



## Review

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## Invasions and extinctions through the looking glass of evolutionary ecology

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Invasive and endangered species reflect opposite ends of a spectrum of ecological success, yet they experience many similar eco-evolutionary challenges including demographic bottlenecks, hybridization and novel environments. Despite these similarities, important differences exist. Demographic bottlenecks are more transient in invasive species, which (i) maintains ecologically relevant genetic variation, (ii) reduces mutation load, and (iii) increases the efficiency of natural selection relative to genetic drift. Endangered species are less likely to benefit from admixture, which offsets mutation load but also reduces fitness when populations are locally adapted. Invading species generally experience more benign environments with fewer natural enemies, which increases fitness directly and also indirectly by masking inbreeding depression. Adaptive phenotypic plasticity can maintain fitness in novel environments but is more likely to evolve in invasive species encountering variable habitats and to be compromised by demographic factors in endangered species. Placed in an eco-evolutionary context, these differences affect the breadth of the ecological niche, which arises as an emergent property of antagonistic selection and genetic constraints. Comparative studies of invasions and extinctions that apply an eco-evolutionary perspective could provide new insights into the environmental and genetic basis of ecological success in novel environments and improve efforts to preserve global biodiversity.

This article is part of the themed issue 'Human influences on evolution, and the ecological and societal consequences'.

## 1. Introduction

Global biodiversity is increasingly under threat from human activity, which has elevated rates of extinction and invasion by several orders of magnitude above historical averages [1,2]. The net result of increasing extinctions and invasions is a homogenization of global biodiversity that may be mitigated by two distinct but complementary goals: (i) suppress long-term viability of invasive populations and (ii) increase population growth rates of endangered native species. Although eradication and enhancement are opposite conservation goals, invasions and extinctions represent two extreme outcomes along a single gradient of ecological success and therefore may be determined by the same core set of ecological and genetic factors. In other words, invasions and extinctions of closely related species may be like reflections in Lewis Carroll's looking glass [3], with similar elements reflecting opposite realities.

Several key environmental and demographic elements that affect population growth and long-term persistence do not differ fundamentally between endangered and invasive species. Both experience strong demographic bottlenecks,

hybridization with divergent lineages, and the demands of surviving and reproducing in novel and changing environments. Yet, these common elements can lead to drastically different 'realities' or ecological outcomes, with invasive species expanding rapidly and endangered species spiralling towards extinction.

One hypothesis for these contrasting fates is that endangered and invasive species possess distinct sets of developmental and life-history characteristics that are either beneficial or detrimental in human-altered environments. For example, some species may be good invaders, because they have co-evolved with increasing human disturbances [4] or fluctuating environments [5] in their native ranges. However, a meta-analysis of 1813 species did not find evidence that invasive and threatened species possess contrasting traits [6]. It is likely that different characteristics are favoured at particular stages of invasion (i.e. transport, introduction, establishment and spread) [7–9]. But many invasive species are close relatives of taxa that are not invasive [10,11], suggesting that any functional basis for being invasive versus of conservation concern is not often phylogenetically conserved. If development, life history or other phylogenetically conserved traits do not differ consistently between endangered and invasive species, then perhaps more transient ecological and genetic factors are responsible for the varied ecological success of species in nature.

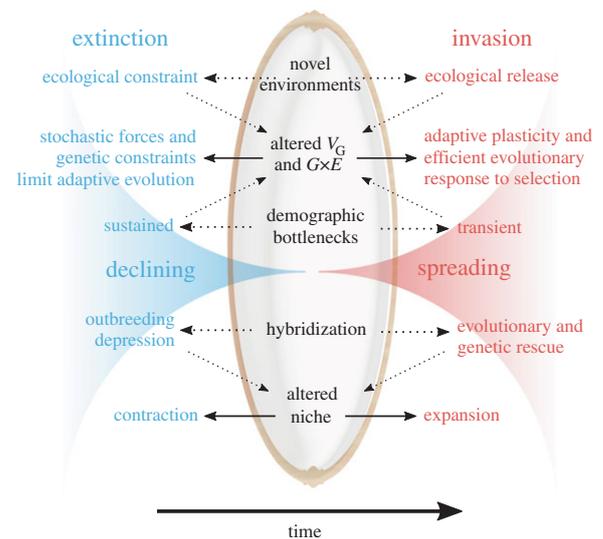
How is it that even related species, having similar growth and life-history traits and encountering similar environmental and demographic challenges, can end up at opposite ends on the spectrum of ecological success? Here, we apply an eco-evolutionary perspective to explore some of the similarities and outline important but often overlooked differences between invasions and extinctions. We focus on three areas of eco-evolutionary theory that reveal important differences between endangered and invasive species likely to affect ecological success: the composition of ecologically relevant genetic variation in natural populations, the genetic basis and evolution of phenotypic plasticity, and evolutionary constraints on the ecological niche. Our overall goal is to examine invasions and extinctions through the same lens of eco-evolutionary theory to suggest common principles for a unified approach to both basic and applied research in these areas.

