

## INVASION GENETICS: THE BAKER AND STEBBINS LEGACY

# The devil is in the details: genetic variation in introduced populations and its contributions to invasion

KATRINA M. DLUGOSCH, SAMANTHA R. ANDERSON, JOSEPH BRAASCH, F. ALICE CANG and HEATHER D. GILLETTE

*Department of Ecology & Evolutionary Biology, University of Arizona, PO Box 210088, Tucson, AZ 85721, USA*

## Abstract

The influence of genetic variation on invasion success has captivated researchers since the start of the field of invasion genetics 50 years ago. We review the history of work on this question and conclude that genetic variation—as surveyed with molecular markers—appears to shape invasion rarely. Instead, there is a significant disconnect between marker assays and ecologically relevant genetic variation in introductions. We argue that the potential for adaptation to facilitate invasion will be shaped by the details of genotypes affecting phenotypes, and we highlight three areas in which we see opportunities to make powerful new insights. (i) The genetic architecture of adaptive variation. Traits shaped by large-effect alleles may be strongly impacted by founder events yet more likely to respond to selection when genetic drift is strong. Large-effect loci may be especially relevant for traits involved in biotic interactions. (ii) Cryptic genetic variation exposed during invasion. Introductions have strong potential to uncover masked variation due to alterations in genetic and ecological environments. (iii) Genetic interactions during admixture of multiple source populations. As divergence among sources increases, positive followed by increasingly negative effects of admixture should be expected. Although generally hypothesized to be beneficial during invasion, admixture is most often reported among sources of intermediate divergence, supporting the possibility that incompatibilities among divergent source populations might be limiting their introgression. Finally, we note that these details of invasion genetics can be coupled with comparative demographic analyses to link genetic changes to the evolution of invasiveness itself.

*Keywords:* admixture, colonization, cryptic variation, genetic architecture, genetic bottlenecks, invasive species

*Received 5 February 2015; revision received 26 March 2015; accepted 27 March 2015*

## Introduction

At a symposium on The Genetics of Colonizing Species in 1964, some of the best minds in evolutionary biology, genetics, ecology and applied biology came together to ponder questions about how the founding of new populations might fundamentally alter the genetics and colonization success of species in novel environments (Baker & Stebbins 1965). Baker & Stebbins

(1965: p.vii) noted in their preface to the proceedings of the symposium that ‘When the approximately thirty biologists who attended started to exchange facts and ideas, all of them realized at once that each had things to say which were of great value to the others, and which were new to them. [...] We hope that some of the spirit of adventure which many of the participants experienced at the symposium will find its way to the readers of this volume’. Indeed, the symposium became the beginning of a vigorous field of enquiry marked by its goal of bridging genetics, evolution and ecology to understand colonization, with particular

Correspondence: Katrina M. Dlugosch, Fax: 1 520 621 9190; E-mail: kdlugosch@email.arizona.edu

insights provided by contemporary species invasions (Barrett 2015; Bock *et al.* 2015).

The symposium was naturally dominated by a discussion of how founding events might diminish genetic diversity within populations. Deceptively simple questions of how much genetic variation establishes in colonizing populations and to what degree the quantity of variation affects the subsequent success of new populations captivated and continue to captivate invasion biologists (Lockwood *et al.* 2005; Dlugosch & Parker 2008a; Uller & Leimu 2011; Blackburn *et al.* 2015). An emphasis on the role of genetic variation in invasion has only grown as evidence has mounted that invaders frequently show evolutionary changes in traits putatively related to fitness and/or the propensity to invade new environments (Hendry *et al.* 1999; Cox 2004; Bossdorf *et al.* 2005; Colautti & Barrett 2013; Colautti & Lau 2015). Thus, it is clear that evolution is happening, seemingly in response to natural selection, but the extent to which adaptation during colonization might be constrained by genetic variation remains largely unknown, despite its fundamental importance.

Here, we trace the history of thought about the role of genetic variation in invasions, and we argue that the nature of genetic variation (the 'details') will be more relevant to facilitating invasion than its total quantity *per se*. We take a closer look at specific attributes of adaptive genetic variation in founding populations, including its genetic architecture, its expression under different environments and its interaction among divergent source populations. All of these aspects of variation show strong potential to influence adaptation during invasion, and open promising avenues for further investigation. We conclude by noting that these details of invasion genetics can allow us to connect the impacts of specific evolutionary changes to population growth and spread, generating a more complete understanding of the importance of genetic variants for the process of invasion itself.

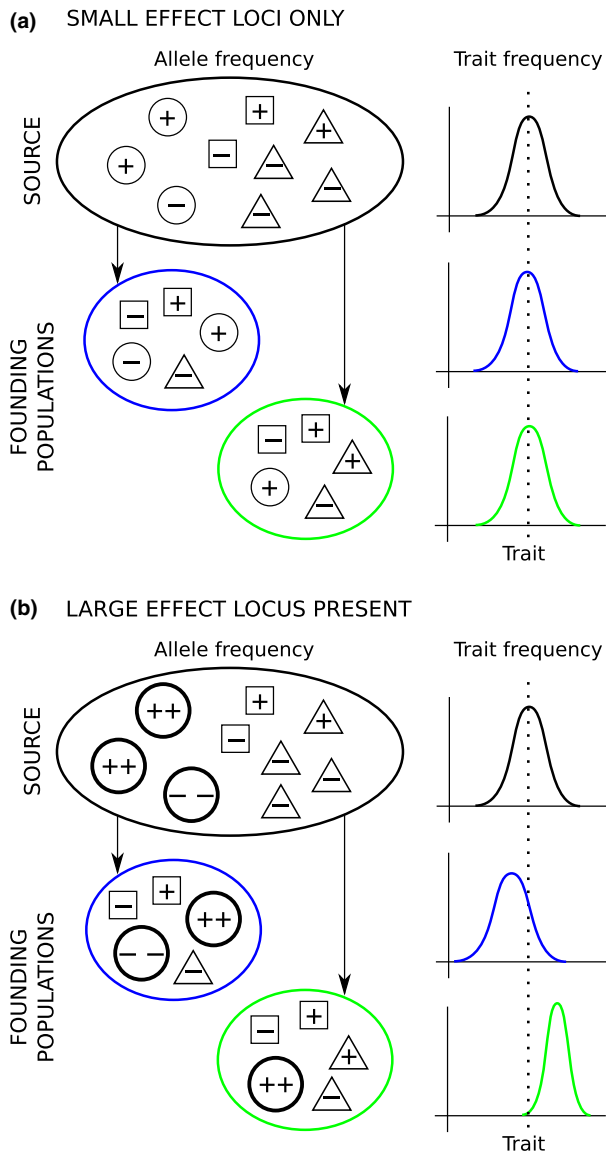
### Genetic variation in invasions: a history

One of the most universal features of invasions is that founding populations will experience demographic bottlenecks of some magnitude after introduction and/or range expansion. Baker (1955) made a powerful case for the potential severity of demographic bottlenecks at founding well before the 1964 symposium. Baker argued that successful long-distance dispersal was strongly associated with species' ability to reproduce without a mate (termed 'reproductive assurance'), using strategies such as self-fertilization or asexual propagation (Baker 1955, 1965). Stebbins (1957) referred to this association of colonization with reproductive strategy as

Baker's Law, and Baker argued that it results from the frequent lack of mates and/or mating opportunities during population establishment (Pannell 2015). In addition to the immediate losses of genetic diversity expected from small numbers of founders, methods of reproductive assurance are generally associated with further declines in genetic variation, all else being equal (Ellstrand & Roose 1987; Hamrick & Godt 1996). For these reasons, Baker predicted that most successful colonizers would be ones to thrive without genetic variation, relying instead upon a single best 'general-purpose-genotype' capable of colonizing a wide variety of environments (Baker 1955, 1974; Ferrero *et al.* 2015).

Despite Baker's assertions, there was much debate at the symposium about the extent to which demographic bottlenecks and self-fertilization/asexuality would actually reduce variation in real founding populations. Many participants assumed that this was so, but some geneticists pointed out important theoretical considerations to the contrary. Confusion on this point culminated in an exposition by Lewontin (Baker & Stebbins 1965; : p. 481), wherein he clarified that while demographic bottlenecks will likely lead to the loss of some rare alleles, they will generally not substantially reduce genetic variance in quantitative traits (determined by common variants at multiple loci; Fig. 1). Mayr (1965a) further argued that new mutations will arise reasonably quickly in founding populations as opportunities for mutants to occur expand with the population (see Box 1). Empirically, Allard (1965) presented data showing a high degree of mating system lability, phenotypic variation and local adaptation in species that are predominantly self-fertilizing, creating a disconnect between traits conferring reproductive assurance in colonizers and a significant lack of genetic variation. Ultimately, this debate could not be settled at the meeting, as data on genetic variation in colonizing populations were almost entirely lacking at the time, outside of chromosomal inversion polymorphisms which showed variable patterns of loss and maintenance of diversity in *Drosophila* (Carson 1965; Dobzhansky 1965; Mayr 1965b).

A separate debate was had at the symposium about whether any lost variation would meaningfully influence the evolutionary and ecological success of founding populations. In line with his hypothesis of the general-purpose-genotype, Baker (1965) suggested that while genetic variation and adaptability could be beneficial or even necessary in the long run, founding populations might have a reduced need for adaptation due to a relatively low-competition environment. Alternatively, Fraser's (1965) discussion of work on the genetics of *D. melanogaster* bristle number highlighted the possibility that lost diversity at some loci could free additive variation at other epistatically interacting loci,



**Fig. 1** Genetic architecture will shape how population bottlenecks during colonization events impact quantitative trait variation. Panels show founding populations sampling allelic variation (acting to increase [+] or decrease [-] the trait value) across loci (shapes). Allelic variants are shown in proportion to their frequency in a population. (a) Traits governed by many loci of small effect are expected to change little in mean or variance, as founding populations sample common allelic variants, and fixation at some loci has little effect on the trait. (b) In contrast, traits that are shaped at least in part by a locus of large effect may shift in both mean and variance in response to either fixation or frequency shifts at these influential loci.

potentially increasing the genetic variation available for adaptation after a bottleneck (i.e. conversion of epistatic to additive variance; see Bock *et al.* 2015). Discussion after Fraser's study further emphasized the possible benefits of genetic drift during colonization, including the potential for higher level selection among divergent founding

demes and shifting balance in adaptive landscapes (Fraser 1965). In a note of caution, however, F. Wilson (1965) conveyed that biocontrol introductions often seemed to show frustratingly low adaptability or ecological amplitude. Biocontrol introductions can be particularly low in diversity—owing to the difficulty identifying, collecting and propagating diversity during deployment—implying that extreme bottlenecks could indeed ultimately limit colonization success (Wilson 1965).

