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Invited Review ══════════

Ecological Genetics of Plant Invasion: What Do We Know?

Sarah M. Ward, John F. Gaskin, and Linda M. Wilson*

The rate at which plant invasions occur is accelerating globally, and a growing amount of recent research uses genetic analysis of invasive plant populations to better understand the histories, processes, and effects of plant invasions. The goal of this review is to provide natural resource managers with an introduction to this research. We discuss examples selected from published studies that examine intraspecific genetic diversity and the role of hybridization in plant invasion. We also consider the conflicting evidence that has emerged from recent research for the evolution of increased competitiveness as an explanation for invasion, and the significance of multiple genetic characteristics and patterns of genetic diversity reported in the literature across different species invasions. High and low levels of genetic diversity have been found in different invading plant populations, suggesting that either selection leading to local adaptation, or pre-adapted characteristics such as phenotypic plasticity, can lead to aggressive range expansion by colonizing nonnative species. As molecular techniques for detecting hybrids advance, it is also becoming clear that hybridization is a significant component of some plant invasions, with consequences that include increased genetic diversity within an invasive species, generation of successful novel genotypes, and genetic swamping of native plant gene pools. Genetic analysis of invasive plant populations has many applications, including predicting population response to biological or chemical control measures based on diversity levels, identifying source populations, tracking introduction routes, and elucidating mechanisms of local spread and adaptation. This information can be invaluable in developing more effectively targeted strategies for managing existing plant invasions and preventing new ones. Future genetic research, including the use of high throughput molecular marker systems and genomic approaches such as microarray analysis, has the potential to contribute to better understanding and more effective management of plant invasions.

Key words: Evolution of increased competitiveness, genetic diversity, hybridization, invasive plants.

The rapid globalization of economies is causing an ever-increasing number of introductions into areas where they are not native. Although it is estimated that only a small fraction of exotic plant introductions lead to economic or environmental consequences, the rate at which plant invasions occur is accelerating (D'Antonio and Vitousek 1992; Mack et al. 2000; Vitousek et al. 1996). Concern for the implications and consequences of nonindigenous

invaders has compelled a considerable amount of research in the past two decades, expanding the discipline of invasion biology (Daehler 2003). Several hypotheses have been proposed to explain the success of invading plants (reviewed in Hinz and Schwarzlaender 2004). It has been observed in some instances that plant species in their invaded range are more vigorous, grow taller, have higher rates of survival and reproduction, and spread more rapidly than in their native range (Crawley 1987; Mack et al. 2000). This has led to suggestions that the success of exotic plants can be attributed to release from natural enemies and more favorable abiotic conditions (Keane and Crawley 2002; Maron and Vila 2001). More specifically, the hypothesis of evolution of increased competitiveness (EICA) predicts that plants in an introduced range encounter altered selection pressures, promoting a shift in resource allocation from defense against natural enemies to

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enhancement of other traits, conferring greater fitness in the novel environment (Blossey and Notzold 1995). However, empirical evidence and support for this has been conflicting (van Kleunen and Schmid 2003; Vila et al. 2003; Willis et al. 2000). Common garden experiments, in which plants from the native and introduced ranges are grown together in standardized environmental conditions, have attempted to test these hypotheses; however, not all results support the claim of greater vigor or competitive ability in the invaded range (see Bossdorf et al. 2004; Goldberg 1996; Thebaud and Simberlofff 2001; Vila et al. 2003, 2005; Williamson and Fitter 1996; and Willis and Blossey 1999).

A considerable amount of research has explored the evolution of invasive plants, and has examined whether certain genotypes within an invading population are more successful (e.g., Maron et al. 2004; Siemann and Rogers 2001; van Kleunen and Schmid 2003; Willis et al. 2000; and reviewed by Bossdorf et al. 2005). These studies have aimed at elucidating whether invasiveness—the ability of exotic plants to establish and rapidly expand in a novel range—is an evolved trait with underlying genetic characteristics. Recent research also explores whether genetic features of individuals or populations explain or predict invasive behavior across species.

In this review we describe examples selected from recent published studies using field and laboratory data to support or refute hypotheses in invasion genetics. First, we consider how information from genetic diversity analysis contributes to our understanding of the causes, mechanisms, and consequences of invasion by plants. We then examine examples of hybridization among invasive plant species, and how it may contribute to the success of plant invasions. Finally, we discuss ways in which improved understanding of the ecological genetics of invasive plant populations can aid the development of more effective management strategies, and we outline some directions for future research. This short overview is intended primarily for the nongeneticist; we hope that readers, including weed and resource managers, will find it a useful introduction to this important aspect of plant invasion biology. A glossary of key genetic terms used herein can be found after the Literature Cited.

