All stressed out and nowhere to go: does evolvability limit adaptation in invasive species?

An introduction to the symposium at the SSE/ASN/SSB meeting, June 2004

George W. Gilchrist · Carol Eunmi Lee

Abstract Introduced and invasive species are major threats native species and communities and, quite naturally, most scientists and managers think of them in terms of ecological problems. However, species introductions are also experiments in evolution, both for the alien species and for the community that they colonize. We focus here on the introduced species because these offer opportunities to study the properties that allow a species to succeed in a novel habitat and the constraints that limit range expansion. Moreover, an increasing body of evidence from diverse taxa suggests that the introduced species often undergo rapid and observable evolutionary change in their new habitat. Evolution requires genetic variation, which may be decreased or expanded during an invasion, and an evolutionary mechanism such as genetic drift or natural selection. In this volume, we seek to understand how natural selection produces adaptive evolution during invasions. Key questions include what is the role of biotic and abiotic stress in driving adaptation, and what is the source of genetic variation in introduced populations.

G. W. Gilchrist (✉)
Department of Biology, College of William & Mary,
Box 8795, Williamsburg, VA 23187-8795, USA
e-mail: gwgilc@wm.edu

C. E. Lee
Wisconsin Institute of Rapid Evolution, Department of
Zoology, University of Wisconsin, 430 Lincoln Drive,
Madison, Wisconsin 53706, USA
e-mail: carollee@wisc.edu

Species introductions and their subsequent range expansions have shaped the biogeography of our planet throughout the history of life. But recently, changes in human activity have accelerated long-distance transport of organisms, greatly increasing the frequency of colonization and inviting the establishment and invasion of non-native populations. Global changes in nutrient cycles and climate may further facilitate the establishment of non-native species by disrupting established patterns of community dynamics and creating ecological opportunities for the invader (Dukes and Mooney 1999). Introduced and invasive species are also among the top contemporary causes of damage to native species and extant biological communities (Pimentel et al. 2000). Although—quite naturally—many researchers think of introduced and invading species largely in ecological or management terms, recent studies demonstrate that significant evolution occurs over ecological time scales (reviewed in Lee 2002; Stockwell et al. 2003) in a diverse range of plants, invertebrates, and vertebrates. Many of these cases of contemporary evolution focus either on evolution of invaders (Gilchrist et al. 2004; Hendry et al. 1996; Johnston and Selander 1964; Lee et al. 2003; Stearns 1983) or on the evolution of native species in response to an invader (Carroll and Boyd 1992; Carroll et al. 1997).

We organized this symposium, entitled "All stressed out and nowhere to go: does evolvability limit adaptation in invasive species?" to begin an exploration of the mechanisms by which adaptive evolution in response to ecological stress takes place during colonization and invasion events. For close to a century, biological invasions have been regarded as "experiments in nature" (Grinnell 1919), offering opportuni-

ties for evolutionary biologists to observe a species as it enters a new habitat, expands its range, and adapts to new biotic and abiotic conditions. A research agenda based on contemporary observations of introduced species was first outlined at a symposium organized by C. H. Waddington in 1963, at Asilomar CA. The resulting volume, "The Genetics of Colonizing Species" (Baker and Stebbins 1965), contains many papers that have become citation classics. Waddington argued that selection on an established non-native species would occur when that species encountered stressful environment conditions during range expansion. Observations of evolution during biological invasions thus offer a unique opportunity to assess the rate (Darwin 1859; Hendry and Kinnison 1999; Simpson 1944) and repeatability (Cooper et al. 2003; Gould and Eldredge 1977; Losos et al. 1998) of natural selection. Furthermore, evolutionary studies of invasions provide much needed information for ecologists and managers seeking to understand ways to predict and mitigate the expansion of invasive species.

