

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

K. M. DLUGOSCH and I. M. PARKER

Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, California 95064, USA

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

Correspondence: Katrina M. Dlugosch, E E Biology/EMS, University of California, Santa Cruz, Santa Cruz, CA 95064. Fax: 831-459-5353; E-mail: katrina.dlugosch@gmail.com

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 epipliron</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.

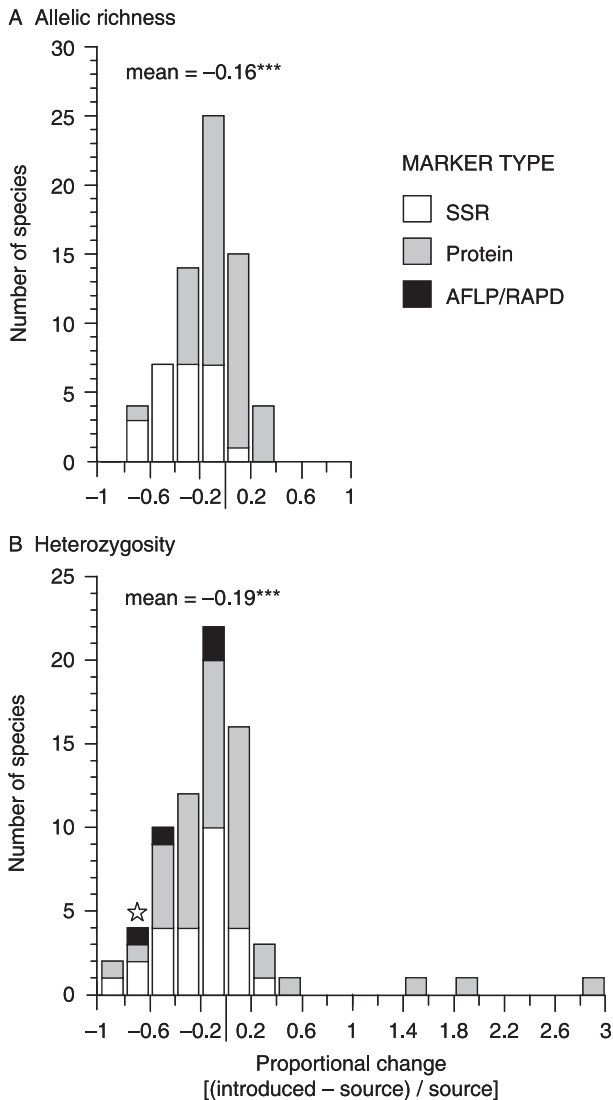


Fig. 1 Histograms showing proportional changes in (A) allelic richness and (B) expected heterozygosity within introduced populations of 80 species, relative to populations within their source region. Values on the x -axis indicate lower bounds of bins. Few large gains in variation have been observed, 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,

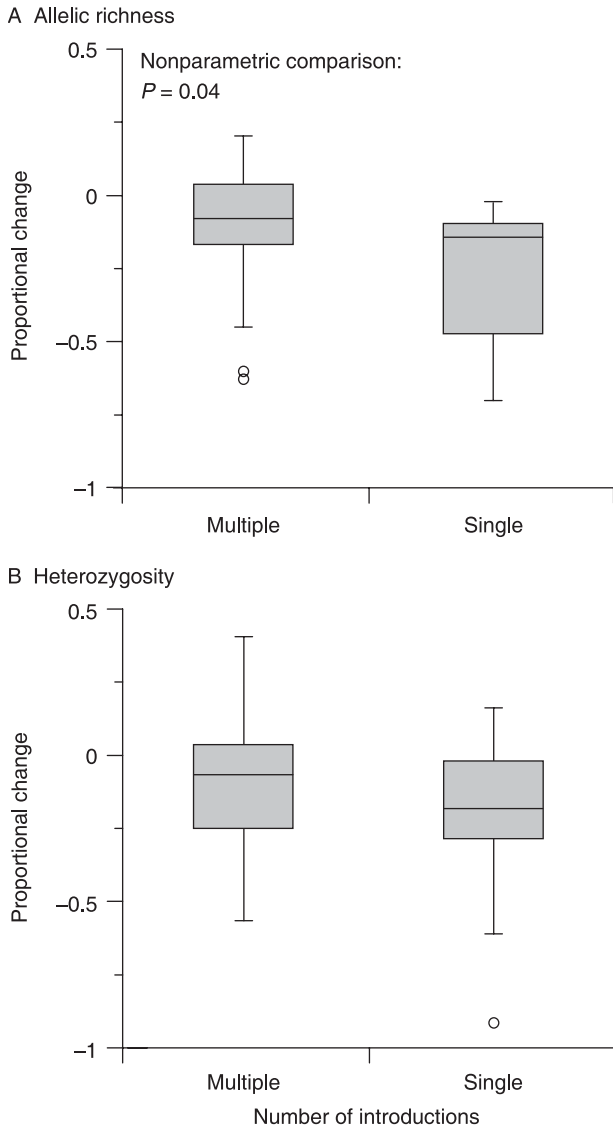


Fig. 2 Box plots showing proportional changes in molecular diversity within populations originating from a single introduction or from multiple introductions, as measured by (A) allelic richness or (B) expected heterozygosity. Single introductions tended to show larger losses of variation than multiple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

