Paradox lost: genetic diversity and the success of aquatic invasions

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There is mounting evidence that reduced genetic diversity in invasive populations is not as commonplace as expected. Recent studies indicate that high propagule vectors, such as ballast water and shellfish transplantations, and multiple introductions contribute to the elimination of founder effects in the majority of successful aquatic invasions. Multiple introductions, in particular, can promote range expansion of introduced populations through both genetic and demographic mechanisms. Closely related to vectors and corridors of introduction, propagule pressure can play an important role in determining the genetic outcome of introduction events. Even low-diversity introductions have numerous means of avoiding the negative impact of diversity loss. The interaction of high propagule vectors and multiple introductions reveal important patterns associated with invasion success and deserve closer scrutiny.

The rise of aquatic invasions

Thousands of estuarine, freshwater and marine species have been dispersed or transplanted throughout the world by humans [1]. In San Francisco Bay, for example, a new species – including plants, protists, invertebrates and vertebrates – becomes established every 14 weeks, compared to every 55 weeks before 1960 [1]. The invasion rate of freshwater cladocera, small crustaceans such as the water flea *Daphnia*, is now 50 000 times higher than background levels before humans played a dominant role in species transport [2].

This startling rise in the success of aquatic invasive species has occurred despite what some have dubbed a 'genetic paradox' (see Glossary). Small founding populations of introduced species are expected to have genetic variation that is lower than that of native populations as a result of bottlenecks [3]. Lessons learned from conservation genetics lead us to expect that such arrivals would be subject to high risk of inbreeding and extinction [4]. Drift and founder events should also limit the ability of such populations to adapt (Box 1). How then do these species become established, expand their invasive range and respond to novel environmental conditions?

Here, we review recent empirical literature comparing the genetic diversity of native and introduced populations in aquatic ecosystems. These systems are particularly interesting for several reasons. First, the rise of transoceanic shipping and globalization, and the subsequent increase in aquatic invasion rates [1,5], has enhanced motivation to understand invasion success, or establishment. Second, the variety of potential vectors for aquatic introductions lets us examine possible relationships between vectors, propagule pressure and genetic diversity. Finally, the number of potential case studies has risen with increased research effort. Many of these studies reveal that multiple introductions play an important role in the expansion of invasive populations.

Glossary

Admixture: The occurrence, in the same population, of individuals from multiple genetically distinct sources. These sources are typically geographically separated native populations of a species, though they can also be temporally distinct samples from the same geographic population or even populations of closely related species. Note that observation of admixture in this sense does not require direct observation of intermediate genotypes, although the generation of such genotypes is the expectation for admixture between populations of the same species.

Bottleneck: Severe reduction in the demographic size of a population.

Corridor: The geographic route along which introduced propagules are conveyed.

Cryptic invasion: Invasion of a species or non-native genotype that goes undetected, often because of morphological similarity with a native or previous invasion; typically resolved by molecular techniques.

Founder effect: Loss of genetic diversity in a population established by a small number of individuals.

Gene flow: Transfer of genetic material from one population to another, also referred to as migration.

Genetic paradox: A dilemma in invasion biology: how do newly founded populations overcome low genetic diversity and expected low evolutionary potential, typically associated with extinction risk, to become established outside of their native range?

Hybridization: The breeding of individuals from genetically distinct populations (either within or between species), resulting in genotypes with novel combinations of alleles.

Inbreeding depression: The reduction of fitness caused by mating between relatives.

Invasion success: The establishment of a non-indigenous species

Invasive species: An introduced species that has become established outside of its native range and is likely to cause ecological or economic harm.

Lag phase: The time between the introduction and establishment of a non-indigenous species.

Outbreeding depression: The reduction of fitness of hybrids.

Overdominance: A condition in which a heterozygote has higher relative fitness than either homozygote, also known as heterozygote advantage.

Propagule pressure: A measure of the number of viable individual non-native organisms introduced to a recipient environment. Equal to the product of inoculum size (the number of propagules released with a single introduction event) and number of introduction events.

Vector: The physical conveyance responsible for moving introduced propagules from source to recipient environments.

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Overcoming the paradox

There have been several proposals to explain how invasive populations overcome the challenge of low genetic diversity. First, it has become clear that introduced populations can succeed despite reduced diversity at neutral genetic loci – the type of diversity most readily measured in natural populations. This might be because variation at most molecular markers underestimates non-neutral genetic diversity (the variation acted upon by selection) and so is of limited importance in assessing ability to respond to new environments [6–9]. Alternatively, demographic bottlenecks might have positive impacts on introduced populations by purging deleterious alleles, preserving highly adapted clonal lineages from sexual recombination, or through other genetic mechanisms (Box 2).

By contrast, recent studies suggest that there simply are no dramatic diversity losses in most successful invasions. In particular, invasive populations can succeed by increasing genetic diversity in their new range through the admixture of lineages from multiple native populations. In such cases, there can be intraspecific hybridization of individuals from genetically distinct sources. For instance, ~69% of invasive plants had genetic diversity that was the same as or higher than that of native populations; many of these species exhibit rapid evolutionary change in novel environments [10]. A similar study of 29 invasive terrestrial and aquatic animals showed that introduced populations maintain on average ~80% of the genetic variation present in native sources [9].

These results appear to be consistent with studies linking increased propagule pressure to invasion success [11], a connection that might be more than just demographic. In their review of propagule pressure and invasion success, Lockwood *et al.* [12] suggested that the relationship between propagule pressure and genetic variation deserves greater attention than it has received. Since then, several authors have remarked on the possible connections between vectors, propagule pressure, multiple invasions and genetic diversity (e.g. [13]), but none have attempted to explicitly examine these relationships.

Living with bottlenecks

Of the 43 introduced populations reviewed here (Box 3), only 16 (37%) showed clear evidence of significant loss of genetic diversity relative to native populations. Unfortunately, although measurements of relative genetic diversity are becoming more common, research into the mechanisms explaining the success of low-diversity populations lags behind considerably. It is interesting to note, however, that our review indicates the possible importance of reproductive mode as a determinant of the capacity of populations to become invasive despite low genetic diversity. Of the 16 invasions exhibiting loss of genetic diversity, 10 (63%) were species capable of reproducing without sexual recombination. By contrast, of 27 successful invasions with no significant loss of diversity, only 5 species (19%) had similar flexibility of mode of reproduction. This correlation does not necessarily indicate causation; asexuals simply might be more prone to loss of diversity through founder events. But it is also possible that the availability of asexual reproduction can mitigate the negative genetic effects of population bottlenecks, particularly in cases in which introduced genotypes exhibit plastic responses to novel environments or possess phenotypes with broad environmental tolerances [14].

Box 2. Molecular diversity might not predict invasion success

Are populations that exhibit high neutral molecular diversity more likely to become invasive? Although conventional wisdom would answer this question with a cautious yes [4,23], several examples suggest that the relationship between genetic diversity and invasiveness might not be straightforward (Figure I).