Waddington (1965) focused on evolvability, the ability of a population to adapt in response to environmentally induced stress, as a function of the degree of canalization or plasticity of ecologically important traits. The phenotypic variants targeted by natural selection may or may not produce an evolutionary response to selection, depending on the genetic architecture of the underlying traits. By genetic architecture, we mean the nature and number of genes, their pattern of regulation, and their dominance, epistatic, and pleiotropic interactions that influence a particular adaptation. Highly canalized architectures imply that the developmental program may allow only a small number of discrete phenotypic states. Such systems limit the possible directions of evolution but may allow a more rapid response to selection because the alternative genetic and developmental pathways are already in place and only a minor transcriptional change might be needed to shift the phenotype (Suzuki and Nijhout 2006; West-Eberhard 2003; Wray et al. 2003). In contrast, highly plastic architectures producing copious continuous variation in traits may allow a more precise fit between trait and environment (Huey et al. 2003) and thus, by reducing selective deaths and expanding the range of expressed genetic variation, plasticity could accelerate evolution (Waddington 1953; West-Eberhard 2003) Alternatively, plastic responses could blunt the blade of selection, potentially retarding evolution (de Jong 2005; Wright 1931). The degree to which natural systems conform to any of these extremes is a subject of current debate. In any case natural selec-

tion can be imposed by abiotic or biotic stress caused by a novel or changing environment encountered during the spread of an invading species. Much of the research featured in this volume uses natural experiments—species introductions—to understand these fundamental factors in evolution. Although our focus is on contemporary evolution, at some point in its history every species has been introduced into a novel environment and has faced many of the same stresses that modern colonizing species encounter but often at a slower rate.

Key questions that we have asked our authors to address here include:

1. Where does the genetic variation that fuels adaptive evolution come from? Introduced species may undergo bottlenecks that could either reduce or enhance the amount of additive genetic variation (V_A) available for selection. Canalization may conceal a reservoir of genetic variation that is expressed only upon encountering a novel stress. New genotypes and traits may be assembled through hybridization.
2. How does genetic architecture influence the evolvability of a species? In particular, what can we learn about the interaction between genotype and phenotype in the source population that may predispose a particular lineage to be a successful colonist? Do plastic responses enable successful colonization? Does plasticity change during introductions?
3. How does environmental stress, either abiotic or biotic, influence the evolutionary trajectory of species? Do patterns of evolution in the introduced population that parallel patterns in the ancestors arise because of similar selection pressures or because of genetic canalization (i.e. parallel genetic mechanisms: Hoekstra et al. 2004)? Does the rate of adaptation to environmental stress determine range limits?

In the pages that follow, we will provide a brief summary of the papers and try to highlight the topics above that were most prominently addressed by the authors.

Genetic variation and biological invasions

Although natural populations generally seem to have abundant genetic variation and significant evolutionary potential (Kingsolver et al. 2001), it must be the case that at least some traits under selection may lack

variation in the dimension required for adaptation. In the case of species introductions, a small founding population may suffer further reduction in ecologically important genetic variation. Species introductions, however, may provide opportunities for hybridization and the acquisition of new genes. Many papers in this volume provide evidence of altered levels of genetic variation in invading populations.

Drosophila melanogaster invaded Australia about 100 years ago. Hoffmann and Weeks (2006) review clinal patterns in various genetic markers that have evolved in populations along the east coast from Queensland to Tasmania. They also examine various quantitative traits, including body size, life history schedules, and physiological tolerances. They find evidence for significant evolution in many traits; however, some expected adaptive patterns in physiology have not evolved in spite of clear geographic variation in environmental stress. *Drosophila melanogaster* has been introduced repeatedly on several continents, so this model system could yield great insight into how genetic variation can be transformed into adaptive traits. The fact that not all of the expected adaptations have been obtained, however, suggests either a lack of genetic variation in the founding population or a lack of understanding about the efficacy of selection due to environmental stress. Studies of additional independently introduced drosophilids would be useful in determining the generality of the observed clinal patterns and aid in anticipating evolutionary responses to range expansion or climate change.

