

Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions

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Abstract

Invasive species are predicted to suffer from reductions in genetic diversity during founding events, reducing adaptive potential. Integrating evidence from two literature reviews and two case studies, we address the following questions: How much genetic diversity is lost in invasions? Do multiple introductions ameliorate this loss? Is there evidence for loss of diversity in quantitative traits? Do invaders that have experienced strong bottlenecks show adaptive evolution? How do multiple introductions influence adaptation on a landscape scale? We reviewed studies of 80 species of animals, plants, and fungi that quantified nuclear molecular diversity within introduced and source populations. Overall, there were significant losses of both allelic richness and heterozygosity in introduced populations, and large gains in diversity were rare. Evidence for multiple introductions was associated with increased diversity, and allelic variation appeared to increase over long timescales (~100 years), suggesting a role for gene flow in augmenting diversity over the long-term. We then reviewed the literature on quantitative trait diversity and found that broad-sense variation rarely declines in introductions, but direct comparisons of additive variance were lacking. Our studies of *Hypericum canariense* invasions illustrate how populations with diminished diversity may still evolve rapidly. Given the prevalence of genetic bottlenecks in successful invading populations and the potential for adaptive evolution in quantitative traits, we suggest that the disadvantages associated with founding events may have been overstated. However, our work on the successful invader *Verbascum thapsus* illustrates how multiple introductions may take time to commingle, instead persisting as a 'mosaic of maladaptation' where traits are not distributed in a pattern consistent with adaptation. We conclude that management limiting gene flow among introduced populations may reduce adaptive potential but is unlikely to prevent expansion or the evolution of novel invasive behaviour.

Keywords: exotic species, genetic bottlenecks, local adaptation, molecular diversity, non-native species, quantitative trait evolution

Received 19 March 2007; revision received 3 July 2007; accepted 8 August 2007

Introduction

During the course of human-mediated introductions, all non-native invasive species have experienced population founding events. Theory predicts that such founding events often establish only a fraction of the genetic variants that occurred in the source population(s) (Nei *et al.* 1975; Barrett & Husband 1990; Box 1). With this prediction in mind,

many studies have compared molecular genetic diversity of invaders to that of either conspecifics in the native range or related noninvasive species. Qualitative reviews of this work (Brown & Marshall 1981; Barrett & Richardson 1986; Gray 1986; Barrett & Husband 1990; Merilä *et al.* 1996b; Lee 2002; Cox 2004; Lambrinos 2004; Lee *et al.* 2004; Bosssdorf *et al.* 2005; Novak & Mack 2005; Wares *et al.* 2005) have highlighted the variety of outcomes observed: many invasive species have reduced genetic variation in their introduced ranges, while many others do not. Several hypotheses have been proposed to explain this variation (e.g. see Allendorf & Lundquist 2003), but despite a long

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Box 1 Bottlenecks and Mendelian trait variation

Molecular markers are discrete traits with Mendelian inheritance, and therefore traditional population genetic theory easily generates predictions about their response to demographic bottlenecks. Nei *et al.* (1975) showed that the loss of genetic diversity is governed by the effective minimum (or founder) population size (N_e) and the growth rate of the population. Lower N_e and/or growth rate will lead to the loss of more alleles, particularly those that are rare. Experimental and observational work has since supported these predictions (e.g. McCommas & Bryant 1990; Leberg 1992; England *et al.* 2003; Eldridge *et al.* 2004). Rare alleles that persist through a bottleneck have the opportunity to become more common, and in general, large shifts in allele frequencies are predicted. For molecular markers, we expect most of these shifts to have no effect on fitness. For other types of Mendelian traits, however, the evolutionary importance of shifts in allele frequencies and losses of rare alleles is likely to be highly idiosyncratic. While many rare alleles

are deleterious, a few, particularly those under frequency dependent selection, may have important fitness consequences (e.g. sex-determining alleles in fire ants, Ross *et al.* 1993; self-incompatibility alleles in plants, Elam *et al.* 2007).

Multiple introductions are predicted to augment Mendelian trait diversity in founding populations by raising both N_e and population growth rate, but even greater increases can be realized if there is differentiation across the geographical distribution of populations in the source region (Ellstrand & Schierenbeck 2000). This is especially true for inbreeding or exclusively clonal species (particularly plants), where native genetic diversity is expected to be low within populations but high among them (Gray 1986; Hamrick & Godt 1989; Barrett & Husband 1990; Schoen & Brown 1991). In these cases, within population diversity is not likely to be unusually low in bottlenecked invasions (just similarly low), and it can easily be higher, if an intentionally mixed stock or multiple introductions combine genotypes from differentiated source populations (Novak & Mack 1993; Novak & Mack 2005).

history of research on genetic diversity in invaders, we still lack clear generalities that describe the genetic changes that occur over the course of an invasion.

Recent discussions of genetic variation in invaders have focused on the role that multiple introductions might play. Multiple introductions seem to be common in invasions (Ellstrand & Schierenbeck 2000; Bossdorf *et al.* 2005; Novak & Mack 2005), and they can bring together unusually large amounts of variation and novel genetic combinations (Box 1). This leads to the hypothesis that many invasions might be successful as a direct result of influxes of genetic variation from multiple introduction events (Ellstrand & Schierenbeck 2000; Allendorf & Lundquist 2003; Facon *et al.* 2003; Kolbe *et al.* 2004; Bossdorf *et al.* 2005; Frankham 2005; Lockwood *et al.* 2005; Novak & Mack 2005; Wares *et al.* 2005), though a general association between multiple introductions and variation in invasions has never been quantified.

The idea that increased genetic diversity contributes to invasion success presupposes that (i) evolution enhances invasions, and (ii) bottlenecks during invasion limit the adaptive evolution of fitness-related traits. From the earliest days of invasion biology, evolutionary biologists postulated that genetic variation and evolution might play an important role in the success of invading species (Baker 1965; Lewontin 1965; Mayr 1965). A growing number of studies show that putatively adaptive traits have evolved in introduced populations (e.g. Brown & Marshall 1981; Stockwell *et al.* 1996; Hendry & Quinn 1997; Huey *et al.* 2000; Koskinen *et al.* 2002a; Blair & Wolfe 2004; Rogers &

Siemann 2004), and sometimes quite rapidly (e.g. Daehler & Strong 1997; reviewed in Thompson 1998; Reznick & Ghalambor 2001). Baker (1965, 1974) described a number of examples of genetically based adaptation in plant invaders, including herbicide resistance and crop mimicry. While a strong believer that plasticity was particularly important to successful invaders (coining the term 'General Purpose Genotype'), he was also one of the first to note that even highly plastic species might benefit from the retention of genetic variation (Baker 1974; for recent discussions see Parker *et al.* 2003; Bossdorf *et al.* 2005; Richards *et al.* 2006). Nevertheless, the observation that some successful invaders have retained putatively adaptive variation is not necessarily inconsistent with the presence of genetic bottlenecks, both because we do not expect founding events to eliminate all variation (Nei *et al.* 1975), and because many fitness-related traits do not lose variation as quickly as do individual loci (Box 2). Direct examinations of evolutionary potential in introduced populations and its implications for invasion success are still required.

The links between bottlenecks, multiple introductions, and invasion success are important for understanding how evolutionary issues may be incorporated into management strategies for invasive species. We need to know how frequently introductions are accompanied by severe genetic bottlenecks, whether bottlenecks constrain adaptive evolution in invaders, and whether multiple introductions and/or contemporary gene flow among introductions represent the key to invasion success. Filling these gaps in

Box 2 Bottlenecks and quantitative trait variation

Quantitative traits integrate across the effects of multiple genes and are characterized by distributions rather than discrete trait values. The portion of a distribution that can be attributed to additive variance is critical for determining the response to selection, since only additive gene action translates parental traits directly into offspring traits. Reductions in additive variation due to demographic bottlenecks are expected to be small, because distributions of quantitative variation are relatively insensitive to the loss of rare alleles (Lande 1980; Barton & Charlesworth 1984). Furthermore, additive variation may increase after a bottleneck due to frequency shifts at loci with nonadditive gene interactions, converting epistatic or dominance variance to additive variance (Goodnight 1988; Whitlock *et al.* 1993; Willis & Orr 1993; Cheverud & Routman 1996; Wang *et al.* 1998; Kirkpatrick & Jarne 2000; López-Fanjul *et al.* 2002; Naciri-Graven & Goudet 2003; Zhang *et al.* 2004; Turelli & Barton 2006; Van Buskirk & Willi 2006; Willi *et al.* 2006). Such increases in additive variation have been observed under experimental conditions, particularly for life-history traits, which are expected to have many nonadditive genetic components (reviewed in Neiman & Linksvayer 2006). Examples from natural systems are rare;

however, in a recent study, higher additive variation was coupled with evidence of a bottleneck in island populations of *Rana arvalis* (Knopp *et al.* 2007).