Decades later, molecular data from protein markers began to shed some light on genetic changes after founding events, and it was clear that real demographic bottlenecks were reducing variation at individual loci in many cases (Barrett & Richardson 1986). In a classic study, Nei *et al.* (1975) published theoretical expectations for the quantity of allelic variation persisting after bottlenecks, showing that founding population size and the rate at which the new population grows both critically determine the loss of variation at markers due to drift. They noted that allelic richness (allele number) will be more sensitive to founding population size and less sensitive to rate of increase, while the reverse is true of heterozygosity, meaning that different metrics of genetic variation will reveal different parts of the story of population history. Nei *et al.* (1975) demonstrated these inferences with an example from invasion biology: the introduction of *D. pseudo-obscura* into Bagota showed a strong loss of allelic diversity consistent with rapid population growth from a small founder number (in line with historical records).

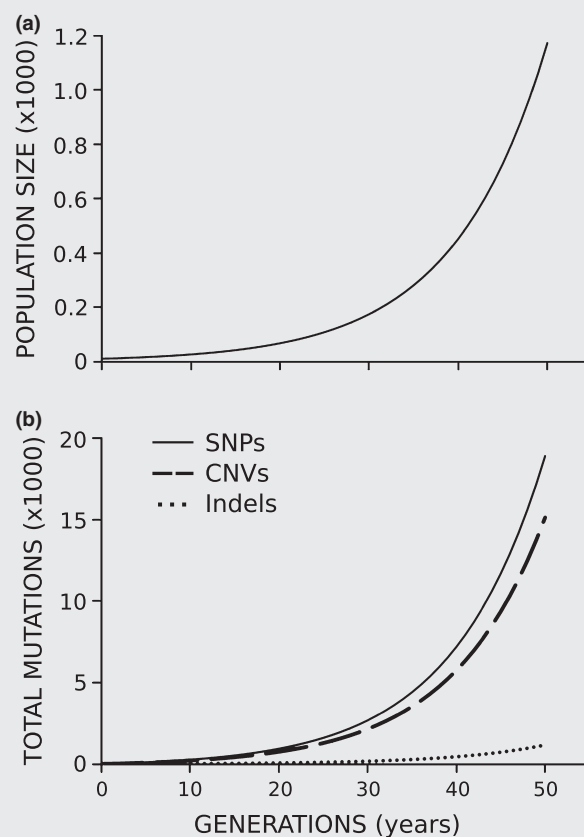
Invasion biologists increasingly questioned how invasions progress despite potentially costly genetic bottlenecks (e.g. Briskie & Mackintosh 2004). An idea developed that invaders must somehow be resolving a 'genetic paradox of invasion' (Allendorf & Lundquist 2003; Frankham 2005), wherein introduced species somehow thrived in new environments when they should be suffering from deleterious losses of genetic diversity. Qualitative reviews of the accumulating empirical data showed little in the way of a consistent pattern of high or low bottleneck severity within successful invasions (Brown & Marshall 1981; Barrett & Richardson 1986; Gray *et al.* 1986; Barrett & Husband 1990; Lee 2002; Cox 2004; Lambrinos 2004; Bossdorf *et al.* 2005), but several reviews did emphasize that invasions were often the result of multiple introductions (Ellstrand & Schierenbeck 2000; Allendorf & Lundquist 2003; Lockwood *et al.* 2005; Novak & Mack 2005; Wares *et al.* 2005; Roman & Darling 2007; Suarez & Tsutsui 2008). Increasing attention was paid to cases of elevated or rising genetic diversity due to multiple introductions, as demonstrations of a potential genetic advantage for invaders and a general resolution to the 'genetic paradox' (e.g. Novak & Mack 1993; Kolbe *et al.* 2004;

**Box 1.** New mutations in colonizing populations

It is reasonable to expect that rapid adaptation which contributes directly to the success of introduced and invasive species will be derived largely from standing genetic variation in the native range, given the short time frame available for response to selection before extinction in struggling founder populations. Nevertheless, recent estimates show that a variety of mutation types occur frequently (Lynch & Conery 2000; Denver *et al.* 2004; Ossowski *et al.* 2010; Stapley *et al.* 2015). Founding populations that are able to increase from small numbers will quickly produce many opportunities for new mutations to appear. Growing populations also provide better opportunities for fixation of rare beneficial variants, which will be the case for new mutations when they arise (Otto & Whitlock 1997).

For example, mutation rates in the model plant *Arabidopsis thaliana* have been estimated conservatively at  $6 \times 10^{-9}$  substitutions/site/generation for single nucleotide polymorphisms ('SNPs', i.e. point mutations; Ossowski *et al.* 2010), 1.3 copies/individual for copy number changes ('CNVs', i.e. gene duplications and deletions; DeBolt 2010; Ossowski *et al.* 2010) and 1.0 mutations/individual for nonmicrosatellite insertion/deletion changes ('indels', including frameshift mutations; Ossowski *et al.* 2010). Assuming a population of 10 annual founder plants growing exponentially at 10% a year, nearly 20 000 different SNP mutations and over 15 000 CNV variants will have occurred in the population within 50 years (Fig. 1). Even if only a small percentage of these mutations have fitness effects (on the order of 20% in *A. thaliana*; Ossowski *et al.* 2010), there will be many opportunities for new mutations to respond to natural selection in the new environment during the early years of population establishment.

Importantly, unlike random SNPs, which should most often be neutral if silent or deleterious if nonsynonymous, copy number changes of intact genes have a much greater potential to result in beneficial phenotypic effects, particularly through changes in gene expression (Kondrashov 2012; Hirase *et al.* 2014; Żmieńko *et al.* 2014). The role of copy number changes in rapid adaptation is largely unknown (Kondrashov 2012) and seems likely to be a promising area of study in invasion genetics.



**Box 1 Fig. 1** New mutations appearing in a theoretical population of *A. thaliana* growing exponentially from 10 founders without selection. (a) Over 50 years, the population size grows to 1174 individuals at a 10% annual rate of increase. (b) During that time, the cumulative number of mutations arising in the population rises sharply according to average rates, particularly for SNPs and CNVs.

Frankham 2005; Lavergne & Molofsky 2007; Roman & Darling 2007; Facon *et al.* 2008; Hufbauer 2008), although arguments lingered that bottlenecks might not be fundamentally problematic for invaders in the first place (e.g. Koskinen *et al.* 2002; Dlugosch & Parker 2008b).

More recently, Dlugosch & Parker (2008a) quantitatively summarized the genetic diversity data available at the time for 80 species of animals, plants and fungi. This analysis showed that changes in intrapopulation genetic variation were generally normally distributed around a modest loss of variation (approx. 15–20%, depending on molecular marker and diversity metric), with larger losses apparent in allelic diversity than in heterozygosity for studies that measured both, as expected. Large increases in diversity were extremely rare, and multiple introductions had only small positive effects on diversity on average. Uller & Leimu (2011) revisited this question with a meta-analysis of the effect size of introduction on heterozygosity (change relative to variance among marker and population) in 85 species of animals and plants. Their results again showed that large changes in diversity have been uncommon. The magnitude of diversity change was unrelated to a metric of invasiveness, and for cases in which founder number was known, large losses of variation (effect size > |2|) were not observed unless founder numbers were extremely small (<15 individuals). These quantitative reviews have largely put to rest the argument that multiple introductions have been critical in providing genetic rescue from severe and deleterious founder effects in most cases.

Taken together, the accumulated data make a strong case that successful invaders frequently experience genetic bottlenecks, but they are neither dramatically depauperate in, nor especially well endowed with, genetic variation relative to native populations of the same species. Certainly, very strong demographic bottlenecks will limit the success of introductions for a variety of reasons (Wilson 1965; Lockwood *et al.* 2005; Agashe *et al.* 2011; Hufbauer *et al.* 2013; Szűcs *et al.* 2014), but demographic barriers to establishment (e.g. stochastic extinction, Allee effects) would seem to be the more important determinants of introduction failure at extremely low founder population sizes (Blackburn *et al.* 2015). Instead, founder populations that are large enough to overcome demographic constraints should consequently retain significant amounts of genetic variation, and indeed this appears to be the case.

### The devil in the details

If changes in genetic variation are not a central determinant of introduction success, are we to conclude that

genetic diversity is not important to invasions? On the contrary, many studies of introduced species indicate that genetics might play an integral role in the progress of an invasion, but they suggest that role is determined by *what* genetic variation is introduced, rather than *how much*. Certainly, total genetic variation has often been intended to serve as a proxy for the likelihood that an adaptive genetic variant is present when the selective environment shifts, but it has become increasingly clear that the disconnect between total and adaptive variation can be large (e.g. Merilä & Crnokrak 2001; McKay & Latta 2002; Leinonen *et al.* 2008). Below we examine three aspects of the nature of genetic variation which will have a particularly significant influence on the adaptive potential of invading populations, all of which have come into focus largely since the formative start of the field of invasion genetics 50 years ago: (i) individual loci whose variants have large phenotypic effects, (ii) cryptic genetic variation that is exposed in the introduced range, and (iii) genetic interactions during admixture of previously isolated alleles that have been brought together by multiple introductions.