Hybridization could contribute to the colonization of novel habitats by creating new genetic combinations on which selection could act, and in some cases enabling selection for "transgressive" traits that transcend parental phenotypes. Rieseberg et al. (2006) review their research on hybrid sunflowers in the genus *Helianthus*. Their work forges a direct link between hybridization, ecological divergence, and colonization of novel habitats. In particular, they review research that investigates the roles of two different types of hybrid lineage formation on phenotypic evolution: introgressive hybridization and recombinational speciation. In the case of introgressive hybridization, *Helianthus annuus* might have been able to expand its range into Texas by hybridizing with the locally adapted native *Helianthus debilis* (forming the hybrid *H. annus texanus)*, and acquiring favorable alleles. Three markers from the locally adapted *H. debilis* were found to be overrepresented in the hybrid *H. annus texanus*, and were likely to have been under positive selection.

Recombinational hybridization and speciation has led to the formation of hybrid sunflower species colonizing extreme habitats. The hybrid species *Helianthus anomalus, Helianthus deserticola*, and *Helianthus paradoxus* are much more limited in geographic distribution than their parents, and occur in desert, sand dune, and saline wetland habitats, respectively. Field experiments demonstrated that many of the extreme traits found in the hybrid species could have arisen via habitat–mediated selection acting on transgressive phenotypes in novel habitats. QTL studies revealed that complementary genes represent "cryptic variation" that is not manifest in parental populations, but can be released following recombination in hybrids and allow for selection on extreme traits. Overall, research on *Helianthus* provides compelling links between hybridization, adaptive evolution, and the colonization of novel habitats.

While in Rieseberg et al's. study, hybrid recombination resulted in specialized lineages, in other cases hybrid recombination could produce genotypes that are broadly adapted across environments (Baker's (1965) "general-purpose genotypes"). Latta et al. (2006) created hybrids between recombinant inbred lines (RILs) derived from two contrasting *Avena barbata* ecotypes (mesic and xeric) and examined the genetic architecture and fitness effects across different environments. They found that recombination among QTLs for a variety of fitness and environmentally related traits generated significant heritable variation among the hybrids. Performance was assayed in the parental xeric and mesic environments in the field, as well as across a range of greenhouse environments crossing high and low water availability with high and low fertilizer availability. Generally, the mesic parental ecotype outperformed the xeric ecotype across all environments in the lab and in the field, suggesting that local adaptation was at best weak and a more "general purpose genotype" was favored. Moreover, whereas most hybrid lines performed less well than their parents, two lines outperformed the parents across nearly all environments, further suggesting that hybrid superiority may be related to better all-around performance than to superior performance in a specific habitat. These results are in contrast to Lee et al.'s (2006) result of tradeoffs between survival in the ancestral source versus in the invaded novel habitats. In Latta et al., many traits showed transgressive segregation caused by recombination of QTL in the parental lineages, and increased fitness of the successful recombinants that could colonize a wide variety of environments.

Although additive genetic variation is clearly important for evolution, several investigators have suggested that non-additive variation may be important in facilitating adaptation to novel conditions (e.g. Bradshaw and Holzapfel 2000; Cheverud and Routman 1996; Goodnight 1995; Lopez-Fanjul et al. 2004). One of the best examples of rapid evolution in response to ''niche opportunity'' is the adaptation of the soapberry bug, *Jadera haematoloma*, to introduced plant species in the family Sapindacea. The native host is the balloon vine, *Cardiospermum corndum*, which has relatively large, high protein seeds. One of the major introduced hosts is the ornamental goldenrain tree, *Koelreuteria elegans* ssp. *formosana*, which has smaller, more lipid-rich seeds with a very different chemical defense relative to the native host. The bugs that have colonized the new host have diverged significantly in many morphological, physiological, and life history traits. Carroll (2006) applies joint-scaling analysis (Mather and Jinks 1982) to bugs from these native and introduced hosts (about 100 generations of divergence) and finds significant dominance, maternal, or epistatic contributions to genetic variation for four of the five traits examined. Similar patterns of adaptation to an entirely different set of native and introduced plant species are seen in the Australian soapberry bug, *Leptocoris tagalicus*. What is not yet known is whether the same contribution of non-additive genetic variation has been important in fueling this parallel diversification.