## 2. Genetic variation

Human activity exposes invasive and endangered species to new adaptive landscapes in which natural selection is fundamentally different from the ancestral environment [12]. Comparing the evolutionary genetics of invasions and extinctions can shed new light on the fate of natural populations exposed to novel and changing environments (figure 1). In this section, we compare the effects of demographic bottlenecks, inbreeding and admixture on invasive and endangered species. We identify key differences that probably contribute to the very different population dynamics of invasions and extinctions.

### (a) Genetic variation and response to selection

Empirical studies show that moderate to severe population bottlenecks can be relatively common for both endangered and invasive species [13–15]. However, post-bottleneck population dynamics differ in several important ways that



**Figure 1.** Extinctions and invasions conceptualized 'Through the Looking Glass' of evolutionary ecology. Extinctions (left side) represent population decline over time, while biological invasions (right side) represent an increase in abundance. Both invasions and extinctions reflect a common set of elements (central column) because subtle but influential ecological and genetic differences (outer columns) can cause opposite population growth trajectories. (Online version in colour.)

translate to large differences in genetic diversity maintained within populations (figure 1). One key difference is the length of the bottleneck period [16], as this directly affects the rate at which genetic diversity is lost [17]. While paired demographic and genetic data are rare for early stage invasions, the magnitude of genetic bottlenecks estimated from neutral markers shows that, on average, invasive populations suffer a detectable but relatively minor loss of genetic diversity [13]. This result suggests that most introduced populations remain small for only a relatively short period before increasing again, because most introductions begin with a strong demographic bottleneck involving a small fraction ( $\ll 1\%$ ) of all individuals present in the native range. Endangered species far more commonly experience extended periods of small population size, greatly increasing the loss of genetic diversity. Even if endangered populations do recover in census size, the genetic effective size of the population ( $N_e$ ) will recover slowly as new mutations introduce variability back to the population.

Another factor mitigating loss of genetic diversity from demographic bottlenecks in invasive species is the high rate of gene flow common among introduced populations, which can promote 'genetic rescue' (alleviating inbreeding depression; [18]) of inbred populations and 'evolutionary rescue' (introduction of an adaptive variant; [19]) of maladapted populations [20–22]. Such increased gene flow is particularly important within a metapopulation context, because the negative demographic and genetic consequences of small population size and local extinction can be mitigated by connectivity with other populations in the region [15,23,24]. Under this model, gene flow shares diversity among populations so the metapopulation as a whole maintains higher  $N_e$  and sustains the invasion even if individual invasive populations are small. By contrast, declining populations of endangered species tend to be few in number and highly isolated, with little connectivity and opportunity for genetic or evolutionary rescue. Efforts to increase population connectivity for endangered species may be particularly

beneficial when isolation is prolonged and population sizes are especially small; however, the benefits of increasing gene flow must be evaluated relative to the risk of compromising locally adapted genotypes.

Because the efficacy of selection is directly proportional to  $N_e$ , genetic drift has a much stronger effect on evolutionary change in species with limited genetic variability and among small, isolated populations, compared with larger well-connected populations. The reduced ability to respond to selection makes endangered populations particularly susceptible to environmental changes that lead to loss of local adaptation. Here too, the metapopulation context distinguishes biological invasions and provides additional opportunities for these species to respond to selection despite founder effects and genetic drift during establishment. Response to selection is more likely for invasive populations when (i) population sizes are large or increasing, (ii) gene flow from neighbouring populations acts as a genetic or evolutionary rescue, and (iii) local extinction of maladapted populations are followed by recolonization from populations with pre-adapted genotypes. This latter example of inter-demic selection within a meta-population context occurs as a result of non-random extinction and recolonization; this may be an under-appreciated mechanism for rapid evolution of invaders in novel environments [23,25]. In this way, invasions might be useful experimental systems for understanding how population connectivity contributes to the survival of individual subpopulations in variable environments, applying this knowledge in turn to restoration strategies and expectations for native species. Population genetic models that assign source populations to colonists and test for genetic associations between source population characteristics (e.g. density, inbreeding rate and phenotypes) and colonization probability may be a particularly useful approach for investigating the effect of metapopulation context on population persistence [24,26].

It is important to recognize that the genetic consequences of small population size affect variation at neutral marker loci differently than quantitative genetic variation in ecologically important traits, and indeed these two types of variance are often poorly correlated [27]. This is likely a consequence of the broadly polygenic basis of most quantitative traits, as individual loci each have only a small effect on the overall trait variance. Previous studies have shown that substantial quantitative genetic variation ( $V_G$ ) can persist for quantitative traits, even when populations show evidence of bottlenecks at individual loci [28,29]. As a result, rapid population growth of invasive species following even a severe demographic bottleneck will have little effect on quantitative genetic variance [30]. Moreover, given that most introductions fail, repeated founding events create opportunities for natural selection to filter the genetic variants that do establish at the scale of genotypes or even entire populations [31], though direct evidence of this process is lacking to date. By contrast, persistent small population sizes over multiple generations in endangered species will erode quantitative genetic variance through genetic drift, limiting adaptive evolutionary responses to changing selection pressures. Few studies have directly addressed the consequences of invasion or colonization on  $V_G$ , although one such study showed a loss of  $V_G$  in younger colonizing populations during (non-invasive) range expansion [32]. A few studies have compared  $V_G$  between native and introduced populations of invasive species