Molecular diversity might not reflect genetic variation relevant to ecological success

Several authors have pointed out the limited relevance of variation in neutral molecular markers for determining the potential of introduced populations to adapt to novel environments [9,10,50]. Whereas diversity at presumably neutral markers (e.g. mtDNA, microsatellites and allozymes) might correlate with diversity at quantitative trait loci if selective forces are insufficient to overcome genetic drift [51], some recent studies reveal that this correlation is often quite weak, particularly for quantitative traits related to fitness [8,52]. Lindholm *et al.* recently found low diversity at mtDNA and nuclear microsatellite loci in introduced populations of the guppy *Poecilia reticulata*, despite previous studies demonstrating high additive genetic variance in several quantitative traits [33,53]. Similarly, the grayling *Thymallus thymallus* has very low microsatellite diversity in intentionally introduced populations, although clear evidence of selection on quantitative traits has been observed [54].

The success of clonal genotypes

In some cases, populations can successfully invade with no genetic variation. Perhaps the most striking example is *Daphnia pulex* in Africa. During the past 75 years, a diverse assemblage of *D. pulex* genotypes has been replaced by a single non-native clone introduced from the Americas [55]. Amazingly, the takeover has occurred despite the presence of resting native egg banks and competition from native *D. pulex* and ten additional daphnid species. Highly successful clonal genotypes have also been reported among invasive plant species [56–58]. The water hyacinth *Eichhornia crassipes,* for example, appears to be predominantly clonal in its introduced range in China, with a single clone representing up to 67% of some populations [57].

The importance of plasticity

Ecological plasticity can complicate the relationship between genetic diversity and invasiveness. For instance, the alligator weed *Alternanthera philoxeroides* is capable of invading aquatic and terrestrial environments despite genetic studies indicating low diversity [59].

Yu-Peng *et al.* recently performed common garden experiments demonstrating a lack of quantitative genetic differentiation between aquatic and terrestrial populations [60]. This absence of diversity parallels a lack of differentiation at neutral loci, suggesting that phenotypic plasticity, not adaptation, has allowed the species to colonize diverse habitats.
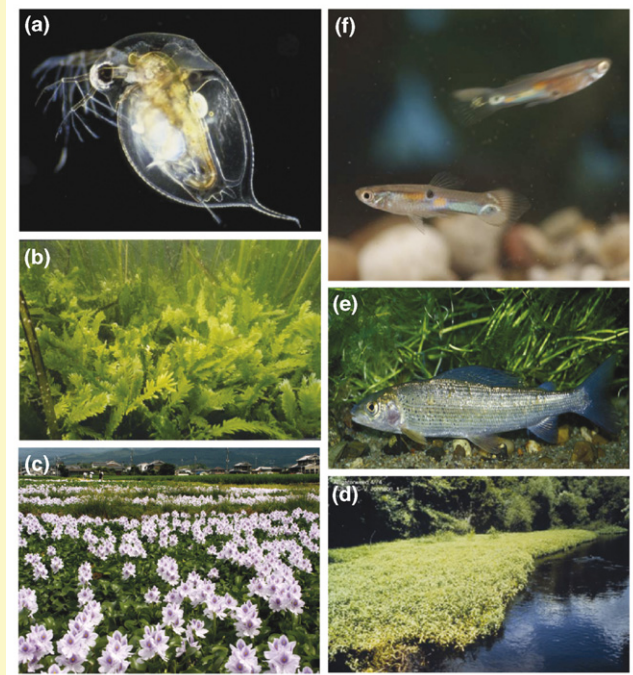

Figure I. Molecular diversity doesn't always predict invasion success. **(a)** The parthenogenic waterflea *D. pulex* and the vegetatively reproducing plants **(b)** *Caulerpa taxifolia* and **(c)** *E. crassipes* all have highly invasive clonal genotypes. **(d)** The alligator weed *A. philoxeroides* exhibits high ecological plasticity, and can invade both terrestrial and aquatic habitats despite very low molecular and quantitative diversity. The invasive fish species **(e)** *T. thymallus* and **(f)** *P. reticulata* possess sufficient additive genetic variance for local adaptation despite low diversity at neutral markers.

The importance of propagule pressure

Propagule pressure is likely to be a significant factor mediating the genetic diversity present in introduced populations, although it is certainly not the only one (Figure 1). To understand the impact that propagule pressure has on genetic diversity, it is necessary to recognize that it is a composite measure of both inoculum size – the number of viable propagules transported with a single introduction event – and number of introduction events [15]. Large inoculum size is likely to have a relatively straightforward impact on genetic diversity. The release of numerous individuals into a new area increases the likelihood that an introduced population will retain representative samplings of source genetic diversity. In addition, large inocula with high effective population sizes are less likely to experience the negative genetic consequences of inbreeding, stochastic diversity loss through drift and lowered response to selection (Box 1).

The number of introduction events might have a less predictable impact. In some cases, multiple introductions can bring additional genetic diversity from the same or similar native sources, essentially equivalent to increasing the size of inocula. But if additional introduction events

derive from genetically diverse native populations, the resulting invasive populations can have greater genetic diversity than those observed in the native range. Such admixture has been demonstrated dramatically by Kolbe
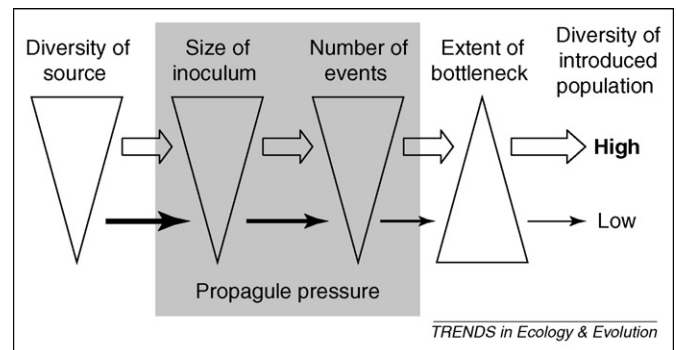
Figure 1. Factors contributing to the genetic diversity of invasive populations. Triangles indicate the magnitude of each factor, tapering from high to low from the base to the point. Arrow thickness indicates the relative genetic diversity preserved from source to introduced populations. The gray box highlights factors explicitly associated with propagule pressure. Genetically diverse invasive populations are likely to derive from high diversity sources and be associated with high propagule pressure from large inocula, multiple introduction events or both. They can avoid extreme or extended population bottlenecks as a result of either large initial founder populations or rapid post-introduction population expansion.

Box 3. Studies assessing the genetic diversity of aquatic introduced populations

Recent empirical studies have challenged the assumption that anthropogenic translocation of species beyond their native ranges is accompanied by loss of genetic diversity [9,10]. Many introduced populations appear to possess levels of diversity at neutral genetic markers comparable to or greater than those of native sources. Several explanations for this phenomenon have been proposed, including the introduction of large propagule pools (thus avoiding founder effects) and multiple introductions from genetically diverse sources [4,16,23].