### Loci of large effect

A major and open question regarding the nature of adaptive genetic variation is the degree to which it is dominated by a small number of genes whose alleles have large effects on the phenotype. Large-effect loci include both those that might contribute to quantitative trait variation and (more obviously) those controlling discrete Mendelian traits. The genetic architecture of quantitative traits is not easily observed, but it will shape patterns of adaptation, and has attracted significant debate (Orr 2005). Fisher's early work on this topic asserted that quantitative traits must be overwhelmingly governed by many loci of small effect (the infinitesimal model; Fisher 1930), predicting that adaptation would proceed continuously towards a fitness optimum at a rate governed by available genetic variance and the strength of selection. Much later, Kimura (1985) pointed out that beneficial large-effect mutations were much less likely than small-effect mutations to be lost to genetic drift because they experience stronger selection. Orr (1998) further argued that mutations involved in the process of climbing to an adaptive optimum should first involve a few large-effect loci, followed by loci with a constant decrease in effect size, a reinvigoration of the geometric model of adaptation originally explored by Fisher (1930). Additional theoretical support for the importance of large-effect loci comes from studies of adaptive landscapes, where interactions among loci create multiple adaptive optima separated by valleys of low fitness (Wright 1932). Complex fitness landscapes appear to be common in nature, and

adaptation under these conditions is much more likely if large-effect loci can facilitate jumps across low-fitness trait space (Whitlock *et al.* 1995; Whitlock 1997; De Visser & Krug 2014).

The architecture of trait variation should be particularly important for adaptive evolution in invading populations for several reasons. First, as articulated so well by Lewontin at the Baker & Stebbins symposium (Baker & Stebbins 1965; : p. 481), traits governed by many small-effect loci should lose little standing variation during founding events, because demographic bottlenecks during colonization will affect genetic variation through the loss of individual allelic variants, particularly rare variants. In contrast, traits that are affected by loci of large effect may experience significant changes in mean and variance purely via sampling effects at these loci (Fig. 1). We expect that the impact of this sampling on traits and fitness would be more negative than positive on average, because large-effect alleles that are *favourable* in a novel environment where adaptation is needed would have been either neutral or selected *against* in the native range (a different environment). Alleles that were deleterious in the native range should be rare and most susceptible to loss during founding. In this way, a large-effect allele can amplify the impacts of founder/bottleneck effects on the phenotype and may therefore have more potential to alter invader establishment and/or spread in often unpredictable ways.

Second, while large-effect loci might have negative impacts on adaptive variation during founder events, these loci may also enhance the response of traits to selection during range expansion. With a greater impact on fitness, beneficial alleles of large effect should respond more strongly to selection and more effectively avoid loss due to drift than individual small-effect alleles (Kimura 1985). Adaptation can and does often proceed successfully via the collective action of many loci of small effect (Olson-Manning *et al.* 2012); however, large-effect alleles may be particularly important to invasions. Invading populations are subject to occasional very low effective population sizes (i.e. strong genetic drift) both during initial founding events and at the invasion front during the process of spatial expansion ('allele surfing'; Hallatschek *et al.* 2007; Excoffier *et al.* 2009; Peischl & Excoffier 2015). Effective population size at the invasion front may be extremely low even if the invading population is large. Strong genetic drift will be particularly problematic for new mutations that might contribute to novel variation in founding populations (Box 1), as these must rise from extreme rarity to contribute to adaptation. Therefore, regardless of their importance to adaptation in stable populations, we predict that the presence or absence of large-effect

loci will influence which traits are able to adapt within invasions.

Recent reviews find that large-effect loci do appear to be an important genetic basis of trait variation. A meta-analysis of QTL effects in plants found that while almost 90% of QTL identified were of small effect, the remaining loci each explained a large proportion of phenotypic variation (estimates >20%) in a study (Louthan & Kay 2011). Certainly, large-effect loci are easier to detect in a QTL analysis and the magnitude of their effects can be inflated by experimental artefacts (Beavis 1994; Otto & Jones 2000), but even in well-studied model organisms such as *Drosophila* and humans, large-effect loci appear to play a significant role in adaptation alongside the many detectable loci of small effect (Olson-Manning *et al.* 2012). Genomic studies have also greatly expanded the types of mutations that we know can have large effects on phenotype, particularly structural mutations such as copy number variation (CNVs, i.e. gene duplications; Lynch & Conery 2000) and inversions (Kirkpatrick 2010), as well as regulatory mutations (Hoekstra & Coyne 2007; Wray 2007). Indeed, copy number variants, largely unappreciated before genome-scale sequencing, are now known to be one of the major forms of mutation differentiating closely related species—such as humans and other apes—and individuals of the same species (Lynch & Conery 2000; Freeman *et al.* 2006). Copy number changes occur at nearly the same rate as point mutations and seem much more likely than other types of mutations to have beneficial effects (Kondrashov 2012; Hirase *et al.* 2014; Żmieńko *et al.* 2014). Thus, it would appear that many types of major mutations are frequent and able to contribute both standing and *de novo* large-effect variants to small founder populations (Box 1).

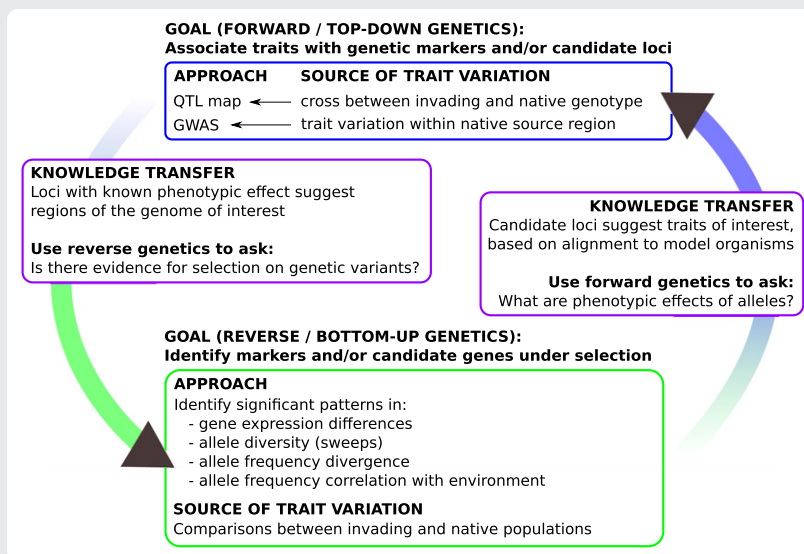
Our first window into the genetic basis of adaptive variation in invasion came from patterns of chromosomal inversions (easily observed in *Drosophila* salivary glands as mentioned above; Carson 1965; Dobzhansky 1965). It is now clear that such structural changes can be associated with large and potentially adaptive phenotypic effects (Hoffmann *et al.* 2004; Kirkpatrick 2010). Through physical rearrangement of loci and/or suppression of recombination, inversions can retain associations between complimentary alleles at multiple loci, preserving coadapted gene complexes and/or making a larger effect locus out of multiple loci of smaller effect (Hoffmann & Rieseberg 2008; Yeaman 2013). The potential for inversions to allow the rapid spread of advantageous loci during invasions seems strong in principle (Kirkpatrick & Barrett 2015). Both the invasion of Australia by *D. melanogaster* (Hoffmann & Weeks 2007) and the invasion of the Americas by *D. subobscura* (Prevosti

**Box 2.** Identifying the genetic basis of adaptive variation

The architecture of adaptive genetic diversity is vastly more observable than ever before (Prentis *et al.* 2008; Stinchcombe & Hoekstra 2008; Stewart *et al.* 2009). When traits are known to have evolved within invasions, or traits are inferred to be under selection via 'reverse' genetics (see below), their genetic basis can be identified using classical 'forward' genetics (Fig. 1). Genome wide markers can be screened across hundreds of individuals in systems with no prior genetic information, using genotype-by-sequencing approaches such as RADseq (Davey *et al.* 2011; Narum *et al.* 2013). Genetic maps can be obtained from sequences of individuals with known genetic relationships (i.e. via controlled crosses or pedigrees), or using genome wide association (GWAS) approaches in natural populations (Narum *et al.* 2013). The final step of associating trait variation with genotypes should work particularly well for invasive species, because trait variation among genotypes is likely to be segregating within extant populations or easily obtained via intraspecific controlled crosses (opportunities not available for most studies of species-level divergence, for example).

In a complimentary fashion, 'reverse' genetics tools that screen loci for evidence of natural selection (e.g. gene expression comparisons, scans for sweeps or differentiation of marker variation, and correlations of allele frequencies with environmental variables; Ekblom & Galindo 2011; Manel & Holderegger 2013) now allow genomic information itself to suggest which loci might be involved in adaptation (Bock *et al.* 2015). Using alignments of genes in candidate regions to loci in model organisms, phenotypic effects can be hypothesized and explored further. Invasions pose particular analytical challenges for reverse genetics, due to their nonequilibrium and often complex demographic history, which may generate allele frequency shifts that mimic signatures of selection (Excoffier *et al.* 2009). Putative loci under selection must be evaluated directly for their phenotypic and fitness effects. For example, Vandepitte *et al.* (2014) recently identified several regions of the Pyrenean rocket (*Sisymbrium austriacum*) genome that have differentiated during invasion, and some of these are located within genes that control flowering time in the closely related model *A. thaliana*. Flowering time can now be evaluated further in this system using 'forward' genetics and field studies of selection on this trait to validate its role in adaptation.

A persistent challenge is to firmly link individual mutations to their phenotypic effects, as mapping of quantitative trait loci or regions under selection can encompass multiple loci and variant sites. For example, multiple mutations in just one gene independently control different aspects of adaptive coat colour variation involved in the colonization of light sand substrate by deer mice (Linnen *et al.* 2013). Nevertheless, by combining 'forward' and 'reverse' genetics, and investigating candidate genes in these regions based on information from model organisms, it is possible to work through these links and build an understanding of the details of the genetics of adaptations (Stinchcombe & Hoekstra 2008; Fig. 1). Indeed, invasions may prove to offer outstanding opportunities to study the rapid evolution of loci in close physical linkage.



**Box 2 Fig. 1** A combination of forward, reverse and candidate gene approaches can resolve the genetic basis of variation that has been involved in the evolution of invaders.

