



Effects of exotic species on evolutionary diversification

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Exotic species invasions create almost ideal conditions for promoting evolutionary diversification: establishment of allopatric populations in new environmental conditions; altered ecological opportunities for native species; and new opportunities for hybridization between previously allopatric taxa. Here, we review recent studies of the evolutionary consequences of species invasions, revealing abundant and widespread examples of exotic species promoting evolutionary diversification via increased genetic differentiation among populations of both exotic and native species and the creation of new hybrid lineages. Our review indicates that, although the well-documented reductions to biodiversity caused by exotic species might outweigh the increases resulting from diversification, a complete understanding of the net effects of exotic species on biodiversity in the long term will require consideration of both.

Exotic species and biodiversity

The literature on exotic species (see Glossary) to date has overwhelmingly emphasized their negative effects on biodiversity. However, there is another, potentially important, part of the equation. Via a variety of mechanisms, exotic species invasions can promote evolutionary diversification and, therefore, offset, at least partially, the losses to biodiversity that they themselves contribute to. Although an increasing amount of attention is being paid to the evolutionary dimensions of exotic species invasions [1–5], the issue of when and how exotic species might promote diversification has not yet been directly addressed, apart from the occasional mention in broader review papers [1]. Here, we review the empirical evidence on this issue, and outline a conceptual framework uniting the various mechanisms by which exotic species might influence diversification.

Exotic species and evolutionary diversification

We define evolutionary diversification as an increase in genetic variation among populations within a particular species or species complex, including adaptive divergence

of lineages as well as the special case of the formation of new hybrid lineages. A stricter definition would insist on the actual creation of new species and, indeed, there are cases described herein of new reproductively isolated lineages adapted to novel conditions whose origin stems from an exotic species introduction. However, whereas evolutionary diversification might ultimately result in speciation, most human-mediated exotic species invasions have occurred too recently for this to have been fully realized. We can nonetheless look for clues that the process is underway. Specifically, we focus here on the early stages of evolutionary diversification, as evidenced by increases in genetic differentiation among populations within particular species for quantitative traits or molecular marker data. We recognize that exotic species can contribute simultaneously to decreases in biodiversity via a variety of ecological or evolutionary interactions with other species, and to increases in biodiversity via evolutionary diversification. This raises the difficult issue of what conservation

Glossary

Allopatric speciation: the creation of new species via genetic divergence in geographically separated populations.

Biodiversity: the sum total of genetically based variation within and among species.

Directional selection: natural selection favoring trait values that are consistently in the same direction away from the population mean.

Disruptive selection: natural selection favoring multiple trait values with lower fitness at intermediate values.

Exotic species: a species with one or more populations that have established outside of its native range.

Evolutionary diversification: an increase in genetic variation among populations within a particular species or species complex, including adaptive divergence of lineages as well as the special case of the formation of new hybrid lineages.

Genetic bottleneck: a reduction in genetic diversity via the sampling of a relatively small number of individuals to form a new population.

Genetic drift: random changes in allele frequencies owing to the sampling of finite numbers of individuals across generations, eventually resulting in reduced genetic diversity.

Hybridization: the production of viable offspring via mating between two distinct species.

Introgression: movement of genetic material from one species or lineage to another via interbreeding.

Species invasion: the spread of an exotic population beyond its initial point of establishment in the non-native range.

Polyploidy: having more than two full sets of homologous chromosomes.

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value we should ascribe to different components of biodiversity, a subject that we address briefly in the discussion. Our interest is largely in evaluating the science behind the mostly ignored positive side of the ledger tallying the effects of exotic species on biodiversity.

Introducing species to new regions far from their native range and with different environmental conditions sets an ideal stage for evolutionary diversification among populations of exotic species. Likewise, the altered selection regime, ecological opportunities, or possibilities for hybridization provided by exotic species might promote diversification of some native species. We consider three categories of evolutionary diversification stimulated by exotic species invasions (Figure 1): (i) diversification of exotic species following introduction to new regions; (ii) diversification of native species in response to exotic species invasion; and (iii) diversification via hybridization, either between native and exotic species, between pairs of exotic species brought into sympatry, or pairs of native species whose interaction is brought about by an exotic species invasion. We outline the theoretical context for each case and review the relevant empirical evidence. Our review of the literature is not exhaustive, but draws on a range of case studies that provide compelling evidence that evolutionary diversification is a frequent result of exotic species invasions with potentially profound implications for the global biota.