These gene interactions, as well as the action of selection, can decouple patterns of quantitative variation from those of discrete molecular markers. This decoupling can make molecular markers poor predictors (typically underestimates) of evolutionary potential in important fitness-related traits (Barrett & Richardson 1986; Pfrender *et al.* 2000; Merilä & Crnokrak 2001; Reed & Frankham 2001; McKay & Latta 2002), though few studies have adequately addressed this comparison (Crnokrak & Merilä 2002; Latta & McKay 2002). Nevertheless, neutral molecular markers should reflect total losses of genetic variation, which may ultimately affect the potential for quantitative traits to achieve extreme phenotypes. For example, Briggs & Goldman (2006) found that bottlenecked populations of *Brassica rapa* initially responded more quickly to artificial selection than did stable populations, but were ultimately more limited in their long-term response. The trade-off between loss of total variation and gain of additive variation has not been explored in natural populations and deserves further attention (Lee 2002). Perhaps the additional genetic diversity contributed by multiple introductions over the long-term will be crucial for sustained adaptive change in founding populations.

our knowledge will help us to assess whether evolutionary considerations are likely to be important in small, isolated founding populations, and whether the movement of genotypes within an invaded range is likely to enhance the fitness of invading species (Stockwell & Ashley 2004).

Here we explore what the current body of genetic and evolutionary work reveals about the adaptive potential of invaders. We use a review of molecular variation in successfully introduced species to gauge changes in diversity during human-mediated founding events, and we ask (i) whether invaders generally show genetic bottlenecks, and (ii) whether we see evidence that multiple introductions rescue particular species from losses of variation. We then review studies of quantitative variation in invaders and ask whether there are indications that founding events might limit the evolution of putatively adaptive traits. Finally, we provide two case studies that illustrate both the opportunities retained and the limitations imposed on introduced species by founding events.

Review of molecular diversity

We reviewed the literature for studies that quantified molecular variation in invasions and their sources. We used

searches of the Web of Science database (combining genetic diversity keywords with invasion biology keywords) and citations in reviews of invasive species evolution (Barrett & Richardson 1986; Molina-Freaner & Jain 1992; Merilä *et al.* 1996b; Kinnison & Hendry 2001; Lee 2002; Cox 2004; Lee *et al.* 2004; Stockwell & Ashley 2004; Bossdorf *et al.* 2005; Novak & Mack 2005; Wares *et al.* 2005). We found that allelic diversity (A) and/or heterozygosity (H) of nuclear markers were the most common metrics of diversity used, and thus we limited our review to studies that reported these values for introduced and source populations. We included only comparisons among naturally reproducing populations, involving human-assisted introductions to areas outside of the range of natural dispersal for each species. We excluded studies of hybrid species where native populations of similar hybrids did not also exist.

We made several important choices when synthesizing these data. We used within-population estimates of allelic richness and heterozygosity rather than regional (pooled) estimates whenever possible, and we averaged across populations and loci. Therefore, our results pertain primarily to the amount of diversity that is available for individual populations to respond to local selective pressures, rather than to the regional variation available for large-scale

Box 3 The challenge of making relevant comparisons with source regions

There are many key questions in invasion biology that rely on comparisons between the native range and the introduced range (Hierro *et al.* 2005). These comparisons are often made by sampling broadly across the native range; however, the entire native range is not the most appropriate comparison for certain types of questions. In particular, to study the genetic changes that may have occurred during and after the introduction process, it is important to identify with as much precision as possible what was the original source for the introduction. Because the source region provides the benchmark against which genetic and evolutionary changes are assessed, it must represent variation from which an introduction was actually derived, otherwise apparent evolutionary changes since introduction may simply reflect regional differences (i.e. local adaptation,

drift, and evolutionary history) between the true source population and the area sampled for study. For this same reason, comparisons between introductions and populations from across a broad source region may obscure important changes in the introductions that appear small against the range of variation in the source region.

Unfortunately, reliable records of the precise origins of introduced populations do not exist for most invaders. Instead, we typically rely on surveys of molecular variation to identify regions that are likely to contain the source of a particular introduction. The accuracy of this approach will be determined by the intensity of sampling in introduced and source areas, by the resolution of the molecular markers involved, and by the scale of differentiation across the potential source area. Future studies that pay close attention to these issues will offer particularly meaningful insights into the evolutionary ecology of introduced species.

processes of gene flow and differentiation. We also restricted our analyses to native range populations and their associated primary introductions, when such data were provided for a particular species. In other words, we tried not to compare native populations to secondary introductions, or primary introductions to their secondary offshoots, or to average across primary and secondary introductions. This allowed us to focus on the consequences of the initial act of transporting species out of their native range. Finally, when multiple articles were available for a single species, we reported all of these data but included only the most comprehensive study in our statistical analyses in order not to average across different methodologies or pseudoreplicate across species (see notations in Table 1).

We identified appropriate studies for 80 species (Table 1), covering 18 plants, 2 fungi, and 60 animals (including 7 birds, 6 reptiles, 8 fish, 3 amphibians, 8 mammals, 13 insects, 4 crustaceans, 6 mollusks, 3 annelids, 1 cnidarian, and 1 tunicate). We used these data to conduct one of the first quantitative summaries of founder effects on molecular variation in introduced species. We calculated proportional losses of variation [(introduced – source)/source] in both expected heterozygosity (or observed in a few cases, see Table 1) and mean number of alleles per locus. These metrics were previously used in a more qualitative review of founding populations in 29 animal species by Wares *et al.* (2005). Our study extends their approach by (i) restricting analyses to human-mediated introductions, (ii) including a greater range and number of taxa, (iii) focusing on comparisons of introduced populations to their immediate sources (Box 3), and (iv) applying statistical approaches to test par-

ticular hypotheses. All calculations were performed using the software JMP version 7 (SAS Institute).

Hypothesis 1: introduced species lose genetic variation relative to source populations

Overall, we found that losses of variation are a frequent feature of introductions, although they are not ubiquitous (Fig. 1). Proportional changes in allelic richness were approximately normally distributed, and showed an overall significant loss of 15.5% of variation in introduced populations ($N = 69$, two-tailed t -test $P < 0.0001$, Fig. 1A). Estimates of heterozygosity revealed three outliers with large increases of diversity (the plants *Bromus tectorum* and *Trifolium hirtum*, and the fish *Percottus glenii*). The two plant species are well-known case studies of increased molecular variation within invading populations and have stimulated much thoughtful discussion (recently reviewed in Novak & Mack 2005), so it is worth noting that here they appear to be truly exceptional among the invaders studied to date. Excluding these three outliers (here and in all analyses of H_E hereafter), heterozygosity was also approximately normally distributed, with a significant average loss of 18.7% of variation across species ($N = 70$, two-tailed t -test $P < 0.0001$, Fig. 1B).

Allelic richness is generally predicted to be more sensitive to founder effects than is heterozygosity (Nei *et al.* 1975; Allendorf 1986; Leberg 1992), and we were able to detect this pattern in our data (Fig. 1). For studies that reported both metrics, a paired comparison showed that proportional losses of allelic richness were on average 5.1% more severe (more negative) than losses of heterozygosity

Table 1 Details of studies of molecular variation in 80 introduced species. Locations reflect the sampling areas used for the introduced (I) and source (S) regions. The number of populations that provided statistical replicates (# Pops) and the average sample sizes per population and locus (N/Pop) are given. Marker types include enzyme variants (Prot.), microsatellites (SSR), amplified fragment length polymorphisms (AFLP) and randomly amplified polymorphic DNA (RAPD). Values for allelic richness (A) and expected heterozygosity (H_E) are averages per locus and population. Historical or genetic indications of the number of introductions into the same region are indicated as multiple (Mult) or Single. Species marked with an asterisk (*) were intentional introductions at a known date and contributed to the analyses of molecular variation across time