Genetic architecture and evolvability of biological invaders

Why do some colonizing species become established and invade, whereas most apparently either fail to become established or persist as small, isolated populations (Williamson and Fitter 1996)? One possibility is a limit on evolvability, defined as the capacity of a set of genotypes to respond to natural selection.

Although natural selection might often facilitate invasions into novel habitats, few direct measurements of selection response exist for invasive populations. Lee et al. (2006) examine the selection response and evolutionary potential of ancestral source and invading populations to changes in salinity. The estuarine and salt marsh copepod *Eurytemora affinis* has repeatedly invaded freshwater ecosystems throughout the world. Using populations from saline source (salinity: 5–40 PSU) and freshwater invading populations (0 PSU), Lee et al. (2006) examine how selection at an intermediate salinity (5 PSU) affects survival and development rate at salinities ranging from 0 to 25 PSU. Both

populations had a significant selection response at 5 PSU, although evolutionary differences persisted between the populations. Both populations experienced a reduction in freshwater (0 PSU) tolerance, consistent with negative genetic correlations found between survivorship at 0 and 5 PSU. Results from this study indicate that both the saline and freshwater populations harbor adequate genetic variation for a fitness-related trait and that selection can act on this variation to induce rapid phenotypic evolution in a novel habitat.

Incorporating genetic model organisms into ecologically relevant studies is one promising avenue to begin dissecting the genetic underpinnings of traits that confer invasive success in related nonmodel species. Weinig et al. (2006) describe state-of-the-art molecular genetic tools, such as association mapping, transgenic complementation, as well as network modeling approaches, which could be used to characterize the genetic basis of adaptation and the genetic targets of selection. For example, the model system *Arabidopsis thaliana* is a recent colonizing species into North America from Eurasia, with close relatives that are invasive. Determining genetic targets of selection associated with range expansions in *A. thaliana*, such as germination and flowering time, water use efficiency, and elongation response, may provide a framework for identifying genes that account for invasiveness in related species.

Environmental stress as a driver of adaptation during invasions

All of the studies in this symposium have focused on some mixture of biotic and abiotic stresses as drivers of evolution. New habitats often present new challenges for colonizing species on many levels. One challenge of broad applied interest is how populations adapt to new pathogens or parasites.

Hess et al. (2006) discuss the evolution of an invasive bird species, the European house finch that has spread across much of North America and Hawaii since its introduction to New York state in the early 1900s, in response to a recently encountered bacterial pathogen, *Mycoplasma gallisepticum*. The study first examines genetic variation among the invaders using AFLPs and finds little sign of a genetic bottleneck on a genome-wide scale. Moreover, although the *Mycoplasma* is exerting significant selective pressure on finches in the Eastern US, the shifts in allele frequencies of a candidate gene in the major histocompatibility complex (MHC) were similar to those observed in controls not exposed to bacteria. Expression studies

indicate decreased expression of the class II MHC locus upon exposure to *Mycoplasma*, a pattern consistent with manipulation of the finch immune system by *Mycoplasma*. Hess et al. do find some apparently large genetic shifts between samples taken before and after the encounter with *M. gallisepticum* at some codons in the peptide binding regions. This suggests that evolution of the MHC complex can readily take place in an invasive species, but that genetic changes that increase fitness in the present of a particular pathogen may not, in fact, be evolving in response to that pathogen. One of the challenges of using invasions as "natural experiments" is that many components of the environment have changed, relative to the ancestral habitat and several selective factors may be acting at once.

Overall, these papers suggest that genetic variation in phenotypic traits must be present among the early generations following the initial colonization for adaptive evolution to occur in response to novel habitats. Phenotypic plasticity, and particularly cross-generational developmental plasticity (i.e. maternal effects), often play a key role in producing phenotypes capable of competing favorably with native species. The genetic basis of this plasticity remains largely unexplored, however recent advances in QTL mapping and the ability to identify and test candidate loci influencing fitness and environmentally related traits are likely to revolutionize our understanding of canalization and plasticity within the next few years. Much of the ability of colonists to invade and adapt depends on existing genetic variation, with some evidence suggesting that non-additive variation may be the main contributor to the rapid evolution frequently seen during biological invasions.

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