[33,34], but in these cases it is difficult to rule out differences among populations in the strength of stabilizing selection. Increasingly, population genomics is enabling the discovery of genes (or closely linked loci) involved in local adaptation, which may allow a more direct integration of molecular data into conservation strategies. More generally, genomic sequencing can now be combined with ecological surveys and field manipulations to better understand the relationship between genome-wide genetic variation and adaptive trait variation in natural populations, and how both are affected by demographic bottlenecks, gene flow and natural selection.

### (b) Genetic load and inbreeding depression

One intriguing difference between endangered and invasive species is the effect of small population size on genetic load and inbreeding depression. Genetic load is a well-established conservation concern for many endangered taxa, as elevated inbreeding in small populations exposes the negative fitness effects of recessive deleterious alleles [17]. These effects directly contribute to increased extinction probability, especially under stressful environments [35]. The genome-wide load of deleterious mutations is sensitive to  $N_e$ , which determines how effectively purifying selection can purge genetic load. In endangered populations that are small, declining, or have undergone a bottleneck, avoiding or mitigating inbreeding is critical to maintain genotypes that carry few deleterious alleles (e.g. avoiding Muller's Ratchet). Invaders may also suffer from inbreeding depression if a colonization bottleneck is severe, as exemplified by a multi-species analysis of birds introduced to New Zealand. In this case, species that experienced strong bottlenecks (less than 150 individuals) showed persistent increases in hatching failure compared with less 'bottlenecked' species [36]. These effects may be transient in growing populations as some empirical studies have found increases in heterozygosity over time, despite bottlenecks as severe as a single pair of breeding individuals [37,38]. This is consistent with an increase in the efficiency of natural selection to 'weed out' homozygous individuals as population sizes increase. However, further studies are needed to determine whether this is a general phenomenon in successful invaders. Invasive species may also accumulate genetic load as a by-product of the range expansion process. Recent theoretical work has shown that small populations at the wavefront of an expanding range face increased probabilities of deleterious mutations drifting to high frequency, termed 'expansion load' [39]. The accumulation of expansion load is predicted to lead to legacies of reduced fitness following expansion [40,41]. Long-range dispersal between multiple introductions from distinct genetic sources could partially mitigate this effect by helping to shelter the genetic load in recently expanded invasive populations [42], but to our knowledge this has not been explored in colonization models.

Why do invasive populations not suffer from inbreeding depression more often? First, as described above, if invaders recover from demographic bottlenecks more quickly, they maintain genetic variation and experience less severe genetic drift and inbreeding. Second, as invasive populations grow in  $N_e$ , selection should become more effective at reducing the frequency of weakly deleterious alleles, thereby reducing the genetic load [43]. Third, the fitness effects of recessive alleles may be conditional on the environment. Phenotypic

effects of deleterious mutations may be conditionally neutral when the environment is benign but amplified by environmental stress, resulting in *inbreeding*  $\times$  *environment* ( $I \times E$ ) interactions [44]. Invasive species tend to experience more benign environments than endangered species, for example, by invading resource-rich or enemy-free environments, and this could mask the expression of deleterious alleles [45]. Consequently, invasive species may avoid the negative fitness effects of inbreeding more often than rare and declining species, even when subject to the same evolutionary dynamics of small population size. An important question is thus how much of the among-population variance in fitness (and underlying allele frequency differentiation) is caused by different degrees of purifying selection acting on weakly deleterious or conditionally neutral ( $I \times E$ ) genetic load? Answering this question could improve insights into the population-level consequences of different amounts of inbreeding in both invasive and endangered species. Spatial comparisons of population demography could be coupled with experimental and/or genomic assessments of genetic load to assess the conditions associated with effective purging. Here, an experimental strength is the high replication potential afforded by many invading populations with different demographic histories.

### (c) The pros and cons of genetic admixture

Admixture is a well-established outcome for invasions and arises when multiple genotypes from genetically divergent populations in the native range come into secondary contact during invasion [46–48]. Hybridization and admixture are also a major issue for species at risk, where declining populations may be intentionally admixed during management efforts or may unintentionally hybridize with more abundant species [49,50]. The immediate fitness consequences of admixture can be complex, depending on the degree of divergence of the parental lineages, and can vary among  $F_1$  and more advanced recombinant hybrid generations [51,52]. Fitness effects can range from highly beneficial outbreeding to severely deleterious hybrid incompatibilities, decreasing in benefit as parental populations become more locally adapted [53].