Genetic Diversity and Genetic Structure in Invasive Plant Populations

Analysis of Genetic Diversity in Invading Plants. Genetic diversity among individuals within a species is reflected in the presence of different alleles in the gene pool, and hence different genotypes within populations. Such diversity was originally detected and studied using phenotypic markers: variation among individual plants for traits, such as leaf shape or flower color that were assumed to be based on differences in the plant's DNA. Enzyme variants such as allozymes were among the first molecular markers to be widely used in genetic diversity studies. More recently, PCR-based molecular marker systems have allowed direct examination of DNA sequence differences, leading to precise and sensitive detection of genetic variation among individuals. Different molecular marker technologies and their uses in population genetic analysis will not be discussed here because they have been the subject of several recent reviews; for example, see Jasieniuk and Maxwell (2001) and Ward (2006a).

The ultimate source of all genetic variation is mutation, which alters the DNA sequence. Fluctuating patterns of genetic variation, seen as changes in allele and genotype frequencies over time, form the basis of population genetics. The forces that drive these changes, and shape the distribution of genetic variation within and among plant populations are well known: selection, gene flow, genetic drift, and breeding system. Measuring the amount of genetic variation present, and mapping its distribution within and among populations, can reveal how these forces have acted on a species in a given environment, and provide insights into population history. However, the relative impact of each force on a population varies over time and also with the spatial scale of analysis (Ward 2006b), so untangling exactly what has shaped genetic structure is not always a straightforward task.

A small but growing number of studies have examined genetic diversity and genetic structure within invading plant species. Some of these studies compare diversity in a species' native range to that in invaded areas to reconstruct invasion history, or search for patterns that might explain or predict invasive behavior. Other studies focus on diversity in invading populations, examining genetic structure in an attempt to understand how nonnative plant populations establish, adapt, and expand in a novel environment. The results of some of these studies, and the emerging patterns they reveal, are discussed in more detail below.

Characteristic Patterns of Genetic Variation Associated with Invasion. Ecological adaptation can be a significant factor in range expansion by a plant species, whether driven by enlargement of the native range, or colonization and subsequent invasion into a completely novel range. One way to achieve such adaptation is through local selection acting on populations of genetically diverse individuals. When this happens, plants with genotypes conferring the highest levels of fitness are expected to survive and reproduce at a greater rate, shifting the gene pool over time towards higher frequencies of those alleles making up the more successful genotypes.

Fisher (1930) connected adaptation to measurable genetic diversity by proposing that a population's rate of

change in response to natural selection is proportional to the amount of additive genetic variation present. Based on this, the literature contains much speculation on the importance and function of genetic diversity in invasion. As a number of authors have noted, founder effect associated with initial colonization can significantly reduce genetic diversity in invasive populations, theoretically also reducing their capacity to adapt to novel conditions (Lee 2002; Sakai et al. 2001; Warwick 1990). Reduced genetic diversity in a plant population can have additional consequences, such as inbreeding depression limiting propagule production and population growth (Ellstrand and Elam 1993). Some authors have suggested that the apparent lag period between initial colonization and subsequent population expansion of a successful invader could be due to the time required to rebuild genetic diversity on which local selection can act (Ellstrand and Schierenbeck 2000; Mack et al. 2000). Several possible ways for a colonizing species to redevelop genetic diversity have been suggested, including multiple introductions bringing additional genotypes from the native range (see Frankham 2005) and hybridization (discussed in more detail below).

Is genetic diversity always a prerequisite for successful plant invasion? We reviewed analyses published between 1997 and 2007 of allozyme and DNA marker-based within-population genetic diversity in nonnative plant populations reported to be expanding within the introduced range, and therefore defined by investigators as invasive. Table 1 summarizes the diversity levels reported in these studies. Some studies we reviewed also investigated the extent of genetic differentiation among populations in the introduced range, and this information is included in Table 1 where available. Our categorization of diversity levels as "low," "medium," or "high" is based on researchers' own definitions; these categories should therefore be considered indicators of general patterns rather than absolute values. As several authors have noted, caution is needed when comparing genetic diversity indices across studies that used different sampling protocols and marker techniques; for examples, see Mohammadi and Prasanna (2003) and Zhao et al. (2006).