Table I collects recent genetic studies of aquatic invasive species that directly compare neutral diversity in introduced and native populations. We have recorded the most likely vectors of introduction for these invasions and, in many cases, whether or not they have derived from single or multiple introduction events. We did not include studies in which taxonomic uncertainty potentially complicated the interpretation of results. Although interspecific hybridization is a mechanism for generating highly diverse populations, it can confound attempts to compare diversity in native and introduced populations. Such studies are avoided here, although several are discussed in the text. Comparisons of genetic diversity are cited as determined by the authors of the papers referenced. Assessments of multiple versus single introductions were listed for cases in which genetic evidence clearly indicates one or the other, for example, cases for which there is clearly admixture from different sources or reliable historical evidence. Vectors and dates of introduction are from discussions in the studies.

Overall, it appears that diverse invasive populations are the norm in aquatic systems and many populations result from multiple introductions. Certain vectors, such as ballast water and shellfish transplantation, seem to regularly convey highly diverse populations, whereas others, such as intentional introductions, show trends toward lowered diversity. This assessment provides a general overview of trends in aquatic invasions and is intended to serve as a stimulus for future study.

Table I. Recent studies assessing the genetic diversity of introduced populations in aquatic systems

Species	Common name	Reproductive mode	Marker(s)[a]	n (native, introduced)[b]	Diversity comparison[c]	Number of introductions	Most likely vector of introduction	Refs
Apollonia melanastomus	Round goby	Sexual	mtDNA	7,6	NC	Multiple	Ballast water	[23]
Cephalopholis argus	Grouper	Sexual	Allozyme	1,1	NC	Single	Intentional release	[61]
Gymnocephalus cernuus	Eurasian ruffe	Sexual	mtDNA, allozyme	7,5	NC	Single	Ballast water	[23]
Lates niloticus	Nile perch	Sexual	Allozyme	2,10	−/NC	Unknown	Intentional release	[62]
Lepomis macrochirus	Bluegill sunfish	Sexual	mtDNA	13,59	−	Multiple[d]	Intentional release	[31]
Lutjanus fulvus	Snapper	Sexual	Allozyme	1,3	NC	Single	Intentional release	[61]
Proterorhinus semilunaris	Tubenose goby	Sexual	mtDNA	3,2	NC	Unknown	Ballast water	[23]
Protopterus aethiopicus	Marbled lungfish	Sexual	mtDNA	5,1	−	Single	Intentional release	[63]
Siganus luridus	Rabbitfish	Sexual	mtDNA, EPIC, ISSR	2,1	NC	Continuous	Lessepsian migrant	[26]
Siganus rivulatus	Rabbitfish	Sexual	mtDNA, EPIC, ISSR	2,1	NC	Continuous	Lessepsian migrant	[29]
Siluris aristotelis	Aristotle's catfish	Sexual	SSR	2,1	NC	Single	Intentional release	[64]
Upeneus molucccensis	Goldband goatfish	Sexual	mtDNA, EPIC	1,1	NC	Continuous	Lessepsian migrant	[28]
Bythotrephes longimanus	Spiny waterflea	Facultative parthenogen	SSR	4,3	NC[e]	Multiple	Ballast water	[25]
Carcinus maenas	Green crab	Sexual	mtDNA	15,25	−/NC	Multiple	Solid ballast, ballast water	[65]
Cercopagis pongoi	Fishhook waterflea	Facultative parthenogen	mtDNA	6,6	−	Unknown	Ballast water	[66]
Chthalamus proteus	Barnacle	Sexual	mtDNA	9,23	+[f]	Multiple	Ship fouling	[67]
Daphnia exilis	Waterflea	Facultative parthenogen	Allozyme	13,1	−	Single	Equipment fouling	[68]
Eriocheir sinensis	Chinese mitten crab	Sexual	SSR	1,7	−	Unknown	Ballast water	[34]
Gammarus tigrinus	Amphipod	Sexual	mtDNA	13,19	−/+[g]	Multiple	Ballast water	[13]
Batillaria attramentaria	Asian mud snail	Sexual	mtDNA	14,4	−	Single	Shellfish transplantation	[22]
Crepidula fornicata	Slipper limpet	Sexual	Allozyme	1,12	NC	Multiple	Shellfish transplantation	[69]
Cyclope neritea	Gastropod	Sexual	mtDNA	14,5	+[h]	Multiple	Shellfish transplantation	[40]

Table I (Continued)

Species	Common name	Reproductive mode	Marker(s)[a]	n (native, introduced)[b]	Diversity comparison[c]	Number of introductions	Most likely vector of introduction	Refs
Dreissena bugensis	Quagga mussel	Sexual	mtDNA, RAPD	9,11	NC	Unknown	Ballast water	[23]
Dreissena polymorpha	Zebra mussel	Sexual	mtDNA, RAPD	18,15	NC	Multiple	Ballast water	[23]
Dreissena rostriformis	Mussel	Sexual	SSR	3,10	NC	Multiple	Ballast water	[70]
Lymnaea truncatula	Snail	Hermaphroditic selfer	SSR	12,13	−	Single	Unknown	[71]
Melanoides tuberculata	Snail	Parthenogen	mtDNA	20,21	NC	Multiple	Aquarium release	[20]
Ocinebrellus inornatus	Asian oyster drill	Sexual	mtDNA, allozyme	3,1	NC	Unknown	Shellfish transplantation	[72]
Perna perna	Brown mussel	Sexual	SSR	6,6	NC	Single	Ballast water	[73]
Potamopyrgus antipodarum	Mud snail	Facultative parthenogen	mtDNA	15,17	−	Unknown	Maritime traffic[i]	[74]
Crambe crambe	Sponge	Sexual, asexual	ITS	9,2	−[j]	Unknown	Ballast water?	[75]
Sabella spallanzanii	Polychaete	Sexual	ITS	9,3	−	Single	Ballast water	[76]
Alternanthera philoxeroides	Alligator weed	Sexual	mtDNA	2,2	NC	Unknown	Agriculture	[59]
Butomus umbellatus	Flowering rush	Sexual and vegetative	RAPD	71,69	−	Unkown	Agriculture	[77]
Phragmites australis	Common reed	Sexual and vegetative	SSR	125,150[k]	NC	Unknown	Solid ballast and marsh fill	[78]
Caulerpa taxifolia	Green alga	Sexual and vegetative	cpDNA, ITS	5,8	−	Multiple	Aquarium release	[58]
Codium fragile	Green alga	Parthenogenic and asexual	cpDNA, SSR	8,10	NC	Multiple	Maritime traffic	[79]
Fucus serratus	Toothed wrack	Sexual	SSR	13,9	NC	Single	Solid ballast	[80]
Polysiphonia harveyi	Red alga	Sexual	cpDNA	4,19	−	Multiple	Maritime traffic	[81]
Undaria pinnatifida	Brown alga	Asexual, sexual	mtDNA	5,16	+	Multiple	Ballast water	[30]
Undaria pinnatifida	Brown alga	Asexual, sexual	mtDNA	5,17	−	Single	Ballast water	[30]
Undaria pinnatifida	Brown alga	Asexual, sexual	mtDNA	5,18	−	Multiple	Aquaculture	[33]