Diversification of exotic species: theory

Exotic species invasions occur when individuals of a species become established and spread in a region outside of their native range. The early stage of the invasion process samples available genetic diversity from the native range of a species and, thus, we expect non-native populations to show reduced genetic variation relative to populations in the native range. Many exotic species, plants in particular, are self-fertilizing or even asexual, in which case genetic bottlenecks can be severe [6] and, therefore, the likelihood of evolutionary divergence minimal. However, the reduction

in genetic diversity of introduced populations is more often modest, as indicated by a review of 29 animal studies that showed an average reduction in heterozygosity of only 17%, with most values considerably lower [7]. Even for self-fertilizing plants, populations in the introduced range can show either reductions in genetic diversity that are minimal or, if there are multiple introduction events or source populations, no reduction at all [6]. In addition, the molecular marker data that are typically used to study population bottlenecks might not accurately reflect genetic variation for traits that might be subject to natural selection [8].

Genetic variation in non-native populations provides the raw material for any response to local selection pressures, and these pressures might be quite novel, considering the distance that individuals are often moved out of their native range [2]. This scenario of introduction of a genetically variable population into a geographically isolated region with a novel selective environment provides all of the key ingredients for the initial steps towards allopatric speciation. Thus, evolutionary theory leads us to expect that invasions will often be followed by evolutionary diversification.

The details of the invasion process might have important consequences for the likelihood of subsequent evolution. Genetic bottlenecks can either constrain evolutionary potential via decreased genetic diversity or, under special circumstances, can shift allele frequencies of interacting genes so as to promote further evolutionary change [9]. If propagules of particular exotic species are introduced repeatedly, or from multiple source regions [10], this gene flow might either inhibit local adaptation or facilitate it by increasing genetic diversity [11]. The key points for our purposes here are that the available evidence suggests that genetic bottlenecks often do not constrain evolutionary change in exotic species, and that selection is often sufficiently strong to result in adaptive evolution in the face of gene flow [6,7].

Evolutionary diversification of exotic species can occur via three main mechanisms (Figure 1). First, bottlenecks