| Species | Location (S > I) | # Pops (S, I) | N/Pop (S, I) | Marker type (# loci) | A (S, I) | H_E (S, I) | # Intro | Data reference |
|---------------------------------|---|---------------|--------------|----------------------|-------------|---------------|---------|--|
| Plants | | | | | | | | |
| <i>Aegilops cylindrica</i> | Mideast (Lebanon) > N. America (CA) | 1, 1 | 20, 30 | Prot. (10) | 1.0, 1.0 | 0, 0 | — | Hegde <i>et al.</i> (2002) |
| <i>Aegilops triuncialis</i> | Mideast (Turkey) > N. America (CA) | 1, 1 | 30, 30 | Prot. (10) | 1.0, 1.3 | 0.00, 0.06 | — | Hegde <i>et al.</i> (2002) |
| <i>Alliaria petiolata</i> | Europe > N. America | 15, 26 | 8, 8 | SSR (8) | 1.63, 1.41 | 0.17, 0.11 | Mult | Durka <i>et al.</i> (2005) |
| <i>Anthrosia artemisiifolia</i> | N. America > Europe (France) | 12, 10 | 30, 30 | SSR (5) | 9.0, 8.5 | 0.756, 0.746 | Mult | Genton <i>et al.</i> (2005) |
| <i>Apera spica-venti</i> | Europe > N. America (Canada) | 6, 9 | 40, 40 | Prot. (17) | 2.53, 2.54 | 0.203, 0.209 | — | Warwick <i>et al.</i> (1987) |
| <i>Avena barbata</i> | Mediterranean > N. America (CA) | 9, 16 | 32, 305 | Prot. (5) | 1.51, 1.22§ | — | Mult | Clegg & Allard (1972) |
| <i>Avena barbata</i> † | Mediterranean (Spain) > N. America | 42, — | 96, — | Prot. (15) | 2.06, — | — | Mult | Garcia <i>et al.</i> (1989) |
| <i>Bromus mollis</i> | Europe (England) > Australia | 10, 10 | — | Prot. (16) | 1.44, 1.50 | 0.121, 0.138† | — | Brown & Marshall (1981) |
| <i>Bromus tectorum</i> | Europe and SW Asia > N. America | 51, 60 | 34, 36 | Prot. (25) | 1.01, 1.05 | 0.005, 0.012 | Mult | Novak <i>et al.</i> (1991); Novak & Mack (1993) |
| <i>Cedrus atlantica</i> * | N. Africa (Algeria) > Europe (France) | 1, 3 | 130, 92 | Prot. (12) | — | 0.186, 0.164 | Single | Lefevre <i>et al.</i> (2004) |
| <i>Chondrilla juncea</i> | Europe (Turkey) > Australia | 1, 1 | 123, 23 | Prot. (8) | 3.4, 2.1 | — | — | Chaboudez (1994) |
| <i>Clidemia hirta</i> | C. America (Costa Rica) > Hawaii | 20, 20 | 12, 12 | Prot. (7) | 1.8, 2.5 | 0.043, 0.060 | — | DeWalt & Hamrick (2004) |
| <i>Echium plantaginatum</i> | Europe > Australia | 2, 8 | 30, 50 | Prot. (16) | 2.61, 2.72 | 0.29, 0.32† | Mult | Burdon & Brown (1986) |
| <i>Epipactis helleborine</i> | Europe > N. America (Canada) | 35, 12 | 23, 26 | Prot. (9) | 1.77, 1.81 | 0.230, 0.231 | — | Squirrell <i>et al.</i> (2001) |
| <i>Hirschfeldia incana</i> | S. Europe > British Isles (Wales) | 4, 13 | 10, 10 | RAPD (30) | — | 0.399, 0.356 | Mult | Lee <i>et al.</i> (2004) |
| <i>Hypericum canariense</i> * | Canary Isl > N. America (CA), Hawaii | 8, 3 | 8, 8 | AFLP (244) | — | 0.175, 0.085 | Single | Dlugosch (2006) |
| <i>Lolium perenne</i> | Europe: Italy > Corsica | 8, 8 | 75, 75 | Prot. (13) | 2.84, 2.79 | 0.326, 0.347 | — | Balfourier & Charmet (1994) |
| <i>Phalaris arundinaceae</i> | Europe > N. America | 8, 8 | — | Prot. (12) | 1.89, 2.27 | — | Mult | Lavergne & Molofsky (2007) |
| <i>Trifolium hirtum</i> * | Mediterranean > N. America (California) | 22, 22 | 50, 50 | Prot. (8) | 1.07, 1.18 | 0.014, 0.055 | Mult | Molina-Freaner & Jain (1992) |
| Fungi | | | | | | | | |
| <i>Ceratomyces fimbriata</i> | N. America (E. USA) > S. Europe | 1, 1 | 33, 27 | SSR (8) | — | 0.218, 0.019 | Single | Engelbrecht <i>et al.</i> (2004) |
| <i>Ophiostoma ips</i> | N. Hemisphere > S. Hemisphere | 4, 3 | 36, 35 | SSR (10) | 2.40, 1.37 | 0.223, 0.112 | — | Zhou <i>et al.</i> (2007) |
| Fish | | | | | | | | |
| <i>Cephalopholis argus</i> * | Tuamotu archipelago > Hawaii | 1, 1 | 50, 25 | Prot. (9) | 4.00, 3.78 | 0.046, 0.045 | Single | Planes & Lecaillon (1998) |
| <i>Gambusia affinis</i> * | N. America (Texas) > Hawaii | 3, 17 | 50, 120 | Prot. (23) | 2.53, 1.85 | 0.136, 0.145 | Single | Stearns (1983); Scribner <i>et al.</i> (1992) |
| <i>Gambusia affinis</i> ¶ | N. America (Texas) > California | 2, 3 | 39, 38 | Prot. (16) | 1.96, 1.61 | 0.138, 0.095 | Mult | Stockwell <i>et al.</i> (1996) |
| <i>Gambusia holbrooki</i> * | N. America > S. Europe (Spain) | 1, 2 | 21, 10 | RAPD (49) | — | 0.352, 0.095 | — | Grapputo <i>et al.</i> (2006) |
| <i>Limnothrissa miodora</i> * | Africa: Lk. Tanganyika > Lk. Kivu | 13, 4 | 38, 50 | Prot. (29) | 1.44, 1.48 | 0.066, 0.066 | Mult | Hauser <i>et al.</i> (1995) |
| <i>Lutjanus kasmira</i> * | Marquesas > Hawaii | 1, 3 | 39, 24 | Prot. (17) | 3.12, 2.76 | 0.085, 0.089 | Single | Planes & Lecaillon (1998) |
| <i>Percottus glenii</i> * | Europe: Russia (Amur basin > Moscow) | 13, 3 | 53, 101 | Prot. (2) | 2.08, 2.83 | 0.151, 0.435 | — | Golubtsov <i>et al.</i> (1993) |
| <i>Poecilia reticulata</i> * | Guyana > Australia | 1, 7 | 39, 45 | SSR (9) | 3.51, 9.4 | 0.68, 0.49 | Mult | Lindholm <i>et al.</i> (2005) |
| <i>Thymallus thymallus</i> * | NW/C Europe > Lk Lesjaskogsvatn | 4, 1 | 38, 52 | SSR (17) | 3.75, 1.90 | 0.435, 0.17 | Single | Koskinen <i>et al.</i> (2002a, b) |
| Amphibians | | | | | | | | |
| <i>Ameiurus vagrans</i> | N. America: California > Vancouver Island | 9, 3 | — | Prot. (27) | 1.07, 1.05 | — | — | Jackman (1998) |
| <i>Bufo marinus</i> * | Hawaii (introduced) > Australia | 5, 5 | 77, 74 | Prot. (10) | 2.24, 2.18 | 0.392, 0.358 | Single | Eastal (1985); Estoup <i>et al.</i> (2001) |
| <i>Rana ridibunda</i> * | Europe: Hungary > England (Romney) | 1, 1 | 32, 37 | SSR (5) | 3.2, 2.2 | 0.522, 0.484 | Single | Zeisset & Beebee (2003) |