*et al.* 1988) show evidence of rapid adaptation in chromosomal inversion frequencies. This is particularly impressive in South America, where *D. subobscura* is inferred to have invaded via just a few founders, yet the species rapidly re-evolved clines in inversion frequency characteristic of the native range (Pascual *et al.* 2007). Inversions are now increasingly identified in studies of the genetic basis of adaptation across taxa; for example, in the post-Pleistocene invasion of freshwater lakes by threespine sticklebacks, an inversion is among several large-effect loci that control the repeated evolution of freshwater and benthic forms (Jones *et al.* 2012).

Studies that map the genetic basis of phenotypic variation in contemporary invasions have been slow to appear, but these clearly indicate an important role for loci of large effect (Bock *et al.* 2015). Paterson *et al.* (1995) were among the first to map QTL in a colonizer, showing that a small number of QTL controlled the propensity of johnsongrass (*Sorghum halepense*) to produce asexually via rhizomes. Linde (2001) similarly found three major QTL controlling flowering time differences among ecotypes of the invasive plant shepherd's purse (*Capsella bursa-pastoris*). Most recently, Whitney *et al.* (2015) have identified three major QTL associated with range expansion in the sunflower *Helianthus annuus texanus*.

As we accumulate information about the genetic basis of invader phenotypes, we can begin to ask what types of traits are most likely to have standing variation in large-effect loci, or to gain it more easily through mutations. One class of traits for which large-effect loci are already well known are those under frequency-dependent selection in the native range. For example, variation at social recognition loci in both the fire ant (*Solenopsis invicta*) and the Argentine ant (*Linepithema humile*) has been lost during founder events, resulting in decreased conspecific aggression and increased invasiveness (Tsutsui *et al.* 2000, 2003; Krieger & Ross 2002), giving us our most famous cases of *positive* effects of genetic bottlenecks on invasion. Another major class of loci under frequency-dependent selection are self-incompatibility (SI) loci in plants, at which loss of alleles can clearly be detrimental to reproduction in founding populations (e.g. Elam *et al.* 2007). These cases demonstrate the important phenotypic effects of the loss of large-effect alleles, through the positive or negative nature of the consequences, are less predictable. There are also many classic examples of invaders circumventing loss of SI diversity by evolving self-compatibility in invading populations (Baker 1965; Barrett 2015; Ferrero *et al.* 2015), emphasizing the impressive adaptability of introduced species under seemingly unlikely conditions.

Interestingly, a recent review of QTL studies in plants concludes that large-effect loci are more com-

monly found in traits governing biotic interactions than in traits associated with adaptation to abiotic conditions (Louthan & Kay 2011). This pattern may be due to greater spatial variation in selection for biotic interactions (i.e. a rougher adaptive landscape) favouring fixation of large-effect alleles, as opposed to the presence of more available large-effect variation in these traits *per se*. Regardless, the maintenance of variation in large-effect loci across populations under spatially and temporally varying selection in native populations may provide more opportunities for adaptation in these traits during invasion. Given that one of the major hypotheses for invasion success is the escape from negative biotic interactions in the native range (Keane & Crawley 2002), the potential for especially high adaptability in traits underlying precisely these interactions should be of great interest to invasion geneticists.

Linking phenotypic variation to its genetic basis is a major undertaking in any study system, but invaders may be especially well suited to these approaches among nonmodel organisms (Box 2). The contemporary nature of their evolutionary changes means that adaptive variation exists within and among current populations across the range, facilitating genetic mapping, identification of current targets of selection, and observation of the impacts of genetic variants on populations in native and invaded environments. An exciting window into the future of these opportunities is provided by Hamilton *et al.* (2015) in this issue, who compare the phenotypic effects of many loci associated with adaptation in the native range of the model *Arabidopsis thaliana* (Fournier-Level *et al.* 2011; Hancock *et al.* 2011) between the native and introduced ranges (Hamilton *et al.* 2015). Their results reveal a large number of loci with conditional effects, altering fitness in only one environment, but just a handful of loci that have significant effects across both ranges, with opposing consequences for fitness in each region (antagonistic pleiotropy). This type of study is powerful for identifying the genetic basis of adaptation to novel ranges, the effect size and number of loci involved, and whether alleles at individual loci can shift populations from one phenotypic optimum in the native range to a new optimum in an invasion. Clearly, important and exciting insights into the connections between genetic architecture and invasiveness await the accumulation of this type of information.

### *Cryptic genetic variation*

To establish adaptive genetic variants in a founding population, it is ideal if these alleles are segregating at high frequency in source population(s). As noted above, we expect that many loci will not contain such varia-

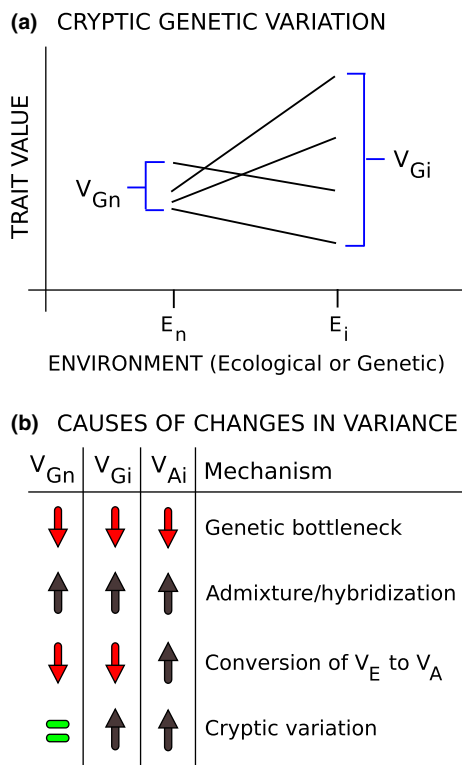


tion, given that source environments differ from the invasion and will have selected for different trait optima. This situation might be avoided if adaptive variation in the new environment is not under selection in the old, as will be the case for ‘cryptic’ genetic variation—that is variation only observed in the invasion. Cryptic genetic variation of a trait is revealed whenever the phenotypic effects of genetic variants differ depending on the ecological environment ( $G \times E$  interactions) or differ depending on the genetic environment (allele frequencies at other loci;  $G \times G$  interactions), such that there is increased genetic variation of the trait within some environments (Hermisson & Wagner 2004; McGuigan & Sgrò 2009; Paaby & Rockman 2014). These previously hidden sources of variation would seem to be particularly important for rapid evolutionary change, and contemporary species introductions should be outstanding places to look for evidence of adaptation via cryptic variants (Lee & Gelembiuk 2008).

There is a long history of interest in the potential for exposure of a population to a stressful environment to increase heritable variation in this way (Waddington 1956; Hoffmann & Merilä 1999; Badyaev 2005). This field has grown out of the well-known pioneering work of Waddington (1956), who argued that selection will act to create buffering mechanisms to stabilize optimal phenotypes under typical conditions (masking genetic variation), but that these buffering mechanisms may fail under atypical/stressful conditions, as he demonstrated in *D. melanogaster*. At the Baker & Stebbins symposium, Waddington (1965) himself raised questions about the stability of phenotypes and the expression of genetic variation during the colonization of new environments.

Evidence is now accumulating that this phenomenon is common under natural environmental variation, in both individual loci as well as quantitative traits (Dworkin *et al.* 2003; Latta *et al.* 2015). Cryptic allelic variants may be strictly neutral in the historical environment, having no phenotypic effects. For example, a large body of work has shown that the heat-shock chaperone protein Hsp90 buffers the effects of mis-folded proteins in a wide variety of taxa, such that genetic variation in those proteins lacks phenotypic effect. When Hsp90 expression is reduced through environmental effects or its own mutations, genetic variation in the associated proteins is exposed and can reveal adaptive variants (Paaby & Rockman 2014). Alternatively, alleles may be under selection for their phenotypic effects, but have new pleiotropic phenotypes expressed in the new environment. For example, Duveau & Félix (2012) showed that a locus under selection for life history variation in *Caenorhabditis elegans* produces novel morphological effects under environmental variation. These observations suggest that cryptic variation may often be present in ecologically relevant traits. Indeed, conditionally neutral allelic variants appear to be a common genetic basis for local adaptations in natural populations (Colautti *et al.* 2012; Olson-Manning *et al.* 2012; Hamilton *et al.* 2015), which means that cryptic variation should have many opportunities to accumulate in traits related to adaptation to a range of environmental variation that is not uncommon within species ranges (Paaby & Rockman 2014).

The exposure of cryptic variation might be especially relevant for species introductions, given that we expect shifts in the genetic background due to founder effects and/or admixture, as well as shifts in the biotic and abiotic ecological environment in the new range. Compelling cases have been made that cryptic variation has played a role in historical cases of adaptation in body size in sticklebacks invading freshwater lakes (McGuigan *et al.* 2011) and in adaptive loss of eyes in cavefish invading caves (Rohner *et al.* 2013). To date,



**Fig. 2** Cryptic genetic variation can be revealed whenever genetic variance increases in a new ecological or genetic environment. (a) If genetic variance increases in the invaded environment (subscript ‘i’), relative to the native environment (subscript ‘n’), cryptic variation might contribute adaptive variation to an invasion. (b) Cryptic variation is one of several potential mechanisms underlying changes in total ( $V_G$ ), additive ( $V_A$ ) and epistatic ( $V_E$ ) genetic variance of a trait in an invading population, relative to its source population(s).

there is no study that we are aware of which tests for evidence of cryptic variation surfacing in a contemporary invasion, although some studies of invader plasticity seem to suggest this possibility (e.g. Purchase & Moreau 2012). A recent demonstration of dominance reversal in allelic effects (where a formally recessive allele becomes dominant) during invasion of the copepod *Eurytemora affinis* highlights the potential for the genetic basis of adaptive variation to change fundamentally in an invader's new environmental context (Posavi *et al.* 2014). In a theoretical analysis, Masel (2006) showed that cryptic variation might often be biased towards adaptive variation (i.e. biased against deleterious mutations), if [source] populations occasionally experience conditions similar to the new environment during their evolutionary history, exposing cryptic variation to selection. Given that invasions often seem to occur in niche space that is similar to native environments (Petitpierre *et al.* 2012; Strubbe *et al.* 2013), it is not unreasonable to imagine that native populations might have experienced relevant conditions in the past.