[a]mtDNA, mitochondrial DNA; EPIC, exon-primed intron crossing PCR; ISSR, intersimple sequence repeats; SSR, simple sequence repeats (microsatellites); RAPD, random amplified polymorphic DNA; ITS, ribosomal internal transcribed spacer; cpDNA, chloroplast DNA

[b]Number of populations studied in native/introduced range

[c]Comparisons are listed as: − (overall loss of diversity in introduced populations); NC (no significant change in diversity); or + (overall gain in diversity)

[d]Multiple known introductions, but all contemporary populations traced to single original introduction (18 individuals)

[e]Likely erosion of initial founder effect because of multiple introductions

[f]Low sampling in native range indicates that diversity might be underestimated

[g]Individual introductions show lowered diversity, admixture zones show increased diversity

[h]Possibly cryptogenic, but multiple introductions contribute to range expansion

[i]Unresolved vector, possibly including ballast water, solid ballast and hull fouling

[j]Introduced status inferred from lowered diversity, possibly cryptogenic

[k]Number of individuals, not populations

et al. in the case of Cuban anoles introduced to Florida [16]. It has also been observed in several aquatic invasive species, such as the European spiny waterflea *Bytho-trephes longimanus*, the amphipod *Gammarus tigrinus* and the European green crab *Carcinus maenas* (Box 4). Newly introduced genotypes can be preadapted to recipient environments in ways that the initial invasive cohort is not or they might simply provide additional raw material to respond to local selection pressures [16,17]. Alternatively, admixture of previously allopatric populations might increase fitness through overdominance effects. Either way, such increases in genetic diversity have the potential to alter the capacity of introduced populations to succeed in their new environments.

Delivering diversity: vectors and corridors

Given the importance of propagule pressure in determining genetic diversity, it stands to reason that certain vectors and invasion corridors are more likely to enhance variation than others. Ballast water has the potential to be an extremely efficient vector for large propagule pools [18]. By contrast, vectors such as aquarium releases, although perhaps responsible for numerous invasions [19], almost certainly introduce only a few propagules per event and would require multiple introductions to generate diverse invasive populations [20].

The empirical literature appears to bear out expectations regarding the role of vectors in determining the genetic diversity of introduced species. Of 15 reports on likely ballast-water-mediated invasions, 10 (66%) show increased or similar levels of genetic diversity in comparison to native populations. Similarly, species accidentally transported with shellfish transplantations tend to be diverse: three out of five studies (60%) showed an increase or no change in genetic diversity. Given the vast quantities of material that have been transported over time, shellfish transplantation has the capacity to deliver large propagule pools; certain translocations, such as the mass movement of both Pacific and Atlantic oysters (*Crassostrea gigas* and *C. virginica*) to the North American West Coast, are particularly likely to have enhanced genetic diversity [21]. Yet transoceanic movement might bring only limited diversity if

sources come from a restricted geographic range. For instance, the mud snail *Batillaria attramentaria*, brought to North America with Pacific oysters, appears to have reduced genetic diversity because all successful transplants are derived from a single prefecture in Japan [22].

It is also important to consider vectors in the context of the corridors along which they act. Perhaps the most notable vector–corridor combination is maritime traffic – especially ballast water transport – between the Ponto-Caspian region, which includes the basins of the Black, Azov and Caspian Seas, and the North American Great Lakes. In their study of invasive Eurasian species in the Great Lakes, Stepien *et al.* [23] noted that all five species analyzed, including the round goby *Neogobius melanostomus*, zebra mussel *Dreissena polymorpha* and quagga mussel *D. bugensis*, exhibited high genetic variability and a large number of founders. Such high diversity and propagule pressure, along with multiple founding sources for four species, probably contribute to the possibility of invasion success and increase the chances of further outbreaks from these new sources. Continuous traffic between these two regions – along with similar habitats and possible facultative interactions between co-evolved invaders – has greatly increased the risk of invasion [23]. Studies of the *B. longimanus* [24,25] support the conclusion that this vector–corridor combination is particularly efficient at conferring high levels of genetic diversity on the recipient system through a combination of large inocula and multiple introduction events.

Although rarely discussed in this context, perhaps because their means of anthropogenic translocation fail to conform well to the classical definition of 'vector', numerous species have expanded their range after the construction of canals and removal of dispersal barriers. Perhaps the most significant event was the excavation of the Suez Canal, completed in 1869. Known as Lessepsian migrants, after Ferdinand de Lesseps, the French diplomat responsible for the construction of the canal, several species have made incursions from the Red Sea into the Mediterranean [26–29]. Genetic studies of several fish species have revealed little to no genetic differentiation between source and introduced populations, and no significant loss of

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Box 4. Contrasting genetic signatures of green crab invasions in the nineteenth and twentieth centuries

Molecular genetics has been used to explore the invasion history of one of the oldest known marine invaders, a species that has probably been traveling in the ballast or among the fouling communities of wooden ships for centuries. With high fecundity, excellent dispersal potential and an ability to survive on a diverse diet, the green crab *Carcinus maenas*, native to the Atlantic coast of Europe and North Africa, is well adapted to modern travel. It has invaded every continent with temperate shores.

The earliest known invasion of this intertidal decapod was in the northwestern North Atlantic, around New York and southern Massachusetts, in 1817. In 1905, the green crab spread north to the Gulf of Maine and, for much of the twentieth century, it remained in the Gulf and along the southern Scotian Shelf. In the 1990s, the species underwent rapid range extension throughout the Canadian Maritimes (Figure Ia). To some observers, it appeared that this expansion was part of a continual advance and retreat in conjunction with climate fluctuations that had been occurring for the past two centuries [82]. Others suggested that the

green crab might have adapted to colder temperatures in the region [83].

Genetic analysis showed that the inoculation of new lineages into Nova Scotia was responsible for this rapid expansion (Figure Ib). Mitochondrial DNA data and frequent shipping between Nova Scotia and the North Sea indicate that these new lineages probably derive from populations on the northern edge of the green crab's native range. Temperature tolerance tests will help determine if these genotypes provided a physiological advantage or if the inoculum had a spatial advantage by arriving in a cul-de-sac up current of the original nineteenth century invasion front.