Table 1 Continued

| Species | Location (S > I) | # Pops (S, I) | N/Pop (S, I) | Marker type (# loci) | A (S, I) | H _E (S, I) | # Intro | Data reference |
|----------------------------------|--|---------------|--------------|----------------------|------------|-----------------------|---------|---|
| Reptiles | | | | | | | | |
| <i>Anolis aeneus</i> | Grenada > Trinidad | 1,1 | 22, 22 | Prot. (23) | — | 0.035, 0.035† | — | Gorman <i>et al.</i> (1978) |
| <i>Anolis extremus</i> | Barbados > Bermuda, St Lucia | 1,2 | 20, 20 | Prot. (21) | — | 0.043, 0.006† | — | Gorman <i>et al.</i> (1978) |
| <i>Anolis grahami*</i> | Jamaica (Kingston) > Bermuda | 1,1 | 38, 43 | Prot. (24) | 1.75, 1.50 | 0.078, 0.064 | Single | Taylor & Gorman (1975) |
| <i>Anolis leachi</i> | Antigua > Bermuda | 1,1 | 20, 20 | Prot. (22) | — | 0.071, 0.040† | — | Gorman <i>et al.</i> (1978) |
| <i>Anolis richardi</i> | Grenada > Tobago | 1,1 | 15, 15 | Prot. (23) | — | 0.049, 0.031† | — | Gorman <i>et al.</i> (1978) |
| <i>Anolis trinitatis</i> | St Vincent > Trinidad | 1,1 | 30, 30 | Prot. (22) | — | 0.068, 0.014† | — | Gorman <i>et al.</i> (1978) |
| Birds | | | | | | | | |
| <i>Acridotheres tristis*</i> | Asia (India) > Fiji, Hawaii, Australia | 7, 5 | 28, 35 | Prot. (21) | 1.43, 1.28 | 0.060, 0.056 | Mult | Baker & Moeed (1987) |
| <i>Acridotheres tristis†</i> | Asia (India) > Hawaii | —, 4 | —, 23 | Prot. (21) | —, 1.33 | — | Mult | Fleischer <i>et al.</i> (1991) |
| <i>Carduelis chloris*</i> | Europe > New Zealand | 14, 7 | 34, 35 | Prot. (40) | 1.19, 1.22 | 0.025, 0.025 | Mult | Merilä <i>et al.</i> (1996a, b) |
| <i>Carpodacus mexicanus*</i> | W. N. America > E. N. America | 1, 1 | 105, 117 | SSR (10) | 16.4, 10.8 | 0.809, 0.771 | Mult | Hawley <i>et al.</i> (2006) |
| <i>Carpodacus mexicanus††</i> | W. N. America > E. N. America | 6, 8 | 9, 10 | AFLP (258) | — | 0.16, 0.16 | Mult | Wang <i>et al.</i> (1998) |
| <i>Fringilla coelebs*</i> | N. Europe > New Zealand | 7, 8 | 26, 29 | Prot. (22) | 1.34, 1.24 | 0.047, 0.066 | Mult | Baker (1992) |
| <i>Passer domesticus*</i> | Europe > Australia, New Zealand | 1, 2 | 90, 90 | Prot. (13) | 2.91, 2.46 | 0.095, 0.091 | Mult | Parkin & Cole (1985) |
| <i>Passer montanus*</i> | Europe (Germany) > N. America (Illinois) | 1, 3 | 30, 31 | Prot. (39) | 1.50, 1.33 | 0.101, 0.078 | Single | St. Louis & Barlow (1988) |
| <i>Sturnus vulgaris*</i> | Europe (UK) > New Zealand | 6, 6 | 50, 50 | Prot. (11) | 1.89, 1.74 | 0.033, 0.043 | Mult | Ross (1983) |
| <i>Sturnus vulgaris†</i> | Europe (United Kingdom) > N. America | —, 4 | —, 33 | Prot. (6) | — | —, 0.032† | Mult | Cabe (1998) |
| Mammals | | | | | | | | |
| <i>Cervus nippon*</i> | Asia (Kyushu) > Europe (UK) | 2, 4 | 18, 9 | SSR (9) | 2.56, 1.89 | 0.32, 0.25 | — | Goodman <i>et al.</i> (2001) |
| <i>Cervus timorensis russa*</i> | New Caledonia (introduced) > Australia | 1, 1 | 120, 37 | SSR (10, 24) | 7.60, 2.29 | 0.595, 0.485 | Single | Bonnet <i>et al.</i> 2002; Webley <i>et al.</i> (2004) |
| <i>Herpestes auroponctatus*</i> | Asia (India) > Jamaica, Fiji, Mauritius | 1, 3 | 35, 41 | SSR (8) | 5.9, 5.2 | 0.539, 0.556 | Single | Thulin <i>et al.</i> (2006) |
| <i>Macropus rufogriseus*</i> | Tasmania > New Zealand | 3, 1 | 29, 44 | SSR (5) | 8.4, 4.6 | 0.767, 0.586 | Single | Le Page <i>et al.</i> (2000) |
| <i>Marmota marmota*</i> | Europe: Austria > Austria, Spain | 3, 5 | 12, 11 | SSR (4) | 2.08, 2.37 | 0.257, 0.338 | Mult | Kruckenhauser <i>et al.</i> (1999) |
| <i>Rangifer tarandus*</i> | Europe: Norway > Iceland | 2, 1 | 100, 74 | Prot. (1) | 8.0, 3.0 | 0.729, 0.332 | Single | Roed <i>et al.</i> (1985) |
| <i>Rattus norvegicus</i> | Europe: France > Brittany islands | 2, 3 | 11, 33 | SSR (7) | 5.85, 3.70 | 0.747, 0.362 | Mult | Calmet <i>et al.</i> (2001) |
| <i>Trichosurus vulpecula*</i> | Australia > New Zealand (grey form) | 2, 5 | 28, 61 | Prot. (45) | 1.17, 1.21 | 0.044, 0.033 | Mult | Triggs & Green (1989) |
| <i>Trichosurus vulpecula††</i> | Australia > New Zealand (black form) | 1, 5 | 53, 43 | Prot. (45) | 1.13, 1.17 | 0.029, 0.049 | Mult | Triggs & Green (1989) |
| Tunicates | | | | | | | | |
| <i>Styela clava</i> | Asia (Japan) > N. America (California) | 1, 1 | 32, 32 | SSR (12) | 4.9, 4.58 | 0.54, 0.56 | Mult | Dupont <i>et al.</i> (2006) |
| Cnidarians | | | | | | | | |
| <i>Aurelia</i> sp. | Asia (Tokyo) > N. America (Foster City) | 1, 1 | 11, 24 | Prot. (14) | 1.29, 1.29 | — | — | Greenberg <i>et al.</i> (1996) |
| Annelids | | | | | | | | |
| <i>Marenzelleria type I</i> | Atlantic: N. America > Europe | 4, 3 | 81, 137 | Prot. (10) | 1.93, 1.70 | 0.124, 0.134 | Mult | Rohner <i>et al.</i> (1996) |
| <i>Marenzelleria type II</i> | Atlantic: N. America > Europe | 4, 4 | 59, 90 | Prot. (10) | 1.78, 2.02 | 0.072, 0.658 | Mult | Rohner <i>et al.</i> (1996) |
| <i>Sabella spallanzanii</i> | Mediterranean Sea > Australia | 3, 3 | 53, 103 | Prot. (23) | 2.31, 1.93 | 0.258, 0.206 | — | Andrew & Ward (1997) |
| Crustaceans | | | | | | | | |
| <i>Bosmina coregoni</i> | Europe > N. America (Great Lakes) | 12, 4 | 34, 38 | Prot. (7) | 1.31, 1.55 | 0.09, 0.08† | Mult | Demelo & Hebert (1994) |
| <i>Carcinus maenas</i> | Europe (Atlantic) > E. N. America, Australia | 2, 2 | — | SSR (5) | 25, 10 | 0.84, 0.74 | Mult | Bagley & Geller (1999) |
| <i>Bythotrephes longimanus</i> | Europe > N. America (Great Lakes) | 3, 3 | 30, 25 | SSR (5) | 4.47, 2.93 | 0.425, 0.186 | Mult | Colautti <i>et al.</i> (2005) |
| <i>Bythotrephes longimanus††</i> | Europe (Lk Ladoga) > N. America | 1, 4 | 73, 62 | Prot. (10) | 1.2, 1.3 | 0.06, 0.06 | Mult | Berg <i>et al.</i> (2002) |
| <i>Pacifastacus leniusculus*</i> | N. America (Pitt R.) > Europe (Sweden) | 1, 1 | 45, 36 | Prot. (4) | 1.50, 1.25 | 0.177, 0.079 | Mult | Agerberg & Jansson (1995) |

Table 1 Continued

| Species | Location (S > I) | # Pops (S, I) | N/Pop (S, I) | Marker type (# loci) | A (S, I) | H _E (S, I) | # Intro | Data reference |
|---------------------------------|---|---------------|--------------|----------------------|------------|-----------------------|---------|--|
| Mollusks | | | | | | | | |
| <i>Arion subfuscus</i> | Europe > N. America (NE USA) | 31, 10 | 24, 20 | Prot. (11) | 1.82, 1.27 | 0.098, 0.045 | Mult | Pinceel <i>et al.</i> (2004); Pinceel <i>et al.</i> (2005) |
| <i>Crepidula fornicata</i> | N. America (MA) > Europe (France) | 1, 12 | 50, 51 | Prot. (8) | 2.63, 2.89 | 0.255, 0.226 | Mult | Dupont <i>et al.</i> (2003) |
| <i>Dreissena bugensis</i> | Europe > N. America | 1, 5 | 25, 22 | RAPD (52) | — | 0.269, 0.237 | — | Stepien <i>et al.</i> (2002) |
| <i>Dreissena polymorpha</i> | Europe: England (introduced) > Ireland | 1, 5 | 31, 31 | SSR (5) | 13.2, 11.0 | 0.849, 0.820 | Mult | Astancet <i>et al.</i> (2005) |
| <i>Dreissena polymorpha</i> ††† | Europe (introduced) > N. America | 6, 7 | 18, 25 | RAPD (63) | — | 0.171, 0.188 | Mult | Stepien <i>et al.</i> (2002) |
| <i>Dreissena polymorpha</i> ††† | Europe (introduced) > N. America | 3, 7 | — | Prot. (11) | 2.61, 2.75 | 0.451, 0.465 | Mult | Boileau & Hebert (1993) |
| <i>Perna perna</i> | Atlantic/Indian O. > Gulf of Mexico | 6, 6 | 31, 37 | SSR (2) | 25.5, 24.2 | 0.945, 0.949 | — | Holland (2001) |
| <i>Theba pisana</i> | Europe (France) > Australia | 2, 4 | — | Prot. (25) | 1.92, 1.25 | 0.176, 0.084 | — | Johnson (1988) |
| Insects | | | | | | | | |
| <i>Aedes albopictus</i> | Japan, SE Asia > Europe (Italy), N. America | 8, 20 | — | Prot. (15) | 2.1, 1.8 | 0.211, 0.177 | Mult | Urbanelli <i>et al.</i> (2000) |
| <i>Ceratitis capitata</i> | Africa: Kenya > Morocco | 1, 1 | 309, 224 | Prot. (26) | 3.7, 2.9 | 0.161, 0.097 | — | Malacrida <i>et al.</i> (1998) |
| <i>Ceratitis rosa</i> | African continent > Mauritius, Reunion | 4, 5 | 22, 26 | SSR (10) | 5.5, 4.18 | 0.672, 0.613 | — | Baliraine <i>et al.</i> (2004) |
| <i>Diaeretiella rapae</i> * | Eurasia/N. Africa > W. Australia | 3, 1 | 46, 56 | SSR (4) | 4.08, 2.25 | 0.555, 0.280 | — | Baker <i>et al.</i> (2003) |
| <i>Drosophila pseudoobscura</i> | North America > New Zealand | 1, 1 | 136, 126 | SSR (10) | 11.5, 5.4 | 0.715, 0.584 | — | Reiland <i>et al.</i> (2002) |
| <i>Drosophila subobscura</i> | Europe > N. America | 5, 2 | 85, 92 | SSR (10) | 15.6, 5.4 | 0.874, 0.700 | Single | Pascual <i>et al.</i> (2001) |
| <i>Drosophila subobscura</i> † | Europe > N. & S. America | 11, 13 | —, 148 | Prot. (15) | 4.33, 1.77 | 0.244, 0.234 | Single | Balanya <i>et al.</i> (1994) and refs therein |
| <i>Erebia epihiron</i> * | Czech Republic (E. > W. Sudetans) | 3, 2 | 40, 41 | Prot. (17) | 1.59, 1.47 | 0.100, 0.116 | Single | Schmitt <i>et al.</i> (2005) |
| <i>Linepithema humile</i> | S. America (Argentina) > N. America (CA) | 1, 1 | 255, 460 | SSR (7) | 8.43, 4.29 | 0.639, 0.204 | — | Tsutsui <i>et al.</i> (2000) |
| <i>Musca autumnalis</i> | Europe > N. America | 4, 4 | 35, 28 | Prot. (6) | 1.55, 1.46 | 0.053, 0.038† | Single | Bryant <i>et al.</i> (1981) |
| <i>Polistes dominulus</i> | Europe > N. America | 1, 1 | 8, 79 | SSR (13) | 8.08, 5.38 | 0.63, 0.69 | — | Henshaw (2000); Johnson & Starks (2004) |
| <i>Rhagoletis completa</i> | N. America: Midwest USA > California | 4, 6 | 30, 30 | SSR (5) | 4.71, 4.28 | 0.52, 0.50 | — | Chen <i>et al.</i> (2006) |
| <i>Solenopsis invicta</i> | S. America (Argentina) > N. America | 2, 1 | (30–36) | Prot. (76) | 1.55, 1.26 | 0.062, 0.048 | — | Ross <i>et al.</i> (1993) |
| <i>Solenopsis richteri</i> | S. America (Argentina) > N. America | 1, 1 | 57, 58 | Prot. (26) | 1.54, 1.15 | 0.032, 0.021 | — | Ross <i>et al.</i> (1987); Ross & Trager (1990) |

