

# What can DNA tell us about biological invasions?

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**Abstract** It is often hoped that population genetics can answer questions about the demographic and geographic dynamics of recent biological invasions. Conversely, invasions with well-known histories are sometimes billed as opportunities to test methods of population genetic inference. In both cases, underappreciated limitations constrain the usefulness of genetic methods. The most significant is that human-caused invasions have occurred on historical timescales that are orders of magnitude smaller than the timescales of mutation and genetic drift for most multicellular organisms. Analyses based on the neutral theory of molecular evolution cannot resolve such rapid dynamics. Invasion histories cannot be reconstructed in the same way as biogeographic changes occurring over millennia. Analyses assuming equilibrium between mutation, drift, gene flow, and selection will rarely be applicable, and even methods designed for explicitly non-equilibrium questions often require longer timescales than the few generations of most invasions of current concern. We identified only a few population genetic questions

that are tractable over such short timescales. These include comparison of alternative hypotheses for the geographic origin of an invasion, testing for bottlenecks, and hybridization between native and invasive species. When proposing population genetic analysis of a biological invasion, we recommend that biologists ask (i) whether the questions to be addressed will materially affect management practice or policy, and (ii) whether the proposed analyses can really be expected to address important population genetic questions. Despite our own enthusiasm for population genetic research, we conclude that genetic analysis of biological invasions is justified only under exceptional circumstances.

**Keywords** Population genetics · Phylogeography · Invasive species · Molecular markers · Nonequilibrium ·  $F_{st}$

## Introduction

Research in invasion biology is often a blend of applied and basic objectives. Applied objectives include predicting, preventing, and controlling undesirable invasions and their ecological or economic consequences. Basic objectives are rooted in the principle that we can address important theoretical questions about natural colonization, adaptation, and biotic interactions by treating species translocations as largescale, long-term experiments in ecology and

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evolutionary biology. Indeed, there are now many examples of successful invasion biology research programs with broadly interesting results in population and community ecology and sociobiology (Sax et al. 2005; Simberloff and Rejmanek 2011). In addition, ecological research has sometimes directly influenced conservation policy and practice (Simberloff 2009). Here we address the question of whether similar success should be expected for population genetics.

Although it might at first seem obvious that biological invasions should provide a rich testing ground for population genetic theories and methods, closer inspection reveals that such theories and methods are rarely applicable to the short timescales and coarse-grained genomic resolution of most biological invasion research. Further, it is unusual to find population genetic questions with any applied relevance for conservation management (though there are notable exceptions). We briefly critique the application of molecular population genetics in four areas of invasion biology: origin and propagule pressure, founder effects, population structure within the invaded range, and hybridization with native species.

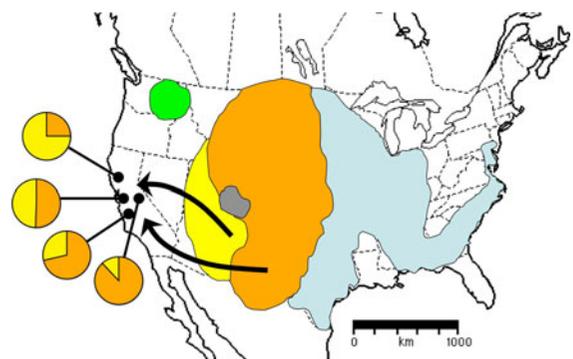
### Origins and propagule pressure

What is the geographic source of an invasive population? Was an invasive species established by a single or multiple introductions? These are forensic questions that might be of some interest for management or law enforcement (Ascunce et al. 2011), and the roles of propagule size and genetic diversity in establishment success are important general issues (Sakai et al. 2001). These questions are reasonably tractable in some cases with good molecular data, and sometimes yield results that would not have been predicted from directly documented histories of translocations.