A distinct benefit of admixture for both invasive and endangered species is increased heterozygosity at loci containing recessive deleterious mutations. Positive effects of admixture have been observed in invasive populations that show heterozygosity-fitness correlations in the introduced range [46,54]. The fitness benefits of a heterozygous genome are likely to be especially strong for small, declining and inbred populations of endangered species that are unable to purge deleterious mutations [55]. This is frequently seen in zoo or other extremely bottlenecked vertebrate populations. For example, the endangered Florida panther population shrank in size to as few as 20 individuals, with reduced heterozygosity at neutral markers and phenotypic evidence of inbreeding depression, including sperm deformities, kinked tails and reduced survival [56]. Intentional release of eight female Texas pumas into Florida created opportunities for admixture, doubling heterozygosity in the population and alleviating inbreeding depression in many traits.

In many cases, admixture also contributes to increases in standing  $V_G$  and can broaden the genotypic space available to selection. When adaptive variants from a genetically

distinct population introgress, natural selection can act on this enhanced standing variation without waiting for new mutations to arise *de novo* [57]. For these reasons, and because invasive species frequently experience novel selective environments in their introduced range, admixture has been implicated as a potential factor fuelling rapid evolution and the generation of novel invasive genotypes [33,48,58]. Nevertheless, direct evidence of a link between introgressed variation and the evolution of invasiveness is largely lacking to date. Population genomic studies of admixture/hybrid zones during invasions could test the adaptive introgression hypothesis using methods that identify the signal of differential introgression of positively selected loci against the null expectation based on the degree of admixture across the genomic background (e.g. *genomic clines analysis*) [59]. The benefit of adaptive introgression should be most pronounced when rates of gene flow and introgression are low relative to  $N_e$  and recombination rate, such that selection can efficiently incorporate beneficial variants while eliminating detrimental alleles. Therefore, adaptive introgression of positively selected genomic regions is likely to be much less common in endangered species, where low population sizes and low effective recombination limit the ability of selection to decouple maladaptive from adaptive introgressed alleles.

Populations of endangered species can also benefit from expanded genotypic variation resulting from admixture. Indeed, this is one reason that wildlife corridors are promoted for conservation [60]. The benefit of admixture is reduced when populations are locally adapted and therefore may be less beneficial for native relative to non-native species. Such an influx of genetic variation would be even more detrimental in small populations where natural selection is less efficient at eliminating locally maladapted alleles [61,62]. This genomic swamping of endangered species has become a serious conservation concern when small native populations meet abundant populations of reproductively compatible invasive species. Many native species show relatively low reproductive isolation from introduced species with which they have had no historical contact, and high numbers of introduced genotypes increase the likelihood of hybridization [63,64]. In addition to swamping locally adapted alleles, these native-invasive hybrids can put legal protections of native species in jeopardy as species definitions become questionable [65].

### 3. Phenotypic plasticity

The developmental, physiological and life-history modifications that have been widely observed in natural populations exposed to altered or novel environments can be due to plastic responses of individuals in a population as well as to selective trait changes [66,67]. To focus on this aspect of diversity, each genotype can be viewed as a repertoire of phenotypes expressed in different environments, or, more technically, a *norm of reaction*. This perspective makes it possible to evaluate both individual adaptive flexibility and genetic variation as expressed in novel environments. It is important to distinguish adaptive plastic responses, which maintain fitness across a range of environments, from phenotypic responses that arise directly from resource limits or other stresses and may not be adaptive. Reaction norms are products of evolution that, like any phenotypic trait, are inevitably subject to developmental, phylogenetic and genetic constraints [68]. Consequently,

individual plasticity is best understood as the result of adaptive and stochastic evolution, rather than as a separate phenomenon [69]. Individual plasticity can play two key roles in the eco-evolutionary dynamics of natural populations. First, the capacity of individuals to express adaptive plasticity in response to novel or changing environments contributes to a population's viability. Second, existing norms of reaction, and genetic variation for these norms, influence the potential for future evolution of adaptive responses to new environments.

### (a) Plasticity and tolerance of novel environments

Adaptive plasticity allows individual organisms to survive and reproduce in a variety of environmental conditions. Such plasticity can buffer populations or species from extinction when conditions change rapidly [70–72]. For example, some birds and mammals can advance life-history schedules through plastic responses to seasonal cues, allowing them to keep pace with altered timing of food availability due to rapid climate change (e.g. [73]); the many taxa whose populations lack such plasticity may face an enhanced risk of extinction [74,75]. Adaptive plasticity can include effects of parental environments on offspring phenotypes (*transgenerational plasticity*). For instance, in the sheepshead minnow, offspring growth rates, body mass and expected fecundity were highest at temperatures previously experienced by parent fish, regardless of whether that temperature was high or low [76]. As a result, warmer water temperatures did not cause negative effects on development and fitness. Adaptive transgenerational effects such as this may be most beneficial to species encountering gradual changes in the environment, including the rise in sea temperatures predicted under current models of global climate change.