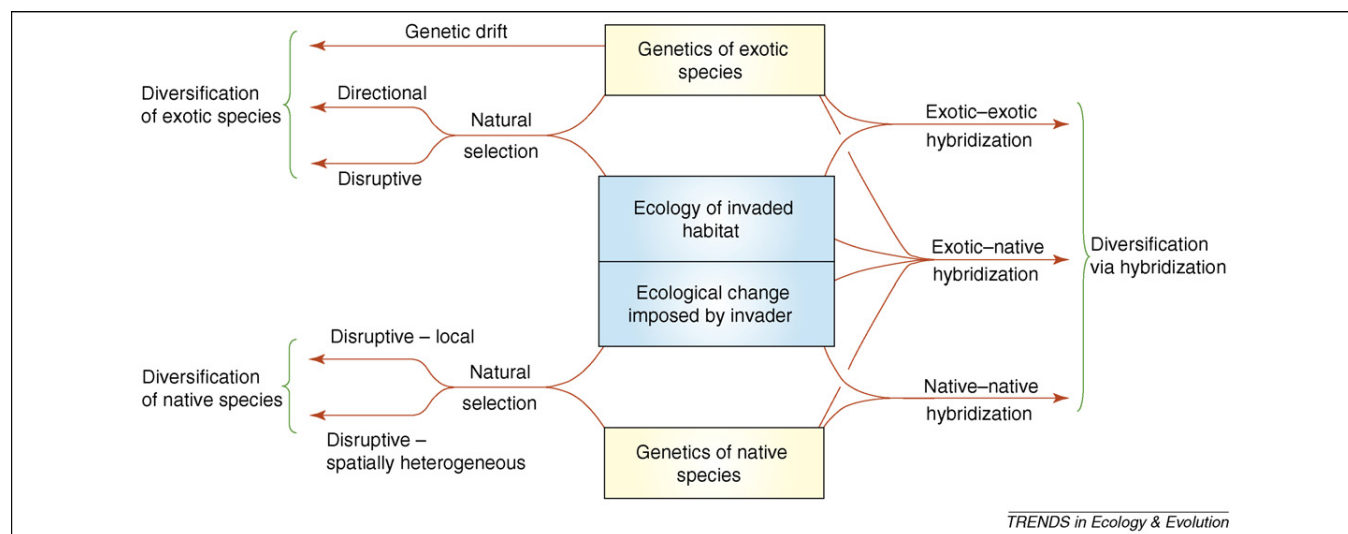


Figure 1. Conceptual framework for understanding effects of exotic species invasions on evolutionary diversification. Characteristics of the genetics of exotic and native species (yellow boxes) and the ecology of their shared habitats (blue boxes) interact via genetic drift, natural selection and hybridization to result in evolutionary diversification of exotic species, native species, or hybrid combinations of one or both of the exotic and native species.

and drift in the new allopatric population might cause it to diverge from populations in the native range. Second, directional selection imposed by the novel environment might cause divergence from populations in the native range. In these two cases, genetic variation in the new range might be no greater than in the native range, but at the species level, genetic differentiation among populations will have increased. Finally, if environmental conditions are sufficiently heterogeneous, disruptive selection can lead to diversification within the introduced range.

Diversification of exotic species: empirical evidence

Data from putatively neutral molecular markers provide some evidence of founder effects and genetic drift causing divergence of populations between native and introduced ranges, and among different areas of introduction. At the species level, overall genetic variation will increase if differentiation measured among both native and exotic populations exceeds that found among only native populations, but relatively few studies address the latter level of differentiation in detail, so the evidence is mostly suggestive rather than conclusive. For example, common mynas *Acridotheres tristis*, introduced to New Zealand, South Africa, Hawaii, Australia and Fiji from India, show genetic differentiation at enzyme loci that exceeds that found among native populations by a factor of four, although native populations were sampled only in the central, albeit large, portion of the native range [12]. In the house finch *Carpodacus mexicanus*, populations introduced into Hawaii and eastern North America show significant differentiation at AFLP markers from populations sampled from across the native range in western North America, and these patterns are consistent with morphological differentiation among the same populations [13].

Differentiation at molecular marker loci by itself does not demonstrate or imply adaptive differentiation among populations or lineages, but examples abound of evolutionary changes in introduced populations owing to directional natural selection [3]. In animals, the traits that respond to selection are varied and include migratory patterns [14], key morphological traits [15], life-history traits [16], body size [17] and host preference [18]. In plants, there has been much recent research on the response of non-native populations to the selective forces imposed by the loss or gain of enemies. The evolution of increased competitive ability (EICA) hypothesis [19] predicts that the loss of enemies causes non-native plant populations to evolve reduced allocation to defense and greater competitive ability, assuming a tradeoff between these two traits. The evidence for EICA is mixed [20–22], but there are several studies that show divergence between non-native plant populations and their native sources that result, at least in part, from a change in interspecific interactions (e.g. Refs [23,24]). Thus, for both animals and plants, selective pressures can act as a mechanism for evolutionary divergence between the native and naturalized ranges of species, although strong conclusions here must be hedged by the fact that sampling of populations in the native range is typically sparse. There are also several spectacular documented cases of adaptive evolutionary divergence within an introduced range (Box 1).

Finally, exotic species might evolve in response to the widespread availability of suitable but unoccupied habitat. In cane toads *Bufo marinus* in Australia, populations at the leading edge of expansion appear to have evolved longer legs and increased locomotion speed because of the substantial fitness advantage of arriving at a site first and forming the founding population [25].

Diversification of native species in invaded regions: theory

Exotic species alter the biotic composition of invaded communities [4] and often the physical and chemical structure of invaded environments [26]. The selective pressures that these changes impose on native species can result in a variety of outcomes, reviewed in detail by Strauss and colleagues [5] and briefly outlined here.

Exotic species can often lead to extinction or severe reductions in abundance of natives, thereby eliminating or greatly reducing the possibility of evolutionary diversification in the affected taxa. However, in many cases, selection-via-invaders is not so strong as to lead to extinction, but strong enough to induce phenotypic change [5]. However, even if a native species evolves in response to an exotic species, selection might be directional and more or less uniform across the range of a native species, thereby resulting in no overall diversification of the native species.

