

Population Genetics of Invasions: Can We Link Neutral Markers to Management?¹

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Abstract: Molecular data are becoming easier to collect and can help us address many important questions in invasion biology. However, for most organisms, the connection between molecular loci and phenotypic traits is not direct. Here, I review some fundamentals of population and ecological genetics and point out limitations of molecular data, particularly when the data are from loci without a known connection to the phenotype. I then discuss the ways that molecular data may facilitate management of invasive weeds, despite the limitations. Key uses of molecular data in invasive weed management include identifying species, determining their origins, and understanding mechanisms and rates of spread.

Additional index words: Biological invasions, ecological genetics, phylogeography.

Abbreviations: AFLP, amplified fragment length polymorphisms; cpDNA, chloroplast DNA; RFLP, restriction fragment length polymorphisms.

INTRODUCTION

Invasive weeds are nonnative plants introduced to a new range that establish and then proliferate to an extent that they are economically or environmentally damaging. Weed scientists, ecologists, and evolutionary biologists are using the tools of population genetics to further their understanding of the causes and consequences of plant invasions (Burdon and Brown 1986; Hollingsworth et al. 1999; Nissen et al. 1992; O'Hanlon et al. 1999; Pester et al. 2003; Ramakrishnan et al. 2004; Rowe et al. 1997; Scott et al. 1998a, 1998b; Walker et al. 2003; Ye et al. 2004). However, the links between neutral genetic markers and management of invasive weeds remain tenuous. Managers need concrete tools to control invaders while promoting desirable plants and guidelines to help them implement and integrate different approaches effectively. Unfortunately, most molecular genetic information does not contribute directly and immediately to management issues. However, population genetic approaches can deepen our understanding of the basic biology of invasive weeds, and basic biology is the foundation upon which sound management efforts are built (Hall et al. 2000; Masters and Sheley 2001). Three aspects of the basic biology of weeds that molecular genetic data can help elucidate, which are crucial for developing appro-

priate management are (1) knowing which species are present, (2) pinpointing areas of origin of invaders, and (3) understanding methods and distance of migration.

In this review, I seek to clarify both the limitations and strengths of population genetic data because they relate to weed management. First, I introduce briefly population genetics and the related field of ecological genetics and review the relationship between neutral loci and ecologically important quantitative traits. Then, I discuss how population genetic data can be brought to bear upon basic biological issues of relevance to weed management.

POPULATION AND ECOLOGICAL GENETICS

Population genetics focuses on describing the amounts and structuring of genetic variation within and among populations and understanding the evolutionary processes that lead to observed patterns. With the advent of molecular methods, one active area is quantifying the structure among and variation within populations in molecular loci. The genetic markers used include DNA sequence data, microsatellite loci, single nucleotide polymorphisms, amplified fragment length polymorphisms (AFLPs), random amplified polymorphic DNA, restriction fragment length polymorphisms (RFLPs), and others. With an appropriate laboratory setup, collecting data on such markers is relatively fast and simple. The utility and characteristics of these markers have been thoroughly reviewed elsewhere (Jasieniuk and Maxwell 2001;

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O'Hanlon et al. 2000; Parker et al. 1998; Sunnucks 2000) and will not be treated in this study. While these DNA markers may be close to genes, they are often in regions of the genome that do not code for proteins and are, therefore, presumed neutral for most analyses. Even if they do play a role in determining the phenotype, typically that role is unknown, except in model organisms.

In contrast to population genetics, ecological genetics is the study of the ecological factors influencing adaptation and evolutionary change and is often experimental rather than descriptive (Ford 1964). It is a discipline founded on quantitative genetic approaches for studying selection and the response to it (Falconer 1989; Lynch and Walsh 1998; Roff 1997). Although quantitative genetics was historically used for animal and plant breeding, ecological genetics turns those tools toward quantifying the structure among, and variation within, populations in ecologically important quantitative traits: traits that affect fitness of individuals and therefore the growth rates of populations. These are traits that generally are coded for by multiple genes, many of which have small effects and some of which have larger effects. These genes may interact with each other in the development of different phenotypes. Examples of ecologically important quantitative traits of weeds include resistance to insects and pathogens used for biological control (Hanley and Groves 2002; Peng et al. 2004) and competitive ability (Burdick and Konisky 2003).

