

Evolutionary genetics of invasive species

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The evolutionary genetics of invasive species has been relatively unexplored, but could offer insights into mechanisms of invasions. Recent studies suggest that the invasion success of many species might depend more heavily on their ability to respond to natural selection than on broad physiological tolerance or plasticity. Thus, these studies stress the importance of genetic architecture, selection upon which could result in evolutionary adaptations and possibly speciation. For instance, epistatic interactions and the action of a few genes could facilitate invasion success. These findings emphasize the utility of genomic approaches for determining invasion mechanisms, through analysis of gene expression, gene interactions, and genomic rearrangements that are associated with invasion events.

INVASIVE SPECIES (see Glossary) and populations pose major threats to biodiversity, ecosystem integrity, agriculture, fisheries, and public health. Economic costs associated with the more publicized exotic invaders, such as weeds, agricultural pests, zebra mussels and plant pathogens, total ~US\$137 billion y^{-1} in the USA [1]. The rapid spread of exotics has received considerable attention within the international community, and has mobilized substantial ecological research. By contrast, evolutionary aspects of INVASIONS have remained relatively unexplored.

Why is evolution integral to the study of invasion biology? Invasions frequently constitute rapid evolutionary events [2], resulting in populations that are genetically dynamic over both space and time. Genetic characteristics of populations have profound impacts on their capacity for range expansions [3–5]. Both natural selection and genetic drift could alter genetic structures of invading populations in ways that modify their tolerance or behavior (see examples below). Invading populations are also capable of inducing evolutionary changes in native species [6,7]. Consequently, incorporating evolutionary genetics is important for revealing characteristics that determine invasion success.

Why is this topic of immediate importance? As impacts of invasions intensify, it is imperative to move beyond treating invasive species as genetic black boxes in mitigation and management strategies. For instance, demographic models that treat invasive species as homogeneous and immutable entities will often fail over extensive spatial or temporal scales. We are in an excellent position to investigate factors that affect invasion success, given recent developments in evolutionary theory and molecular genetics. Technical innovations in GENOMICS (e.g. MICROARRAY TECHNOLOGY and QUANTITATIVE TRAIT

LOCI (QTL) MAPPING) and BIOINFORMATICS offer many opportunities for exploring GENETIC ARCHITECTURE and gene expression patterns of invading populations. Effective application of these tools requires an assessment of the current literature. Thus, here I review recent studies on genetic characteristics and adaptative responses of successful invaders, and recommend topics for future research.

Genetic architecture of invasive species

The importance of natural selection

Biological invasions present interesting evolutionary problems because they are stochastic events often involving small populations that can survive rapid habitat transitions. The classic symposium volume *The Genetics of Colonizing Species* [8] was influential for focusing on evolutionary mechanisms of invasions. In this text, C.H. Waddington asked how genetic architecture might impact the propensity to invade. Mounting evidence supports the importance of genetic attributes for invasion success, such as ADDITIVE GENETIC VARIANCE (AGV) [7,9–11], EPISTASIS [7,12–14], hybridization [4,15], genetic tradeoffs [6,16], the action of small numbers of genes [5,17,18] and, possibly, genomic rearrangements [15,19,20].

Thus, invasion success could be facilitated by the presence of genetic substrate in source populations upon which natural selection could act. In some cases, genetic drift alone has promoted successful invasions [3], but such cases probably represent exceptions rather than the rule. Broad tolerance and PLASTICITY are commonly invoked to explain invasion success [21–23], but often fail upon close examination [24,25]. For example, the copepod complex *Eurytemora affinis* is considered a euryhaline species because it inhabits broad salinity ranges from hypersaline marshes to freshwater lakes [23]. However, certain populations cannot tolerate or acclimatize to the full range of salinities occupied by this species complex, but instead experience strong selection and heritable shifts in tolerance when they invade new habitats [24,26].

Genetic variance

Sufficient AGV is essential for evolutionary ADAPTATION in response to environmental change [27]. Several recent studies have found high levels of AGV within source populations for traits that facilitate invasions [7,9–11]. The observed lag time commonly preceding successful invasions could result from the

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need to accumulate adequate levels of AGV, rather than the need to attain sufficient population size [4]. An exception to this generalization, among others, is the case of the Argentine ant *Linepithema humile*, for which loss of genetic diversity following invasion into North America has resulted in reduced intraspecific aggression, leading to the formation of 'super colonies' [3].