To identify the geographic source of introduced populations and determine the number of introductions, the native range of the invasive species must be thoroughly sampled and potential source populations must be sufficiently differentiated. If genetic variation is highly structured in the native range (i.e., high levels of among-population variation), then genotypes found in introduced populations might be assigned with high probability to geographic

locations within the native range using clustering or assignment methods (Excoffier and Heckel 2006). For example, Johnson et al. (2011) used mtDNA to show that introduced tiger salamanders (*Ambystoma mavortium*) in California originated from source populations in both the Great Plains and Southwest regions of North America, and not from the Pacific Northwest or east of the Mississippi River (Fig. 1). Moreover, at least 20 unique maternal lineages were identified in the introduced range (Johnson et al. 2011). These genetic results are consistent with the reported introduction history, involving multiple releases of salamanders from Texas, Colorado, and New Mexico (Riley et al. 2003). Integrating molecular and historical information, Ascunce et al. (2011) inferred that the United States has been the major source of invasive fire ants (*Solenopsis invicta*), a worldwide bridgehead effect for this native of South America. In contrast, Thulin et al. (2006) could say only that introduced populations of the small Indian mongoose (*Herpestes auropunctatus*) carried alleles not found in native samples from Bangladesh or Pakistan, but could not identify putative sources owing to inadequate sampling of the native range (because of restrictions on scientific collecting in India and the Middle East).

As in the case of the tiger salamanders, multiple introductions can be inferred if alleles that do not co-occur in native populations are found in introduced



**Fig. 1** Introduced tiger salamanders in California (samples represented by pie charts) show mitochondrial haplotypes from both the Southwestern (yellow) and Great Plains (orange) groups, consistent with multiple introductions from Colorado, New Mexico, and Texas (Riley et al. 2003; Johnson et al. 2011). Pacific Northwest (green), San Juan (gray), and Eastern (blue) groups are not represented in the introduced range

samples (Johnson et al. 2011). Multiple introductions from different sources can increase within-population genetic variation of introduced populations relative to native populations (Kolbe et al. 2004). This is indicative of increased propagule pressure and likely enhances the probability of establishment (Frankham 2005). Additionally, introductions from different sources into different extralimital sites are the primary source of variation among introduced populations because mutation and drift are unlikely to generate intrinsic population differentiation over historical timescales. Thus, the extent of differentiation among introduced populations is likely dominated by introduction history rather than steady state dynamics (Marisco et al. 2011). Ultimately, the accuracy of estimated numbers of introductions and origins of introduced populations is determined by sampling intensity in both the introduced and native ranges, the resolution of the molecular markers employed, and the scale of genetic differentiation across the native range (Dlugosch and Parker 2008).

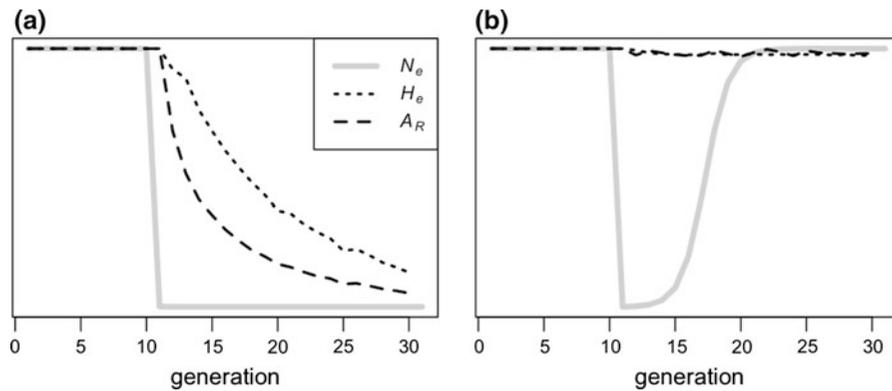
### Founder effects

Detecting bottlenecks in recent invasions seems to be a common component of attempting to assess genetic structure of invasive species. Investigators are interested in understanding the initial conditions of the invasion in order to better control and predict future invasions (Dlugosch and Parker 2008; Sakai et al. 2001). Bottlenecks during initial colonization might mean that (i) the invaders are vulnerable to inbreeding depression and have a reduced evolutionary potential (Frankham 2005), and (ii) that the invasive populations are the result of a single colonization event and not subject to recurrent gene flow (Russell et al. 2009).