†Observed heterozygosity reported (H_E unavailable).

‡ Study not included: another study of the same species with direct comparison of source and introduced populations available.

§Regional (pooled) values have been reported in other reviews [(2.4, 2.2)in Clegg & Brown 1983; Molina-Freaner & Jain 1992; Lee *et al.* 2004], but we show within-population averages.

¶ Study not included: another study of the same species with more comprehensive sampling available.

†† Study not included: another study of the same species with more sensitive codominant marker available.

††† Study not included: another study with samples sizes reported and more apparent source region available.

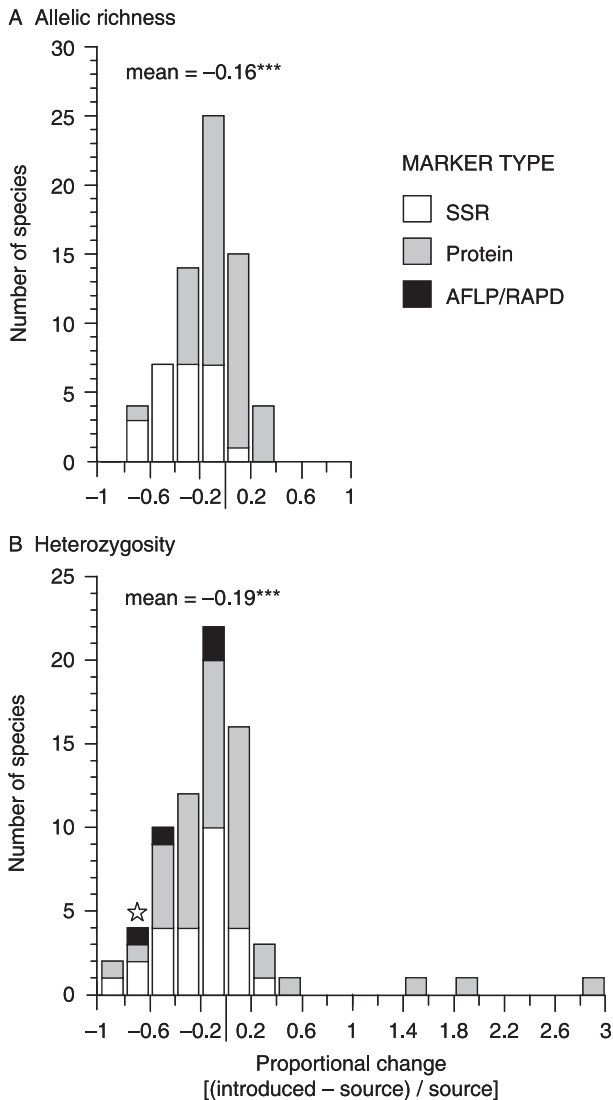


Fig. 1 Histograms showing proportional changes in (A) allelic richness and (B) expected heterozygosity within introduced populations of 80 species, relative to populations within their source region. Values on the x-axis indicate lower bounds of bins. Few large gains in variation have been observed, and both metrics show losses of variation overall ($^{***}P < 0.0001$). Shading indicates the type of molecular marker used in each study; microsatellites (SSR) tended to reveal larger losses of allelic richness than did proteins ($P < 0.0001$). The star indicates the average loss of variation in introduced *Hypericum canariense* populations.

($N = 59$, two-tailed t -test $P = 0.037$). This difference is expected because allelic richness will reflect the loss of rare alleles that contributed little to heterozygosity (Box 1). Likewise, markers that contain many rare alleles (such as microsatellites) should be especially sensitive to founder effects (Spencer *et al.* 2000). Our data included primarily protein and microsatellite markers, and indeed we found that

microsatellites revealed much greater proportional losses of allelic diversity than did protein markers on average (two-tailed t -test $P < 0.0001$; proteins: $N = 44$, mean = -5.8% ; microsatellites: $N = 25$, mean = -32.7% , Fig. 1A). This same discrepancy between markers was not significant in the heterozygosity data ($P = 0.13$, protein: $N = 40$, mean = -14.3% ; microsatellite: $N = 26$, mean = -22.6%).

Regardless of metric or marker, the above analyses clearly show substantial average losses of diversity within populations of introduced species. Because many of the studies did not standardize sampling effort among introduced and source populations (Table 1), it is possible that this pattern could be an artefact of differences in sample size. Ideally, subsampling or rarefaction should be used to address this problem, but we found that most studies did not provide the data needed for such re-analysis. Nevertheless, the ratio of introduced to source sample size does not correlate with the corresponding ratio for allelic richness (Spearman's rank correlation: $N = 62$, $P = 0.50$), and shows only a weak and marginally significant correlation with heterozygosity ratios ($N = 64$, $P = 0.06$, and $P = 0.10$ when *Polistes dominulus* outlier excluded). Furthermore, only 17 species in our review were undersampled in the introductions by more than 5% of the source sample (out of 73 studies clearly reporting sample sizes), and the majority of species were oversampled in the introductions (Table 1). Therefore, the data set should be generally conservative with respect to the detection of founder effects in the invasions. We conclude that these studies generally reflect true losses of variation within introduced populations.

Hypothesis 2: multiple introductions rescue invaders from losses in diversity

Our review identified an overall loss of molecular diversity within populations of introduced species, but it also illustrated substantial differences among species, and a lack of founder effects in some cases. For species such as *Bromus tectorum*, it is clear that multiple introductions have contributed to gains of within-population diversity (Novak & Mack 1993; Novak & Mack 2005), but whether this occurs regularly among invaders is less certain. We compared proportional changes in variation (one-tailed Wilcoxon's signed-rank tests) between species with records of single introductions and those with clear indications (genetic or historical) of multiple introductions into the same region (Table 1). We detected a significant increase in the proportion of allelic richness maintained in invasions where multiple introductions were implied ($P = 0.04$; multiple: $N = 29$, median = -7.9% ; single: $N = 15$, median = -14.3% ; Fig. 2A), but not in the proportion of heterozygosity maintained ($P = 0.18$; Fig. 2B).