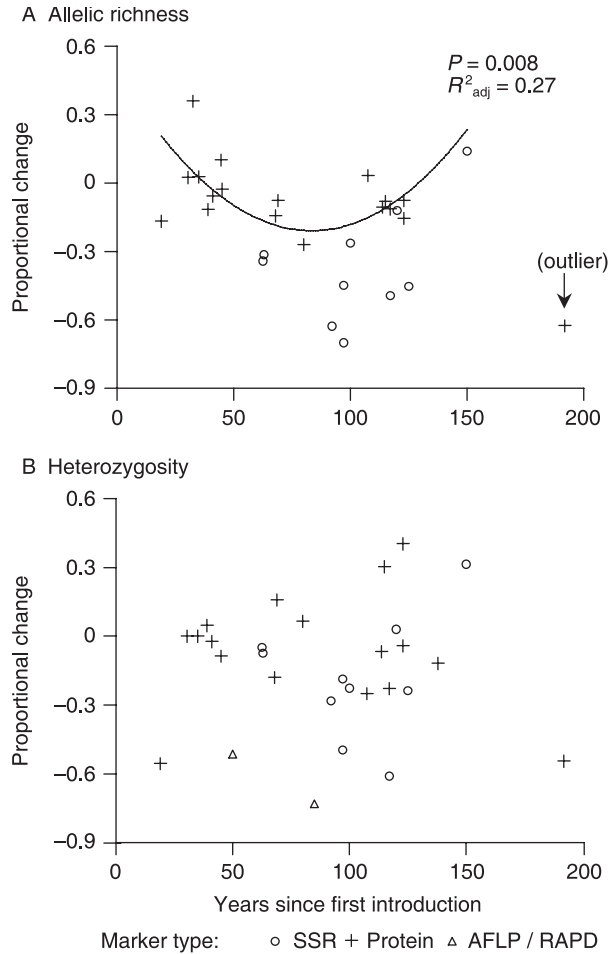


Fig. 3 Proportional changes in (A) allelic richness and (B) heterozygosity by the years since initial introduction, for species where the date of the first introduction is known. Symbols indicate the type of molecular marker used in each study. The allelic richness data are fit by a quadratic relationship 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 segrui* 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 spica-venti*) 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

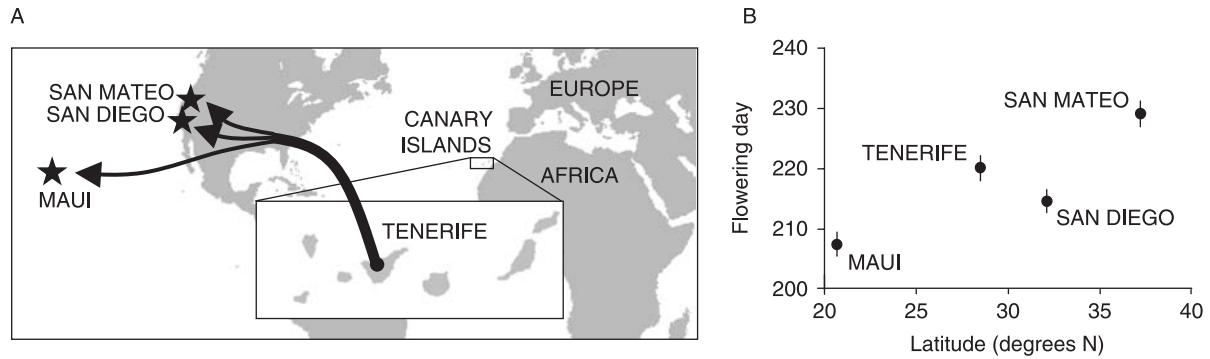


Fig. 4 Local adaptation among introductions of *Hypericum canariense* from a common source. (A) Sequence and AFLP data have indicated that three introductions in North America and Hawaii have originated from a single collection on the native Canary island of Tenerife. (b) Flowering date (Julian day)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

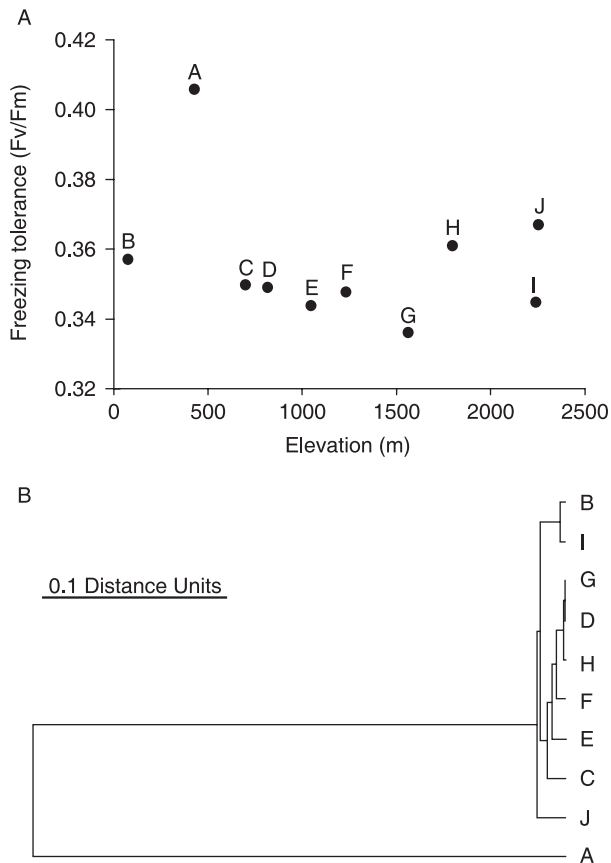


Fig. 5 A mosaic of maladaptation for freezing tolerance in *Verbascum thapsus*. (A) Freezing tolerance (ratio of variable to maximum florescence of common garden plants exposed to freezing temperatures) of populations from different elevations in California (based on data from Parker *et al.* 2003), 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 lead 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).