Carcinus also sheds light on the importance of vectors in changing genetic diversity. Historical invasions might be characterized by reduced genetic diversity. In the case of the green crab, one likely vector for the nineteenth century invasion is the ballast rocks of a sailing ship. Only a few adults would probably survive among this dry ballast. By contrast, a modern ship exchanging millions of liters of ballast water can release thousands of crab larvae.
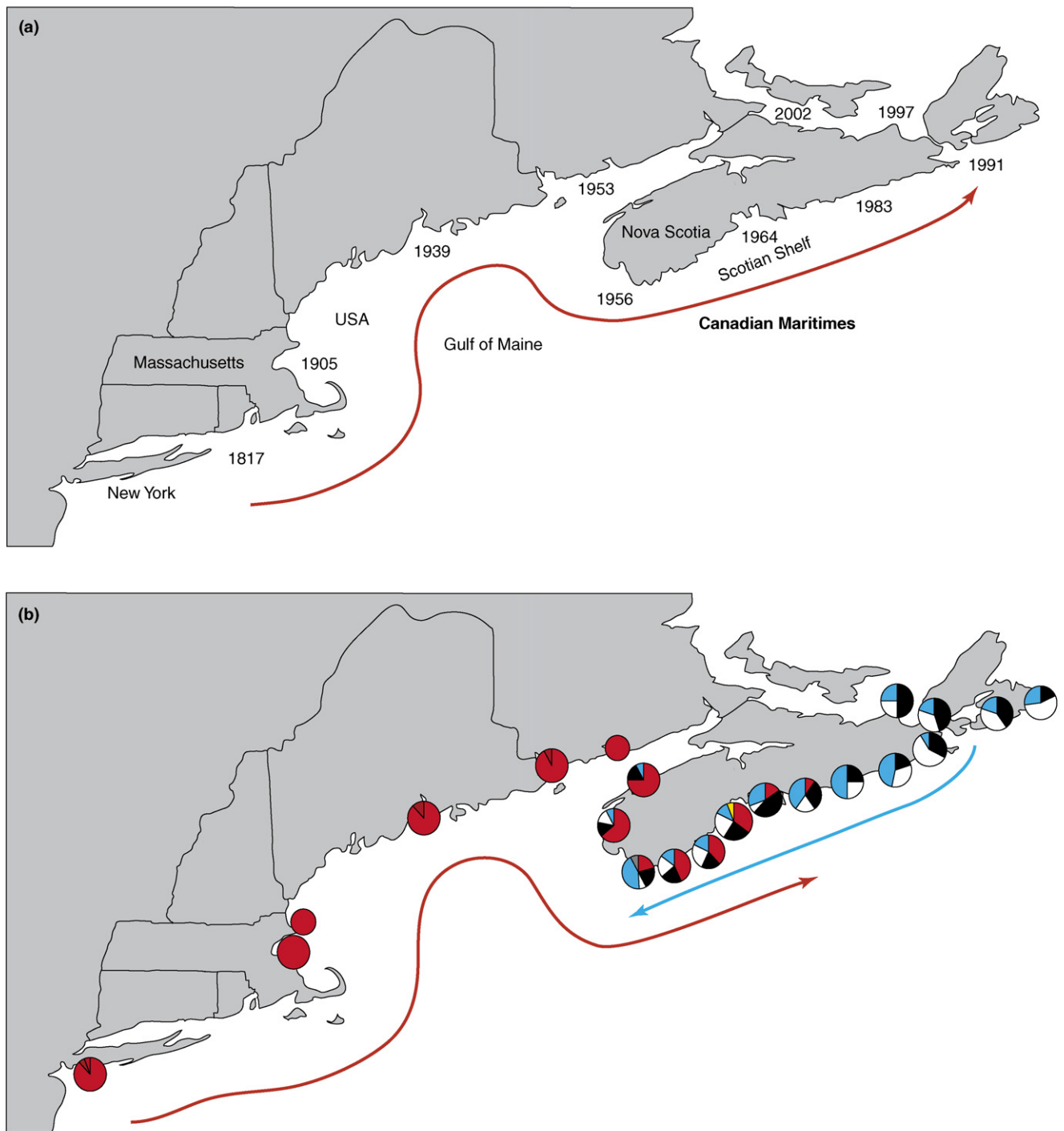
(a)

(b)

Figure I. Cryptic invasion of green crabs revealed in North America. **(a)** Range expansion of the invasive green crab *C. maenas* in North America. Dates represent first confirmed sightings of the species (adapted from [83]). The red arrow represents the presumed pathway of range expansion from the original nineteenth century introduction in the mid-Atlantic. **(b)** Actual expansion in the Canadian Maritimes (blue arrow) was a result of multiple invasions in the northern part of eastern North America in the 1980s or 1990s. Each color in the pie chart represents a genotype of the mitochondrial cytochrome oxidase I gene [65].

diversity following the transition to the Mediterranean [28]. In retrospect, it is not surprising that such introductions maintain native variation, as propagule pressure might be more or less continuous.

Although few studies have directly assessed the relative strengths of different vectors in delivering high genetic diversity to recipient systems, one recent study deserves mention. In their analysis of the edible brown alga *Undaria pinnatifada*, Voisin *et al.* found significantly different patterns of genetic diversity in two regions where this Asian native has been introduced [30]. Introduced Australasian populations possessed high haplotype and nucleotide diversity at two mitochondrial DNA (mtDNA) loci, but European populations showed dramatically lower diversity, primarily because of the predominance of a single haplotype. This disparity probably stems from different invasion dynamics. Australasian populations probably result from accidental translocations associated with maritime traffic, whereas

European populations are derived from intentional aquacultural introductions or accidental introductions associated with Pacific oyster (*C. gigas*) transplants. Cultivated strains of the alga dominate European populations, whereas Australasia has received far more diversity from the source region.

It is interesting to note that intentional introductions do not always show high levels of genetic diversity; in several cases, diversity decreased despite known multiple introductions from native sources [31–33]. Intentional releases encompass a broad class of vectors, ranging from small-scale unsanctioned attempts to establish local fisheries to large commercial aquaculture efforts. Illegal releases might consist of only few individuals, but the *Undaria* example suggests that, even in cases of large-scale aquaculture, propagule pools can derive from a small subset of the natural diversity associated with cultivation. For aquacultural species, source diversity might be far lower than native diversity.

Temporal change

When temporal data are available, the genetic diversity of many invasive species increases over time, apparently as a result of anthropogenic gene flow through multiple release events. Allozyme analysis of *B. longimanus*, for example, showed evidence of a founder effect in North America during initial surveys of the invasive population in 1989 [24]. By 1996, the genetic structure was similar to that of native European populations and founder effects had disappeared. Similarly, in Europe, homogenizing gene flow has reduced founder effects of Chinese mitten crabs *Eriocheir sinensis* and admixture among invasive populations has increased genetic diversity over time [34]. Twelve of sixteen studies (75%) reported to have multiple invasions showed an increase or no change in genetic diversity compared to native sources. (Six of twelve studies assumed to have been single invasions showed a decline in diversity; as expected, none showed an increase.) Human-mediated transport appears to remain a significant factor in the dispersal and gene flow of many invasive species long after initial establishment (Box 4).

The presence of a previously established population can help new propagules avoid the consequences of Allee effects, such as decreased likelihood of establishment, increased lag time between introduction and establishment, and slower spread [35]. This situation could result in a positive feedback loop: the presence of a few established lineages increases the probability that new propagules will successfully reproduce; in turn, new lineages enhance diversity and enable previously established populations to persist and perhaps expand their range.