Despite these limitations, the studies summarized in Table 1 do reveal two apparently contradictory trends. Some invasive plants possess significant genetic diversity within the invaded range, and in several of the investigated species listed here, including reed canarygrass (*Phalaris arundinacea*), garlic mustard (*Alliaria petiolata*), kudzu (*Pueraria lobata*), and leafy spurge (*Euphorbia esula*), molecular data and historical records point to multiple introductions as the most likely source of such diversity. In studies we examined that partitioned the amount of genetic diversity within vs. among populations, distribution patterns generally reflected the reproductive biology of the plant in question. Cross-pollinating plant species tend to have high levels of genetic variation within populations but low levels of genetic differentiation among populations, whereas self-pollinating species typically have less within-population genetic variation and more diversity among populations (Hamrick and Godt 1983, 1996). Clonal reproduction also might reduce genetic diversity within populations, as better-adapted clonal genotypes expand and dominate available resources (e.g., Scheepens et al. 2007). In some plant species, however, maintenance of sexual reproduction can result in surprisingly high levels of within-population genetic diversity even when combined with clonal spread. This pattern has been reported in several of the invasive plant species listed in Table 1, including kudzu, Canada goldenrod (*Solidago canadensis*), and yellow toadflax (*Linaria vulgaris*). Table 1 also shows that some plant species can invade aggressively despite having little or no genetic diversity. The most striking example is Japanese knotweed (*Fallopia japonica* [=*Polygonum cuspidatum*]), which Hollingsworth and Bailey (2000) reported to be genetically identical across invasion sites sampled throughout the United Kingdom. Invasive populations of alligator weed (*Alternanthera philoxeroides*) and water hyacinth (*Eichhornia crassipes*) in China are also reported to have very low levels of genetic diversity (Geng et al. 2007; Ren et al. 2005). Rapid clonal spread and dispersal via root or stem fragments in these species has been suggested as a major factor in their lack of genetic diversity and population genetic structure. The capacity of these invasive plants to adapt to different conditions might be the result of a preadaptational capacity for phenotypic plasticity rather than local selection acting on genetic diversity; this is discussed further below.

Not all invasive plant species with limited genetic diversity in the invaded range are clonally reproducing perennials. Table 1 also includes two related self-pollinating annuals in this category, *Aegilops triuncialis* and *Aegilops cylindrica*, and a perennial bunchgrass spread by apomictic wind-dispersed seed (*Pennisetum setaceum*). This suggests that multiple invasive plant species with different life histories and reproductive biologies show a high degree of individual buffering: genetically similar plants in the invading populations can tolerate environmental heterogeneity and a range of associated stresses, with potentially variable phenotypic expression in response to different conditions.

Genetic Diversity and Adaptive Strategy in Invasive Plants. Whether the ability of some plants to invade a wide range of habitats is due to phenotypic plasticity, or to selection leading to locally adapted ecotypes, has been debated for more than a decade (for example, see Sultan 1995). Parker et al. (2003) suggested that factors such as number of introductions and breeding

Table 1. Summary of results from 20 published analyses of genetic diversity in invasive plants.

Species	Native range	Invaded range	Total GD[a]	Within/among[b]	Breeding system	Life history	Markers used[c]	Reference
Euphorbia esula	Eurasia	North America	High	Low/high	Clonal/outcrossing	Perennial	cpDNA and RAPD	Rowe et al. 1997
Poa annua	Europe	North America	High	High/low	Selfing	Annual	RAPD	Mengistu et al. 2000
Pilosella officinarum	Europe	New Zealand	Medium	Low/medium	Clonal	Perennial	ISSR	Chapman et al. 2000
Alliaria petiolata	Europe	North America	High	Low/high	Predominantly selfing	Biennial	SSR	Durka et al. 2005
Chromolaena odorata	South America	China	Low	Low/high	Clonal/outcrossing	Perennial	ISSR	Ye et al. 2003
Pueraria lobata	SE Asia	United States	High	High/low	Clonal/outcrossing	Perennial	ISSR	Sun et al. 2005
Kochia scoparia	Eurasia	United States	High	High/low	Outcrossing	Annual	ISSR	Mengistu and Messersmith 2002
Ambrosia artemisiifolia	North America	France	High	High/low	Outcrossing and selfing	Annual	SSR	Genton et al. 2005
Phalaris arundinacea	Europe	United States	High	High/medium	Clonal/outcrossing	Perennial	Allozymes	Lavergne and Molofsky 2007
Aegilops cylindrica	Eurasia	United States	Very low	Not analyzed	Selfing	Annual	AFLP and RAPD	Pester et al. 2003
Clidemia hirta	South America	Hawaii	Low	High/low	Agamospermy	Perennial	Allozymes	DeWalt and Hamrick 2004
Fallopia japonica (=*Polygonum cuspidatum*)	Japan	United Kingdom	None detected	Not analyzed	Clonal	Perennial	RAPD	Hollingsworth and Bailey 2000
Egeria densa	South America	United States	Low	Not analyzed	Clonal	Perennial	RAPD	Carter and Sytsma 2001
Eichhornia crassipes	South America	China	Low	Low/low	Clonal/outcrossing	Perennial	RAPD	Ren et al. 2005
Linaria vulgaris	Europe	United States	High	High/low	Clonal/outcrossing	Perennial	ISSR	Ward et al. 2006
Pennisetum setaceum	Middle East	United States	None	Not analyzed	Agamospermy	Perennial	ISSR	Poulin et al. 2005
Aegilops triuncialis	Eurasia	United States	Low	Low/low	Selfing	Annual	SSR	Meimberg et al. 2006
Solidago canadensis	North America	China	High	High/low	Clonal/outcrossing	Perennial	ISSR	Dong et al. 2006
Alternanthera philoxeroides	South America	China	Low	Low/low	Clonal	Perennial	ISSR	Geng et al. 2007
Hieracium glomeratum	Europe	North America	None detected	Not analyzed	Apomixis	Perennial	SSR	Wilson et al. 2006

[a] Overall intraspecific genetic diversity within the invaded range.