Under at least two scenarios, we can expect exotic species to promote the evolutionary diversification of native species (Figure 1). First, invaders might impose disruptive selection locally, within populations of native species, for example by providing an alternative host for herbivorous insects. Second, if only some populations of native species are being impacted by an exotic species, even selection of similar direction and magnitude in different invaded populations will lead to diversification via genetic differentiation between invaded and uninvaded populations.

Diversification of native species in invaded regions: empirical evidence

Shifts of native phytophagous insects onto novel exotic host plants provide the most striking and common empirical examples of native evolutionary diversification in response to invaders (Box 2). Exotic species might also impose directional selection on native species and, in many cases, this selection occurs in only a subset of the populations of native species, thereby leading to evolutionary diversification. Indeed, the comparison of evolutionary changes in invaded versus uninvaded habitat patches frequently contributes to the evidence that exotic species act as agents of evolutionary change in native species [3,5].

Exotic species impose selection via a variety of competitive and trophic interactions. Examples of competition-mediated evolutionary change include the shift of native brook charr *Salvelinus fontinalis* towards a predominantly pelagic feeding habitat in lakes invaded by benthic white suckers *Catostomus commersoni* [27,28], and the evolution of tolerance in native rangeland plants to allelopathy by exotic spotted knapweed *Centaurea maculosa* in western North America [29]. Native prey might evolve resistance, tolerance, or avoidance of exotic

Box 1. Evolution of geographical clines following invasion

Environmental gradients can impose spatially varying selection on exotic species, which, in turn, can lead to evolutionary diversification within the introduced range. A century after house sparrows *Passer domesticus* were introduced from England and Germany into North America, there was clear evidence for adaptive divergence under different climatic conditions [58,59]. Birds from cool and humid climates were darker in plumage than were birds in hot and dry climates. Similarly, birds living in boreal climates with severe winters were larger in body size compared with those living in milder climates. These patterns conform to plumage and body size clines found among native North American bird species and follow the well-documented Gloger's and Bergmann's rules, respectively, for native species [60]. To the extent that these patterns mirror those

found along the latitudinal gradient in Europe, they might not represent an increase in genetic variation among populations of house sparrows, but instead a duplication of variation found in the native range.

However, similar studies of genetically based clines in introduced taxa of *Drosophila subobscura* [15] provide evidence to the contrary. After 20 years in the New World, separate *D. subobscura* populations in both North and South America had evolved a pattern of increased wing length with increasing latitude that mirrored the pattern found in the Old World (Figure 1a), but the developmental and genetic basis of the variation in wing length varied among the three continents (Figure 1b). Thus, similar phenotypic patterns were underlain by evolutionary diversification in *D. subobscura*.