Population bottlenecks cause a loss of alleles at a faster rate than a loss of gene diversity, generating a pattern of “heterozygosity excess” or deficiency of rare alleles (Nei et al. 1975). Recent bottlenecks can be detected by examining allele frequencies at polymorphic loci within an extant population and testing for reduced allele number and excess heterozygosity compared to that expected for an equilibrium population (Cornuet and Luikart 1996; Luikart et al. 1998). Cornuet and Luikart (1996) conducted power analyses of sign and regression tests for bottlenecks, two tests

implemented in BOTTLENECK (Piry et al. 1999), and demonstrated that statistical power derives from a narrow combination of factors in the analysis. In particular, very recent bottlenecks (0.01–0.025  $N_e$  generations ago) are difficult to detect because the expected deviation from mutation-drift equilibrium appears after several generations of reduced population size. Further, Cornuet and Luikart (1996) simulated only isolated populations experiencing a sudden decline without recovery. Rapid recovery to the original effective population size reduces the genetic impact of a bottleneck (Nei et al. 1975). In Fig. 2, we illustrate the expected effects of genetic drift on gene diversity ( $H_e$ ) and allelic richness over time after a severe reduction in population size without recovery (Fig. 2a) versus with rapid recovery (Fig. 2b). Other simulations show that recovery and/or immigration can make severe bottlenecks or founder effects undetectable (Reynolds 2011), and spatial population structure might give false signals of bottlenecks (Chikhi et al. 2010). Given that most invasions of interest involve rapid population growth and expansion, the standard bottleneck tests are unlikely to recover genetic signatures characteristic of sustained reduction in effective population size (Fig. 2).

Testing for bottlenecks has been justified as a way to determine the relative importance of population size to invasibility, or to demonstrate that the invasive species has overcome the genetic and demographic consequences of small population size (e.g., Alexander et al. 2009; Russell et al. 2009). This is perhaps by definition a post-hoc tautological test— if most invasive species are the result of small numbers of propagules then demonstrating that a successful colonist has undergone a bottleneck merely extends the notion that invasive species are good at dealing with the deleterious effects of small population size. It is not clear how such information might help manage invasive species (Simberloff 2003). Alternatively, low genetic diversity might indicate low adaptive potential to overcome control measures (Le Roux et al. 2008). However, molecular genetic variation is a poor indicator of additive genetic variance for any particular trait (Lynch and Walsh 1998; Reed and Frankham 2001) and the actual adaptive potential will not be known until selection is applied. It is important to recognize that inbreeding depression (low fitness of inbred offspring) is not the same thing as inbreeding (the simple fact of breeding



**Fig. 2** Founder effects on average gene diversity ( $H_e$ ) and allelic richness ( $A_R = \text{number of alleles} - 1$ ). **a** During a sustained bottleneck of effective population size  $N_e = 10$ , the more rapid decline in  $A_R$  versus  $H_e$  gives the characteristic genetic signature of a bottleneck (Cornuet and Luikart 1996). **b** The effect is undetectable when a founder population of  $N_e = 10$  rapidly increases to  $K = 10,000$  following the

between related individuals) and neither of these can be diagnosed by molecular patterns alone. Although  $F_{IS}$  is sometimes called an “inbreeding coefficient”, it is only a measure of deviation from expected Hardy–Weinberg genotype frequencies and does not directly indicate anything about mating system, population size, or fitness (Hartl and Clark 1997; Templeton and Read 1994).

Among the more interesting results relating founder effects to invasions is the expression of unicoloniality in invasive ants, such as the Argentine ant, *Linepithema humile* (Tsutsui et al. 2000). Owing to severely reduced genetic variation in the introduced range, workers from different colonies are rarely able to differentiate their true sisters from workers from other colonies. As a result, territoriality is rare and cooperative behavior is extended across massive supercolonies occupying hundreds of  $\text{km}^2$ . However, in many study systems, introduced populations harbour levels of genetic variation similar to native populations (Dlugosch and Parker 2008). This is probably explained by the fact that genetic drift is not expected to remove substantial amounts of variation from expanding populations (Fig. 2).