To understand whether cryptic variation is important to invasions, we must disentangle it from a set of non-mutually exclusive factors that can influence adaptive variation in these populations (Fig. 2). Admixture or hybridization (and specifically the transgressive segregation that these foster) can also clearly increase genetic variance during invasion, particularly in traits that are divergent in source populations/species, but this increase should be robust to environmental context. Conversion of epistatic to additive variance has also been of long-standing interest as a way in which additive variation (but not total genetic variation) can increase during invasion (Goodnight 1988), although the conditions under which conversion is expected are relatively narrow and there is little evidence for its role to date (Turelli & Barton 2006; Van Heerwaarden *et al.* 2008). In contrast, cryptic variation should increase total genetic variance only in the novel environment (Fig. 2). This context-dependent variation highlights an important point: our null expectation for variation in a founder population should be that expressed by founder genotypes in their *source* environment, something which is rarely examined. As loci underlying adaptations in invaders are identified, a key area of interest should be their effects under different environmental conditions and genetic backgrounds, particularly the comparison of native vs. invading contexts.

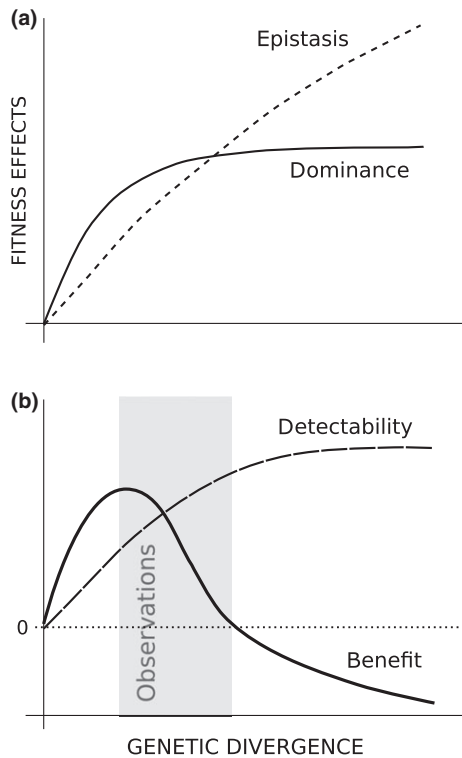
### Admixture

Thus far, we have considered the details of genetic diversity in founding events derived from a single source, but we know that multiple introductions are

very common features of invasions (Dlugosch & Parker 2008a; Uller & Leimu 2011). As discussed above, multiple introductions appear to have modest effects on the total amount of genetic variation in most introduced populations, as measured by molecular markers. In contrast, there is a very strong potential for multiple introductions to have significant impacts on adaptive variation in invading populations if the introductions come from different areas of the native range, resulting in admixture of divergent source populations (Ellstrand & Schierenbeck 2000; Verhoeven *et al.* 2011; Rius & Darling 2014). Admixture can infuse the invasion with novel alleles, which can have particularly strong effects on phenotype for loci of large-effect and/or cryptic variants arising from a history of spatially varying selection across native sources. Perhaps most importantly, admixture creates unique opportunities for genetic interactions among previously isolated alleles and/or loci, which can dramatically affect phenotypes and fitness in admixed genotypes (Waser & Price 1989; Lynch 1991; Edmands 1999; Keller & Waller 2002).

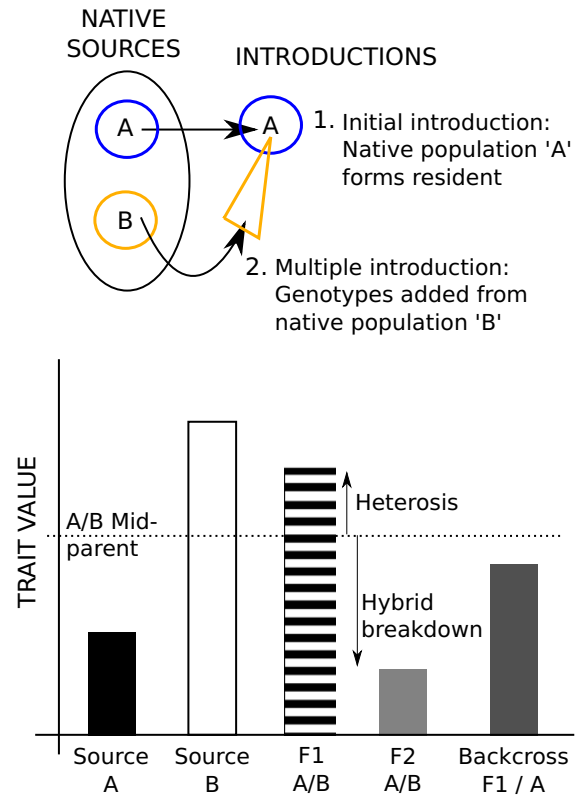
Genetic interactions are well known from studies of inbreeding depression, outbreeding depression, and heterosis observed through genetic crosses. These observations are part of a general set of expectations for the fitness effects of crosses between parents of varying genetic distances, based on the mechanisms underlying the genetic interactions (Lynch 1991; Fig. 3). Outcrossing is expected to be beneficial when a focal population has some fixed recessive deleterious alleles—genetic load—that can be rescued through dominance interactions with more fit alleles, generating diminishing returns as genetic distance increases and genetic load is relieved. In contrast, the effects of epistatic interactions among alleles at different loci rise or even accelerate as genetic distance between parents increases. Epistatic interactions are expected to build up in relatively isolated populations due to selection for locally coadapted gene complexes or to genetic drift (creating Bateson-Dobzhansky-Muller incompatibilities), acting separately in each population (Lynch & Walsh 1998). Epistatic effects in the F1 generation may sometimes be positive (heterotic) but are expected to become increasingly negative with genetic distance, particularly in the F2 and later generations when co-evolved multilocus genotypes are broken apart by recombination (i.e. 'hybrid breakdown'; Fig. 4; Orr & Turelli 2001; Bomblies *et al.* 2007).

Although both positive and negative genetic interactions are expected, admixture has generally been hypothesized to be beneficial to invasions. Signatures of positive genetic interactions have been sought by looking for correlations between heterozygosity and fitness traits (Heterozygosity-Fitness Correlations, 'HFCs'; Rius & Darling 2014). It is important to note that these analyses



**Fig. 3** Genetic divergence between potential source regions will shape both their genetic interactions and our ability to observe their admixture when present. (a) Dominance interactions (positive effects from the rescue of loci homozygous for deleterious recessive alleles) are maximized at low levels of divergence, while the fitness effects of epistatic interactions (often negative due to incompatible allele combinations, particularly in F2 and later generations) continue to increase with divergence among loci. (b) The power to detect admixture in a data set increases with genetic divergence, as native subpopulations become more identifiable, but net fitness benefits from their genetic interactions should become increasingly negative. As a result, observations of admixture are predicted to concentrate at intermediate levels of genetic divergence (after Lynch 1991).

typically use molecular marker heterozygosity under the assumption that it is in linkage disequilibrium with sites that affect fitness. Linkage disequilibrium with neutral markers is expected to decay quickly in most cases, and so there is a limited window in which this type of analysis is expected to reveal positive effects of admixture when they are present. Moreover, if presumed fitness-rated traits are also varying due to local adaptation in the native source range (Colautti *et al.* 2009), and/or if epistatic genetic interactions are generating nonlinear fitness effects of heterozygosity, then HFCs are no longer expected (Lynch & Walsh 1998; Chapman *et al.* 2009; Szulkin *et al.* 2010). Nevertheless, significant HFCs have shown apparent benefits of admixture during invasion. For example, Keller *et al.* (2014) elegantly showed a positive HFC for reproduction in admixed introductions of



**Fig. 4** A realistic scenario for the effects of admixture on fitness-related traits. Multiple introductions are likely to occur via input of new genotypes ('B') into an existing introduced population of genotypes ('A'). If fitness-related traits (e.g. body size, seed number) in the source populations differ genetically, then the expected result of the F1 cross is the mid-parent value. F1 progeny may experience heterosis or 'hybrid vigour' due to genetic interactions between sources A and B, but these often break down in the F2. Hybrid breakdown might often be ameliorated by backcrosses to the resident population, a likely scenario for introgression of new genotypes during invasion.

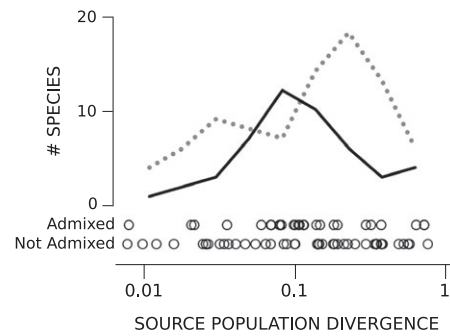
the plant *Silene vulgaris*, a relationship that was not present in a zone of historical admixture in the native range. This approach may be best suited to detecting fitness effects of very recent admixture (relative to recombination rate), particularly among sources with a low degree of divergence, such that epistatic interactions are expected to be minimal.

In place of HFC searches, it might be ideal to combine genetic surveys of invasion history with experimental crosses of known or potential sources, looking directly for the fitness effects of crossing at varying levels of divergence. Experimental crosses have the particular benefit of allowing progeny performance to be evaluated against a mid-parent expected value (Fig. 4). Mid-parent comparisons are important because source populations will often have divergent life history and/or morphological traits due to local adaptation, and

these are often the same traits that are used to quantify fitness effects (e.g. body size, offspring size or number). For example, an invading population with an offspring number that is intermediate between values observed in source populations may in fact be experiencing 'hybrid vigour', if reproduction exceeds the mid-parent expectation. Traits of experimental progeny can be evaluated at the F1, F2 and backcross generations and compared to invading genotypes that are potentially the products of these histories (Facon *et al.* 2008; Turgeon *et al.* 2011).