Although AGV provides the main substrate for selection, recent studies indicate that EPISTATIC GENETIC VARIANCE might also be important [7,12,14]. Without the generation of new mutations, epistasis could provide novel substrate for selection either between or within populations. Fixed epistatic variance between populations could arise through genetic drift, natural selection, or both [7,14]. In the soapberry bug *Jadera haematoloma*, which colonizes different host plants, selection has presumably resulted in large epistatic variance (40–78% of total GENETIC VARIANCE) in traits with fitness tradeoffs on different hosts [7].

Alternatively, theoretical studies have shown that dominance [28] and epistatic variance [29,30] within populations could be converted into AGV through genetic drift. Recent empirical studies [31,32] support these theoretical predictions. Hence, a temporary bottleneck might expose nonadditive genetic variance to selection, and contribute to rapid rates of evolution observed during invasion events [2]. However, the potential tradeoff between AGV loss during FOUNDER EVENTS versus AGV gain from variance conversion deserves further investigation.

Hybridization

Inter- or intraspecific hybridization of invasive populations, with native or other non-native populations, could alleviate loss of additive genetic variance during founder events, and generate novel genotypes [4]. Numerous studies have documented positive effects of hybridization on invasibility, such as faster growth, greater size and increased aggression [4,33], possibly as a result of increased genetic variance, new gene interactions, masking or unloading of deleterious recessive alleles, or the transfer of favorable genes [4,13]. Examples of adaptation through hybridization include the acquisition of herbicide resistance in weeds from genetically engineered crops [34] and possibly the transfer of cold tolerance [35]. Given that hybridization is detrimental in many cases, successful invasions probably result from selection on numerous hybrid combinations [4].

Among plants, recently formed ALLOPOLYPLOID hybrids typify many widespread and successful weed species [4,15,36]. Thus, invasion potential in plants might be somewhat predictable given that spontaneous hybridization is concentrated within certain families and genera [37]. POLYPLOID hybrids in plants tend to have greater fitness than do diploid hybrids, possibly because of increased heterozygosity

and reduced inbreeding depression [15]. In addition, much genetic variation could arise from multiple origins of polyploidy within allopolyploid 'species', and the prevalence of genomic rearrangements [15]. In sterile and asexual allopolyploids, additional benefits could arise from FIXED HETEROSIS [15]. For such sterile allopolyploids, tradeoffs between benefits of fixed heterosis and costs of lowered AGV are poorly understood [4]. Levels of AGV vary considerably among sterile allopolyploids, being low in the smooth cordgrass *Spartina anglica* (Poaceae) [4], but unexpectedly high in triploid populations of the dandelion *Taraxacum officinale* (Asteraceae) from recombination between chromosomal homologues [38].

Genotype \times environment interaction

Fitness tradeoffs in different environments (GENOTYPE \times ENVIRONMENT INTERACTION) can lead to diversifying selection among populations invading different habitats [6,7,16]. For example, selection on fitness tradeoffs on introduced apple *Malus pumila* and native hawthorn *Crataegus* spp. hosts has led to divergence in phenology and physiology in the fly *Rhagoletis pomonella* [6]. Apples ripen earlier than hawthorn and have higher internal temperatures, advancing the seasonal distribution of apple-maggot flies by 3–4 weeks and leading to high temperature adaptation [6]. In COMMON-GARDEN EXPERIMENTS using hawthorn larvae, warmer rearing conditions (26°C) selected for alleles common in apple-fly populations, whereas cooler conditions (17°C) selected for alleles common in hawthorn fly populations [6]. Thus, selection on pre-existing fitness tradeoffs in source populations could result in distinct physiological races.

The role of particular genes

Small numbers of genes could have profound impacts on colonizing ability. A notable example is the possible effect of a single gene on social organization in the fire ant *Solenopsis invicta* [5], which invaded the southeastern USA ~60 years ago from South America. Colonies of multiple unrelated queens (polygyne) have become prevalent in the USA, with greater nest densities and greater impacts on native ant populations than from single-queen colonies [39]. Polygyne colonies possess particular worker genotypes at the gene *Gp-9*, which encodes a pheromone-binding protein [5]. This gene, or a gene closely linked to it, might affect the ability of workers to recognize queens and regulate their numbers [5]. Through different mechanisms, the outcome of large polygyne colonies is similar to that of the Argentine ant *Linepithema humile* [3]. In both cases, loss of self-recognition has led to a large and dense colony structure. Such a strategy might be effective for invading new territories, but is not evolutionarily stable in the long term [40]. Following establishment in new territories, intraspecific selection should

promote the acquisition of selfish worker strategies, leading to the breakdown of super colonies [40].