The degree of overlap between diversity metrics in the 'multiple' and 'single' introduction categories was striking,

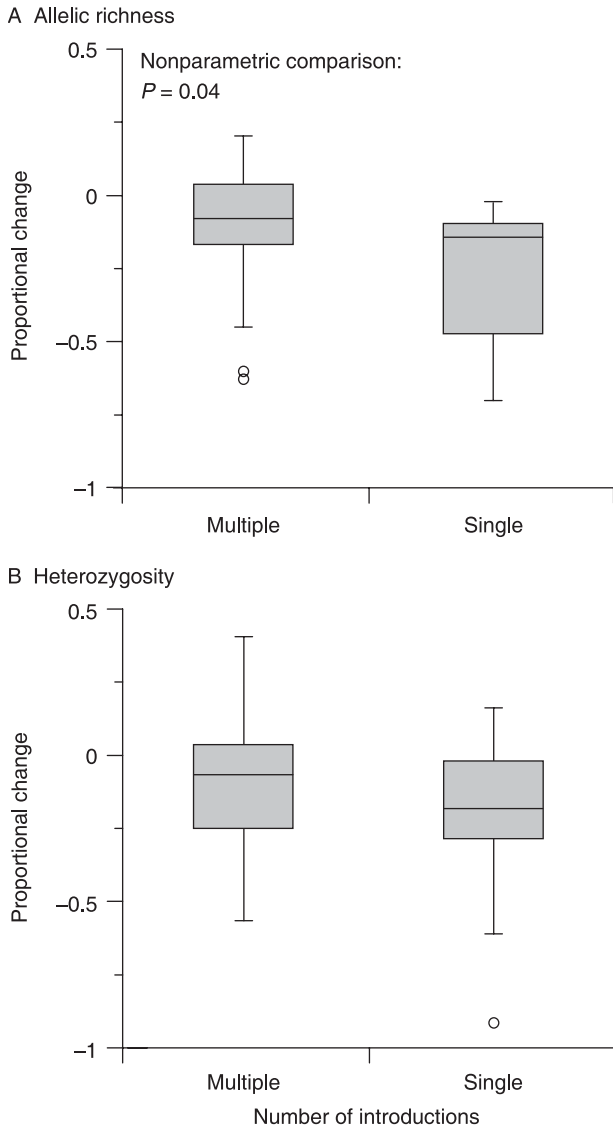


Fig. 2 Box plots showing proportional changes in molecular diversity within populations originating from a single introduction or from multiple introductions, as measured by (A) allelic richness or (B) expected heterozygosity. Single introductions tended to show larger losses of variation than multiple introductions, and this difference was significant for the allelic richness data.

and many species with indications of multiple introductions still showed large deficiencies of variation (Fig. 2). Certainly, many factors within each invasion will affect the genetic outcome of multiple introductions, but we may be able to identify some general features that shape the incorporation of genetic variation across introduced species. By definition, multiple introductions comprise separate dispersal events, and imply the passage of time. Moreover, time will be required for genes from new arrivals to spread in established populations. We postulated that older popu-

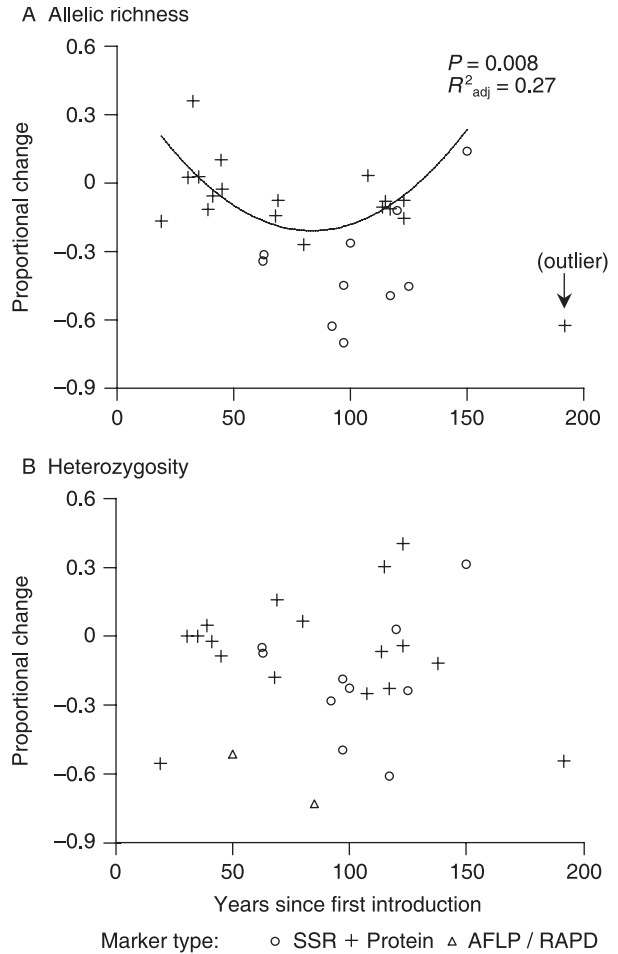


Fig. 3 Proportional changes in (A) allelic richness and (B) heterozygosity by the years since initial introduction, for species where the date of the first introduction is known. Symbols indicate the type of molecular marker used in each study. The allelic richness data are fit by a quadratic relationship with time, excluding one outlier (*Rangifer tarandus*, the only single-locus study examined).

lations would benefit most from the accumulation of genetic material from repeated introductions, and that this process might explain some of the variation in diversity among species. To explore this idea, we plotted the proportional change in molecular variation against the time since first introduction for intentionally introduced species with appropriate records (Table 1). Time since introduction was calculated as the years between the first record of an invasion (averaged across separate introductions) and the year of sampling reported in the study. If no date was given for sampling, we used 1 year prior to publication.

For allelic richness, we found a pattern that was best fit by a quadratic relationship, such that introductions of intermediate ages showed the highest losses of diversity relative to their sources (Fig. 3A, $N = 27$, $r^2_{adj} = 0.27$, $P = 0.008$,

minimum at 83.6 years, [prop. loss = $-0.26 + 0.0006 \cdot (\text{years}) + 0.0001 \cdot (\text{years}-86.4)^2$]). The ratio of introduced to source sample size per population did not show a relationship with time ($N = 30, P = 0.81$), indicating that a sampling artefact could not produce the pattern in the allelic richness data. No quadratic relationship was apparent in the heterozygosity data ($P = 0.37, N = 28$, Fig. 3B). One outlier was excluded from these analyses (Fig. 3): *Rangifer tarandus* showed an unusually large loss of alleles for its duration at a single enzyme locus (the only single-locus study in our review).

We have already noted that protein and microsatellite markers differ in their sensitivity to changes in rare alleles (see above), and it is apparent that studies using each of these markers are unequally distributed across time since first introduction (Fig. 3). The preponderance of microsatellite-based studies at intermediate years is likely to amplify the trough in the distribution. Interestingly, the microsatellite data alone are fit by quadratic relationships for both allelic richness ($N = 10, P = 0.033, r_{\text{adj}}^2 = 0.52$) and heterozygosity ($N = 10, P = 0.049, r_{\text{adj}}^2 = 0.46$). The protein data are not ($A: N = 17, P = 0.34; H: N = 16, P = 0.30$). A variety of additional factors could contribute to these across-species patterns (e.g. differences in generation time, mating system, dispersal vector), and we encourage direct tests of these relationships within individual species or taxa. Some studies have already touched on this approach by detailing diversity at different times in the same introduction (e.g. Berg *et al.* 2002), or in separate introductions of different ages (see Thulin *et al.* 2006 for a particularly outstanding example).

If this U-shaped pattern of diversity loss proves to be a common feature of invasions, it has some important implications. The pattern suggests a decline in molecular variation over several decades, followed by a return to similar levels of diversity as found in source populations. This scenario seems plausible given that drift and strong selection are likely to drive losses of genetic variation during the first decades of population establishment and growth (Nei *et al.* 1975). Over time, however, larger populations should experience reduced drift and become increasingly interconnected, integrating across multiple introductions and rising in diversity relative to native source populations. Consistent with this pattern, Kolbe *et al.* (2004) found that large increases in genetic variation from multiple introductions of the lizard *Anolis segei* were probably not achieved until about a century after the initial introduction.

From this perspective, genetic bottlenecks do not end at establishment, and the benefits of multiple introductions might not be realized for decades (see case study of *Verbascum thapsus* below). This would suggest that most invaders experience a loss of diversity at some point, and that the particular time of study might affect the ability to detect this loss.

Review of quantitative trait diversity

The conjecture is often made that losses of molecular variation during invasion imply lost opportunities for adaptive evolutionary change (e.g. Sakai *et al.* 2001; Allendorf & Lundquist 2003). However, many fitness-related traits are quantitative in nature, and quantitative variation (particularly additive variation) may not decline as readily as molecular variation during demographic bottlenecks (Box 2). We reviewed the literature for studies comparing within-population variation between native and introduced ranges for quantitative traits, and again focused only on human-mediated introductions. We distinguished among studies that quantified additive genetic variation specifically, those that assessed broad-sense genetic variation in common environments (i.e. additive plus nonadditive), and those that surveyed phenotypic variation in wild-caught individuals.