[b] Proportion of total genetic diversity found within populations *vs.* among populations in the invaded range.

[c] Marker acronyms: AFLP = amplified fragment length polymorphism; cpDNA = chloroplast DNA; ISSR = inter-simple sequence repeat; RADP = randomly amplified polymorphic DNA; SSR = simple sequence repeat.

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system determine whether phenotypic plasticity or local selection is the most important adaptive mechanism for an invasive plant species. Multiple introductions and outcrossing (including hybridization with native or other introduced species) generate genetic diversity within invading plant populations on which selection can act. Alternatively, limited introductions combined with inbreeding or clonal reproduction would favor plastic phenotypic expression by genetically similar plants colonizing different environments. A complicating factor is that some genotypes are more plastic than others, so the capacity for phenotypic plasticity is itself under genetic control and subject to selection (Via et al. 1995). Such selection might have already taken place in the native range to produce pre-adapted colonizing plants, or it might occur following introduction so that subsequent invasive spread is achieved by a small number of phenotypically plastic genotypes. Our understanding of the adaptive strategies of invasive plants would be enhanced by determining genetic diversity levels in additional species of concern, and by relating patterns of diversity distribution to modes of reproduction and spread.

Meanwhile, it seems that both phenotypic plasticity and adaptation can play a role in plant invasion. Evidence for plasticity comes from a recent common garden study by Geng et al. (2007), in which genetically identical alligator weed plants collected from different locations in China showed similar changes in root/shoot biomass partitioning when grown in terrestrial vs. aquatic environments. Geng and coworkers suggest that this flexibility in growth habit allows alligator weed to flourish in a wide range of habitats, despite extremely limited genetic diversity in invading populations. In another example, Parker et al. (2003) used common-garden experiments to evaluate fitness traits in invasive populations of mullein (*Verbascum thapsus*) collected from different elevations. Although measurable genetic diversity was found, mainly as differences among populations, results of this study again pointed to plasticity of phenotypic expression in different environments as the key to success of invasive plants, rather than adaptation. Lavergne and Molofsky (2007) also detected plasticity in the expression of several phenotypic traits in genetically diverse invasive populations of reed canary grass. These results suggest that the importance of phenotypic plasticity in plant invasion is not limited to invading species with little or no genetic diversity.

In contrast, evidence for local adaptation of an invasive plant through selection acting on within-species diversity comes from Maron et al. (2004) who reported substantial genetic variation among populations of St. John's wort (*Hypericum perforatum*), and also latitudinally-based differences in plant size and seed production among plants from the North American invaded range that were similar to differences seen in the native European range. These researchers concluded that St. John's wort invading North America is responding to selection along an environmental gradient by redeveloping adaptations that mirror those it previously evolved elsewhere. Leger and Rice (2007) describe a similar pattern of response to abiotic selection in introduced populations of California poppy (*Eschscholzia californica*) in Chile, where in less than 150 years adaptive changes in growth patterns and flowering times along a precipitation gradient have developed that resemble those seen in native Californian populations.

Using Genetic Diversity Analyses to Reconstruct Invasion Histories. Comparisons of genetic diversity in the invaded and native ranges of an invasive plant can potentially pinpoint which native populations were the sources of the invader, show how much genetic diversity was lost due to founder effect during the invasion process, and provide evidence for multiple introductions (Sakai et al. 2001). This kind of analysis involves large numbers of samples across locations that are often on different continents, so it is not surprising that so far relatively few such studies have been published. Comparisons of genetic diversity across native and introduced ranges assume that present patterns of diversity in the native range have not changed since the founding plants or propagules were transported to their new home. If plant introduction resulting in invasion occurred a long time ago, or if the native range has since undergone major environmental change, this might not be the case. Another limitation is that this type of analysis is easier in species where either inbreeding or asexual reproduction preserves identifiable genetic lineages, as opposed to outcrossing species with a high degree of recombination. Nevertheless, comparative diversity studies have provided useful insights into the invasion histories of a handful of species; some examples are summarized below.

As already described, loss of genetic diversity due to founder effect associated with plant introduction has been proposed as a barrier that invasive plants must overcome to expand successfully in a new range. Some comparative studies have shown founder effect to be real: for example, Meimberg et al. (2006) reported only three different genotypes in invading populations of barbed goatgrass (*Aegilops triuncialis*), compared to 36 genotypes in populations sampled in the native Eurasian range. These authors noted, however, that loss of genetic diversity was not preventing this species from expanding into new habitats in California. Other studies have found that any initial founder effect in nonnative plant invaders has now disappeared; for example, Durka et al. (2005) compared genetic diversity in invasive North American and native European populations of garlic mustard (*Alliaria petiolata*), finding slightly reduced diversity in the invaded range but also multiple genotypes indicating repeated introductions.