Similarly, a small number of genes might affect capacity for range expansion in some plant species. QTL-mapping has revealed small numbers of genes associated with traits affecting 'weediness' (growth, dispersal and persistence) in the allopolyploid johnsongrass *Sorghum halepense* (Poaceae), distinguishing it from closely related crop plants [17]. Likewise, in different colonizing ecotypes of Shepherd's purse *Capsella bursa-pastoris* (Brassicaceae), QTL-mapping has also revealed only a few genes linked to flowering time, which is an important trait for colonizing different habitats [18].

Genomic rearrangements

Genomic rearrangements might provide important substrates for adaptation during invasion events [15]. For example, in the fruitfly *Drosophila subobscura*, selection has independently resulted in identical patterns of chromosomal inversions along a latitudinal gradient on three continents [19], suggesting a functional role for those arrangements. In another fruitfly *D. buzzatii*, the frequency of a particular chromosomal rearrangement is associated with temperature adaptation [41]. Transposable elements might be responsible for these genomic rearrangements [20]. Future genomic analyses should offer explanations for these clines, perhaps by identifying locations and functions of genes or regulatory elements.

Adaptation following invasion events

Given the importance of genetic substrate for selection in many invasive species, on which traits does selection act? Initially, selection might act on dispersal capacity [42] or physiological tolerance in response to immediate stresses in new habitats [24]. Following invasion events, adaptation would proceed in response to selective pressures in the new environment. Selection might occur in response to environmental gradients, such as temperature, photoperiod, or climate [6,18,43–48], or to resident species, as competitors, predators, or prey [6,7,16,49]. Common responses include changes in morphology [7,16,44,45,49], physiology [42,46], phenology [6,18,47,48], or plasticity [16].

Getting there: selection on dispersal

Incipient adaptations in response to invasions are difficult to detect because they occur rapidly. Not surprisingly, the more common examples include selection on dispersal capacity [42] and on physiological tolerance to immediate environmental stress [24]. For example, a common-garden experiment on populations of the butterfly *Pararge aegeria* revealed greater investment in traits related to flight (wings and thorax) relative to reproduction (abdomen) in recently (<20 years) colonizing populations, suggesting that evolutionary

changes in flight morphology accompanied the act of colonization [42].

Response to environmental gradients

Many studies document rapid evolution in response to environmental gradients. *Drosophila subobscura* displayed a rapid morphological response to latitude following introduction into North America from Europe [44]. A cline in wing length that was not apparent after one decade appeared within two decades after introduction, replicating the pattern present in ancestral Europe of increased wing length with latitude [44]. Interestingly, these changes were achieved by disparate means, through lengthening of different portions of the wings [44].

In response to a thermal gradient, populations of the European wild rabbit *Oryctolagus cuniculus*, introduced into Australia in 1859, evolved leaner bodies and longer ears in the warmer climate [45]. This morphological cline resulted from both a genetic and PLASTIC RESPONSE to temperature. The morphological traits were heritable based on the persistence of differences over two generations under common-garden conditions [45]. The Eurasian barnyard grass *Echinochloa crus-galli* (Poaceae) recently invaded colder climates (Quebec, Canada) from southern regions of North America [46]. This grass has a C4 photosynthetic system, which confines this and many other species to warmer geographical regions. Recent studies show that the Quebec population evolved enhanced catalytic efficiency of some enzymes [50].

In angiosperms, flowering time is an important trait for colonization, affecting survival in different climates. In response to latitude, two goldenrods *Solidago altissima* and *S. gigantea* (Asteraceae) introduced into Europe from North America ~250 years ago, exhibited a cline in flowering time that resembled the cline in their native range [47]. Common-garden experiments revealed a genetic basis for the phenological difference [47], and the authors speculate that the cline in the introduced populations resulted from selection both on existing variation and on new mutations [47]. Similarly, shepherd's purse *Capsella bursa-pastoris* (Brassicaceae) has a range of genetically determined ecotypes with striking differences in flowering time [18]. Allozyme data suggest that multiple pre-adapted ecotypes were introduced into California from Europe, and that selection during invasions resulted in the prevalence of early-flowering ecotypes in the desert, and late-flowering ecotypes in coastal and snow-forest regions [48].

Response to resident species

Interspecific interactions in newly colonized habitats pose many challenges for invading species. Some species have evolved plastic responses to accommodate unpredictable conditions. The velvetleaf *Abutilon theophrasti* (Malvaceae) was

introduced to the USA from southeast Asia probably before 1700, but in the past 100 years it has become an aggressive invader in cultivated fields of the Midwestern USA. In response to interspecific competition for light, the velvetleaf has evolved different life-history strategies depending on the nature of the competition [16]. When competing with soybean, velvetleaf populations evolved a plastic growth response to light quality, because such a response enables velvetleaf to outgrow soybean. By contrast, the inability of velvetleaf to outgrow corn presents no advantage for plasticity, leading to the evolution of canalized growth at later life-history stages [16].