### Population structure in the introduced range

Characterizing the processes that have caused and maintain the population structure of an invasive

Beverton–Holt model with  $R = 3$ . For each variable, the abscissa is scaled from zero to its maximum value. Initial allele frequencies were based on microsatellite data from a native population of small Indian mongoose (Thulin et al. 2006). Lines represent averages over 100 simulations of genetic drift given each demographic scenario (Online Resource 1)

species is, on the surface, an appealing prospect. Invasion biologists might be interested in knowing, for example, whether significant migration occurs among established populations. Such information might be used to intuit the factors that either inhibit, or facilitate, gene flow among populations. Similarly, information regarding the historical spread of an invasive species might be useful for understanding the factors that influence the rate of spread, or the location of the initial introduction, much as the field of phylogeography aims at understanding the history of native taxa. Describing geographic relationships might also be important for management efforts, where distinctly different populations can be considered unique management units, similar to the approach used for endangered species, but with an opposing objective (Chadès et al. 2011). Although the motivation for understanding the patterns and processes responsible for population structure has virtue (but see Simberloff 2003), application of population genetic methods to elucidate the mechanisms responsible for patterns of variation have limited utility.

The most commonly used approach to describe among-population variation, as well as migration among populations, is to interpret Wright’s  $F$ -statistics, in particular  $F_{ST}$  (including the analogs  $G_{ST}$ ,  $R_{ST}$ , and  $\Phi_{ST}$ ). These statistics provide a framework for understanding how genetic variation is partitioned among a priori defined populations. Under equilibrium conditions, there is a direct inverse relationship

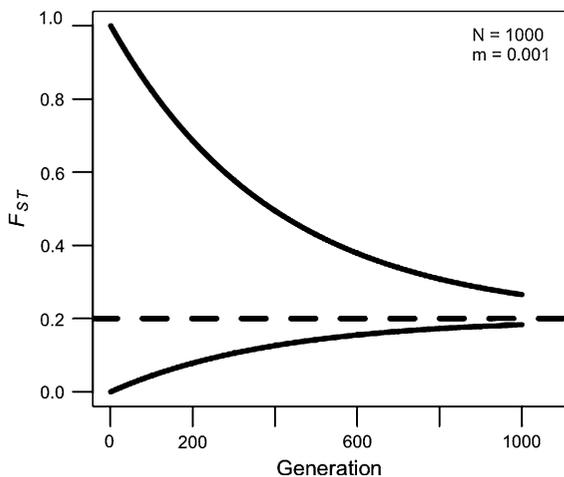
between  $F_{ST}$  and rates of dispersal between populations (Wright 1931). However, the form of this relationship depends on other assumptions (Rousset 1997; Whitlock and McCauley 1999) and minimally requires a balance between mutation and immigration, which introduce genetic variation into a population, and drift, the stochastic process that tends to remove variation. It takes many generations for  $F_{ST}$  to approach its expected steady-state value (Fig. 3), usually in excess of the number of generations associated with a typical human-mediated biological invasion. Therefore, population genetic inferences of migration rates among introduced populations are unlikely to be valid.

Even methods described as “non-equilibrium” rely on specific assumptions about population structure and history that might be greatly disrupted by recent translocations. The most promising approach is to develop custom models incorporating explicit geographic and historical scenarios based on the particular study system. However, as demonstrated by Estoup et al. (2010), the most important result of such efforts might be that ecological and historical survey data are much more informative than genetic data. A potentially informative area for future research is to ascertain whether the resolving power of next-generation DNA technologies can be combined with new

computational methods and custom historical models (Estoup et al. 2010; Gompert and Buerkle 2011; Gompert et al. 2010; Peter et al. 2010) to provide useful insights about biological invasions.

Most invasive species that receive attention are introduced species and, by definition, in violation of the underlying assumptions of population genetic tools used to estimate among-population structure or migration rates. Specifically, the time since the initial introduction and subsequent expansion of range of an introduced invasive species is too recent for the effects of mutation and drift to be at equilibrium, particularly when effective population sizes are large (Rieux et al. 2011). Furthermore, by their very nature that causes them to be classified as invasive species, population size will clearly not be constant over the amount of time required to understand, or estimate the important parameters of, the processes of mutation and drift. Thus, beyond characterizing how variation is partitioned among locales, there is little information provided by implementing population genetic theory to most cases of invasion biology. One potential exception is for invading species with a short generation time and relatively high mutation rates, such as pathogenic bacteria or viruses.

