length with latitude formed in North America following introduction, replicating the pattern present in ancestral Europe. The cline in wing length that was not apparent after one decade appeared within two decades after introduction. Interestingly, these changes were achieved by disparate means for the different clines, through lengthening of different portions of the wings. In response to a thermal gradient in the invaded range, populations of the European wild rabbit *Oryctolagus cuniculus*, introduced into Australia in 1859, evolved leaner bodies and longer ears in the warmer climate. For the invasive plant St. John's wort (*Hypericum perforatum*), clines in the introduced range in North America tended to converge with those found in native Europe. The native and introduced populations show parallel latitudinal clinal variation in plant size, leaf area, and fecundity.

The need for adequate genetic variation might account for the lengthy lag period that often precedes the onset of population and range expansion, following the initial stages of invasions. The 150–170 year lag period that has been observed in some cases might result from the need for multiple invasions to facilitate a sufficient evolutionary response. Multiple or repeated invasions might be required to accumulate sufficient additive genetic variance upon which selection could act.

Rapid evolution following invasions could result from relaxed selection in the invaded range, due to release from a selective force that was important in the native range. A commonly invoked mechanism for invasive success of plants is the enemy release hypothesis (ERH), which postulates that invasive species become more vigorous in their invaded ranges due to escape from natural enemies from their native ranges (i.e., pathogens, parasites, and predators). Of the ERH hypotheses, the evolution of increased competitive ability (EICA) hypothesis, proposed by Blossey and Nötzold in 1995, has been particularly influential. According to the EICA hypothesis, there might be an evolutionary tradeoff between resource allocation toward defense against enemies and allocation toward fitness-related traits, such as increased growth or reproduction. Given such a tradeoff, relaxed selection for enemy defense in the introduced range should allow selection to favor increased growth or reproduction (termed “competitive traits”). A prediction of this hypothesis is that, when reared under identical conditions, introduced populations should display greater biomass or fitness than the source populations and should simultaneously show reduced resistance against specialist herbivores.

Support for the enemy release hypothesis, based on field comparisons and laboratory experiments, has been mixed. In general, introduced species do appear to lose their natural enemies at a biogeographical scale. Field comparisons generally show increased vigor and reduced herbivory in introduced plant populations, while some common-garden experiments appear to show rapid evolution of reproductive traits, consistent with the EICA hypothesis.

However, studies testing enemy release hypotheses have mostly been correlative, and few studies have rigorously tested whether a tradeoff actually exists between defense and fitness or growth, and whether enemy release is directly responsible for the phenotypic shifts observed. Other factors might account for phenotypic shifts in plant traits in the invaded range. For example, a meta-analysis of common-garden studies of many plant species found that differences in plant size between the native and invaded range depended heavily on latitudinal

differences between the native and invading populations. Thus, observed differences in plant size between native and introduced populations might have resulted from clinal variation in traits (in both the native and invaded ranges) rather than from enemy release following invasions. Additionally, as many of the comparative studies did not include analyses of genetic structure, it is unclear whether they examined closely related populations from the native and invaded range, rather than highly divergent populations or those of different ploidy. A strong inference approach is required, where competing hypotheses are tested and all plausible mechanisms for phenotypic shifts are addressed.

Environmental shifts during invasions could also alter the structure of genetic correlations between traits, as genetic correlations are environment specific. Such effects are relevant for trait evolution in invasive populations, because genetic correlations dictate how selection on a particular trait would affect the evolution of other traits. For instance, negative genetic correlations between fitness-related traits might often be associated with fitness tradeoffs, such that shifts in genetic correlations with environmental change might be accompanied by altered fitness tradeoffs. A shift from resource-rich to resource-poor environments might shift genetic correlations between traits, as genetic correlations among traits might often be positive when resources are abundant, but negative when they are scarce. Such alterations in genetic correlations with environmental change would make evolutionary trajectories difficult to predict for populations undergoing environmental change.

In terms of long-term trajectories, do some invasive populations fail in the long run relative to others? It would be informative to determine how adaptations important for initial success differ from those that promote population persistence, and whether there are tradeoffs between early versus long-term success. It would be also be useful to investigate factors that are responsible for the observed lag periods that precede rapid growth and large-scale spread of invasive populations. Finally, knowledge on changes in genetic architecture of invasive populations over extended periods of time would provide key insights into evolutionary factors that affect long-term persistence.

FUTURE DIRECTIONS

Considerable progress has been made in reconstructing geographic pathways of invasions, characterizing patterns of phenotypic evolution, and documenting levels and effects of hybridization among invasive and between invasive and native populations. Some studies have also shed light on

specific genetic changes that occur during adaptation in the novel range. However, the evolutionary mechanisms that make some populations or lineages more successful as invaders remain poorly understood. What evolutionary forces shape the intrinsic properties of invasive populations? The role of evolutionary history and selective forces in the native range has been hypothesized but inadequately tested.

SEE ALSO THE FOLLOWING ARTICLES

Disturbance / Enemy Release Hypothesis / Evolutionary Response, of Natives to Invaders / Genotypes, Invasive / Hybridization and Introgression / Lag Times / Ponto-Caspian: Invasions / Range Modeling / Taxonomic Patterns

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