Identifying admixture and/or its potential source regions for further study introduces its own challenges. While historical records can indicate multiple introductions, ultimately it is essential to observe genetic mixing directly to be certain admixture is present. A typical approach is to survey marker variation in the native and invaded ranges as broadly as possible, delineate any distinct genetic subpopulations in the native source region and identify signatures of these subpopulations mixing in the introduced range (Cristescu 2015). There are two underappreciated challenges associated with these steps. First, sampling in the native range must be sufficient for a reasonable argument to be made that invaders are truly admixed, and not simply derived from an unsampled region in the native range (including a zone of historical admixture). Second, sampling in the native range and marker variability must be high enough to resolve different source populations as unique. This latter concern is particularly serious, because admixture may have important phenotypic effects at low levels of divergence among sources (Fig. 3).

Genetic reconstructions of invasion history are accumulating, affording opportunities to examine the conditions under which admixture is detectable and potentially affecting invader fitness. Reports of admixture to date are reasonably common (37% of 70 invaders studied with nuclear markers; Fig. 5), but they appear to be underrepresented at both low and high levels of source population divergence (Fig. 5). This pattern matches our expectation that admixture should be harder to detect at low levels of source divergence, and is consistent with our prediction that admixture might be unfavourable at higher levels of source divergence. We can imagine a variety of alternative factors that will also affect these patterns (e.g. sampling design, mating system, generation time, bottleneck severity, number of introductions and introduction vector), but the idea that there might be conditions under which genetic variation itself resists multiple introductions is in direct opposition to the long-held view that admixture should be beneficial during invasions. There is clearly a need for direct examination of the fitness consequences of admixture among potential source populations, particularly across both low and high levels of divergence.



**Fig. 5** A survey of studies reporting admixture or no admixture in introduced species (circles), as a function of genetic differentiation among sites in the native range ( $F_{ST}$  and related metrics, based on nuclear genetic markers;  $N = 70$  species). Lines show the number of species for which admixture was reported (heavy line) or not reported (dashed line) in a sliding window of width  $1.0 \ln(F_{ST})$ . Data are available at Dryad doi:10.5061/dryad.s2948.

### Contributions of genetic diversity to invasion

In the event that we are able to identify genetic changes that have been adaptive in invading populations, we will have outstanding opportunities to assess the contribution of adaptation to the process of invasion itself. We typically do not know whether adaptations that we observe in well-established invaders reflect higher fitness in the novel environment postinvasion without contribution to the process of invasion itself. A potential example of adaptation unrelated to invasiveness is provided by the highly invasive plant garlic mustard (*Alliaria petiolata*) in North America, which is thought to have invaded largely due to its allelopathic inhibition of competing species. Recent studies suggest some populations may be evolving reduced allelopathic activity in the face of competition with resistant conspecifics and increasingly resistant natives (Lankau *et al.* 2009), a putative shift away from the traits that facilitated the invasion itself.

In general, we have little knowledge of the population-level consequences of individual genetic changes (Kinnison & Hairston 2007; Gaston 2009). We routinely assume that invading genotypes with higher reproduction and/or survival relative to other lineages must be invading with increased population growth, density and/or spread. While selection will favour the evolution of the invading population towards such a high-fitness genotype, there may be extrinsic factors limiting the consequences of adaptation for population growth itself. One of the primary barriers to connecting the fitness of individual genotypes with population-level performance is density-dependent changes in vital rates that occur as a population grows (Antonovics & Levin

1980; Ozgul *et al.* 2009), as will often be the case when invaders reach the high densities that can be a hallmark of 'invasiveness'. Density dependence is an extremely common property of populations, but in general we know almost nothing about how fitness differences among genotypes change under competition with density of conspecifics, within invasions or any other system. Fisher (1930) went so far as to suggest that fitness increases could even contribute to 'environmental degradation', imposing limits on population growth as high-fitness individuals consumed more resources. Invasions offer particularly outstanding opportunities to study density dependence in genotype performance, as many invasions have active expansion fronts at which density is currently varying under relevant conditions.

Whether adaptation or beneficial admixture ultimately matter to population establishment, persistence, spread and 'invasiveness' merits careful consideration (Molofsky *et al.* 2014). A promising way forward is to integrate comparative demography into the study of the evolution of invaders. The best example of this that we are aware of to date is in work seeking to understand the contribution of evolutionary increases in leg length/individual dispersal speed of cane toads (*Bufo marinus*) to the rate of expansion of its invasion into Australia (Perkins *et al.* 2013). In this case, it seems likely that adaptation for dispersal has changed the rate of spread at least in part, although adaptation may not have played much role in the successful establishment and severe ecological impact of this species once established.

### Future directions

The issues that we have considered above suggest many opportunities for new insights into the importance of genetic variation in invasion, including the following:

- The genetic basis of variation in ecologically relevant traits. Invasions provide outstanding opportunities to understand the contributions of different classes of mutations—such as chromosomal inversions and copy number variants—to rapid adaptive evolution. We predict that evolutionary changes that are important to invasion by introduced species will more often occur in traits affected by large-effect loci, through unpredictable founder/bottleneck effects at these loci, through the arrival of new mutations that are able to rise quickly in frequency, and through response to selection at low effective population size during range expansion.
- The relative contribution of large-effect loci in abiotic vs. biotic trait variation. Where the genetic basis of adaptive variation in invaders can be identified, it could reveal important connections between evolutionary and ecological opportunities for introduced species. Nonnative species are particularly likely to experience alterations in biotic interactions; if these same interactions are more evolutionarily labile due to underlying trait architecture, then invaders may be predisposed to benefit from adaptation during invasion.
- The genetic variation within founder genotypes in the invaded vs. the native environment. Disentangling potential bottleneck, admixture and cryptic variation effects will enable a deeper understanding of the realized evolutionary constraints and opportunities experienced by founding populations.
- The fitness effects of genetic admixture between source populations with different levels of genetic divergence. In particular, experimental crosses and comparisons to mid-parent values should reveal the potential fitness benefits of multiple introductions of modest genetic differentiation, as well as the potential resistance to admixture from negative genetic interactions among more divergent sources.
- The demographic impacts of evolutionary change. Comparative demography of genetic variants can be used to connect individual evolutionary changes to their consequences for aspects of invasiveness (population growth, density and spread) across all stages of invasion.

Baker often referred to his study of the genetics of colonizers as 'genecology' (Baker 1965), and this connection between genes and ecology remains a worthy goal 50 years later. By understanding the details of invader genetics, we can move towards understanding how their ecology might realistically evolve.

### Acknowledgements

We would like to thank the organizers and participants of Invasion Genetics: The Baker and Stebbins Legacy Symposium held at Asilomar, California, USA, in 2014, which celebrated 50 years of invasion genetics and inspired this synthesis. Comments from RI Colautti, G Baucom and an anonymous reviewer substantially improved this manuscript.

### References

- Agashe D, Falk JJ, Bolnick DI (2011) Effects of founding genetic variation on adaptation to a novel resource. *Evolution*, **65**, 2481–2491.
- Allard R (1965) Genetic systems associated with colonizing ability in predominantly self-pollinated species. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 49–76. Academic Press, New York.
- Allendorf FW, Lundquist LL (2003) Introduction: population biology, evolution, and control of invasive species. *Conservation Biology*, **17**, 24–30.