It is possible that the lag time that often precedes invasion reflects the accumulation of adequate levels of additive genetic variance, rather than simply being a function of propagule pressure [7]. One key to the success of introduced species across a wide environmental gradient might be the result of a shift from genetic variation in native populations resulting from population structure (i.e. genetic variation among populations) to variation that occurs within admixed populations in invasive areas [16]. It is unclear whether such high genetic diversity

typically functions as a rescue effect – increasing diversity after an initial lag time – or whether some aquatic introductions succeed because genetic diversity is high at the outset. In particular, it remains to be seen if the infusion of new lineages can cause a non-native species to become invasive.

Studies of terrestrial and aquatic invasive plants show that hybridization between individuals from different source populations can lead to a reduction in mutational genetic load and the production of novel genotypes or phenotypes that do not occur in the native range [36]. Increased genetic variation can also provide an opportunity for natural selection to bring about adaptive evolutionary change. Although several non-native cord grasses (*Spartina* sp.) have been introduced to San Francisco Bay, these intertidal species have exhibited limited success compared to populations derived from hybridization between introduced *S. alterniflora* and native *S. foliosa* [37]. Hybridization in marine invertebrates is more likely to be between intraspecific populations that have evolved allopatrically. To date, we are aware of no invertebrate species known to have become invasive as a result of interspecific hybridization. Kelly *et al.* [13] have shown that the amphipod *G. tigrinus* has two patterns of invasion: single-source low-diversity populations and high-diversity admixture zones. Unlike monomorphic populations, with restricted distribution, the high-diversity amphipods are found across brackish and freshwater habitats in Eastern Europe. Multiple introductions appear to have accelerated the range expansion and habitat distribution of the amphipod.

In some cases, the role of admixture in invasion success might be less a factor of increasing genetic diversity than of genetic novelty. Hybridization of admixed populations can result in the production of novel genotypes, even if overall diversity remains low, and these genotypes might provide the opportunity for innovative responses to non-native environments. For instance, populations of *S. alterniflora* in Willapa Bay, Oregon, although exhibiting relatively low neutral genetic variation in the introduced region, possess hybrid genotypes from previously allopatric populations that were independently introduced to the estuary [38]. These unique genotypes might have some advantages over non-hybrids, although this is yet to be demonstrated.

The leading edge

Multiple introductions can play an important role at the leading edge of an invasion front, by supplying established populations with adequate genetic variation to sustain population viability or respond to selection and adapt to a new environment [39]. In addition, they can lead to the influx of propagules to areas that are up current of previously introduced populations in coastal or marine systems. Simon-Bouhet *et al.* [40] have shown that multiple invasions of the mollusk *Cyclope neritea* promoted range expansion along the coast of France. Elevated levels of genetic diversity on the northern edge of the species range indicated that recurrent human-mediated introductions from several geographic areas were involved in the expansion. The admixture of several evolutionary lineages might have assisted in extending the species range, although warming temperatures could also have played a role.

Similar results were found for range expansion of the green crab *C. maenas,* in North America in the 1990s (Box 4). These examples illustrate the potential importance of multiple introductions to range expansion, and the difficulties of inferring causal relationships between increases in diversity and invasiveness.

It has been noted that changes in water temperature are likely to promote the establishment of invasive species at the expense of natives in the coming years [41]. The frequency of multiple introductions might exacerbate that trend. Warmer conditions favor longer growing seasons and earlier reproduction and migration for many species, increasing growth and dispersal rates, and accelerating the rate of expansion [42]. Increased within-population genetic variation from multiple introductions can enhance the ability of introduced populations to respond to these changing environmental conditions.

Paradox lost

Genetic studies of aquatic species indicate that, in many cases, large propagule pools and multiple introduction events overwhelm the effects of founder events. Our study, along with other recent reviews [9,10], suggests that the genetic paradox can now be put to rest. Successful invasive species do not, as a rule, exhibit the genetic signatures of population bottlenecks. And even when they do, enough has been said regarding possible mechanisms for avoiding the negative impact of low population size that we should no longer be surprised at the success of even genetically depauperate introductions.

This conclusion might raise as many questions as it addresses. The apparent importance of the flexibility of reproductive mode to the success of low diversity invasions suggests that there is much to learn regarding how evolutionary history and life history characteristics affect the invasiveness of species. Some successful invaders, such as the Ponto-Caspian populations of *Dreissena,* might have evolved traits associated with environmental fluctuations and severe bottlenecks, such as broad salinity tolerance, that allow them to colonize new areas with relatively low levels of genetic diversity [43]. Although plasticity and generalism are reasonable hypotheses for the success of low diversity populations, the importance of these mechanisms needs to be directly tested.

Given widespread patterns of multiple introductions, one challenge for future research is examining how the introduction of new lineages affects invasion success. Projections of the impact of increased genetic variation will be aided by a better mechanistic understanding of ecological and evolutionary responses to multiple invasions among admixed populations. For instance, whereas much of the existing work on hybridization and the effects of admixture has been addressed in terrestrial vascular plants [36], such studies must similarly be undertaken in the aquatic realm. Do hybrid genotypes typically result in novel physiological adaptations in fish and aquatic invertebrates, or is outbreeding depression more common in animals than in plants?

Many invasive species have independently introduced populations in multiple geographic regions. In some cases, they clearly display different patterns of genetic

diversity [30]. These populations might let us examine the relationship between neutral and quantitative genetic variation and patterns of expansion. Greater vigilance in early detection and monitoring can also provide opportunities to track genetic change over time and perhaps relate these patterns to invasion failure – either by the disappearance of transient populations or by their inability to expand.

Multiple introductions can be used to examine patterns of larval dispersal and genetic change over time in aquatic animals. For example, the two invasion fronts discovered among green crabs in northeastern North America (Box 4) present a unique opportunity to test models of larval retention and track potential genetic turnover as newly arrived lineages spread through a long-established population. Whether such range expansions are because of the influx of novel genetic diversity, the arrival of new propagules in habitats previously inaccessible to larval dispersal, or some combination of the two is an important issue to managers of aquatic invasives and researchers interested in the role of dispersal in coastal systems.

To meet the challenge of reducing the rate of aquatic invasions, management strategies will be needed to control propagule supply, before and after establishment. The rapid growth of invasion genetics can play an important role in assessing the risks associated with particular vectors and potential invaders by increasing our understanding of the relationship between vectors, propagule pressure and genetic diversity. Molecular studies might also be important in developing strategies for the post-invasion control of marine introductions. An understanding of population genetics will be critical in assessing proposed control efforts using genetic engineering or biological control agents such as parasites and pathogens.