Comparison of allele frequencies in native and introduced gene pools pointed to the British Isles and north Europe as the most likely source regions. Similarly, world-wide sampling and genetic analysis of downy brome (*Bromus tectorum*) by Mack and coworkers has revealed a complex history of multiple introductions for this species, spreading from its European origins to one new country, then another, in patterns closely tied to global migration of European human settlers (see Novak and Mack 2001 for a summary of this research).

Reconstructions of invasion histories sometimes produce unexpected results. For example, Saltonstall (2002) analyzed changes in the genetic composition of North American populations of common reed (*Phragmites australis*) by comparing chloroplast DNA sequences from herbarium specimens with samples collected from present-day field sites. This revealed that a globally distributed haplotype historically confined to common reed populations on the northeastern United States coast has undergone rapid recent range expansion across North America, displacing other native haplotypes. The mechanism driving this previously undetected cryptic invasion is unclear. The invading haplotype might represent a more aggressively colonizing genotype, or its expansion might be driven by changes in land use. In another study with quite different—but also unexpected—results, Amsellem et al. (2000) analyzed genetic diversity patterns in *Rubus alceifolius*, a bramble native to southeast Asia that has invaded Madagascar and spread across a number of Indian Ocean islands. Repeated introductions from the native range were thought to be the source of these island invasions. However, results revealed reduction in genetic diversity in the Madagascar populations compared to the native range, with successive nested founder effects progressively reducing diversity further as subpopulations of *R. alceifolius* leapfrogged from one island to the next. Understanding that new islands are being invaded in this way will facilitate redirection of control measures, hopefully leading to more effective management of this species.

As with genetic diversity studies, research using genetic analysis to reconstruct plant invasion histories has so far revealed several general trends rather than a clear predictive pattern. First, reduced genetic diversity due to founder effect does occur in colonizing plant populations, but is not always a barrier to subsequent range expansion. Second, although multiple introductions have played a role in triggering a number of plant invasions, as proposed by Frankham (2005), some plant invasions appear to have been initiated by a mere handful of introductions, or possibly even a single event. Third, genetic analysis provides additional evidence that many plant invasions involve either deliberate or inadvertent introduction by humans. The role of human activity in transporting plant species with unintended and undesirable consequences has been discussed elsewhere; see, for example, Mack (1991), Mack and Lonsdale (2001), and Mooney and Cleland (2001). As genetic analysis sheds light on more invasion histories, however, the need to translate this knowledge into more effective regulation of nonnative plant introductions becomes even clearer.

Hybridization in Plant Invasion

Hybridization and Genetic Diversity. Hybrids are the result of sexual reproduction between individuals from different species (interspecific hybridization) or from different populations within the same species or lineages (intraspecific hybridization). The critical element that separates hybridization from typical sexual reproduction is that the parents have had some level of reproductive and/or geographic isolation from each other in the past, and during that long period of time they have evolved and become genetically distinct (as discussed in Rhymer and Simberloff 1996). Past events that might have isolated the parental lineages include the movement of continents, topographical and climate changes, and long-distance dispersal. Recently (within the last few centuries), we have seen acceleration in the movement of plants to new areas of the globe, mostly—as already noted—mediated by humans. This has brought together some closely related plant species and populations that previously had been evolving in isolation from each other, providing unprecedented opportunities for hybridization.

As described above, there is often a lag time between a species' introduction and the beginning of invasive spread, and in many examples multiple introductions of a species are noted before invasion occurs. Both of these observations support the proposal that events occurring after introduction, such as hybridization between an introduced plant and a closely related native plant, or between two closely related introduced plants, can stimulate invasiveness in some species (Abbott 1992; Ellstrand and Schierenbeck 2000; Lee 2002; Rieseberg et al. 2007; Sakai et al. 2001). This is possible because hybridization is an extremely rapid mechanism for increasing genetic variation and producing novel gene combinations on which natural selection can act (Anderson 1949; Lewontin and Birch 1966; Stebbins 1959). As already noted, increasing genetic variation can be especially important for an introduced species that has lost much of its genetic variation due to founder effect. Certainly not all new genetic combinations are beneficial, and many of the hybrids created will not survive as well as their parents did, but hybridization is common enough in plants (Rieseberg 1997; Stebbins 1969) that an estimated 11% of species are derived from hybrid origins (Ellstrand et al. 1996).