References

- Agerberg A, Jansson H (1995) Allozymic comparisons between 3 subspecies of the fresh-water crayfish *Pacifastacus leniusculus* (Dana), and between populations introduced to Sweden. *Hereditas*, **122**, 33–39.
- Allendorf FW (1986) Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology*, **5**, 181–190.
- Allendorf FW, Lundquist LL (2003) Introduction: population biology, evolution, and control of invasive species. *Conservation Biology*, **17**, 24–30.
- Andrew J, Ward RD (1997) Allozyme variation in the marine fanworm *Sabella spallanzanii*: comparison of native European and introduced Australian populations. *Marine Ecology Progress Series*, **152**, 131–143.
- Astane I, Gosling E, Wilson J, Powell E (2005) Genetic variability and phylogeography of the invasive zebra mussel, *Dreissena polymorpha* (Pallas). *Molecular Ecology*, **14**, 1655–1666.
- Bagley MJ, Geller JB (1999) Microsatellite DNA analysis of native and invading populations of European green crabs. In: *Marine Bioinvasions: Proceedings of the 1st National Conference* (ed. Pederson J), pp. 241–243. MIT Sea Grant Program, Cambridge, Massachusetts.
- Baker HG (1965) Characteristics and modes of origins of weeds. In: *The Genetics of Colonizing Species* (eds Baker HG, Stebbins GL), pp. 141–172. Academic Press, London.
- Baker HG (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.
- Baker AJ (1992) Genetic and morphometric divergence in ancestral European and descendant New Zealand populations of chaffinches (*Fringilla coelebs*). *Evolution*, **46**, 1784–1800.
- Baker DA, Loxdale HD, Edwards OR (2003) Genetic variation and founder effects in the parasitoid wasp, *Diaeretiella rapae* (M'intosh) (Hymenoptera: Braconidae: Aphidiidae), affecting its potential as a biological control agent. *Molecular Ecology*, **12**, 3303–3311.
- Baker AJ, Moeed A (1987) Rapid genetic differentiation and founder effect in colonizing populations of common mynas (*Acridotheres tristis*). *Evolution*, **41**, 525–538.
- Balanya J, Segarra C, Prevosti A, Serra L (1994) Colonization of America by *Drosophila subobscura*: the founder event and a rapid expansion. *Journal of Heredity*, **85**, 427–432.
- Balfourier F, Charmet G (1994) Geographical patterns of isozyme variation in Mediterranean populations of perennial ryegrass. *Heredity*, **72**, 55–63.
- Baliraine FN, Bonizzoni M, Guglielmino CR *et al.* (2004) Population genetics of the potentially invasive African fruit fly species, *Ceratitis rosa* and *Ceratitis fasciventris* (Diptera: Tephritidae). *Molecular Ecology*, **13**, 683–695.
- Barrett SCH, Husband BC (1990) The genetics of plant migration and colonization.
- Barrett SCH, Richardson BJ (1986) Genetic attributes of invading species. In: *Ecology of Biological Invasions* (eds Groves RH, Burdon JJ), pp. 21–33. Cambridge University Press, New York.
- Barton NH, Charlesworth B (1984) Genetic revolutions, founder effects, and speciation. *Annual Review of Ecology and Systematics*, **15**, 133–164.
- Berg DJ, Garton DW, MacIsaac HJ, Panov VE, Telesh IV (2002) Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga. *Russia Freshwater Biology*, **47**, 275–282.
- Blair AC, Wolfe LM (2004) The evolution of an invasive plant: An experimental study with *Silene latifolia*. *Ecology*, **85**, 3035–3042.
- Boileau M, Hebert PDN (1993) Genetics of the zebra mussle (*Dreissena polymorpha*) in populations from the Great Lakes region and Europe. In: *Zebra Mussels: Biology, Impacts, and Control* (eds Nalepa T, Schloesser D), pp. 227–238. Lewis Publishers, Boca Raton, Florida.