Applying phylogeographic methodologies to invasive species is even more fraught with difficulties. Methods that assess concordance between geography and the topology of phylogenetic trees, or networks, require sufficient time (generations) for drift and mutation to affect the distribution of molecular marker variation. These considerations also affect applicability of methods designed to infer histories of range expansion on post-glacial timescales (e.g., Hewitt 2000; Ibrahim et al. 1996). Even under ideal circumstances, multiple processes can give rise to indistinguishable phylogeographic or population genetic patterns (Bloomquist et al. 2010; Hey and Machado 2003; Nielsen and Beaumont 2009; Panchal and Beaumont 2010). This is made worse in biological invasions where compressed timescales and idiosyncracies of introduction/translocation histories can confound interpretation of patterns of molecular variation. As with methods based on population genetic theory, phylogeographic methods show more promise for invasive species with short generation time and high mutation rates. In all cases, it is important to ask how knowledge of population genetic structure might inform management and then



**Fig. 3** Expected trajectory of  $F_{ST}$  as a system of populations slowly approaches migration-drift equilibrium (dashed line). Values are based on the infinite island model with  $N_e = 1000$  and  $m = 0.001$  ( $Nm = 1$ ). The recursion is  $F_{ST}(t + 1) = [1/(2N_e) + [1 - 1/(2N_e)]F_{ST}(t)](1 - m)^2$  (Crow and Aoki 1984; Hartl and Clark 1997). Similar trajectories can be obtained from simulations of finite systems (Online Resource 2)

carefully evaluate the feasibility of obtaining answers or parameter estimates with sufficient accuracy.

## Hybridization

One area where molecular studies have had significant impact on invasion biology and conservation is the detection and characterization of interbreeding between introduced and native populations. Most invasions involve introduced species that negatively impact native species or crops via ecological interactions. When introduced or cultivated individuals interbreed with wild natives, additional, uniquely genetic issues arise. These issues include (i) the question of whether introgression of introduced alleles into native populations should be considered a minor evolutionary change or a “genomic extinction”, (ii) the legal problem of establishing criteria for protection when endangered species might have received gene flow from non-natives, and (iii) the possibility that recombinant hybrid genotypes might express novel phenotypes with detrimental ecological effects (Allendorf et al. 2001; Chapman and Burke 2006; Ellstrand and Schierenbeck 2000; Rhymer and Simberloff 1996).

Hybridization can sometimes be detected from the presence of morphological intermediates, but generally must be confirmed with DNA analysis (and sometimes cannot be detected by any other means). The clearest way to test whether individuals are hybrids is to find diagnostic markers in samples from genetically “pure” reference populations of the native and introduced lineages. Individuals with hybrid ancestry are expected to show mosaics of native and introduced alleles. Codominant markers with simple alternative allelic states (e.g., SNPs) provide the most straightforward evidence: heterozygotes and recombinant multi-locus genotypes can be identified with little ambiguity. Uniparentally inherited markers (mitochondrial or chloroplast DNA) are, by themselves, of no use. Introgression of such markers can be assessed only within the context of other markers or diagnostic morphology.

In the absence of reference samples or diagnostic markers, hybridization might be inferred from patterns of genetic variation that are inconsistent with population genetic equilibria (Anderson and Thompson 2002; Pritchard et al. 2000). If native and introduced forms