Hybridization Leading to Invasion. The first (F$_1$) generation of plants produced by hybridization usually contains a diverse collection of genetic material from each parent. The offspring might be able to sexually reproduce among themselves, creating further generations of hybrid types. Repeated backcrossing of hybrid offspring with the same parental line can transfer individual genes and associated traits from one parent population (or species) to the other. In reality, it is probable that many invasive hybrid plant populations represent a continuum of hybrid types, ranging from new F$_1$ hybrids to highly introgressed individuals that more closely resemble one parent with less genetic contribution from the other (Abbott 1992).

Examples of traits that invaders have acquired through hybridization include tolerance for local temperatures (Milne and Abbott 2000), herbivore resistance (Whitney et al. 2006), increased clonal growth (Vila and D'Antonio 1998), and attractiveness to locally available pollinators (Abbott et al. 2003).

Besides being adapted to the habitat, invasive plants must also be able to reproduce and spread effectively. First generation hybrids, due to chromosomal incompatibilities, are not always able to produce viable seed from sexual reproduction, but there are methods of clonal reproduction that can keep a hybrid lineage expanding, such as agamospermy, vegetative spread, or production of bulbils. Heterosis in early generation hybrids normally breaks down in later generations in sexual populations, but some species avoid that problem by reproducing primarily through vegetative propagation, and are thus able to fix and retain successful hybrid genotypes (e.g. Moody and Les 2002).

Another way for hybrids to escape infertility is by polyploidization. Polyploids are common, making up an estimated 30 to 80% of the angiosperms (Soltis and Soltis 2000). Allopolyploids are plants derived from a hybridization event between different species followed by a doubling of the chromosomes (Stebbins 1950). Because allopolyploids are derived from diverse parents, they and their offspring can be fixed as heterozygous for many of their genes, insuring high levels of genetic variation for the lineage. These polyploids can be less prone to inbreeding depression, and are thus more tolerant of selfing than the parental lineages that created them via hybridization, a characteristic that can be adaptive during the range expansion stage of invasion (Soltis and Soltis 2000). Examples of polyploidization that have allowed subsequently invasive hybrids to escape from infertility include *Spartina* in the British Isles (Raybould et al. 1991; Ayres and Strong 2001; Ainouche et al. 2004) and *Fallopia* in the Czech Republic (Pyšek et al. 2003; Mandák et al. 2005).

Hybridization between native and nonnative plants can be a way for introduced species to gain adaptive traits from native species. It is also possible for genetic material from the introduced plants to be transferred to native popula-

tions. This process is variously referred to as "genetic assimilation," "genetic pollution," or "genetic swamping" (Levin et al. 1996; Mooney and Cleland 2001; Petit 2004; Rhymer and Simberloff 1996; Vila et al. 2000). These citations discuss examples of hybridization involving rare and common plants (not necessarily invasives), in which the rarer species has been or is in eminent danger of assimilation. Recent examples of potential genetic assimilation involving invasives include hybridization between introduced and native dandelions (*Taraxacum officinale* and *T. ceratophorum*, respectively) in the United States (Brock 2004), *Eucalyptus* spp. in Tasmania (Barbour et al. 2006), and *Spartina alterniflora* in California (Anttila et al. 1998). Even if there is no introgression between native and introduced plant species, natives can suffer by being swamped with pollen from the closely related introduced species, reducing seed set or producing only sterile or weak progeny (e.g., native *Lythrum* in Brown and Mitchell 2001).

How Can Population Genetics Research Contribute to Invasive Plant Management?

Genetic Diversity Analyses. Research so far reveals no single pattern of genetic diversity that can explain or predict plant invasion. In addition, because population genetic structure and diversity levels can change dramatically during the course of invasion, most diversity studies at best provide a one-time snapshot of an ongoing process. Nevertheless, using genetic diversity analyses to reconstruct invasion history and determine current genetic structure can provide valuable insights to help manage invasive plants.

As Sakai et al. (2001) pointed out, knowing the amount and distribution of genetic diversity in an invasive plant species can help predict its response to chemical and biological control. Populations with limited genetic diversity are theoretically less likely to contain or rapidly evolve herbicide-resistant individuals, or plant genotypes that are unattractive to biocontrol agents. Several authors have argued that both herbicides and biocontrol are likely to have more immediate impact and longer-term efficacy when used on invasive plant populations with lower levels of genetic diversity (e.g., Nissen et al. 1995; Ye et al. 2003).