Invasive pest species evolve quickly in response to human efforts to eradicate them. For instance, agricultural practices have resulted in diverse defense strategies of weed populations. Some weed species that are closely associated with agricultural crops have evolved crop mimicry to evade eradication [49]. For some species mimicry is aided by genetic exchange with crop species, but in the barnyard grass *Echinochloa crus-galli* rice mimicry is achieved through strong selection [49]. This species is a rice mimic where there is intensive handweeding, but not in places where mechanized or chemical weed control is practiced [49]. In cases where chemical weed control is used, genetic exchange between weeds and genetically engineered crops has resulted in herbicide resistance in several species [34,51].

Adaptation could also occur in response to environmental shifts presented by introduced host plant species. For instance, in *R. pomonella*, selection on fitness tradeoffs on different host plants has led to divergence in temperature tolerance and phenology [6]. Likewise, a change in hosts within the past 50 years (~100 generations) has resulted in rapid morphological and life-history adaptations in the North American soapberry bug *Jadera haemotoloma* [7]. For instance, some soapberry bugs have colonized the introduced southeast Asian goldenrain tree *Koeleruteria elegans* (Sapindaceae), which bear smaller fruit than do their native host, the balloon vine *Cardiospermum corindum* (Sapindaceae) [7]. To access smaller fruit of the introduced host, soapberry bugs have evolved shorter (~30%) stylets relative to those associated with the native host [7].

Release from predation in the new environment

In response to the lack of predators in the new habitat, increase in size has been proposed to occur in plants as a result of shunting investment to growth rather than to predator defenses [52]. This idea was challenged by Willis *et al.* [53,54], based on a common-garden experiment on four invasive plant species, which found no evidence of size difference between invasive and native populations. Potentially, removal of predation and competition in newly invaded

habitats would relax selection pressure on the invader, releasing defensive traits from evolutionary CANALIZATION and resulting in rapid evolution. Such a scenario is worth exploring.

Invasions as speciation events

Rapid speciation following invasions could occur both through neutral [55] and selective [56] processes. According to theoretical predictions, even relatively weak selection for local adaptation could dramatically decrease the waiting time to speciation [57]. Significant genotype \times environment interaction [6,16] could promote speciation if diversifying selection results in preference for isolated microhabitats or divergent mate choice. Speciation could also conceivably arise from genetic drift in mate preference following colonization.

Relatively few studies have explicitly examined reproductive isolation and speciation associated with biological invasion events. The most commonly reported examples pertain to allopolyploid hybridization in plants and host-race formation in insects. Allopolyploid hybridization can lead to reproductive incompatibility with parental species, resulting in instantaneous speciation coupled with the emergence of invasiveness [4]. Colonization of new host plants frequently results in reproductive isolation and speciation because of the evolution of host specificity [6,7].

Other than the scenarios discussed above, reproductive isolation has rarely been measured following an invasion event. Reproductive isolation was inferred from patterns of genetic divergence between an introduced population of beach-breeding sockeye salmon *Oncorhynchus nerka*, separated by ~13 generations from its riverine source [58]. Patterns of microsatellite variation revealed that the two populations remained genetically distinct in spite of immigration from the river into the beach populations, suggesting that reproductive isolation had evolved [58]. This study has provoked some controversy [59]. In another example, reproductive isolation appears to have occurred between a recently derived population of the copepod *Eurytemora affinis* on the Pacific coast of the USA and an ancestral population from the Atlantic coast [60,61]. In this case, it is not certain that reproductive isolation followed the invasion event because the exact source population was not used in the mating experiment.

The possibility of rapid speciation following biological invasions deserves further exploration, given that geographic isolation caused by invasion events promotes the formation of new EVOLUTIONARY SPECIES. For example, many invasive populations have colonized environments that are radically different from their sources and have evolved fitness tradeoffs in their new environments [6,7,24,58]. Physiological and other adaptations could hinder gene flow, even if intermating was technically possible. Eventually, this

Acknowledgements

I thank Greg Gelembiuk, Michael Bell, James Crow, George Gilchrist, Don Waller, Tony Ives, David Baum, Neil Tsutsui and members of my laboratory for thoughtful discussion and useful comments. Helen Moorhead assisted with library research. This study was supported by NSF DEB-0130543 to C.E.L.

Glossary

Adaptation: genetic change in a population resulting from natural selection, whereby the average state of a character becomes improved with respect to a specific function, or a population becomes better suited to its environment.