Along with promoting species persistence, adaptive plasticity can facilitate the rapid spread of invasive species across diverse new habitats [77–79]. In both animals and plants, the ability to maintain net reproductive rates in contrasting environments promotes invasive spread [80,81]. Additionally, a plastic response to sharply increase fecundity in resource-rich environments may be an important attribute of invasive taxa [82,83] because it increases the 'propagule pressure' that fuels colonization [84,85]. Theoretical work indicates that greater adaptive plasticity should be associated with higher rates of colonization of new, and more diverse, environments [86]. However, recent meta-analyses disagree as to whether invasive species consistently show higher plasticity in general than native congeners [82,87]. This inconsistency in part reflects the different plasticity metrics and choice of traits used in various studies. Results of native versus invasive comparisons also depend on environmental variability in the home range that favours high plasticity, and on norm of reaction evolution following a species' introduction (for instance, canalization of a new adaptive phenotype following initially high plasticity) [88].

In addition to maintaining fitness across environments, adaptive plasticity can prevent a decrease in ecological breadth when a genetic bottleneck occurs, as each genotype can accommodate diverse conditions. Such plasticity can mitigate the ecological consequences of a prolonged bottleneck in an endangered species [89] or a short-term bottleneck due to an introduction event [90,91]. In these cases, geographically isolated populations may share similar broad patterns of individual plasticity instead of divergent,

locally adapted norms of reaction [92,93]. However, as adaptive plasticity itself has a genetic basis, it can be compromised by the negative consequences of inbreeding and sustained bottlenecks. Moreover, two critical factors will determine the effectiveness of plasticity relative to selective evolution in maintaining the viability of populations exposed to novel environments. First, norms of reaction that evolved under past selection pressures may not encompass the range of phenotypes required to maintain fitness in the new circumstances, and can even produce a disrupted, maladaptive phenotype in response to a novel stress [94]. Second, even with sufficient existing plasticity, adaptive phenotypes will not be produced if changed cues fail to provide accurate information to elicit appropriate and timely responses [69,95]. In such cases, plasticity can promote extinction rather than persistence [29]. This potential adaptive limit may be particularly important in human-altered environments or following introduction to a new continent where abiotic and biotic factors that organisms have evolved to use as plasticity cues may be absent or disrupted.

### (b) Plasticity and evolutionary potential

Phenotypic plasticity can allow a population to persist following a change in local conditions or introduction to a new range. If pre-existing reaction norms do not produce sufficiently adaptive phenotypes to maintain a population's viability (e.g. [96]), then further adaptive evolution of plasticity is an essential step to either avoid extinction or permit establishment (modelled by Chevin & Lande [97]; see [98–100] on selective evolution of reaction norms). In invasive species, rapid plasticity evolution can promote subsequent spread into new habitats. For instance, cane toads (*Rhinella marina*) that have spread to colder regions in Australia have evolved higher metabolic plasticity [101]; invasive freshwater populations of the marine-native copepod *Eurytemora affinis* have evolved increased ion-transport plasticity [96]; and a shrubby South African *Senecio* introduced into Spain has evolved greater reproductive output in wet conditions without any loss of fitness in its ancestral dry habitat [102].

Expanded repertoires of adaptive plasticity can result from the environmental heterogeneity encountered within and among sites in the new range, rather than from a changed directional selection pressure compared to the native range [103]. This finding is consistent with theoretical predictions that increased adaptive plasticity is selectively favoured in populations and metapopulations that encounter variable environments ([68,86,104–108] and references therein). This particular selective property may lead to a positive evolutionary feedback for greater invasiveness in non-native taxa that have sufficiently broad norms of reaction to survive their initial introduction. Because successful non-natives tend to (i) colonize disturbed, variable habitats and (ii) have high dispersal capabilities that would cause them to encounter diverse sites, they may be especially likely to evolve greater adaptive plasticity post-introduction [109]. Evolution of increasingly generalist norms of reaction will in turn promote an even broader ecological distribution across habitats ([67] and references therein), expanding the invasion front and possibly creating more contiguous populations that will accelerate colonization of new sites [85,110]. Conversely, if endangered taxa initially have less-plastic norms of reaction that confine them

to a narrow range of conditions, they may not encounter the environmental variability that promotes evolution of broader plasticity.

Although a cost of plasticity could in theory limit this type of evolution, evidence for such a cost is weak [107,111], and recent models assume that any plasticity costs are outweighed by benefits (e.g. [97]). Indeed, the previous examples show that increasingly broad adaptive norms of reaction can evolve, at least in certain taxa, without fitness trade-offs that would entail a loss of adaptive responses to ancestral environments. In any given case, the evolution of greater plasticity—like that of any adaptive trait—depends on whether or not genetic or developmental constraints are present that limit the potential for selective change. How widespread among invasive taxa is the potential to evolve ‘jack of all trades’ genotypes? Is the lag phase between introduction and invasion commonly characterized by the evolution of greater adaptive plasticity? These questions can be explored through resurrection experiments designed to compare environmental response patterns of genotypes sampled from introduced taxa across time (e.g. [103]).