- Antonovics J, Levin D (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*, **11**, 411–452.
- Badyaev A (2005) Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 877–886.
- Baker H (1955) Self-compatibility and establishment after “long-distance” dispersal. *Evolution*, **9**, 347–349.
- Baker H (1965) Characteristics and modes of origin of weeds. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 147–172. Academic Press, New York.
- Baker H (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.
- Baker H, Stebbins G (eds) (1965) *The Genetics of Colonizing Species*. Academic Press, New York.
- Barrett SCH (2015) Foundations of invasion genetics: the legacy of Baker and Stebbins. *Molecular Ecology*, **24**, 1927–1941.
- Barrett SCH, Husband BC (1990) The genetics of plant migration and colonization. In: *Plant Population Genetics, Breeding, and Genetic Resources* (eds Brown AHD, Clegg MT, Kahler AL, Weir BS), pp. 254–277. Sinauer Associates Inc., Sunderland.
- Barrett SCH, Richardson BJ (1986) Genetic attributes of invading species. In: *Ecology of Biological Invasions, an Australian Perspective* (eds Groves R, Burdon JJ), pp. 21–33. Australian Academy of Sciences, Canberra.
- Beavis WD (1994) The power and deceit of QTL experiments: lessons from comparative QTL studies. *Proceedings of the Forty-ninth Annual Corn and Sorghum Industry Research Conference*, **49**, 250–266.
- Blackburn T, Lockwood JL, Cassey P (2015) The influence of numbers on invasion success. *Molecular Ecology*, **24**, 1942–1953.
- Bock D, Caseys C, Cousens R *et al.* (2015) What we still don't know about invasion genetics. *Molecular Ecology*, **24**, 2277–2298.
- Bomblies K, Lempe J, Epple P *et al.* (2007) Autoimmune response as a mechanism for a Dobzhansky-Muller-type incompatibility syndrome in plants. *PLoS Biology*, **5**, e236.
- Bossdorf O, Auge H, Lafuma L *et al.* (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.
- Briskie JV, Mackintosh M (2004) Hatching failure increases with severity of population bottlenecks in birds. *Proceedings of the National Academy of Sciences of the USA*, **101**, 558–561.
- Brown A, Marshall D (1981) Evolutionary changes accompanying colonization in plants. In: *Evolution Today, Proceedings of the Second International Congress of Systematic and Evolutionary Biology* (eds Scudder G, Reveal J), pp. 351–353. Hunt Institute, Pittsburgh, Pennsylvania.
- Carson H (1965) Chromosomal morphism in geographically widespread species of *Drosophila*. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 503–531. Academic Press, New York.
- Chapman JR, Nakagawa S, Coltman DW, Slate J, Sheldon BC (2009) A quantitative review of heterozygosity-fitness correlations in animal populations. *Molecular Ecology*, **18**, 2746–2765.
- Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science*, **342**, 364–366.
- Colautti RI, Lau JA (2015) Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology*, **24**, 1999–2017.
- Colautti RI, Maron JL, Barrett SCH (2009) Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evolutionary Applications*, **2**, 187–199.
- Colautti RI, Lee C-R, Mitchell-Olds T (2012) Origin, fate, and architecture of ecologically relevant genetic variation. *Current Opinion in Plant Biology*, **15**, 199–204.
- Cox GW (2004) *Alien Species and Evolution: The Evolutionary Ecology of Exotic Plants, Animals, Microbes, and Interacting Native Species*. Island Press, Washington.
- Cristescu ME (2015) Genetic reconstructions of invasion history. *Molecular Ecology*, **24**, 2212–2225.
- Davey JW, Hohenlohe PA, Etter PD *et al.* (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nature Reviews Genetics*, **12**, 499–510.
- De Visser JAGM, Krug J (2014) Empirical fitness landscapes and the predictability of evolution. *Nature Reviews Genetics*, **15**, 480–490.
- DeBolt S (2010) Copy number variation shapes genome diversity in *Arabidopsis* over immediate family generational scales. *Genome Biology and Evolution*, **2**, 441–453.
- Denver DR, Morris K, Lynch M, Thomas WK (2004) High mutation rate and predominance of insertions in the *Caenorhabditis elegans* nuclear genome. *Nature*, **430**, 679–682.
- Dlugosch KM, Parker IM (2008a) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, **17**, 431–449.
- Dlugosch KM, Parker IM (2008b) Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. *Ecology Letters*, **11**, 701–709.
- Dobzhansky T (1965) “Wild” and “domestic” species of *Drosophila*. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 533–551. Academic Press, New York.
- Duveau F, Félix M-A (2012) Role of pleiotropy in the evolution of a cryptic developmental variation in *Caenorhabditis elegans*. *PLoS Biology*, **10**, e1001230.
- Dworkin I, Palsson A, Birdsall K, Gibson G (2003) Evidence that Egfr contributes to cryptic genetic variation for photoreceptor determination in natural populations of *Drosophila melanogaster*. *Current Biology*, **13**, 1888–1893.
- Edmunds S (1999) Heterosis and outbreeding depression in interpopulation crosses spanning a wide range of divergence. *Evolution*, **53**, 1757–1768.
- Eklom R, Galindo J (2011) Applications of next generation sequencing in molecular ecology of non-model organisms. *Heredity*, **107**, 1–15.
- Elam DR, Ridley CE, Goodell K, Ellstrand NC (2007) Population size and relatedness affect fitness of a self-incompatible invasive plant. *Proceedings of the National Academy of Sciences of the USA*, **104**, 549–552.
- Ellstrand NC, Roose ML (1987) Patterns of genotypic diversity in clonal plant species. *American Journal of Botany*, **74**, 123–131.
- Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the USA*, **97**, 7043–7050.
- Excoffier L, Foll M, Petit RJ (2009) Genetic consequences of range expansions. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 481–501.
- Facon B, Pointier J-P, Jarne P, Sarda V, David P (2008) High genetic variance in life-history strategies within invasive

- populations by way of multiple introductions. *Current Biology*, **18**, 363–367.
- Ferrero V, Barrett S, Castro S *et al.* (2015) Invasion genetics of the Bermuda buttercup (*Oxalis pes-caprae*): complex intercontinental patterns of genetic diversity, polyploidy and heterostyly characterize both native and introduced populations. *Molecular Ecology*, **24**, 2143–2155.
- Fisher RA (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Fournier-Level A, Korte A, Cooper MD *et al.* (2011) A map of local adaptation in *Arabidopsis thaliana*. *Science*, **334**, 86–89.
- Frankham R (2005) Resolving the genetic paradox in invasive species. *Heredity*, **94**, 385.
- Fraser A (1965) Colonization and genetic drift. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 117–125. Academic Press, New York.
- Freeman JL, Perry GH, Feuk L *et al.* (2006) Copy number variation: new insights in genome diversity. *Genome Research*, **16**, 949–961.
- Gaston KJ (2009) Geographic range limits of species. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 1391–1393.
- Goodnight CJ (1988) Epistasis and the effect of founder events on the additive genetic variance. *Evolution*, **42**, 441–454.
- Gray AJ, Mack RN, Harper JL *et al.* (1986) Do invading species have definable genetic characteristics? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **314**, 655–674.
- Hallatschek O, Hersen P, Ramanathan S, Nelson DR (2007) Genetic drift at expanding frontiers promotes gene segregation. *Proceedings of the National Academy of Sciences of the USA*, **104**, 19926–19930.
- Hamilton J, Okada M, Korves T, Schmitt J (2015) The role of climate adaptation in colonization success in *Arabidopsis thaliana*. *Molecular Ecology*, **24**, 2253–2263.
- Hamrick JL, Godt MJW (1996) Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351**, 1291–1298.
- Hancock AM, Brachi B, Faure N *et al.* (2011) Adaptation to climate across the *Arabidopsis thaliana* genome. *Science*, **334**, 83–86.
- Hendry AP, Kinnison MT, Dec N (1999) The pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**, 1637–1653.
- Hermisson J, Wagner GP (2004) The population genetic theory of hidden variation and genetic robustness. *Genetics*, **168**, 2271–2284.
- Hirase S, Ozaki H, Iwasaki W (2014) Parallel selection on gene copy number variations through evolution of three-spined stickleback genomes. *BMC Genomics*, **15**, 735.
- Hoekstra HE, Coyne JA (2007) The locus of evolution: evo devo and the genetics of adaptation. *Evolution*, **61**, 995–1016.
- Hoffmann AA, Merilä J (1999) Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution*, **14**, 96–101.
- Hoffmann AA, Rieseberg LH (2008) Revisiting the impact of inversions in evolution: from population genetic markers to drivers of adaptive shifts and speciation? *Annual Review of Ecology and Systematics*, **39**, 21–42.
- Hoffmann AA, Weeks AR (2007) Climatic selection on genes and traits after a 100 year-old invasion: a critical look at the temperate-tropical clines in *Drosophila melanogaster* from eastern Australia. *Genetica*, **129**, 133–147.
- Hoffmann AA, Sgrò CM, Weeks AR (2004) Chromosomal inversion polymorphisms and adaptation. *Trends in Ecology & Evolution*, **19**, 482–488.
- Hufbauer RA (2008) Biological invasions: paradox lost and paradise gained. *Current Biology*, **18**, 246–247.
- Hufbauer RA, Rutschmann A, Serrate B, Vermeil de Conchard H, Facon B (2013) Role of propagule pressure in colonization success: disentangling the relative importance of demographic and habitat effects. *Journal of Evolutionary Biology*, **26**, 1691–1699.
- Jones FC, Grabherr MG, Chan YF *et al.* (2012) The genomic basis of adaptive evolution in threespine sticklebacks. *Nature*, **484**, 55–61.
- Keane R, Crawley M (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164–170.
- Keller L, Waller D (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, **17**, 230–241.
- Keller SR, Fields PD, Berardi AE, Taylor DR (2014) Recent admixture generates heterozygosity-fitness correlations during the range expansion of an invading species. *Journal of Evolutionary Biology*, **27**, 616–627.
- Kimura M (1985) *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge.
- Kinnison MT, Hairston NG (2007) Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Functional Ecology*, **21**, 444–454.
- Kirkpatrick M (2010) How and why chromosome inversions evolve. *PLoS Biology*, **8**, e1000501.
- Kirkpatrick M, Barrett B (2015) Chromosome inversions, adaptive cassettes, and the evolution of species' ranges. *Molecular Ecology*, **24**, 2046–2055.
- Kolbe JJ, Glor RE, Rodríguez Schettino L *et al.* (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**, 177–181.
- Kondrashov FA (2012) Gene duplication as a mechanism of genomic adaptation to a changing environment. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 5048–5057.
- Koskinen MT, Haugen TO, Primmer CR (2002) Contemporary fisherian life-history evolution in small salmonid populations. *Nature*, **419**, 826–830.
- Krieger MJB, Ross KG (2002) Identification of a major gene regulating complex social behavior. *Science*, **295**, 328–332.
- Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061–2070.
- Lankau RA, Nuzzo V, Spyreas G, Davis AS (2009) Evolutionary limits ameliorate the negative impact of an invasive plant. *Proceedings of the National Academy of Sciences of the USA*, **106**, 15362–15367.
- Latta LC, Peacock M, Civitello DJ *et al.* (2015) The phenotypic effects of spontaneous mutations in different environments. *The American Naturalist*, **185**, 243–252.
- 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 of the USA*, **104**, 3883–3888.
- Lee CE (2002) Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, **17**, 386–391.