It is important that managers understand the distinction between population and ecological genetics to avoid the misconception that the molecular genetic data used for population genetic analyses provide direct information about particular ecological traits of the weeds that they are managing. Three recent meta-analyses have reviewed the relationship between molecular genetic variation and phenotypic variation (McKay and Latta 2002; Merila and Crnokrak 2001; Reed and Frankham 2001). Reed and Frankham (2001) found only a weak correlation between genetic diversity and ecologically relevant traits that explained only 4% of the variation, whereas Merila and Crnokrak (2001) found a somewhat stronger correlation but with much scatter. All three studies found that among quantitative traits, morphological traits were more strongly correlated with neutral markers than were ecologically important life-history traits. It is probable that this pattern is due to morphological traits being subject to weaker selection than ecologically important traits (Kingsolver et al. 2001) and so is more likely to evolve in similar manner as selectively neutral molecular markers.

These reviews of the relationship between molecular and quantitative variation show that neutral loci sometimes will not match patterns in ecologically important traits. One common pattern that the reviews brought to light is that there often is less variation and geographic structure in molecular markers than in ecologically important traits (Armbruster et al. 1998; Bekessy et al. 2003; Cai et al. 2004; Palo et al. 2003; Steinger et al. 2002). For example, Steinger et al. (2002) found greater divergence in quantitative traits than AFLPs among populations of common groundsel (*Senecio vulgaris*). The patterns in the quantitative traits suggested that the plants are responding to different selection pressures in ruderal and agricultural habitats. This was not reflected in the neutral loci (Steinger et al. 2002). In a study of wild rice (*Oryza sativa*), a common weed in cultivated rice, Cai et al. (2004) explored molecular genetic and phenotypic variation across its native range. They found that RFLPs showed a pattern of isolation by distance, whereas ecotypic variation was found in breeding system that varied with habitat type and was not reflected in the RFLP markers (Cai et al. 2004). Thus, population genetic data often cannot substitute for ecological experiments.

The relationship found between molecular markers and phenotypic traits depends upon the predominant evolutionary forces (mutation, genetic drift, selection, or gene flow) and also on the particular molecular markers and phenotypic traits measured. If the molecular markers themselves truly are neutral, then whether they reflect patterns in an ecological trait of interest will depend on their physical relationship with the genes coding for the trait of interest. If a molecular marker is close to a functional gene underlying the trait of interest, then it is likely to show similar structure of variation because of genetic hitchhiking (Slatkin 1995), whereas if it is remote from such functional genes, then it is likely to show patterns of variation shaped by genetic drift.

Clearly, the more of the genome that is assayed, the more likely it is that a molecular marker will be found that reflects differences in ecologically important traits. AFLPs are used widely in plant breeding because they provide a wide assay of the genome, and often, particular AFLP loci are linked to traits of interest. Quantitative trait locus mapping (Asins 2002; Jones et al. 1997) and other means of developing functional molecular markers that are linked to traits of interest (Andersen and Lubberstedt 2003; van Tienderen et al. 2002) are becoming more feasible. However, developing such markers requires time and dedicated funding. Weed science is moving toward having the tools of functional genomics (Wel-

ler et al. 2001), but currently, only the best-studied plants are understood at that level. For most species, we lack direct links between the genotype and the phenotype. Thus, most molecular markers may not be able to tell us whether a population or an individual has a certain ecological characteristic of interest, but they can provide information that is important for understanding the basic biology of weed invasions.

APPROPRIATE USES FOR MOLECULAR MARKERS

The main contribution of molecular markers in weed management is to provide information regarding the identity of weeds, their origins, and their spread.

Species Identity. The identity of invasive weeds is not always known, yet it can influence the goals of management (e.g., population regulation below economic or environmental thresholds, containment to a particular area, eradication) and the choice of management tools. Although many integrated weed management tools are useful across multiple taxa, knowing exactly which taxa are present can aid in choosing the most appropriate tools. This is particularly relevant for biological control where the control agents may only be effective against a single species or even particular genotypes within a species (Lym and Carlson 2002; Lym et al. 1996) and can also be vital for managing resistance to herbicides (Jasieniuk and Maxwell 1994). Thus, it is vital to know the identity of the invasive weeds, both at the species level and below the species level if there are important ecological variants within the species. In addition, it is important to know whether weeds are hybridizing, which may complicate both identification and management.