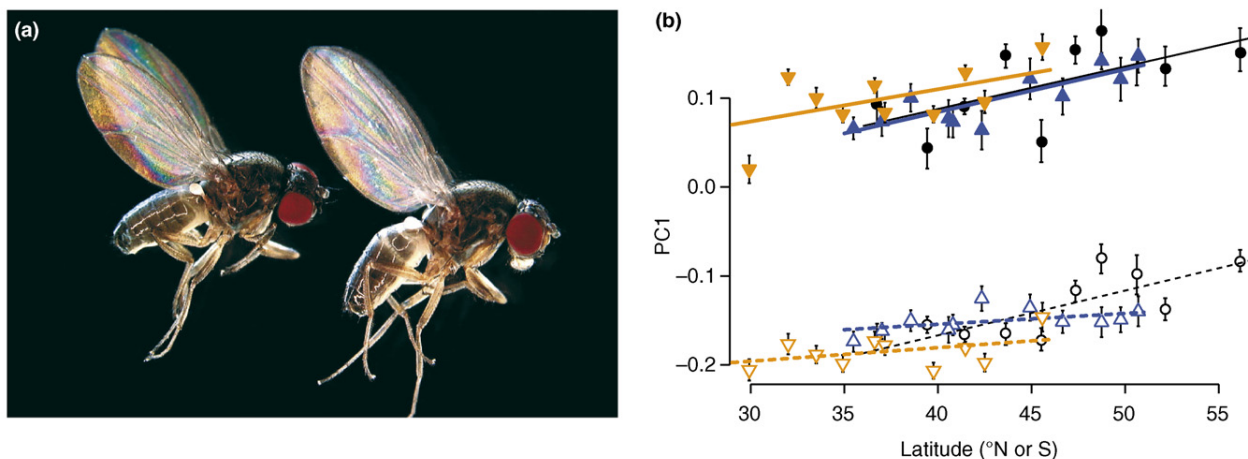


Figure 1. Evolution of geographical clines in an exotic species. (a) *Drosophila subobscura* from Barcelona, Spain (39° latitude, left) and Aarhus, Denmark (56° latitude, right) demonstrating the latitudinal cline in wing size that has evolved in the native European range, and also in the introduced North and South American ranges. (b) Latitudinal clines in wing size in Old World (black circles), North American (blue triangles), and South American (orange inverted triangles) populations. Filled and empty symbols are for females and males, respectively. PC1 refers to the first principal component of the three wing dimensions: length of the wing along the proximal portion of vein IV, length of the wing along the distal portion of vein IV and wing width. Reproduced with permission from G. Gilchrist; data from Ref. [15].

predators, as in the case of red-legged frogs *Rana aurora*, which have evolved avoidance strategies in the face of invasion by bullfrogs *Rana catesbeiana*, in some but not all ponds in Oregon, USA. [30]. Likewise, native predators might evolve to cope with abundant exotic prey; for example, Australian black snakes *Pseudechis porphyriacus* have evolved resistance to the toxins in exotic cane toads in invaded sites [31].

Hybridization: theory

Hybridization initiated by exotic species invasions provides some of the most unambiguous cases of rapid evolutionary diversification [32]. Exotics can hybridize with other exotics [33] or with native species [34]. Additionally, exotic species invasions can alter community structure and lead to hybridization between two formerly distinct native species (e.g. Ref. [35]; Figure 1). Results of any of these hybridization events can include the formation of new species, introgression of genetic material into one or both original species, or the formation of hybrid swarms, depending on the genetics and ecology of the two species.

Hybridization can have both positive and negative roles in the generation of biodiversity. Hybridization and introgression between populations in distinct selective environments can inhibit local adaptation and prevent speciation

[36]. Hybridization can swamp local gene pools via interbreeding or competitive superiority of hybrids, such that rare species might be driven to extinction by more abundant, closely related invaders [32,37]. At the same time, hybridization can lead to speciation, with many plant species thought to be of hybrid origin [38,39]. Hybridization can also accelerate adaptation in both plants and animals [40,41] and might have an important role in adaptive radiation [42,43].

For hybrids to persist as new species, both genetic and ecological criteria must be satisfied. Genetically, there must be factors, such as polyploidy or other chromosomal changes, that prevent the expansion or collapse of the hybrid zone through gene flow and introgression [44]. Ecologically, distinctness of the new species from any parental species with which it shares habitat will promote persistence of the hybrid [45]. For hybridization to increase diversity directly in the long term, the new hybrid taxon must be stable and exist without leading to the extinction of either parental form, which can be facilitated by spatial separation as well as ecological distinctness of the hybrids.

Hybridization: empirical evidence

Particular case studies often reveal a complex combination of processes by which exotic species invasions ultimately

Box 2. Host shifts of native insects onto exotic plants

Some of the clearest examples of evolutionary diversification of native species in response to invaders come from host shifts in phytophagous insects. The two best-documented cases are that of native apple maggot fly *Rhagoletis pomonella*, which has evolved genetically differentiated ecotypes that feed on native hawthorns and introduced apples in North America [61,62] (Figure 1) and the North American soapberry bug *Jadera haematoloma*, which has evolved different beak lengths to feed on the fruit from exotic tree species [63]. In both cases, genetically differentiated populations feed on native and exotic host plants, with restricted gene flow between the new and old host races.

Additional empirical examples of genetically based host shifts include Colorado potato beetles *Leptinotarsa decemlineata* shifting from native Solanaceae to introduced potatoes and tomatoes [64]; common sulfur butterflies *Colias philodice* shifting onto introduced alfalfa [65]; and the weevil *Euhrychiopsis lecontei* shifting from native to exotic watermilfoil [66]. There are several additional examples [5] of what appears to be a widespread phenomenon of native insect species genetically diversifying in response to exotic host plants.