Additive genetic variance: the proportion of genetic variance in a character that is due to the additive component of allelic effects. Genetic diversity is used frequently to indicate the potential for evolutionary adaptation, but it is additive genetic variance rather than genetic diversity *per se* that responds to natural selection. Genetic diversity encompasses polymorphism at all markers, including neutral markers, whereas additive genetic variance pertains to variance of particular phenotypic traits.

Allopolyploid (= amphidiploid): a hybrid between different species in which chromosomes of both parental species are retained. Allopolyploidy is common in plants but rare in animals. Allopolyploids with odd copy numbers of chromosomes are usually sterile, but can often propagate asexually. Most allopolyploid 'species' are polyphyletic, or comprise individuals that have been derived from multiple independent hybridization events between the same parental species [a].

Bioinformatics: the creation and development of information and computational technologies for storing, retrieving and analyzing biological data, such as DNA, RNA, or protein sequences, structures, functions, pathways and genetic interactions.

Canalization: limitation of possible phenotypes because of constraints imposed by a developmental pathway.

Common-garden experiment: an experiment in which individuals from different populations or treatments are reared together under identical conditions.

Epistatic genetic variance: genetic variance attributable to the interaction of two or more loci.

Epistasis: interaction between two or more gene loci where the joint effect on the phenotype differs from the sum of the loci taken separately.

Evolutionary species: populations or groups of populations that share a common evolutionary fate through time [b,c]. Unlike the biological species concept, a group of reproductively compatible populations could be classified as separate 'evolutionary species' if they are on independent evolutionary trajectories.

Fixed heterosis: the maintenance of hybrid vigor in a fixed manner in a population because the individuals reproduce asexually and favorable genotypes do not recombine.

Founder event: the occurrence in which founders of a new population carry only a fraction of the total genetic variation in the source population because of sampling error resulting from their small numbers.

Genetic architecture: the number of loci and the number and frequency of alleles at those loci that affect a particular trait, their allelic (dominance) and genic (epistatic) interactions, and their relationship to other traits (pleiotropy) [d].

Genetic variance: the degree of phenotypic variance within populations that is due to genetic differences among individuals (as opposed to environmental or chance factors), including dominance, additive genetic and epistatic genetic variance.

Genomics: the global study of all genes and noncoding sequences as a dynamic system, including their identity, location, interaction, integrated functions and expression over time.

Genotype x environment interaction: changes in rank or level of performance among genotypes when tested in different environments.

Invasion (= biological invasion): the event in which a population is moved beyond its natural range or natural zone of potential dispersal through human-mediated transport. Invasions are distinct from colonizations, which are often viewed as natural range expansions.

Invasive species: a species that contains populations that invade. Invasive species typically refer to introduced species that cause negative impacts on the environment, human activities, or human health. Among species that are introduced, only a very small proportion become established and then invasive [e]. This paper includes examples from species with no known harmful effects to illustrate important evolutionary concepts relevant to invasions.

Microarray technology: a relatively new method of examining differential expression or presence and interaction of genes. A robot applies droplets of DNA or RNA onto glass slides (microarray gene chips), encompassing all or part of a genome. Fluorescently labeled DNA or RNA from the organism or cell of interest is then hybridized to the gene chips to determine the expression or presence of particular genes [f].

Plastic response: a response of a given genotype that can vary depending on external conditions.

Plasticity (= phenotypic plasticity): the capacity of a given genotype to develop one of several phenotypic states depending on the environment.

Polyploid: having more than two sets of chromosomes.

Quantitative trait loci (QTL) mapping: mapping onto the genome the location of a gene that affects a quantitative trait (a measurable trait that shows continuous variation and that is encoded by multiple genes) [g].

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isolation might lead to speciation and the formation of species complexes.

Conclusions and future directions

Biological invasions are quintessential models for rapid evolution [2]. The examples above illustrate cases in which: (1) invasion success was influenced by genetic architecture within source populations; and (2) natural selection on this genetic substrate has led to rapid adaptations in the new environments. In particular, recent studies indicate that: (1) epistatic interactions could contribute to adaptation during

invasions; and that (2) small numbers of genes could have profound effects on invasion success. These conclusions touch on controversial topics in evolutionary biology dating back to the Fisher–Wright debates [62]. These intriguing results emphasize the utility of exploring genomic characteristics of invasive species, such as genes, gene complexes, and epistatic interactions that promote invasive behavior. Such information could yield insights into the relationship between genetic architecture and rate of evolution, and evolutionary versus ecological factors which confer invasion success.

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