Genetic data can be used to identify invasive species and determine whether or not hybridization is occurring. Sequence data from the nuclear and organellar genomes can inform robust systematic analyses that can be used in taxonomic revisions of problematic groups. Molecular genetic data also can be useful for distinguishing among species in groups that are difficult to distinguish morphologically.

An example of the use of molecular markers in weed identification comes from Wetzell et al. (1999), who published a set of molecular markers to identify difficult native and exotic *Amaranthus* species. Another complex weedy genus is *Centaurea*. Molecular data (chloroplast DNA [cpDNA] sequences) suggest that there may be a cryptic invasion of a closely related species *C. vallesiaca* into North America (Hufbauer et al. 2004). The land managers in the areas known to have the *C. vallesiaca*-

like cpDNA haplotypes are attempting to eradicate their populations (D. Woods, personal communication), an effort that might reduce the possibility of future hybridization of this species with other closely related *Centaurea*.

Another cryptic invasion appears to be occurring below the species level with common reed (*Phragmites australis*) in North America (Saltonstall 2002). Molecular markers show that there is an invasive exotic genotype of this native species. This would have been difficult to verify with other means. Knowing that the expansion of common reed is because of an invasion has spurred research on how it differs from the native genotypes in ways that can be used by managers. It has been found that the specialized herbivore complex of the invasive genotype differs from native genotypes, making classical biological control a possible option for management (Blossey 2003). There are also differences in the physical regime that the invasive genotype of common reed can tolerate and in its competitive abilities, leading to management approaches aimed at reducing human disturbance (Burdick and Konisky 2003). Ludwig et al. (2003) argue that whether or not common reed should be considered an invasive weed that requires active management or not, is something that will need to be determined on a case-by-case basis, with the genetic identity of the plant a primary consideration. Saltonstall (2003) has developed a technique for relatively rapid identification of the invasive genotype that should facilitate using the Ludwig et al. (2003) decision tree.

Gaskin and Schaal (2002, 2003) explored the identity of invasive *Tamarix* in North America and found four distinct genetic groups representing four to six species. In addition, many individuals are hybrids that are unique to the invasive range. The frequency of hybridization may help explain the invasiveness of *Tamarix* and also may influence the ability of biological control agents to effectively control them (Gaskin and Schaal 2002). The population genetic data were used in the design and interpretation of host-specificity tests of the leaf beetle biological control agent *Diorhabda elongata* (Coleoptera: Chrysomelidae) (DeLoach et al. 2003).

These recent examples show that molecular genetic data are being used actively to help determine the identity of weeds and that knowing the identity can contribute to developing and implementing weed management strategies.

Provenance of Invasions. The provenance of an invasion is the particular location within the native range that served as the source of an introduction into a new range.

The traits that are present in invasive species depend largely on the provenance of the invasion. For example, if an introduction of a widespread species was from an area with a cold climate, the invaders would be more likely to be cold tolerant than if the introduction was from an area with a mild winter. The amount of genetic variation in traits depends upon the number of individuals introduced and whether there were multiple introductions from different locations or only one. Knowing the provenance of a weed, and whether or not multiple introductions have occurred, is important for some types of management, particularly biological control. Although historical records can reveal much about weed origins, genetic data can expose introductions not found in historical records and may show that not all known introductions have contributed to invasions. The process of determining the genealogical relationships among geographically separated individuals is called phylogeography (Avice 2000). Roderick (2004) provides a nice review of the strengths and weaknesses of phylogeographic approaches in attempting to determine relationships among populations and origins of invasive species. It is only possible to pinpoint the areas of origin of invaders using molecular markers if there exists relevant variation in the genetic marker of interest in the native range. This is easy to understand at the extreme end of no variation in the marker: if all individuals and populations across the native range share the same genotype, then there will be no distinguishing feature with which to associate a particular population in the native range with the invasive population. However, a variable marker does not necessarily mean that it will be possible to find the source of an invasion. The marker must be both variable and have a definite geographic signature. For example, if all regions within the native range share all the variants, then identifying which region an invasion containing a particular variant is from will not be possible. However, if different regions have different genetic variants, then the genotypes in the invasive range should be able to be matched to a specific region of the native range.