As with any phenotypic trait, evolution of plasticity requires genetic variation—in this case, genetic differences in reaction norms measured as *genotype*  $\times$  *environment* ( $G \times E$ ) variance in a statistical model ([67,68,112,113] and references therein). Like other aspects of genetic diversity, populations and taxa will differ in  $G \times E$  variation due to previous mutation, drift and selection. A defining feature of  $G \times E$  variation is that a given set of genotypes may express different phenotypes in certain environments, but converge on similar phenotypes in others: in other words, genetic variance itself differs from one environment to another [114,115]. A novel environment such as a new range or altered habitat can lead to rapid adaptive evolution if genotypes in a population express different phenotypes [116]. By contrast, evolutionary response to natural selection is buffered in a new environment where similar phenotypes occur [69,95,117]. Consequently, differences in patterns of  $G \times E$  variation will influence the ability of populations to evolve new adaptive responses following introduction or *in situ* environmental challenges. In addition, a better understanding of the genetic architectures underlying reaction norms, such as the effects of modularity versus pleiotropy of regulatory pathways [118], will better inform models of constraint on plasticity evolution in natural populations [67,119].

In general, it is not known whether phenotypes in natural populations are more likely to differ or converge in predicted future environments such as high CO<sub>2</sub> and higher temperatures [120,121]. The question of adaptive evolutionary potential is of particular concern with respect to species that may face extinction in the absence of altered plasticity patterns. A case in point is reptiles with temperature-dependent sex determination, which are predicted to produce female-biased sex ratios in warmer future climates [122]. In a study of the leopard gecko *Eublepharis macularius* [123], populations were found to contain  $G \times E$  variation for the proportion of males produced at different likely incubation temperatures. Such variation could fuel the selective evolution of new temperature thresholds for sex determination in future populations, promoting the species’ persistence. Similarly, certain European populations of great tits (*Parus major*) contain genetic variation for temperature-based plasticity of reproductive timing, providing the potential for

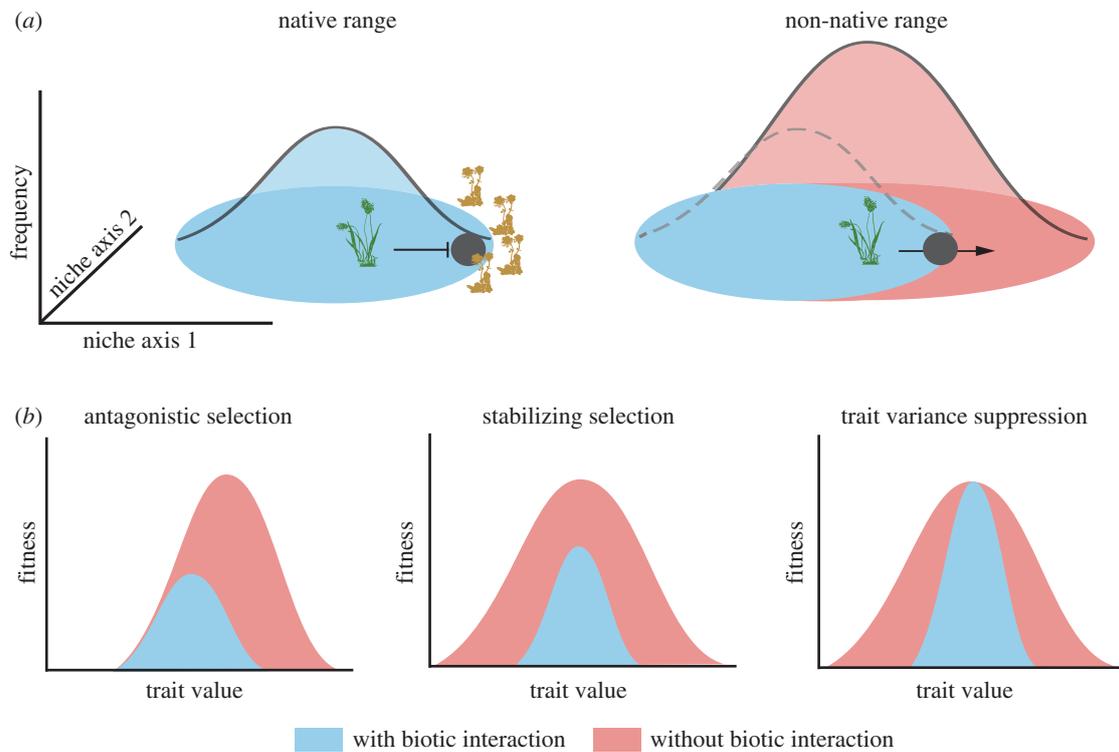
adaptive evolution of life-history plasticity in response to altered seasonal timing of food availability [124]. Examining norm of reaction diversity in populations of various organisms, including its expression under predicted future conditions, is a crucial step to assess (i) the potential for plasticity evolution to prevent extinction and (ii) the critical differences in evolutionary potential between endangered and invasive species.