- Bonnet A, Thevenon S, Maudet F, Maillard JC (2002) Efficiency of semi-automated fluorescent multiplex PCRs with 11 microsatellite markers for genetic studies of deer populations. *Animal Genetics*, **33**, 343–350.
- Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.
- Briggs WH, Goldman IL (2006) Genetic variation and selection response in model breeding populations of *Brassica rapa* following a diversity bottleneck. *Genetics*, **172**, 457–465.
- Brooks R, Endler JA (2001a) Direct and indirect sexual selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). *Evolution*, **55**, 1002–1015.
- Brooks R, Endler JA (2001b) Female guppies agree to differ: phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution*, **55**, 1644–1655.
- Brown AHD, Marshall DR (1981) Evolutionary changes accompanying colonization in plants. In: *Evolution Today* (eds Scudder GGE, Reveal JL), pp. 351–363. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania.
- Bryant EH, van Dijk H, van Delden W (1981) Genetic variability of the face fly, *Musca autumnalis* Degeer, in relation to a population bottleneck. *Evolution*, **35**, 872–881.
- Burdon JJ, Brown AHD (1986) Population genetics of *Echium plantagineum* L. — target weed for biological control. *Australian Journal of Biological Sciences*, **39**, 369–378.
- Cabe PR (1998) The effects of founding bottlenecks on genetic variation in the European starling (*Sturnus vulgaris*) in North America. *Heredity*, **80**, 519–525.
- Calmet C, Pascal M, Samadi S (2001) Is it worth eradicating the invasive pest *Rattus norvegicus* from Molene archipelago? Genetic structure as a decision-making tool. *Biodiversity and Conservation*, **10**, 911–928.
- Carronero W, Hamrick JL (2005) The mating system of *Verbascum thapsus* (Scrophulariaceae): The effect of plant height. *International Journal of Plant Sciences*, **166**, 979–983.
- Chaboudez P (1994) Patterns of clonal variation in skeleton weed (*Chondrilla juncea*), an apomictic species. *Australian Journal of Botany*, **42**, 283–295.
- Chen YH, Opp SB, Berlocher SH, Roderick GK (2006) Are bottlenecks associated with colonization? Genetic diversity and diapause variation of native and introduced *Rhagoletis completa* populations. *Oecologia*, **149**, 656–667.
- Cheverud JM, Routman EJ (1996) Epistasis as a source of increased additive genetic variance at population bottlenecks. *Evolution*, **50**, 1042–1051.
- Clegg MT, Allard RW (1972) Patterns of genetic differentiation in the slender wild oat species *Avena barbata*. *Proceedings of the National Academy of Sciences, USA*, **69**, 1820–1824.
- Clegg MT, Brown AHD (1983) The founding of plant populations. In: *Genetics and Conservation* (eds Schonewald-Cox CM, Chambers SM, MacBryde B, Thomas WL), pp. 216–228. Benjamin Cummings, Menlo Park, California.
- Colautti RI, Manca M, Viljanen M *et al.* (2005) Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. *Molecular Ecology*, **14**, 1869–1879.
- Cox GW (2004) *Alien Species and Evolution*. Island Press, Washington.
- Crnokrak P, Merilä J (2002) Genetic population divergence: markers and traits. *Trends in Ecology & Evolution*, **17**, 501.
- Daehler CC, Strong DR (1997) Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia*, **110**, 99–108.
- Demelo R, Hebert PDN (1994) Founder effects and geographical variation in the invading cladoceran *Bosmina (Eubosmina) coregoni* Baird 1857 in North America. *Heredity*, **73**, 490–499.
- DeWalt SJ, Hamrick JL (2004) Genetic variation of introduced Hawaiian and native Costa Rican populations of an invasive tropical shrub, *Clidemia hirta* (Melastomataceae). *American Journal of Botany*, **91**, 1155–1163.
- Dhondt AA, Badyaev AV, Dobson AP *et al.* (2006) Dynamics of mycoplasmal conjunctivitis in the native and introduced range of the host. *Ecohealth*, **3**, 95–102.
- Dlugosch KM (2006) *Adaptation and colonization in Hypericum canariense: past and present invasions of an island endemic*. PhD Thesis, University of California Santa Cruz.
- Dlugosch KM, Parker IM (2007) Molecular and quantitative trait variation across the native range of the invasive species *Hypericum canariense*: evidence for ancient patterns of colonization via pre-adaptation? *Molecular Ecology*, **16**, 4268–4282.
- Dupont L, Jollivet D, Viard F (2003) High genetic diversity and ephemeral drift effects in a successful introduced mollusc (*Crepidula fornicata*: Gastropoda). *Marine Ecology Progress Series*, **253**, 183–195.
- Dupont L, Viard F, Bishop JDD (2006) Isolation and characterization of twelve polymorphic microsatellite markers for the invasive ascidian *Styela clava* (Tunicata). *Molecular Ecology Notes*, **6**, 101–103.
- Durka W, Bossdorf O, Prati D, Auge H (2005) Molecular evidence for multiple introductions of garlic mustard (*Alliaria petiolata*, Brassicaceae) to North America. *Molecular Ecology*, **14**, 1697–1706.
- Easteal S (1985) The ecological genetics of introduced populations of the giant toad *Bufo marinus*: 2. effective population size. *Genetics*, **110**, 107–122.
- Elam DR, Ridley CE, Goodell K, Ellstrand NC (2007) Population size and relatedness affect fitness of a self-compatible invasive plant. *Proceedings of the National Academy of Sciences*, **104**, 549–552.
- Eldridge MDB, Rummery C, Bray C, Zenger KR, Browning TL, Close RL (2004) Genetic analysis of a population crash in brush-tailed rock-wallabies (*Petrogale penicillata*) from Jenolan Caves, south-eastern Australia. *Wildlife Research*, **31**, 229–240.
- Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants. *Proceedings of the National Academy of Sciences, USA*, **97**, 7043–7050.
- Engelbrecht CJB, Harrington TC, Steimel J, Capretti P (2004) Genetic variation in eastern North American and putatively introduced populations of *Ceratocystis fimbriata f. platani*. *Molecular Ecology*, **13**, 2995–3005.
- England PR, Osler GHR, Woodworth LM, Montgomery ME, Briscoe DA, Frankham R (2003) Effects of intense versus diffuse population bottlenecks on microsatellite genetic diversity and evolutionary potential. *Conservation Genetics*, **4**, 595–604.
- Estoup A, Wilson JJ, Sullivan C, Cornuet JM, Moritz C (2001) Inferring population history from microsatellite and enzyme data in serially introduced cane toads, *Bufo marinus*. *Genetics*, **159**, 1671–1687.
- Facon B, Pointier JP, Glaubrecht M, Poux C, Jarne P, David P (2003) A molecular phylogeography approach to biological invasions of the New World by parthenogenetic Thiarid snails. *Molecular Ecology*, **12**, 3027–3039.
- Fisher RA (1958) *The Genetical Theory of Natural Selection*. Dover, Toronto.