The data that are best suited to phylogeography are DNA sequence data, particularly from uniparental, non-recombining sources such as cpDNA. The lack of recombination means that different mutations remain linked, and this makes it simpler to infer the genealogical relationships of given strings of sequences, rather than using overall similarity, which can give biased patterns because of convergent evolution (Avice 2000). Nuclear regions also can be used (Gaskin and Schaal 2002), par-

ticularly short regions with a low probability of recombination, but cloning may be necessary to determine the haplotypes of heterozygotes.

An excellent example of using phylogeography to develop appropriate management is found in the work of Goolsby et al. (2004). Goolsby et al. (2004) explored cpDNA sequences of Old World climbing fern (*Lygodium microphyllum*) from invasive populations in Florida and populations from the native range and were able to find a single location that matched the haplotype of the Florida invaders exactly. They compared the ability of a mite (*Floracarus perrepae*, Eriophyidae) from several locations in the native range to feed on and damage the genotype of the weed present in Florida. Genotypes of *F. perrepae* from the putative source of the fern were most damaging. Prerelease research on the specificity and efficacy of *F. perrepae* is in progress, and it appears to be a promising tool for managing this weed invasion.

Clear patterns of variation such as those discovered by Goolsby et al. (2004) are not always found. In fact, a main problem with sequence data is that even noncoding regions may not have the requisite variation to reveal origins. In addition, they can be time consuming and expensive to collect. Markers such as allozymes, microsatellites, and various fingerprinting techniques are typically much more variable than sequence data, and some are also less expensive. With these types of markers, similarity among populations can be inferred, and assignment test approaches (Pritchard et al. 2000) can be quite useful in elucidating weed origins. In addition, they may reveal aspects of the basic biology of the weeds that can be useful to managers. For example, AFLP variation in invasive Japanese knotweed (*Polygonum cuspidatum*) in the U.K. suggests that it is composed of a single self-incompatible clonal individual (Hollingsworth et al. 1998). This makes it particularly important that border officials and weed managers guard against further introductions, which would enable sexual reproduction and dispersal of the invasive weed through seeds as well as clonally.

Migration. Understanding the methods by which invasive weeds spread, and the distance that they spread, can aid in the planning of control measures (Cook et al. 1996; Hall et al. 2000; Prather and Callihan 1993; Smith et al. 1999; Thill and Mallory-Smith 1997). This is particularly important in efforts to contain an invasive weed within a particular area or eradicate it all together, because estimates of dispersal distance and knowing which life stages to search for can guide deployment of limited resources. There are many means of measuring weed dis-

persal, including direct measurement (Gardener et al. 2003; Grice 1998), Geographic Information Systems (Prather and Callihan 1993), and genetic approaches (Khudamrongsawat et al. 2004; Scott et al. 1998b). Collecting genetic data has limitations and can be costly but can provide unique information not available from other approaches. In particular, genetic approaches to estimating migration rates give an average through time that may capture rare, long-range dispersal events that approaches such as mark-recapture miss (Slatkin 1987). However, many assumptions are involved in the calculations of migration rates, and those assumptions are unlikely to be met in introduced weed populations (Whitlock and McCauley 1999). In particular, the assumption that there is no selection is probably not realistic in populations of invasive weeds that are being actively managed because most management approaches impose selection. Also, the assumption that the populations are at equilibrium between migration and genetic drift is probably not realistic for populations of invasive weeds that have been introduced recently because it takes some time for mutation–drift equilibrium to establish. Given these difficulties, direct measurement of movement is often preferable to estimates derived from molecular data. Thus, molecular genetic data are applied less often to understanding spread than they are to determining the identity and provenance of weeds.

CONCLUSIONS

Studying the population genetics of weed invasions has the potential to provide insights into the evolutionary consequences of invasion, and in the long run, should improve our ability to prevent and manage invasions. However, population genetics data can rarely be directly and immediately applied to the management of environmentally and economically disastrous weed invasions. In this review, I have discussed three main ways in which population genetic data on neutral molecular loci can contribute to management: identifying species, determining origins, and evaluating dispersal. Population genetic data can play a particularly important role in the first two. For population genetics to offer more to weed management, the scientists conducting the research need to focus their work on questions relevant to managers and to communicate their findings to managers. An excellent way for this to happen is the development of knowledge networks, as proposed by Jordan et al. (2003). The linking of scientists and managers in such networks should lead to innovation in both groups.

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