#### 4. Ecological niche

Invasive and endangered species exist at opposite ends of ecological spectra in geographical range size, niche breadth and population density [125–127] (figure 1). Geographical range size correlates positively with both local abundance [128,129] and niche breadth [130]. Therefore, understanding eco-evolutionary constraints on the ecological niche and local abundance could improve our understanding of why some species remain rare while others become invasive [127]. We use the term ‘ecological niche’ in the broad sense, as the range of environmental conditions and resources that influence the viability of local populations, either in the absence (fundamental niche) or in the presence (realized niche) of biotic interactions [131]. In this section, we apply the eco-evolutionary framework to the ecological niche concept and ask how differences in genetic variation and plasticity might explain niche differences in invasive and endangered species.

Some invasive species have evolved rapidly along environmental gradients during range expansion, increasing genetic variation for ecologically important traits and potentially expanding the niche well beyond that of the founder population(s). For example, clinal genetic variation in traits such as size and phenology have been documented in a number of widespread invasive species across geographical gradients, including latitude (e.g. [132]), elevation (e.g. [133]) and continentality (e.g. [134]). Interestingly, a species’ climatic niche breadth in its non-native range often does not exceed its niche breadth in the native range—in other words, climatic niches are frequently conserved between ranges [135]. This raises a biological conundrum: if introduced populations evolve and plasticity allows persistence in a range of environments, why are similar climatic limits re-established in introduced populations [136]?

One explanation is the presence of constraints on niche breadth along environmental gradients that are also conserved across ranges [137]. Genetic constraints on niche breadth could include inbreeding depression, maladaptive gene flow or low heritable genetic variability in single traits, and also along multivariate trait axes (i.e. core trade-offs; reviewed by [138,139]). Core trade-offs provide perhaps the most convincing explanation for why niche limits should be conserved across disparate geographical ranges, despite the evolution of local adaptation [136]. For example, natural selection favours early flowering time and larger size at flowering across the native and introduced ranges of *Lythrum salicaria*, but evolution of these traits is constrained by a trade-off [132,140]. This trade-off limits the reproductive output of earlier flowering plants in high-latitude populations, helping to set the northern range limit in both the non-native and native ranges. Therefore, while adaptive evolution during invasion can contribute to the niche expansion



**Figure 2.** Eco-evolutionary model of the ecological niche as an emergent property of genetic constraints and spatial variation in abiotic and biotic sources of natural selection. (a) The number of individuals in a population ( $y$ -axis) depends on environmental variables that vary along geographical gradients (niche axes 1 and 2), for example, moisture and temperature. Additional constraints on the niche of the focal species (darker green plant) are imposed by negative biotic interactions, such as a competitor (lighter yellow plants). Escape from negative biotic interaction represents an ecological release, which increases population vital rates across a range of environments and thereby expands the ecological niche. (b) Three evolutionary consequences of relaxed biotic interactions for an individual population, measured near the edge of the range of the focal plants (black circles in (a)). Selection at this location is measured either in the presence (lighter blue curve) or in the absence (darker red curve) of competition: *antagonistic selection*—ecological release relaxes antagonistic selection on a trait that is also under abiotic selection (e.g. phenology) or on a genetically correlated trait (e.g. size at reproduction); *stabilizing selection*—ecological release relaxes the strength of stabilizing selection across a range of trait values; *trait variance suppression*—competition suppresses the expression of heritable genetic variation, which increases following ecological release. In the first two cases, ecological release is also accompanied by an increase in absolute fitness as negative selection pressures are removed.

of founder populations, genetic architecture can limit the extent of adaptive evolution and niche breadth. As outlined in previous sections, several genetic attributes of non-native populations promote adaptive evolution of niche breadth. By contrast, high genetic drift, genetic load and small population will limit adaptive responses and could contribute to narrow niche breadth in endangered species.

In addition to selection from abiotic factors, biotic interactions can influence range margins [141], and are likely to differ in importance between native and introduced ranges as well as between invasive and endangered species. There are several mechanisms by which negative interactions (e.g. competition or predation) could contribute to evolutionary constraints on niche breadth (figure 2). First, if selection imposed by species interactions is antagonistic to abiotic selection pressures, this can limit the fitness of local populations and ultimately restrict niche breadth. This would occur if either the same trait was under antagonistic selection from abiotic and biotic factors, or if multiple genetically correlated traits were under antagonistic selection. For example, the evolution of increased competitive ability (EICA) hypothesis predicts a trade-off between herbivore defence and competitive ability in plants [142]. Non-native species that escape regulation by natural enemies, particularly specialists, would therefore experience relaxed selection on traits associated with defence, allowing a response to selection for

increased competitive ability. While there is support for the EICA hypothesis in some species [143], the consequences for niche breadth in the non-native range of invasive species have, to our knowledge, not been investigated. Second, resource competition can constrain niche evolution by imposing strong selection against resource switching (i.e. stabilizing selection) even as resource availability drops to unsustainable levels [144,145]. Third, competition that reduces fitness of a focal species can suppress the expression of genetic variation for ecologically important traits, limiting the potential for selective changes in niche breadth. In an elegant experiment across a depth gradient in Californian vernal pools, release from competition enabled the annual plant *Lasthenia fremontii* to expand its niche breadth, and exposed additive genetic variation in the fundamental niche for which there was positive selection [146]. These examples suggest that a relaxation in evolutionary constraints caused by biotic interactions is likely to facilitate niche expansion, and could contribute to the success of invasive species that experience ecological release from native-range competitors or natural enemies. By contrast, biotic interactions might impose particularly strong evolutionary constraints on endangered species with narrow niche breadth, compounded by low genetic variation or plasticity in traits affecting the outcome of interactions.