- Fleischer RC, Williams RN, Baker AJ (1991) Genetic variation within and among populations of the common myna (*Acridotheres tristis*) in Hawaii. *Journal of Heredity*, **82**, 205–208.
- Frankham R (2005) Invasion biology: resolving the genetic paradox in invasive species. *Heredity*, **94**, 385–385.
- Garcia P, Vences FJ, Perez de la Vega M, Allard RW (1989) Allelic and genotypic composition of ancestral Spanish and colonial Californian gene pools of *Avena barbata*: evolutionary implications. *Genetics*, **122**, 687–694.
- Genton BJ, Shykoff JA, Giraud T (2005) High genetic diversity in French invasive populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of introduction. *Molecular Ecology*, **14**, 4275–4285.
- Gilchrist GW, Huey RB, Serra L (2001) Rapid evolution of wing size clines in *Drosophila subobscura*. *Genetica*, **112**, 273–286.
- Golubtsov AS, Ilyin II, Mina MV (1993) Polymorphisms at 2 enzyme loci (Sod and Odh) in populations of the Amur sleeper, *Perccottus glenii* (Pisces, Eleotrididae), from its native range and the colonized area — the effect of introduction on genetic variation. *Zeitschrift Fur Zoologische Systematik und Evolutionsforschung*, **31**, 269–279.
- Goodman SJ, Tamate HB, Wilson R *et al.* (2001) Bottlenecks, drift and differentiation: the population structure and demographic history of sika deer (*Cervus nippon*) in the Japanese archipelago. *Molecular Ecology*, **10**, 1357–1370.
- Goodnight CJ (1988) Epistasis and the effect of founder events on the additive genetic variance. *Evolution*, **42**, 441–454.
- Gorman GC, Kim YJ, Yang SY (1978) Genetics of colonization: loss of variability among introduced populations of anolis lizards (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology*, **12**, 47–51.
- Grapputo A, Bisazza A, Pilastro A (2006) Invasion success despite reduction of genetic diversity in the European populations of eastern mosquitofish (*Gambusia holbrooki*). *Italian Journal of Zoology*, **73**, 67–73.
- Gray AJ (1986) Do invading species have definable genetic characteristics? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **314**, 655–674.
- Greenberg N, Garthwaite RL, Potts DC (1996) Allozyme and morphological evidence for a newly introduced species of *Aurelia* in San Francisco Bay, California. *Marine Biology*, **125**, 401–410.
- Hamrick JL, Godt MJW (1989) Allozyme diversity in plant species. In: *Plant Population Genetics, Breeding and Genetic Resources* (eds Brown AHD, Clegg MT, Kahler AL, Weir BS), pp. 43–63. Sinauer Associates, Sunderland.
- Hauser L, Carvalho GR, Pitcher TJ (1995) Morphological and genetic differentiation of the African clupeid *Limnothrissa miodon* 34 years after its introduction to Lake Kivu. *Journal of Fish Biology*, **47**, 127–144.
- Hawley DM, Hanley D, Dhondt AA, Lovette IJ (2006) Molecular evidence for a founder effect in invasive house finch (*Carpodacus mexicanus*) populations experiencing an emergent disease epidemic. *Molecular Ecology*, **15**, 263–275.
- Hegde SG, Valkoun J, Waines JG (2002) Genetic diversity in wild and weedy *Aegilops*, *Amblyopyrum*, and *Secale* species: a preliminary survey. *Crop Science*, **42**, 608–614.
- Hendry AP, Quinn TP (1997) Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 75–84.
- Henshaw MT (2000) Microsatellite loci for the social wasp *Polistes dominulus* and their application in other polistine wasps. *Molecular Ecology*, **9**, 2155–2157.
- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5–15.
- Holland BS (2001) Invasion without a bottleneck: microsatellite variation in natural and invasive populations of the brown mussel *Perna perna* (L.). *Marine Biotechnology*, **3**, 407–415.
- Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L (2000) Rapid evolution of a geographic cline in size in an introduced fly. *Science*, **287**, 308–309.
- Hufbauer RA, Roderick GK (2005) Microevolution in biological control: mechanisms, patterns, and processes. *Biological Control*, **35**, 227–239.
- Jackman TR (1998) Molecular and historical evidence for the introduction of clouded salamanders (genus *Aneides*) to Vancouver Island, British Columbia, Canada, from California. *Canadian Journal of Zoology*, **76**, 1570–1580.
- Johnson MS (1988) Founder effects and geographic variation in the land snail *Theba pisana*. *Heredity*, **61**, 133–142.
- Johnson RN, Starks PT (2004) A surprising level of genetic diversity in an invasive wasp: *Polistes dominulus* in the northeastern United States. *Annals of the Entomological Society of America*, **97**, 732–737.
- Kaufman SR, Smouse PE (2001) Comparing indigenous and introduced populations of *Melaleuca quinquenervia* (Cav.) Blake: response of seedlings to water and pH levels. *Oecologia*, **127**, 487–494.
- Kinnison MT, Hendry AP (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica*, **112**, 145–164.
- Kirkpatrick M, Jarne P (2000) The effects of a bottleneck on inbreeding depression and the genetic load. *American Naturalist*, **155**, 154–167.
- Kliber A, Eckert CG (2005) Interaction between founder effect and selection during biological invasion in an aquatic plant. *Evolution*, **59**, 1900–1913.
- Knopp T, Cano JM, Crochet PA, Marila J (2007) Contrasting levels of variation in neutral and quantitative genetic loci on island populations of moor frogs (*Rana arvalis*). *Conservation Genetics*, **8**, 45–56.
- Kolbe JJ, Glor RE, Schettino LRG, Lara AC, Larson A, Losos JB (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**, 177–181.
- Koskinen MT, Haugen TO, Primmer CR (2002a) Contemporary Fisherian life-history evolution in small salmonid populations. *Nature*, **419**, 826–830.
- Koskinen MT, Nilsson J, Veselov AJ, Potutkin AG, Ranta E, Primmer CR (2002b) Microsatellite data resolve phylogeographic patterns in European grayling, *Thymallus thymallus*, Salmonidae. *Heredity*, **88**, 391–401.
- Kruckenhauser L, Haring E, Pinsker W (1999) Microsatellite variation in two species of the genus *Marmota* (Rodentia, Sciuridae). *Folia Zoologica*, **48**, 29–36.
- Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061–2070.
- Lande R (1980) Genetic variation and phenotypic evolution during allopatric speciation. *American Naturalist*, **116**, 463–479.
- Latta RG, McKay JK (2002) Genetic population divergence: markers and traits — response. *Trends in Ecology & Evolution*, **17**, 501–502.

- Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proceedings of the National Academy of Sciences, USA*, **104**, 3883–3888.
- Le Page SL, Livermore RA, Cooper DW, Taylor AC (2000) Genetic analysis of a documented population bottleneck: introduced Bennett's wallabies (*Macropus rufogriseus rufogriseus*) in New Zealand. *Molecular Ecology*, **9**, 753–763.
- Leberg PL (1992) Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. *Evolution*, **46**, 477–494.
- Lee CE (2002) Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, **17**, 386–391.
- Lee JC (1992) *Anolis sagrei* in Florida: phenetics of a colonizing species. III. West Indian and Middle American comparisons. *Copeia*, **1992**, 942–954.
- Lee PLM, Patel RM, Conlan RS, Wainwright SJ, Hipkin CR (2004) Comparison of genetic diversities in native and alien populations of hoary mustard (*Hirschfeldia incana* L. Lagreze-Fossat). *International Journal of Plant Sciences*, **165**, 833–843.
- Lefevre F, Fady B, Fallour-Rubio D, Ghosn D, Bariteau M (2004) Impact of founder population, drift and selection on the genetic diversity of a recently translocated tree population. *Heredity*, **93**, 542–550.
- Leger EA, Rice KJ (2003) Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters*, **6**, 257–264.
- Lewontin RC (1965) Comment on chapter by E. Mayr. In: *The Genetics of Colonizing Species* (eds Baker HG, Stebbins GL), pp. 481–484. Academic Press, London.
- Lindholm AK, Breden F, Alexander HJ, Chan WK, Thakurta SG, Brooks R (2005) Invasion success and genetic diversity of introduced populations of guppies *Poecilia reticulata* in Australia. *Molecular Ecology*, **14**, 3671–3682.
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.
- López-Fanjul C, Fernández A, Toro MA (2002) The effect of epistasis on the excess of the additive and nonadditive variances after population bottlenecks. *Evolution*, **56**, 865–876.
- Malacrida AR, Marinoni F, Torti C *et al.* (1998) Genetic aspects of the worldwide colonization process of *Ceratitix capitata*. *Journal of Heredity*, **89**, 501–507.
- Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecological Monographs*, **74**, 261–280.
- Martins PS, Jain SK (1979) Role of genetic variation in the colonizing ability of rose clover (*Trifolium hirtum* All.). *American Naturalist*, **114**, 591–595.
- Mayr E (1965) The nature of colonizations in birds. In: *The Genetics of Colonizing Species* (eds Baker HG, Stebbins GL), pp. 29–43. Academic Press, London.
- McCommas SA, Bryant EH (1990) Loss of electrophoretic variation in serially bottlenecked populations. *Heredity*, **64**, 315–321.
- McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution*, **17**, 285–291.
- Merilä J, Björklund M, Baker AJ (1996a) Genetic population structure and gradual northward decline of genetic variability in the greenfinch (*Carduelis chloris*) *Evolution*, **50**, 2548–2557.
- Merilä J, Björklund M, Baker AJ (1996b) The successful founder: genetics of introduced *Carduelis chloris* (greenfinch) populations in New Zealand. *Heredity*, **77**, 410–422.
- Merilä J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, **14**, 892–903.
- Molina-Freaner F, Jain SK (1992) Isozyme variation in Californian and Turkish populations of the colonizing species *Trifolium hirtum*. *Journal of Heredity*, **83**, 423–430.
- Müller-Schärer H, Schaffner U, Steinger T (2004) Evolution in invasive plants: implications for biological control. *Trends in Ecology & Evolution*, **19**, 417–422.
- Naciri-Graven Y, Goudet J (2003) The additive genetic variance after bottlenecks is affected by the number of loci involved in epistatic interactions. *Evolution*, **57**, 706–716.
- Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. *Evolution*, **29**, 1–10.
- Neiman M, Linksvayer TA (2006) The conversion of variance and the evolutionary potential of restricted recombination. *Heredity*, **96**, 111–121.
- Novak SJ, Mack RN (1993) Genetic variation in *Bromus tectorum* (Poaceae): comparison between native and introduced populations. *Heredity*, **71**, 167–176.
- Novak SJ, Mack RN (2005) Genetic bottlenecks in alien plant species: influences of mating systems and introduction dynamics. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 201–228. Sinauer Associates, Sunderland, Massachusetts.
- Novak SJ, Mack RN, Soltis DE (1991) Genetic variation in *Bromus tectorum* (Poaceae): population differentiation in its North American range. *American Journal of Botany*, **78**, 1150–1161.
- Parker IM, Gilbert GS (2004) The evolutionary ecology of novel plant–pathogen interactions. *Annual Review of Ecology Evolution and Systematics*, **35**, 675–700.
- Parker IM, Rodriguez J, Loik ME (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. *Conservation Biology*, **17**, 59–72.
- Parkin DT, Cole SR (1985) Genetic differentiation and rates of evolution in some introduced populations of the house sparrow, *Passer domesticus*, in Australia and New Zealand. *Heredity*, **54**, 15–23.
- Pascual M, Aquadro CF, Soto V, Serra L (2001) Microsatellite variation in colonizing and palearctic populations of *Drosophila subobscura*. *Molecular Biology and Evolution*, **18**, 731–740.
- Pfrender ME, Spitz K, Hicks J, Morgan K, Latta L, Lynch M (2000) Lack of concordance between genetic diversity estimates at the molecular and quantitative-trait levels. *Conservation Genetics*, **1**, 263–269.
- Pinceel J, Jordaens K, Van Houtte N, De Winter AJ, Bäckeljau T (2004) Molecular and morphological data reveal cryptic taxonomic diversity in the terrestrial slug complex *Arion subfuscus/fuscus* (Mollusca, Pulmonata, Arionidae) in continental north-west Europe. *Biological Journal of the Linnean Society*, **83**, 23–38.
- Pinceel J, Jordaens K, Van Houtte N, Bernon G, Bäckeljau T (2005) Population genetics and identity of an introduced terrestrial slug: *Arion subfuscus* s.l. in the north-east USA (Gastropoda, Pulmonata, Arionidae). *Genetica*, **125**, 155–171.
- Pitcairn MJ (2000) *Verbascum thapsus*. In: *Invasive Plants of California's Wildlands* (eds Bossard CC, Randall JM, Hoshovsky MC), pp. 321–326. University of California Press, Berkeley, California.
- Planes S, Lecaillon G (1998) Consequences of the founder effect in the genetic structure of introduced island coral reef fish populations. *Biological Journal of the Linnean Society*, **63**, 537–552.