The use of diversity data to reconstruct invasion histories, and reveal how a nonnative plant adapts and expands into new territory, can also lead to more effective management strategies. One example is the use of genetic comparisons to identify source populations in an invader's original range and focus the search for new biocontrol agents. Herbivorous insects or pathogens that coevolved with an invasive plant in its native environment have a higher likelihood of effective establishment on invasive populations of that plant in an introduced range elsewhere

(Goolsby et al. 2006; Hopper et al. 1993). Population genetic diversity analysis can also help inform decisions on whether efforts to prevent additional introductions of a nonnative plant would be worthwhile. Frankham (2005) proposed such measures as a priority to prevent resurgence of genetic diversity in the invaded range and reduce the capacity of an alien species to adapt and spread. However, as already discussed, some aggressive invasions involve plant populations with virtually no genetic diversity, so knowing whether ecotype selection or phenotypic plasticity is the most important adaptive strategy for an invader could be helpful. As previously described, for example, Japanese knotweed, water hyacinth, and alligator weed have each demonstrated the ability to invade without first redeveloping genetically diverse populations, and the role of phenotypic plasticity in invasion of different environments has been experimentally demonstrated in alligator weed. Consequently, the appearance of even isolated individuals of these species in a previously uninvaded area should be an immediate cause for concern.

On a smaller local scale, for invasive plant species that combine sexual with clonal reproduction, genetic diversity analysis can determine the relative importance of seedling recruitment or vegetative propagation in patch spread. This is information that can also be used to develop more effective management protocols. For example, in a species that invades a site primarily through rhizomatous patch expansion, biocontrol agents such as ovule-feeding insects could reduce seed production but still not be effective at controlling local spread.

Hybridization Studies. The increase in examples of hybridization involved in invasions should serve as a warning against future importation of nonnative varieties, genotypes, and species when closely related plants—either native or introduced—already exist in the region. Hybridization following such introductions can increase genetic variation, adaptation and invasiveness in introduced plant populations, in addition to swamping native gene pools. Hybridization events add layers of difficulty to the control of plant invasions. For example, when native and introduced species hybridize, leading to genetic pollution of native lineages, decisions have to be made regarding the amount of introgression that will be tolerated in plant populations before they are considered nonnative (Petit 2004). Additionally, some species contain high levels of morphological variation, making hybrids difficult to identify, or hybrids can be morphologically cryptic, looking like either parental type, and thus be undetected.

In cases where hybridization is suspected but there is little or no evidence from morphology, molecular analysis can expose cryptic hybridization events. Recent examples of hybridization revealed by molecular analysis include Gaskin and Schaal (2002), who examined nuclear DNA sequences from saltcedar (*Tamarix* spp.) invasion in North America, which was thought to involve two distinct Asian species. They found that the most common invasive genotypes were in fact hybrids not found in the native Asian range. In another example, Williams et al. (2005) showed the invasion of Florida by Brazilian peppertree (*Schinus terebinthifolius*) to contain morphologically cryptic hybrids derived from separately introduced populations with different South American origins. Hybridization between these different peppertree introductions created invasive populations in Florida with high levels of genetic variation, in addition to novel hybrid genotypes.

Detecting introgression using either morphology or molecular tools can be even more difficult than detecting first generation (F_1) hybrids, because repeatedly backcrossed plants might ultimately retain only a fraction of the genetic material from the other parental lineage. For example, in an analysis of hybridization between *Rorippa sylvestris* and *R. austriaca* in Germany, some hybrids were found to have morphology similar to one of their parents, *R. sylvestris*, and a clear estimate of levels of hybridization would not have been accurate using morphology alone (Bleeker 2003).

Hybridization events also can complicate biological control of invasive plants. As already discussed, classical biological control relies on coevolution of the target plant species and the control agent, usually an insect or pathogen. The host-specificity of the agent is optimally limited to the target species, but can occasionally be even more limited if the agent attacks only certain genotypes or varieties of the target plant (e.g., Bruckart et al. 2004; Burdon et al. 1984; Goolsby et al. 2006). If a biological control agent is effective against only a small number of genotypes in an invasive plant population, there is potential for the uncontrolled genotypes to increase their range. This has been reported with ecotypes of *Chondrilla juncea* in Australia (Burdon et al. 1981). For this reason, when hybridization is suspected in an invasion, resulting in the formation of novel genotypes, host-specificity testing of biological control agents should be carried out on a range of parental and hybrid types.

Future Research Directions

Information on intraspecific genetic diversity and population genetic structure is currently available for only a small number of invasive plants. Future research in this area should not only include genetic diversity analyses for additional species, but also enlarge the scope and scale of such studies. The use of high-throughput molecular marker systems now found in many crop breeding programs, combined with the increasing availability of more powerful and user-friendly analytical software for population genetics, enables larger numbers of samples to be efficiently

processed. Expansion of genetic structure and diversity analyses to regional or continental spatial scales for more invasive plant species would greatly enhance our understanding of global plant invasions and associated evolutionary processes.

Hybridization in plant invasion has now been reported for a number of species, based on morphological observations or, more recently, determined by molecular analyses. Further research is needed to assess these situations by examining the relative abundance of hybrid or introgressed offspring compared to their parents, and how the different types are distributed. With this information we can determine if hybrids are more widespread and invasive than the parents in certain habitats, although we still might not know the mechanisms responsible for the hybrid's invasion success. Ultimately, as suggested by Abbott et al. (2003), Rieseberg et al. (2007), and Whitney et al. (2006), a better understanding of how hybridization can enhance invasiveness will come from comparisons of suspected adaptive traits in both parental and hybrid lineages.