Ecological release is a common explanation for why some invasive species attain higher abundance in their new range

[147], and release from negative interactions with competitors and pathogens even appears to have allowed some non-native species to expand their realized niches [148–150]. Indeed, there are examples of species that are considered endangered in their native range, sometimes restricted to a few populations, yet can attain broad non-native ranges (e.g. plants used in horticulture or forestry such as *Pinus radiata*, *Lotus maculatus*, *Melaleuca quinquenervia*) [149,151,152]. Niche expansion following invasion is usually interpreted as a purely ecological response to an altered biotic environment; the possible contribution and relative importance of evolution and phenotypic plasticity, though acknowledged, is rarely tested [149]. Hill *et al.* [153] showed that niche shifts are associated with the evolution of thermal tolerance in the mite, *Halotydeus destructor*, in Australia. Evolution has also been associated with the invasion of a narrowly endemic Canary Island shrub across large parts of California [34]. Another form of niche expansion is host shifting in herbivorous insects, including those introduced for biocontrol. For example, non-native populations of the beetle *Ophraella communa* in Japan have evolved to use *Ambrosia trifida* as a host, even though this plant is not used by *O. communa* in its native range. This host shift is partly explained by relaxed herbivore defences in non-native populations of *A. trifida*, after having escaped natural enemies for approximately 50 generations [154]. However, the contribution of relaxed selection to niche expansion and the role of genetic constraints are still unresolved.

Overall, endangered species can be predicted to experience stronger constraints on niche breadth than invasive taxa for several reasons. First, endangered species might experience greater genetic constraints than invasive species for reasons outlined in the previous sections (e.g. genetic bottlenecks and inbreeding). Second, endangered species might be characterized by especially strong negative biotic interactions. Indeed, invasive and endangered species can be discriminated by the strength of negative interactions with pathogens [155] and competitors [156]. Nonetheless, while rapid evolution associated with environmental gradients is recognized as being important for the persistence of endangered species in changing environments [157] and for the dynamics of species invasions [158], we know much less about the contribution of changing biotic interactions to niche evolution in invasive and endangered species [159]. Understanding whether negative biotic interactions impose constraints on niche evolution, in addition to a purely ecological restriction of niche breadth, is important for accurately predicting evolutionary responses of endangered and invasive species experiencing novel and changing environments.

## 5. Conclusion and future directions

Like Lewis Carroll's looking glass, endangered and invasive species appear similar at first glance, as both often (i) experience strong demographic bottlenecks, (ii) are subject to hybridization and introgression from other species or divergent populations, and (iii) encounter fitness challenges due to novel and changing environments. Yet these apparently similar reflections differ in key elements that lead to very different eco-evolutionary realities. Specifically, the potential for adaptive evolution of phenotypes and broad individual plasticity is predicted to be higher in invading species as a

result of (i) rapid population growth following transient demographic bottlenecks, (ii) lower genetic load, (iii) greater environmental variability, and (iv) relaxed selection from natural enemies and competition. These evolutionary differences directly affect the breadth of the realized ecological niche and ultimately determine the abundance and distribution of species in nature.

Our discussion identifies key elements of what we believe could be a robust framework for exploring eco-evolutionary dynamics using comparative studies of invasive and endangered species. Contrasting invasive and rare or endangered species is not a novel concept, but has tended to focus on interspecific comparisons of functional traits rather than on the local ecological and demographic conditions that directly influence population dynamics. Understanding limits to adaptive evolution (including appropriate plasticity patterns) at the population level may be a more promising avenue of research. We believe these kinds of comparisons between endangered and invasive species represent an under-exploited opportunity to better understand and manage the abundance and distribution of species at both ends of the ecological spectrum. Experimental manipulations could compare phenotypic selection, reaction norms, neutral and functional genetic diversity of closely related endangered and invasive species in several different environments to better understand evolutionary potential and constraints. Endangered (or at least rare native) species that are invasive or spreading elsewhere would be particularly useful study systems to investigate in this way.

One potential obstacle to developing such a framework is the fact that researchers investigating invasive and endangered species rarely collaborate—indeed the authors of this paper work primarily on invasive species and as a result our discussion is more heavily weighted towards this area. Nevertheless, we hope that this review will encourage better communication between these two fields. After all, the goals of conserving endangered species and preventing invasions both require a comprehensive understanding of the evolutionary and ecological factors that affect population persistence in a changing world. Combining knowledge gained from the thousands of published ecological, evolutionary and population genetic studies of invasive and endangered species could lead to more robust tests of theoretical foundations of conservation biology, and to a comprehensive, unified framework for the management of global biodiversity.

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