- Lee CE, Gelembiuk GW (2008) Evolutionary origins of invasive populations. *Evolutionary Applications*, **1**, 427–448.
- Leinonen T, O'Hara RB, Cano JM, Merilä J (2008) Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *Journal of Evolutionary Biology*, **21**, 1–17.
- Linde M (2001) Flowering ecotypes of *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae) analysed by a cosegregation of phenotypic characters (QTL) and molecular markers. *Annals of Botany*, **87**, 91–99.
- Linnen CR, Poh Y-P, Peterson BK *et al.* (2013) Adaptive evolution of multiple traits through multiple mutations at a single gene. *Science*, **339**, 1312–1316.
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.
- Louthan AM, Kay KM (2011) Comparing the adaptive landscape across trait types: larger QTL effect size in traits under biotic selection. *BMC Evolutionary Biology*, **11**, 60.
- Lynch M (1991) The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution*, **45**, 622–629.
- Lynch M, Conery JS (2000) The evolutionary fate and consequences of duplicate genes. *Science*, **290**, 1151–1155.
- Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits*. Sinauer Associates Inc., Sunderland.
- Manel S, Holderegger R (2013) Ten years of landscape genetics. *Trends in Ecology & Evolution*, **28**, 614–621.
- Masel J (2006) Cryptic genetic variation is enriched for potential adaptations. *Genetics*, **172**, 1985–1991.
- Mayr E (1965a) The nature of colonization in birds. In: *The Genetics of Colonizing Species* (eds Baker HG, Stebbins GL), pp. 29–47. Academic Press, New York.
- Mayr E (1965b) Summary. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 553–562. Academic Press, New York.
- McGuigan K, Sgrò CM (2009) Evolutionary consequences of cryptic genetic variation. *Trends in Ecology & Evolution*, **24**, 305–311.
- McGuigan K, Nishimura N, Currey M, Hurwit D, Cresko WA (2011) Cryptic genetic variation and body size evolution in threespine stickleback. *Evolution*, **65**, 1203–1211.
- McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution*, **17**, 285–291.
- Merilä J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, **14**, 892–903.
- Molofsky J, Keller SR, Lavergne S, Kaproth MA, Eppinga MB (2014) Human-aided admixture may fuel ecosystem transformation during biological invasions: theoretical and experimental evidence. *Ecology and Evolution*, **4**, 899–910.
- Narum SR, Buerkle CA, Davey JW, Miller MR, Hohenlohe PA (2013) Genotyping-by-sequencing in ecological and conservation genomics. *Molecular Ecology*, **22**, 2841–2847.
- Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. *Evolution*, **29**, 1–10.
- 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: the influence of mating systems and introduction dynamics. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds Sax D, Stachowicz J, Gaines S), pp. 201–228. Sinauer Associates Inc., Sunderland, Massachusetts.
- Olson-Manning CF, Wagner MR, Mitchell-Olds T (2012) Adaptive evolution: evaluating empirical support for theoretical predictions. *Nature Reviews Genetics*, **13**, 867–877.
- Orr HA (1998) The population genetics of adaptation: the distribution of factors fixed during adaptive evolution. *Evolution*, **52**, 935–949.
- Orr HA (2005) The genetic theory of adaptation: a brief history. *Nature Reviews Genetics*, **6**, 119–127.
- Orr HA, Turelli M (2001) The evolution of postzygotic isolation: accumulating Dobzhansky-Muller incompatibilities. *Evolution*, **55**, 1085–1094.
- Ossowski S, Schneeberger K, Lucas-Lledó JI *et al.* (2010) The rate and molecular spectrum of spontaneous mutations in *Arabidopsis thaliana*. *Science*, **327**, 92–94.
- Otto SP, Jones CD (2000) Detecting the undetected: estimating the total number of loci underlying a quantitative trait. *Genetics*, **156**, 2093–2107.
- Otto SP, Whitlock MC (1997) The probability of fixation in populations of changing size. *Genetics*, **146**, 723–733.
- Ozgul A, Tuljapurkar S, Benton TG *et al.* (2009) The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science*, **325**, 464–467.
- Paaby AB, Rockman MV (2014) Cryptic genetic variation: evolution's hidden substrate. *Nature Reviews Genetics*, **15**, 247–258.
- Pannell JR (2015) Evolution of the mating system and ability to self-fertilize in colonizing plants. *Molecular Ecology*.
- Pascual M, Chapuis MP, Mestres F *et al.* (2007) Introduction history of *Drosophila subobscura* in the New World: a micro-satellite-based survey using ABC methods. *Molecular Ecology*, **16**, 3069–3083.
- Paterson AH, Schertz KF, Lin YR, Liu SC, Chang YL (1995) The weediness of wild plants: molecular analysis of genes influencing dispersal and persistence of johnsongrass, *Sorghum halepense* (L.) Pers. *Proceedings of the National Academy of Sciences of the USA*, **92**, 6127–6131.
- Peischl S, Excoffier L (2015) Expansion load: recessive mutations and the role of standing genetic variation. *Molecular Ecology*, **24**, 2084–2094.
- Perkins TA, Phillips BL, Baskett ML, Hastings A (2013) Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecology Letters*, **16**, 1079–1087.
- Petitpierre B, Kueffer C, Broennimann O *et al.* (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science*, **335**, 1344–1348.
- Posavi M, Gelembiuk GW, Larget B, Lee CE (2014) Testing for beneficial reversal of dominance during salinity shifts in the invasive copepod *Eurytemora affinis*, and implications for the maintenance of genetic variation. *Evolution*, **68**, 3166–3183.
- Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ (2008) Adaptive evolution in invasive species. *Trends in Plant Science*, **13**, 288–294.
- Prevosti A, Ribo G, Serra L *et al.* (1988) Colonization of America by *Drosophila subobscura*: experiment in natural populations that supports the adaptive role of chromosomal-inversion polymorphism. *Proceedings of the National Academy of Sciences of the USA*, **85**, 5597–5600.



- Purchase CF, Moreau DTR (2012) Stressful environments induce novel phenotypic variation: hierarchical reaction norms for sperm performance of a pervasive invader. *Ecology and Evolution*, **2**, 2567–2576.
- Rius M, Darling JA (2014) How important is intraspecific genetic admixture to the success of colonising populations? *Trends in Ecology & Evolution*, **29**, 233–242.
- Rohner N, Jarosz DF, Kowalko JE *et al.* (2013) Cryptic variation in morphological evolution: HSP90 as a capacitor for loss of eyes in cavefish. *Science*, **342**, 1372–1375.
- Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution*, **22**, 454–464.
- Stapley J, Santure A, Dennis S (2015) Transposable elements as agents of rapid adaptation may explain the genetic paradox of invasive species. *Molecular Ecology*, **24**, 2241–2252.
- Stebbins G (1957) Self fertilization and population variability in the higher plants. *The American Naturalist*, **91**, 337–354.
- Stewart CN, Tranel PJ, Horvath DP *et al.* (2009) Evolution of weediness and invasiveness: charting the course for weed genomics. *Weed Science*, **57**, 451–462.
- Stinchcombe JR, Hoekstra HE (2008) Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity*, **100**, 158–170.
- Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography*, **22**, 962–970.
- Suarez A, Tsutsui N (2008) The evolutionary consequences of biological invasions. *Molecular Ecology*, **17**, 351–360.
- Szűcs M, Melbourne BA, Tuff T, Hufbauer RA (2014) The roles of demography and genetics in the early stages of colonization. *Proceedings of the Royal Society B-Biological Sciences*, **281**, 20141073.
- Szulkin M, Bierne N, David P (2010) Heterozygosity-fitness correlations: a time for reappraisal. *Evolution*, **64**, 1202–1217.
- Tsutsui N, Suarez A, Holway D, Case T (2000) Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences of the USA*, **97**, 5948–5953.
- Tsutsui ND, Suarez A, Grosberg RK (2003) Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. *Proceedings of the National Academy of Sciences of the USA*, **100**, 1078–1083.
- Turelli M, Barton NH (2006) Will population bottlenecks and multilocus epistasis increase additive genetic variance? *Evolution*, **60**, 1763–1776.
- Turgeon J, Tayeh A, Facon B *et al.* (2011) Experimental evidence for the phenotypic impact of admixture between wild and bio-control Asian ladybird (*Harmonia axyridis*) involved in the European invasion. *Journal of Evolutionary Biology*, **24**, 1044–1052.
- Uller T, Leimu R (2011) Founder events predict changes in genetic diversity during human-mediated range expansions. *Global Change Biology*, **17**, 3478–3485.
- Van Heerwaarden B, Willi Y, Kristensen TN, Hoffmann AA (2008) Population bottlenecks increase additive genetic variance but do not break a selection limit in rain forest *Drosophila*. *Genetics*, **179**, 2135–2146.
- Vandepitte K, de Meyer T, Helsen K *et al.* (2014) Rapid genetic adaptation precedes the spread of an exotic plant species. *Molecular Ecology*, **23**, 2157–2164.
- Verhoeven KJF, Macel M, Wolfe LM, Biere A (2011) Population admixture, biological invasions and the balance between local adaptation and inbreeding depression. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 2–8.
- Waddington C (1956) Genetic assimilation of the bithorax phenotype. *Evolution*, **10**, 1–13.
- Waddington C (1965) Introduction to the symposium. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), pp. 1–6. Academic Press, New York.
- Wares J, Hughes A, Grosberg K (2005) Mechanisms that drive evolutionary change: insights from species introductions and invasions. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds Sax D, Stachowicz J, Gaines S), pp. 229–257. Sinauer Associates Inc, Sunderland, Massachusetts.
- Waser NM, Price MV (1989) Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution*, **43**, 1097–1109.
- Whitlock MC (1997) Founder effects and peak shifts without genetic drift: adaptive peak shifts occur easily when environments fluctuate slightly. *Evolution*, **51**, 1044–1048.
- Whitlock MC, Phillips PC, Moore FB-G, Tonsor SJ (1995) Multiple fitness peaks and epistasis. *Annual Review of Ecology and Systematics*, **26**, 601–629.
- Whitney KD, Broman K, Kane N *et al.* (2015) QTL mapping identifies candidate alleles involved in adaptive introgression and range expansion in a wild sunflower. *Molecular Ecology*.
- Wilson F (1965) Biological control and the genetics of colonizing species. In: *The Genetics of Colonizing Species* (eds Baker H, Stebbins G), 307–329. Academic Press, New York.
- Wray GA (2007) The evolutionary significance of cis-regulatory mutations. *Nature Reviews Genetics*, **8**, 206–216.
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding, and selection in evolution. In: *Proceedings of the Sixth International Congress on Genetics*, **1**, pp. 356–366.
- Yeaman S (2013) Genomic rearrangements and the evolution of clusters of locally adaptive loci. *Proceedings of the National Academy of Sciences of the USA*, **110**, E1743–E1751.
- Żmieńko A, Samelak A, Kozłowski P, Figlerowicz M (2014) Copy number polymorphism in plant genomes. *TAG. Theoretical and Applied Genetics*, **127**, 1–18.

---

K.M.D. designed the review; K.M.D., S.R.A., J.B., F.A.C. and H.D.G. performed the literature searches and summarized the data; K.M.D. analysed the data; and K.M.D. wrote the manuscript.

---

### Data accessibility

Molecular genetic diversity data from literature review are available through Dryad; Dryad doi:10.5061/dryad.s2948.