- Reed DH, Frankham R (2001) How closely correlated are molecular and quantitative measures of genetic variation? *Evolution*, **55**, 1095–1103.
- Reiland J, Hodge S, Noor MAF (2002) Strong founder effect in *Drosophila pseudoobscura* colonizing New Zealand from North America. *Journal of Heredity*, **93**, 415–420.
- Reznick DN, Ghalambor CK (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, **112**, 183–198.
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**, 981–993.
- Robson N (1996) Studies in the genus *Hypericum* L. (Guttiferae) 6: sections 20. *Myriandra* to 28. *Elodes Bulletin of the Natural History Museum London (Botany)*, **26**, 75–217.
- Roed KH, Soldal AV, Thorisson S (1985) Transferring variability and founder effect in Iceland reindeer, *Rangifer tarandus* L. *Hereditas*, **103**, 161–164.
- Rogers WE, Siemann E (2004) Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. *Journal of Applied Ecology*, **41**, 561–570.
- Rohner M, Bastrop R, Jursk K (1996) Colonization of Europe by two American genetic types or species of the genus *Marenzelleria* (Polychaeta: Spionidae): an electrophoretic analysis of allozymes. *Marine Biology*, **127**, 277–287.
- Ross HA (1983) Genetic differentiation of starling (*Sturnus vulgaris*: Aves) populations in New Zealand and Great Britain. *Journal of Zoology*, **201**, 351–362.
- Ross KG, Trager JC (1990) Systematics and population genetics of fire ants (*Solenopsis saevissima* complex) from Argentina. *Evolution*, **44**, 2113–2134.
- Ross KG, Vargo EL, Fletcher DJC (1987) Comparative biochemical genetics of 3 fire ant species in North America, with special reference to the 2 social forms of *Solenopsis invicta* (Hymenoptera, Formicidae). *Evolution*, **41**, 979–990.
- Ross KG, Vargo EL, Keller L, Trager JC (1993) Effect of a founder event on variation in the genetic sex-determining system of the fire ant *Solenopsis invicta*. *Genetics*, **135**, 843–854.
- Sakai AK, Allendorf FW, Holt JS *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.
- Schmitt T, Cizek D, Konvicka M (2005) Genetics of a butterfly relocation: large, small and introduced populations of the mountain endemic *Erebia epiphron silesiana*. *Biological Conservation*, **123**, 11–18.
- Schoen DJ, Brown AHD (1991) Intraspecific variation in population gene diversity and effective population size correlates with the mating system in plants. *Proceedings of the National Academy of Sciences, USA*, **88**, 4494–4497.
- Scribner KT, Wooten MC, Smith MH, Kennedy PK, Rhodes OE (1992) Variation in life history and genetic traits of Hawaiian mosquitofish populations. *Journal of Evolutionary Biology*, **5**, 267–288.
- Simberloff D, Dayan T, Jones C, Ogura G (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology*, **81**, 2086–2099.
- Spencer CC, Neigel JE, Leberg PL (2000) Experimental evaluation of the usefulness of microsatellite DNA for detecting demographic bottlenecks. *Molecular Ecology*, **9**, 1517–1528.
- Squirrel J, Hollingsworth PM, Bateman RM *et al.* (2001) Partitioning and diversity of nuclear and organelle markers in native and introduced populations of *Epipactis helleborine* (Orchidaceae). *American Journal of Botany*, **88**, 1409–1418.
- St Louis VL, Barlow JC (1988) Genetic differentiation among ancestral and introduced populations of the Eurasian tree sparrow (*Passer montanus*). *Evolution*, **42**, 266–276.
- Stearns SC (1983) A natural experiment in life history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution*, **37**, 601–617.
- Stepien CA, Taylor CD, Dabrowska KA (2002) Genetic variability and phylogeographical patterns of a nonindigenous species invasion: a comparison of exotic vs. native zebra and quagga mussel populations. *Journal of Evolutionary Biology*, **15**, 314–328.
- Stockwell CA, Ashley MV (2004) Diversity, rapid adaptation and conservation. *Conservation Biology*, **18**, 272–273.
- Stockwell CA, Mulvey M, Vinyard GL (1996) Translocations and the preservation of allelic diversity. *Conservation Biology*, **10**, 1133–1141.
- Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, **18**, 94–101.
- Summers K, McKeon S, Sellars J *et al.* (2003) Parasitic exploitation as an engine of diversity. *Biological Reviews of the Cambridge Philosophical Society*, **78**, 639–675.
- Talbot J (1993) Hypericaceae. In: *The Jepson Manual: Higher Plants of California* (ed. Hickman JC), pp. 708–709. University of California Press, Berkeley, California.
- Taylor CE, Gorman GC (1975) Population genetics of a colonizing lizard: natural selection for allozyme morphs in *Anolis grahami*. *Heredity*, **35**, 241–247.
- Thompson JN (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, **13**, 329–332.
- Thulin CG, Simberloff D, Barun A, McCracken G, Pascal M, Islam MA (2006) Genetic divergence in the small Indian mongoose (*Herpestes auropunctatus*), a widely distributed invasive species. *Molecular Ecology*, **15**, 3947–3956.
- Triggs SJ, Green WQ (1989) Geographic patterns of genetic variation in brushtail possums *Trichosurus vulpecula* and implications for pest control. *New Zealand Journal of Ecology*, **12**, 1–16.
- Tsutsui ND, Suarez AV, Holway DA, Case TJ (2000) Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences, USA*, **97**, 5948–5953.
- Turelli M, Barton NH (2006) Will population bottlenecks and multilocus epistasis increase additive genetic variance? *Evolution*, **60**, 1763–1776.
- Tutin TG (1964) *Flora Europaea*. Cambridge University Press, Cambridge.
- Urbanelli S, Bellini R, Carrieri M, Sallicandro P, Celli G (2000) Population structure of *Aedes albopictus* (Skuse): the mosquito which is colonizing Mediterranean countries. *Heredity*, **84**, 331–337.
- Van Buskirk J, Willi Y (2006) The change in quantitative genetic variation with inbreeding. *Evolution*, **60**, 2428–2434.
- Wagner WL, Herbst DR, Sohmer SH (1999) *Manual of the Flowering Plants of Hawaii*. University of Hawaii and Bishop Museum Press, Honolulu.
- Wang Z, Baker AJ, Hill GE, Edwards SV (2003) Reconciling actual and inferred population histories in the house finch (*Carpodacus mexicanus*) by AFLP analysis. *Evolution*, **57**, 2852–2864.
- Wang JL, Caballero A, Keightley PD, Hill WG (1998) Bottleneck effect on genetic variance: a theoretical investigation of the role of dominance. *Genetics*, **150**, 435–447.
- Wares JP, Hughes AR, Grosberg RK (2005) Mechanisms that drive evolutionary change: insights from species introductions and