Despite the crucial link between additive genetic variation and the potential for adaptive evolution to contribute to invasion success (Fisher 1958), we found no studies that statistically compared this variation between introduced and native populations. We did find two assessments of additive variation in invading populations. Koskinen *et al.* (2002a, b) assessed both molecular variation and additive variance in populations of arctic grayling fish (*Thymallus thymallus*) in Norway. Despite losing ~50% of molecular variation during an initial introduction, followed by losses of ~10–15% during secondary and tertiary introductions, most morphological and life-history traits showed no apparent decline in additive variation during the secondary and tertiary introductions, and displayed evidence of adaptive divergence. Studies of guppies (*Poecilia reticulata*) introduced to Australia also revealed a strong genetic bottleneck in the invasions (Lindholm *et al.* 2005) despite the presence of substantial additive variation (Brooks & Endler 2001a, b).

Many studies have examined quantitative variation in a broad sense by growing genotypes from introduced and source populations in a common environment. These data are subject to the influence of maternal effects and do not parse out additive from nonadditive variation, but they can suggest whether there might be large differences in quantitative variance among populations. The vast majority of these studies (see reviews in Kinnison & Hendry 2001; Bossdorf *et al.* 2005) find or assume equal variance among populations as part of the application of analysis of variance statistical methods. We found only one study that reported an inability to homogenize variances (Leger & Rice 2003), and this did stem in part from higher variance within native populations (E. Leger personal communication). We found five studies that explicitly compared variance among populations, and all of these found similar levels of variance in introduced and source populations (silky bentgrass, Warwick *et al.* 1987; paperbark tree,

Kaufman & Smouse 2001; St John's wort, Maron *et al.* 2004; flowering rush, Klüber & Eckert 2005; walnut husk fly, Chen *et al.* 2006). Warwick *et al.* (1987) compared 31 morphological and life-history characters between native and introduced populations of silky bentgrass (*Apera spicaventi*) and found that 25 characters showed no statistical difference in variation, and the remaining six were split evenly between increased and decreased variation in the introductions.

We found a single record of a substantial decline in phenotypic variance in an introduction. Simberloff *et al.* (2000) surveyed field-collected specimens of the small Indian mongoose in its native range (India) and in introductions to Jamaica, Fiji, and Mauritius. They found reduced variation in both tooth diameter and skull length in the introductions. Without an examination of individuals reared in a common environment, it is unclear whether these changes are genetic or environmentally induced. It is also interesting to note that microsatellite studies show relatively modest losses of allelic variation in this species (Thulin *et al.* 2006). Other studies of phenotypic variation have found little change in variance (Eurasian tree sparrow, St Louis & Barlow 1988; *Anolis* lizard, Lee 1992; Atlantic cedar, Lefevre *et al.* 2004).

Taken together, the available evidence to date suggests that losses of quantitative variation in invasions may be minimal compared with losses of molecular variation. The abundant evidence for adaptive differentiation in invaders (e.g. Kinnison & Hendry 2001; Bossdorf *et al.* 2005) supports the idea that genetic variation, even if lost, may not be limiting at least in the short term. In particular, several studies have identified both a molecular genetic bottleneck and evidence for substantial adaptive evolution in quantitative traits. In addition to the case of *T. thymallus* described above, bottlenecked introductions of western mosquitofish (*Gabusia affinis*) have adapted to different hydrology regimes (Stockwell *et al.* 1996), those of *Drosophila subobscura* have developed latitudinal clines in wing size (Gilchrist *et al.* 2001), and those of our own study species Canary Island St John's wort (*Hypericum canariense*) have shown adaptation in growth rate and flowering phenology (see below).

Case study no. 1: single introductions, bottlenecks, and rapid evolution in *Hypericum canariense*

Our review of molecular diversity data suggests that most invaders will go through reductions in genetic diversity, and certainly all species are likely to experience periods where founding populations are isolated from gene flow. We have been studying the evolutionary consequences of these circumstances in *Hypericum canariense* L. (Canary Island St John's wort, Hypericaceae), a perennial plant. This species is a multistemmed shrub that can reach 3 m in height. It produces hundreds of large, showy yellow flowers

and has been distributed around the globe by collectors and botanical gardens as a rare ornamental garden plant. It appears to be pollinated by generalist insects and has a mixed mating system, assuring production of hundreds of its tiny seeds per flower (Dlugosch 2006).

Hypericum canariense is a native endemic of the Canary Islands (Robson 1996), but it has escaped cultivation in a variety of locations with Mediterranean-type climates (mild wet winters, and hot dry summers). We have investigated evolutionary changes in three isolated locations where small-scale plantings of *H. canariense* have spread aggressively in less than 50 years: Kula on Maui in the Hawaiian islands (Wagner *et al.* 1999), Point Loma in San Diego and coastal San Mateo county in California, USA (Talbot 1993). These plants form areas of continuous *H. canariense* cover over tens of hectares at each site. The severity of these invasions has come to the attention of conservation agencies, which have placed *H. canariense* on watch lists of invasive species (e.g. The Nature Conservancy Weed Alert, California Invasive Plant Council Weed List).

We have used the source region for these introductions as a benchmark against which we can assess genetic and evolutionary changes. Identifying a source population precisely can be challenging if the potential source region is large and difficult to sample (Box 3). A special opportunity is provided when the native range is highly restricted and can be fully sampled, as is the case with *H. canariense*. We have genotyped several hundred individuals from throughout the native distribution as well as from each invasion (Dlugosch 2006; Dlugosch & Parker in press). Sequence data (internal transcribed spacer region of nuclear ribosomal DNA) placed invaders within the *H. canariense* var. *canariense*, which is distributed across the three Canary Islands of Tenerife, La Gomera, and El Hierro (Dlugosch & Parker in press). Amplified fragment length polymorphism (AFLP) data further identified the source of the invasions as Tenerife, and the genetic similarity of the invasions to one another suggested that they shared a common source (i.e. a single horticultural collection) (Fig. 4A). Tenerife is only 2034 km² in size, providing an unusually precise source region for these invasions.

The invasions of *H. canariense* show both genome-wide losses of variation and evidence of adaptive evolution. Each invasion has lost ~45% of the expected heterozygosity observed in populations from Tenerife, indicating a strong bottleneck relative to other invaders (Fig. 1). Despite the loss of genome-wide variation, these populations have already shown large, rapid, and apparently adaptive genetic changes (Dlugosch 2006; Dlugosch & Parker in press). We have found evidence for increased growth rates (in common gardens) of plants from all three invasions, and of selection for increased growth in terms of both survival and reproduction. In addition, a latitudinal cline in

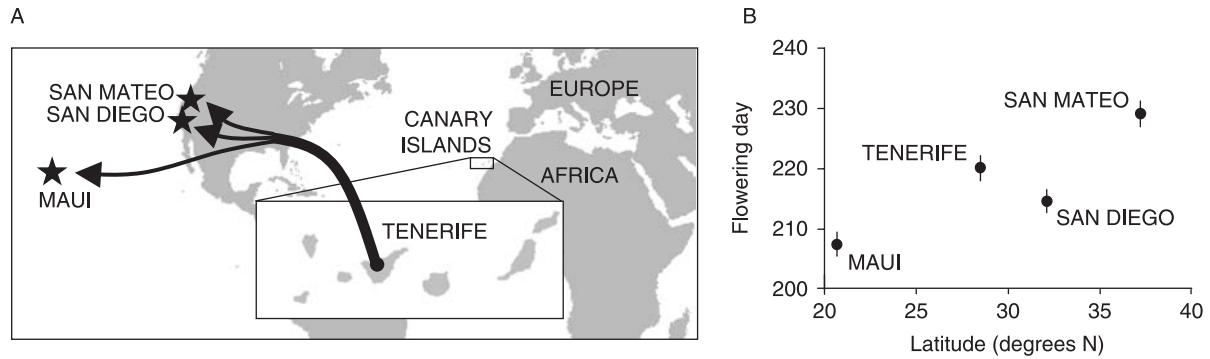


Fig. 4 Local adaptation among introductions of *Hypericum canariense* from a common source. (A) Sequence and AFLP data have indicated that three introductions in North America and Hawaii have originated from a single collection on the native Canary island of Tenerife. (b) Flowering date (Julian day) has diverged among the introduced populations according to latitude (based on data from Dlugosch 2006).

flowering time has developed among the invasions (Fig. 4B). This cline is particularly exciting in that it represents rapid local adaptation among introductions from the same source, where that source is a region with minimal latitudinal range itself. Thus, novel differentiation can arise even in a case where it would seem highly unlikely, and our studies provide an illustration of local adaptation proceeding despite strong founder effects.

Case study no. 2: multiple introductions and a 'geographical mosaic of maladaptation' in *Verbascum thapsus*

Multiple introductions do have the potential to introduce novel genetic variants to invading populations, but this process will be governed by the spatial and temporal nature of the invasion. Our review of molecular variation detected a general pattern wherein the accumulation of genetic material within invading populations was time-dependent (see above). As multiple introduction foci spread across the landscape, the details of history will influence patterns of genetic variation among and within populations, including variation for traits with consequences for fitness across environments in the new region. The haphazard nature of introduction and the delay in movement of genes among populations would be expected to generate a 'mosaic of maladaptation', in which trait values in one population would actually be more optimal in a different local context.