An unresolved issue that looms large in the ecological genetics of plant invasion is whether key genes mediate invasive behavior, what might be the functions of such genes, and whether they are unique to one invasive plant or shared by multiple species. Plant genomics techniques such as microarray analysis could be invaluable in answering such questions, although the lack of resources needed to develop microarrays for diverse weedy plant species remains a barrier. More immediately accessible are new methods of statistical analysis that probe molecular marker data for signatures of local selection (for an example, see Schlötterer 2002). This approach to genetic analysis deserves more widespread application, and could provide an alternative route to identification of alleles contributing to invasion.

Research using plant invasions as model systems to explore various hypotheses in ecology and evolutionary biology will undoubtedly continue. However, from the perspective of invasion management, perhaps the most fundamental question in the ecological genetics of plant invasion is whether aggressive range expansion by non-natives is driven primarily by genetically-determined traits innate to a species, environmental factors such as disturbance, or the interaction of the two. We propose this should be a major focus of future research; more complete answers could guide land and resource management practices toward a future less dominated by unwelcome aliens.

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GLOSSARY OF GENETIC TERMS

Additive genetic variation: variation for a trait controlled by multiple genes. Alleles at the different loci each contribute a fixed amount to the trait, so the genetic component of the final phenotype is the sum of the effects of these contributing alleles.

Allele: One of two or more different versions of a gene found at the same position (**locus**) on a chromosome. Different versions of a gene arise through changes in the DNA sequence (**mutation**).

Allele frequency: relative proportion of a given allele in the gene pool. Frequency estimates provide a measure of how common an allele is in a population.

Apomixis: asexual production of seeds without fertilization. **Agamospermy** is a form of apomixis in which an embryo

forms from the nucellar tissue. Apomictic offspring are genetically identical to the parent plant.

Backcross: crossing of hybrid offspring with one of its parents or parental lines.

Ecological genetics: branch of population genetics integrating field and laboratory investigations into the origin and maintenance of genetic variation within and among natural populations, and the genetic basis of population change and adaptation in natural environments.

Founder effect: reduction in genetic diversity seen when a small subset of individuals separates from a larger more diverse group to form the basis of a new population

Gene flow: movement of alleles from one population to another. In plants this occurs through movement of pollen, seed, or other propagules.

Gene pool: the sum total of all the alleles present in a population.

Genetic drift: random change in allele frequency. This can occur in populations with a small number of reproducing individuals, so the limited number of gametes forming the next generation does not fully represent the genetic diversity of the previous generation.

Genetic structure: pattern created by nonrandom distribution of diverse genotypes within or among populations.

Genetic swamping: loss of genetic identity or purity in one lineage or species resulting from dilution of the gene pool through hybridization with another lineage or species.

Genotype: combination of all alleles possessed by an individual; subject to recombination in subsequent generations in sexually reproducing organisms.

Haplotype: combination of linked alleles on the same DNA strand transmitted together from one generation to the next.

Heterosis: "hybrid vigor" in hybrid offspring expressed as increase in size, growth rate, fecundity or other adaptive traits conferring greater fitness than seen in either of the parent lines.

Heterozygous: The two (or more) alleles present at a given set of chromosomal loci are different sequences, so a cell contains more than one version of a gene.

Homozygous: the two (or more) alleles present at a given set of chromosomal loci are identical sequences, so a cell contains more than one identical copy of a gene.

Hybridization: interbreeding between plants of different taxa (interspecific hybridization) or between plants from different populations of the same taxon (intraspecific hybridization) that have undergone some degree of evolutionary separation and hence genetic differentiation.

Inbreeding depression: reduced fitness in offspring from mating between related individuals. In plants this can be seen as reduced output of viable seed, poor germination and/or loss of seedling vigor.

Introgression: transfer of allele(s) from one species or lineage to the gene pool of another through repeated backcrossing.

Phenotype: physical expression of a trait (or traits) in an individual.

Plasticity: ability of a single genotype to produce more than one phenotype, usually in response to environmental variables.

Polymerase chain reaction (PCR): molecular technique for synthesizing multiple copies of a designated DNA sequence.

Polyploidy: possession of more than two copies of each chromosome per cell. E.g., **triploids** have three copies of each chromosome, **tetraploids** have four copies, **octoploids** have eight copies, etc.

Preadaptation: development of a phenotypic characteristic before selection in a particular environment imposes a need for it. For example, an already drought-tolerant plant species could be described as preadapted to expand its range into a novel arid environment.

Selection: in populations under selection, individuals with more adaptive (and hence advantageous) traits have greater reproductive success and contribute more of their alleles to the gene pool of the succeeding generation.