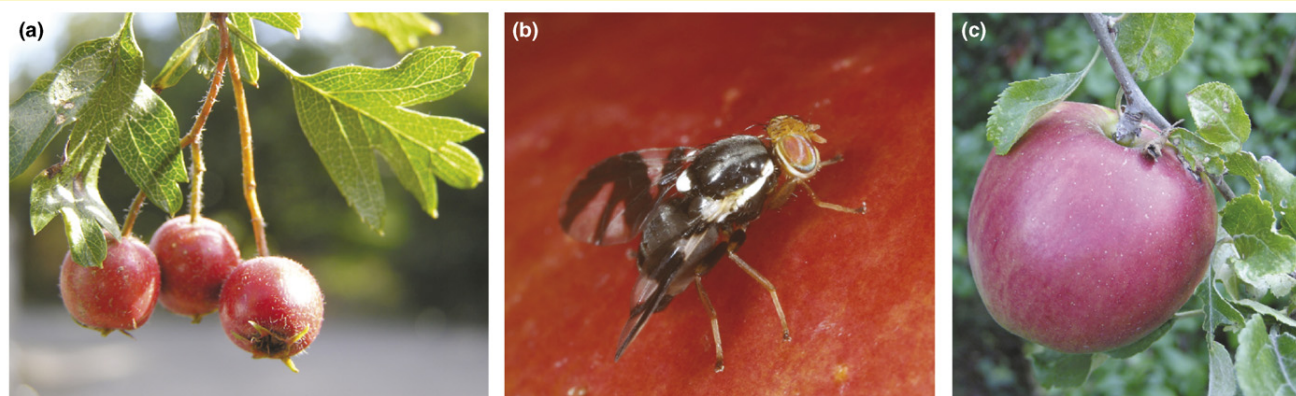


Figure 1. Host shifts onto exotic plants. Hawthorn *Crataegus* spp. (a) are the native host plant for the apple maggot fly *Rhagoletis pomonella* (b) in North America. Following the introduction of apples *Malus* spp. (c) to North America, *R. pomonella* has evolved a genetically differentiated ecotype that feeds on apples. Reproduced with permission from M. Vellend (a,c) and A. Forbes (b).

result in evolutionary diversification via hybridization. Exotic and native cordgrass *Spartina* spp. in Great Britain and San Francisco Bay illustrate how ecological and genetic factors can interact to determine the impacts of hybridization on diversity during invasions.

In Great Britain, native *Spartina maritima* hybridized with exotic *Spartina alterniflora* introduced from eastern North America. This hybridization was followed by chromosome doubling, which led to a new, reproductively isolated species, *Spartina anglica* [46]. Coexistence with native *S. maritima* was facilitated by the fact that the new species can occupy a habitat, bare tidal flats, which is not available to either parental species [47]. However, in San Francisco Bay, hybridization of native *Spartina foliosa* with the same exotic species, *S. alterniflora*, has resulted in hybrids that occupy the same habitats, and can interbreed with and outcompete the native species [48], suggesting that evolutionary diversification is unlikely.

Thus, although strikingly similar hybridization events can have different results, evolutionary diversification is one possible outcome. There are many additional examples of stable new plant species formed through invasion and hybridization (e.g. *Circaea* [49], *Mentha* [50], *Viola* [51], *Rhododendron* [52], *Tragopogon* [53] and *Plantanus* [37]). Another particularly compelling study illustrating a complex combination of factors involved in exotic-native hybridizations involves ragworts in the genus *Senecio* (Box 3).

Invasions associated with hybridization are not unique to plants, as illustrated by the fruit flies of the genus *Rhagoletis*. Schwarz *et al.* [35] describe a recent speciation event in the *Rhagoletis pomonella* complex associated with

a host shift onto exotic honeysuckle (genus *Lonicera*). The new species is a hybrid between two natives, *Rhagoletis mendax* and *Rhagoletis zephyria*, specialized to different host plants. Presumably, the host shift onto the exotic honeysuckle provided the ecological separation needed for hybrid speciation without a change in chromosome number in these flies [35]. This also illustrates that invasions can spur hybridization between two native species.