- invasions. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 229–257. Sinauer Associates, Sunderland, Massachusetts.
- Warwick SI, Thompson BK, Black LD (1987) Genetic variation in Canadian and European populations of the colonizing weed species *Apera spica-venti*. *New Phytologist*, **106**, 301–317.
- Webley LS, Zenger KR, English AW, Cooper DW (2004) Low levels of genetic variation within introduced Javan rusa deer (*Cervus timorensis russa*) in Australia. *European Journal of Wildlife Research*, **50**, 137–140.
- Whitlock MC, Phillips PC, Wade MJ (1993) Gene interaction affects the additive genetic variance in subdivided populations with migration and extinction. *Evolution*, **47**, 1758–1769.
- Willi Y, Van Buskirk J, Hoffmann AA (2006) Limits to the adaptive potential of small populations. *Annual Review of Ecology Evolution and Systematics*, **37**, 433–458.
- Willis JH, Orr HA (1993) Increased heritable variation following population bottlenecks: the role of dominance. *Evolution*, **47**, 949–957.
- Zeisset I, Beebee TJC (2003) Population genetics of a successful invader: the marsh frog *Rana ridibunda* in Britain. *Molecular Ecology*, **12**, 639–646.
- Zhang XS, Wang JL, Hill WG (2004) Redistribution of gene frequency and changes of genetic variation following a bottleneck in population size. *Genetics*, **167**, 1475–1492.
- Zhou XD, Burgess TI, Beer ZW *et al.* (2007) High intercontinental migration rates and population admixture in the sapstain fungus *Ophiostoma ips*. *Molecular Ecology*, **16**, 89–99.

Katrina Dlugosch's research centres on the evolutionary ecology of colonization events, with a particular focus on adaptation in invasive plants. She is a postdoctoral scholar at the University of California Santa Cruz, having recently finished her PhD under Ingrid Parker. She will move to a postdoctoral position at the University of British Columbia with Loren Rieseberg in the fall of 2007. Ingrid Parker holds the Jean H. Langenheim Chair in Plant Ecology and Evolution at the University of California Santa Cruz. Her research interests span topics in plant-pollinator and plant-pathogen interactions as well as the evolutionary ecology of invasive and domesticated species.