Our studies of the herbaceous plant, *Verbascum thapsus* L. (common mullein, Scrophulariaceae), provide an illustration of the implications of such a mosaic. *V. thapsus* is a rosette-forming, semelparous ('biennial') species, known for carpeting disturbed or naturally open sites in montane areas (Pitcairn 2000). It reproduces via generalist insect pollination and can self-fertilize (Carronero & Hamrick

2005). This species was introduced to California from Europe at some time in the 1800s and is perceived as an invasive threat to some native plant communities (Pitcairn 2000). It is now distributed across more than 2000 m of evaluation range with California (Fig. 5A). Growth chamber and greenhouse experiments showed significant differentiation among populations from across this gradient for a wide range of morphological and physiological traits (Parker *et al.* 2003). However, none of the traits was associated with altitude in a way that would suggest adaptive differentiation *in situ*.

Interestingly, one population from the Sierra foothills was a strong outlier for a number of traits that we expected a priori to be associated with high altitude, e.g. tight rosettes, short leaves, high reflectance, and particularly high freezing tolerance (see population 'A' in Fig. 5A). Although it acts like a high-altitude ecotype, this population was collected from one of the lowest altitudes we sampled. We used AFLPs (130 loci from 10 primer pairs) to ascertain patterns of genetic relatedness among the populations (Fig. 5B). We found no evidence for isolation by distance among the populations (Mantel test of geographical distance vs. Nei's genetic distance: $P = 0.58$). In contrast, there was a strong pattern of association between genetic similarity and physiological similarity (Mantel test of genetic distance vs. difference in freezing tolerance: $P = 0.03$, $R = 0.92$). The population with high-altitude traits (population 'A') appears to be a separate introduction from the native range, where *V. thapsus* occupies a wide altitudinal gradient and comprises a number of differentiated ecotypes (Tutin 1964).

Through a combination of invasive spread and gene flow among populations, these high-altitude traits are expected over time to reach high-altitude sites, with implications for the invasiveness of this plant and our ability to control its spread and impacts. In the meantime, invading populations have been able to expand without the benefit

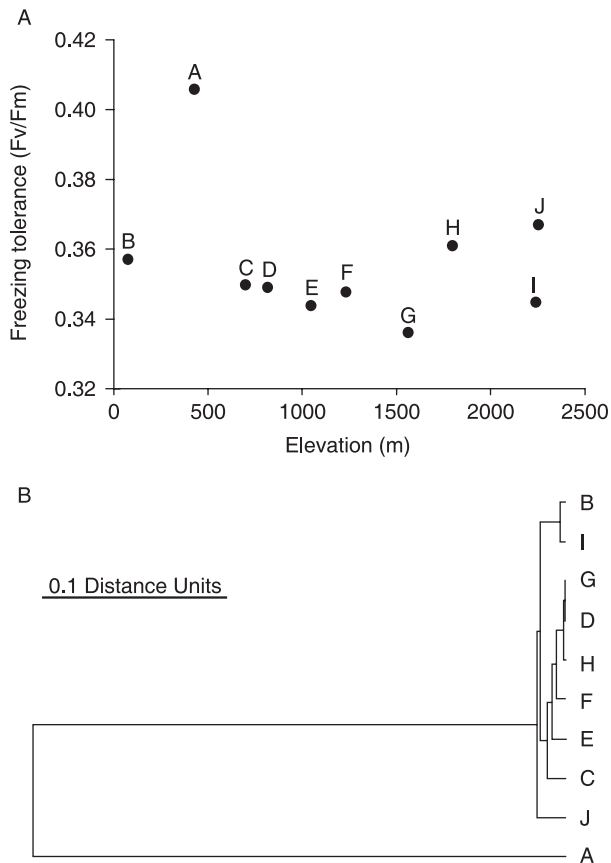


Fig. 5 A mosaic of maladaptation for freezing tolerance in *Verbascum thapsus*. (A) Freezing tolerance (ratio of variable to maximum florescence of common garden plants exposed to freezing temperatures) of populations from different elevations in California (based on data from Parker *et al.* 2003), where population 'A' is an outlier with high freezing tolerance at low elevation. (B) Phenogram of Nei's genetic distances among the same populations, based upon 130 AFLP markers, showing that population 'A' is genetically distinct from the other populations and likely to be a separate introduction.

of this gene flow. Our previous work led to the suggestion that *V. thapsus* represents a 'General Purpose Genotype' (Baker 1965) strategy of invasion (Parker *et al.* 2003). Therefore, multiple introductions may augment the evolutionary and invasive potential of these populations over the long-term, but they have not yet led to a mingling of variants within populations, and are clearly not a necessary condition for invasion success in this case.

Conclusions and implications for management

Our review of the literature on molecular diversity in invading populations across taxonomic groups reveals that many, perhaps most, invading species experience substantial losses

of Mendelian genetic variation during introduction. A few celebrated cases of successful invaders (e.g. *Bromus tectorum*, *Ambrosia artemisiifolia*) show large increases in diversity in the introduced range, apparently caused by the mixing of introductions from different source regions (Novak & Mack 1993; Genton *et al.* 2005). However, our review demonstrates that such increases are rare.

Genes that offer resistance to pathogens and parasites offer one example of traits with strong fitness effects that are often Mendelian in nature. The bottlenecks observed with molecular marker studies may be predictive of changes in plant and animal immune response loci, for which both heterozygosity and allelic diversity may be important (Summers *et al.* 2003; Parker & Gilbert 2004). Low diversity has been implicated in the spread of a *Mycoplasma* epidemic through invading populations of the house finch (*Carpodacus mexicanus*), although it is unclear if the epidemic itself has affected diversity levels in this species (Wang *et al.* 2003; Dhondt *et al.* 2006; Hawley *et al.* 2006). If introduced populations do lack variation at resistance loci, these populations might be easier to manage using biological control techniques; however, more research is needed to explore the link between genetic diversity and control success (Müller-Schärer *et al.* 2004; Hufbauer & Roderick 2005). We have shown that diversity loss varies widely among introduced populations and may change over time, and it is not clear whether such changes would have a predictable and/or meaningful impact on susceptibility to pathogens or parasites.

While genetic bottlenecks may be pervasive for Mendelian markers, such losses of diversity may not predict patterns of variation in quantitative traits, which include many or most ecologically important traits. Our review of the literature shows that quantitative genetic traits appear to maintain relatively large amounts of variation, although more data are clearly needed in this area. A number of studies have shown the potential for rapid adaptive evolution in invading populations. Our case study of *Hypericum canariense* demonstrates that even isolated founding populations with strongly reduced genetic variation may still adapt quickly. Contrary to inferences from small, isolated populations of native species, this suggests that restricted, seemingly innocuous introductions can have the ability to evolve novel invasive behaviour (Stockwell *et al.* 2003; Stockwell & Ashley 2004). Therefore, it is most prudent to target isolated introductions for eradication before they are able to adapt to their novel environments.

Multiple introductions and/or gene flow do not seem to be an indispensable force driving successful invasion. Our analyses imply that these processes do not generate increases in molecular variation for many decades, during which time invaders have already begun expanding successfully. We would not argue, however, that multiple introductions and gene flow are irrelevant to invasion dynamics. Increased diversity through gene flow may still allow the evolution

of extreme phenotypes or movement of the organism into novel habitats or geographical areas. Indeed, our case study of *Verbascum thapsus* illustrates how additional variation from separate introductions can fail to reach nearby sites where it might be most useful. This means that preventing gene flow into isolated introductions could help to reduce adaptive potential in some invaders; it also argues in favour of policies that restrict movement of introduced species within or between regions and minimize the importation of new individuals of species that are already present.

In order to say definitively to what extent genetic bottlenecks may influence invasion success, we would like to compare the performance of founding populations with different degrees of loss of genetic diversity. Unfortunately, we are missing a key piece of information: genetic data on species that were introduced and died out. Such data are nearly unattainable, except in experimental systems (e.g. Martins & Jain 1979) or highly controlled intentional introductions (e.g. biological control introductions, fish stocking). Another approach to the problem would be to try to correlate loss of diversity with degree of invasion success (e.g. local population growth rate, density, rate of spread, perceived impact) using extant introduced populations. We were unable to do this with our data sets because of the difficulty of quantifying invasion success, particularly across the wide range of taxa included in our survey. The lack of data on failed introductions and on invasion success points to an opportunity for evolutionary biologists to collaborate more effectively with applied biologists to gauge the outcomes of founding events. Our data indicate that even successful invaders lose genetic variation after introduction, and future studies will be challenged with understanding how the particular nature of this variation (perhaps rather than its quantity per se) impacts the establishment and spread of introduced species.

Acknowledgements

This manuscript was inspired by the Summit on Micro-Evolutionary Change in Human-Altered Environments (UCLA, February 2007), and we thank T. Smith and L. Bernatchez for organizing and inviting our participation. K. Andonian, E. Cuevas, A. Griffith, S. Swope, N. Wolf, and four anonymous reviewers gave very helpful comments on earlier drafts of this manuscript. Funding during preparation was provided by a United States Department of Agriculture grant to IMP (USDA-NRI no. 2003-35320).

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