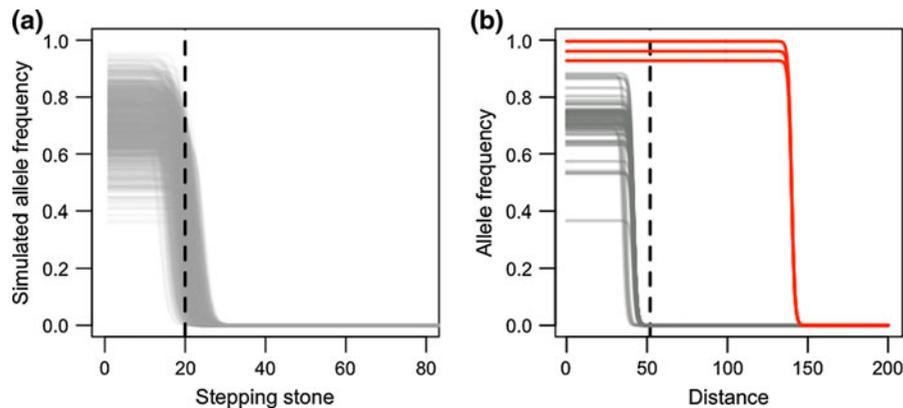
interbreed freely and there is no selection against hybrids, deviations from Hardy–Weinberg and linkage equilibria are expected to become undetectable within a few generations, and the only evidence of admixture would depend on comparison to reference populations. However, if admixture is restricted by geography, behavior, or selection, more-or-less distinct genetic clusters might persist for many generations. For example, Fitzpatrick et al. (2010) simulated neutral admixture (dispersal and drift only) in a stepping stone model where introductions occurred in the first 20 of 100 populations. The transition from genetically mixed to “pure” native populations remained steep and consistent among neutral markers for many generations under a variety of population sizes and dispersal rates (Fig. 4a).

Once detected, more detailed genetic analysis of hybrid invasions can illuminate important questions about their dynamics and consequences. In a few cases, such analyses have shown that hybridization is not a significant issue for a particular endangered species (Pasachnik et al. 2009). In other cases, molecular data have confirmed that genetically “pure” native taxa have been replaced by admixed or introgressed genotypes (Fig. 4b). However, the value of such genetically modified populations is not an entirely scientific issue. Loss of any native allele can be defined as “genomic extinction” (Allendorf et al. 2001; Rhymer and Simberloff 1996) or as a minor genetic change that does not affect the identity or legal status of the native taxon (Daniels and Corbett 2003; Fitzpatrick et al. 2010).

Ecological effects of hybridization, i.e., impacts on “third party” community members not genetically involved in the hybridization, have been less well documented. Important examples include the *Spartina* cord grasses of San Francisco Bay (Neira et al. 2005) and the *Ambystoma* tiger salamanders in the central coast region of California (Ryan et al. 2009). In these cases, understanding the causal links between non-native DNA and ecologically undesirable phenotypes might be important for monitoring and managing detrimental impacts of invasion.

## Conclusions

Molecular genetics can be useful as a forensic tool to discriminate alternative sources of non-native



**Fig. 4** Spread of introduced alleles over short timescales with and without selection. **a** We used the simulation model of Fitzpatrick et al. (2010) in which novel genotypes are introduced (initial frequency 70%) into each of the first 20 out of 100 demes in a stepping stone configuration. Each deme had  $N_e = 100$  diploid individuals and the dispersal rate between neighboring demes was  $m = 0.25$ . That is, on average 12.5% of the individuals in a deme immigrated from each of the two neighboring demes. The vertical dashed line illustrates the edge of the region of introduction. 10,000 independent

simulations of 60 years are illustrated in gray. **b** Clines fitted to data from wild tiger salamander populations (Fitzpatrick et al. 2010) revealed three exceptional markers where introduced alleles have become fixed in populations up to 95 km from the northernmost known introduction site (vertical dashed line). For both simulated and observed data, nonlinear regression was used to fit sigmoid clines of the form  $p = L/(1 + e^{x-M})$ , where  $L$  is the average allele frequency in the region of introduction and  $M$  is the midpoint of the cline

species, distinguish single versus multiple invasion scenarios, and identify hybridization and introgression. However, implementing methods aimed at determining population structure and demographic history should be interpreted with caution, as the assumptions underlying these methods are generally and severely violated in most cases of interest. Although using molecular genetic tools to reconstruct invasion history might have obvious appeal, traditional population genetic methods and markers cannot resolve recent, rapid dynamics. The assumptions of analytical approaches are generally not valid because the processes that generate variation (mutation) and structure (drift and gene flow) play out over timescales much longer than typical human-mediated biological invasions. In most cases, we have little reason to expect an informative relationship between patterns of variation in putatively neutral molecular markers and the ecological and evolutionary processes affecting the success and impact of biological invasions. Investigators of invasive species should appreciate the limitations of molecular tools and consider first whether answering genetic questions is likely to affect invasive species policy or management, and second, whether the important questions can really be addressed with available markers and

methods. Often, resources might be better invested in research on control or eradication efforts.

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