References

1 Cohen, A.N. and Carlton, J.T. (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279, 555–558
2 Hebert, P.D.N. and Cristescu, M.E.A. (2002) Genetic perspectives on invasions: the case of the Cladocera. *Can. J. Fish. Aquat. Sci.* 59, 1229–1234
3 Allendorf, F.W. and Lundquist, L.L. (2003) Introduction: population biology, evolution, and control of invasive species. *Conserv. Biol.* 17, 24–30
4 Frankham, R. (2005) Invasion biology – resolving the genetic paradox in invasive species. *Heredity* 94, 385
5 Ricciardi, A. *et al.* (2000) Toward a global information system for invasive species. *Bioscience* 50, 239–244
6 Hufbauer, R.A. (2004) Population genetics of invasions: can we link neutral markers to management? *Weed Technol.* 18, 1522–1527

7 Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends Ecol. Evol.* 17, 386–391

8 Reed, D.H. and Frankham, R. (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution Int. J. Org. Evolution* 55, 1095–1103

9 Wares, J.P. *et al.* (2005) Mechanisms that drive evolutionary change. Insights from species introductions and invasions. In *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (Sax, D.F. *et al.*, eds), pp. 229–257, Sinauer Press

10 Bossdorf, O. *et al.* (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144, 1–11

11 Von Holle, B. and Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86, 3212–3218

12 Lockwood, J.L. *et al.* (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20, 223–228

13 Kelly, D.W. *et al.* (2006) Contrasting patterns in genetic diversity following multiple invasions of fresh and brackish waters. *Mol. Ecol.* 15, 3641–3653

14 Sakai, A.K. *et al.* (2001) The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32, 305–332

15 Drake, J.M. *et al.* (2005) Propagule pressure and persistence in experimental populations. *Biol. Lett.* 1, 480–483

16 Kolbe, J.J. *et al.* (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431, 177–181

17 Frankham, R. (2005) Genetics and extinction. *Biol. Conserv.* 126, 131–140

18 MacIsaac, H.J. *et al.* (2002) Biological invasions of aquatic habitats in Europe and the Great Lakes: modeling ships' ballast water as invasion threats to the Great Lakes. *Can. J. Fish. Aquat. Sci.* 59, 1245–1256

19 Padilla, D.K. and Williams, S.L. (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Front. Ecol. Environ.* 2, 131–138

20 Facon, B. *et al.* (2003) A molecular phylogeography approach to biological invasions of the New World by parthenogenetic Thiarid snails. *Mol. Ecol.* 12, 3027–3039

21 Fofonoff, P.W. *et al.* (2003) In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the coasts of North America. In *Invasive Species: Vectors and Management Strategies* (Ruiz, G.M. and Carlton, J.T., eds), pp. 152–182, Island Press

22 Miura, O. *et al.* (2006) Introduced cryptic species of parasites exhibit different invasion pathways. *Proc. Natl. Acad. Sci. U. S. A.* 103, 19818–19823

23 Stepien, C.A. *et al.* (2005) Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. *Risk Anal.* 25, 1043–1060

24 Berg, D.J. *et al.* (2002) Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga. Russia. *Freshw. Biol.* 47, 275–282

25 Colautti, R.I. *et al.* (2005) Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. *Mol. Ecol.* 14, 1869–1879

26 Azzurro, E. *et al.* (2006) Genetics of the early stages of invasion of the Lessepsian rabbitfish *Siganus luridus. J. Exp. Mar. Biol. Ecol.* 333, 190–201

27 Bucciarelli, G. *et al.* (2002) Genetic cryptic species as biological invaders: the case of a Lessepsian fish migrant, the hardyhead silverside *Atherinomorus lacunosus. J. Exp. Mar. Biol. Ecol.* 273, 143–149

28 Hassan, M. and Bonhomme, F. (2005) No reduction in neutral variability of mitochondrial and nuclear genes for a Lessepsian migrant, *Upeneus moluccensis. J. Fish Biol.* 66, 865–870

29 Hassan, M. *et al.* (2003) Lessepsian invasion without bottleneck: example of two rabbitfish species (*Siganus rivulatus* and *Siganus luridus*). *J. Exp. Mar. Biol. Ecol.* 291, 219–232

30 Voisin, M. *et al.* (2005) Differential shuffling of native genetic diversity across introduced regions in a brown alga: Aquaculture vs. maritime traffic effects. *Proc. Natl. Acad. Sci. U. S. A.* 102, 5432–5437

31 Kawamura, K. *et al.* (2006) Origin and dispersal of bluegill sunfish, *Lepomis macrochirus,* in Japan and Korea. *Mol. Ecol.* 15, 613–621

32 Kreiser, B.R. *et al.* (2000) Single versus multiple sources of introduced populations identified with molecular markers: a case study of a freshwater fish. *Biol. Invasions* 2, 295–304

33 Lindholm, A.K. *et al.* (2005) Invasion success and genetic diversity of introduced populations of guppies *Poecilia reticulata* in Australia. *Mol. Ecol.* 14, 3671–3682

34 Herborg, L.M. *et al.* (2007) Genetic population structure and contemporary dispersal patterns of a recent European invader, the Chinese mitten crab, *Eriocheir sinensis. Mol. Ecol.* 16, 231–242

35 Taylor, C.M. and Hastings, A. (2005) Allee effects in biological invasions. *Ecol. Lett.* 8, 895–908

36 Ellstrand, N.C. and Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc. Natl. Acad. Sci. U. S. A.* 97, 7043–7050

37 Ayres, D.R. and Strong, D.R. (2001) Origin and genetic diversity of *Spartina anglica* (Poaceae) using nuclear DNA markers. *Am. J. Bot.* 88, 1863–1867

38 Blum, M.J. *et al.* Geographic structure, genetic diversity, and source tracking of *Spartina alterniflora. J. Biogeogr.* (in press) 10.1111/j.1365-2699.2007.01764.x

39 Allendorf, F.W. and Luikart, G. (2007) *Conservation and the Genetics of Populations,* Blackwell Publishing

40 Simon-Bouhet, B. *et al.* (2006) Multiple introductions promote range expansion of the mollusc *Cyclope neritea* (Nassariidae) in France: evidence from mitochondrial sequence data. *Mol. Ecol.* 15, 1699–1711

41 Stachowicz, J.J. *et al.* (2002) Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci. U. S. A.* 99, 15497–15500

42 Garcia-Ramos, G. and Rodriguez, D. (2002) Evolutionary speed of species invasions. *Evolution Int. J. Org. Evolution* 56, 661–668

43 Gelembiuk, G.W. *et al.* (2006) Phylogeography and systematics of zebra mussels and related species. *Mol. Ecol.* 15, 1033–1050

44 Hedrick, P.W. and Kalinowski, S.T. (2000) Inbreeding depression in conservation biology. *Annu. Rev. Ecol. Syst.* 31, 139–162

45 Keller, L.F. and Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends Ecol. Evol.* 17, 230–241

46 Kristensen, T.N. and Sorensen, A.C. (2005) Inbreeding – lessons from animal breeding, evolutionary biology and conservation genetics. *Anim. Sci.* 80, 121–133

47 Lynch, M. *et al.* (1995) Mutational meltdowns in sexual populations. *Evolution Int. J. Org. Evolution* 49, 1067–1080

48 Neiman, M. and Linksvayer, T.A. (2006) The conversion of variance and the evolutionary potential of restricted recombination. *Heredity* 96, 111–121

49 Vrijenhoek, R.C. (1998) Animal clones and diversity. *Bioscience* 48, 617–628

50 Lee, C.E. *et al.* (2007) Response to selection and evolvability of invasive populations. *Genetica* 129, 179–192

51 Merilä, J. and Crnokrak, P. (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *J. Evol. Biol.* 14, 892–903

52 McKay, J.K. and Latta, R.G. (2002) Adaptive population divergence: markers, QTL and traits. *Trends Ecol. Evol.* 17, 285–291

53 Brooks, R. and Endler, J.A. (2001) Direct and indirect sexual selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). *Evolution Int. J. Org. Evolution* 55, 1002–1015

54 Koskinen, M.T. *et al.* (2002) Contemporary fisherian life-history evolution in small salmonid populations. *Nature* 419, 826–830

55 Mergeay, J. *et al.* (2006) Invasion of an asexual American water flea clone throughout Africa and rapid displacement of a native sibling species. *Proc. R. Soc. Lond. B. Biol. Sci.* 273, 2839–2844

56 Liu, J. *et al.* (2006) Invasive alien plants in China: role of clonality and geographical origin. *Biol. Invasions* 8, 1461–1470

57 Ren, M.X. *et al.* (2005) Random amplified polymorphic DNA markers reveal low genetic variation and a single dominant genotype in *Eichhornia crassipes* populations throughout China. *Weed Res.* 45, 236–244

58 Meusnier, I. *et al.* (2002) Polymerase chain reaction-single strand conformation polymorphism analyses of nuclear and chloroplast DNA provide evidence for recombination, multiple introductions and nascent speciation in the *Caulerpa taxifolia* complex. *Mol. Ecol.* 11, 2317–2325

59 Wang, B.R. *et al.* (2005) Genetic diversity of *Alternanthera philoxeroides* in China. *Aquat. Bot.* 81, 277–283

60 Yu-Peng, G. *et al.* (2007) Phenotypic plasticity rather than locally adapted ecotypes allows the invasive alligator weed to colonize a wide range of habitats. *Biol. Invasions* 9, 245

61 Planes, S. and Lecaillon, G. (1998) Consequences of the founder effect in the genetic structure of introduced island coral reef fish populations. *Biol. J. Linn. Soc.* 63, 537–552

62 Hauser, L. *et al.* (1998) Genetic affinities of an introduced predator: Nile perch in Lake Victoria, East Africa. *Mol. Ecol.* 7, 849–857

63 Garner, S. *et al.* (2006) Genetic variation in the marbled lungfish *Protopterus aethiopicus* in Lake Victoria and introduction to Lake Baringo, Kenya. *J. Fish Biol.* 69, 189–199

64 Triantafyllidis, A. *et al.* (2002) Microsatellite analysis of the genetic population structure of native and translocated Aristotle's catfish (*Silurus aristotelis*). *Aquat. Living Resour.* 15, 351–359

65 Roman, J. (2006) Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proc. R. Soc. Lond. B. Biol. Sci.* 273, 2453–2459

66 Cristescu, M.E.A. *et al.* (2001) An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. *Limnol. Oceanogr.* 46, 224–229

67 Zardus, J.D. and Hadfield, M.G. (2005) Multiple origins and incursions of the Atlantic barnacle *Chthamalus proteus* in the Pacific. *Mol. Ecol.* 14, 3719–3733

68 Hairston, N.G. *et al.* (1999) Population biology of a failed invasion: Paleolimnology of *Daphnia exilis* in upstate New York. *Limnol. Oceanogr.* 44, 477–486

69 Viard, F. *et al.* (2006) Dispersal ability and invasion success of *Crepidula fornicata* in a single gulf: insights from genetic markers and larval-dispersal model. *Helgol. Mar. Res.* 60, 144–152

70 Therriault, T.W. *et al.* (2005) Invasion genetics of a freshwater mussel (*Dreissena rostriformis bugensis*) in eastern Europe: high gene flow and multiple introductions. *Heredity* 95, 16–23

71 Meunier, C. *et al.* (2001) Lack of molluscan host diversity and the transmission of an emerging parasitic disease in Bolivia. *Mol. Ecol.* 10, 1333–1340

72 Martel, C. *et al.* (2004) Invasion by the marine gastropod *Ocinebrellus inornatus* in France. II. Expansion along the Atlantic coast. *Mar. Ecol. Prog. Ser.* 273, 163–172

73 Holland, B.S. (2001) Invasion without a bottleneck: microsatellite variation in natural and invasive populations of the brown mussel *Perna perna* (L). *Mar. Biotechnol.* 3, 407–415

74 Stadler, T. *et al.* (2005) Mitochondrial haplotypes and the New Zealand origin of clonal European *Potamopyrgus*, an invasive aquatic snail. *Mol. Ecol.* 14, 2465–2473

75 Duran, S. *et al.* (2004) Phylogeographical history of the sponge *Crambe crambe* (Porifera, Poecilosclerida): range expansion and recent invasion of the Macaronesian islands from the Mediterranean Sea. *Mol. Ecol.* 13, 109–122

76 Patti, F.P. and Gambi, M.C. (2001) Phylogeography of the invasive polychaete *Sabella spallanzanii* (Sabellidae) based on the nucleotide sequence of internal transcribed spacer 2 (ITS2) of nuclear rDNA. *Mar. Ecol. Prog. Ser.* 215, 169–177

77 Kliber, A. and Eckert, C.G. (2005) Interaction between founder effect and selection during biological invasion in an aquatic plant. *Evolution Int. J. Org. Evolution* 59, 1900–1913

78 Saltonstall, K. (2003) Microsatellite variation within and among North American lineages of *Phragmites australis*. *Mol. Ecol.* 12, 1689–1702

79 Provan, J. *et al.* (2005) Tracking the invasive history of the green alga *Codium fragile* ssp tomentosoides. *Mol. Ecol.* 14, 189–194

80 Coyer, J.A. *et al.* (2006) Origin of *Fucus serratus* (Heterokontophyta; Fucaceae) populations in Iceland and the Faeroes: a microsatellite-based assessment. *Eur. J. Phycol.* 41, 235–246

81 McIvor, L. *et al.* (2001) rbcL sequences reveal multiple cryptic introductions of the Japanese red alga *Polysiphonia harveyi*. *Mol. Ecol.* 10, 911–919

82 Yamada, S. (2001) *A Global Invader: The European Green Crab,* Oregon State University

83 Audet, D. *et al.* (2003) Geographic expansion of a nonindigenous crab, *Carcinus maenas* (L.), along the Nova Scotian shore into the southeastern Gulf of St Lawrence, Canada. *J. Shellfish Res.* 22, 255–262