Lessons from the fossil record

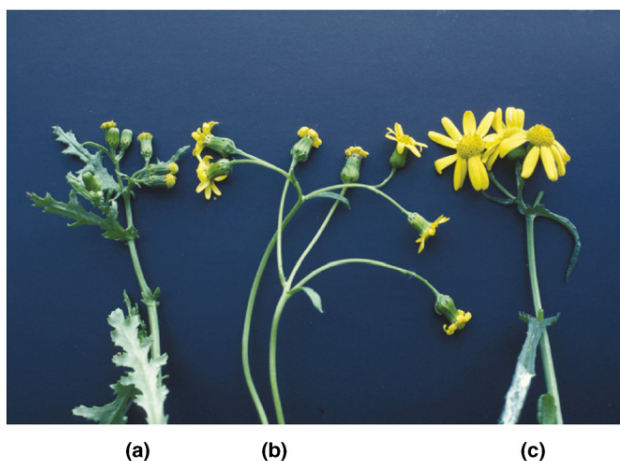
Although it is difficult, if not impossible, to predict accurately the long-term consequences of human-mediated exotic species invasions, biotic exchanges recorded in the fossil record can nonetheless provide some potentially important clues. Large-scale biotic exchanges, in which the elimination of dispersal barriers enabled hundreds or thousands of species to be exchanged between formerly isolated regions, have occurred repeatedly during the history of the Earth, such as when the Panama land bridge formed ~3.5 million years ago connecting the terrestrial biotas of North and South America.

Vermeij [54] has shown that, in general, the number of species driven extinct by invasions was less than the number of species generated by adaptive radiations and evolutionary diversification of invading species in the fossil record. Clearly, there are several differences between biotic exchanges of the past and current patterns of invasion; for example, species are currently transported much greater distances than in the past, and many contemporary exotic species in one region derive from multiple source regions simultaneously. Although the uniqueness of the

Box 3. Geographical isolation and hybrid speciation

Ragworts, *Senecio* spp., provide a fascinating example of the factors influencing genetic stability in exotic hybrids [67]. Two species, *Senecio aethnensis* and *Senecio chrysanthemifolius*, form a natural hybrid zone on Mount Etna, Sicily. Where the native ranges of these two species overlap, there is evidence for extensive hybridization, and for the maintenance of the hybrid zone by a balance between dispersal and extrinsic selection [67].

Within the past 300 years, individuals from this hybrid zone were introduced to the British Isles, where they have spread as an exotic species, known as *Senecio squalidus*, which is morphologically and ecologically distinct from both parents and also from individuals in the hybrid zone in the native range. It is likely that spatial segregation that was lacking in the native range provided the impetus needed for hybrid speciation without a change in chromosome number [67]. Thus, the invasion facilitated a speciation event that has not occurred in the native range where these two species hybridize. As an additional complication, the new exotic species (Figure 1c; reproduced with permission from R. Abbott) has hybridized with a local native species, *Senecio vulgaris* (Figure 1a), leading to the origin of three new hybrid taxa, *S. vulgaris* var. *hibernicus* [68] *Senecio eboracensis* [69] and *Senecio cambrensis* [70] (Figure 1b).



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Figure 1.

present situation makes predictions based on past patterns of change difficult, our review illustrates that the processes involved in evolutionary diversification in past biotic exchanges appear also to be operating today.

Spatial and temporal scale

Consideration of biotic exchanges in the fossil record highlights the important issue of temporal and spatial scales over which we expect present-day exotic species introductions to generate new biodiversity. The examples provided here illustrate that evolutionary diversification occurs over a wide range of scales. In terms of temporal scale, there is no discrete point during the process of diversification after which speciation has occurred. Rather, the process is continuous such that populations or lineages vary continuously in their degree of adaptive differentiation and reproductive isolation [55], and even most lineages that we call species are not 100% reproductively isolated from their closest relatives [55].

For new lineages created by hybridization, adaptive differentiation and reproductive isolation can occur essen-

tially overnight, and we have described several examples in which exotic species introductions have led to the creation of such new hybrid lineages. Adaptive diversification of native phytophagous insects onto exotic plants can also occur relatively quickly, within a century in the case of soapberry bugs evolving to exploit introduced plants in the Sapindaceae (Box 2). For non-hybrid exotic or native species, significant adaptive genetic differentiation among populations can occur over a period of years to decades [15], but in most cases we would predict a high degree of reproductive isolation (i.e. what might be considered new species) to take thousands or millions of years to evolve [55], and, at present, we can only speculate that reproductive isolation will eventually evolve between native and introduced ranges.

The spatial scale of diversification also varies tremendously. For some exotic species, genetic differentiation occurs among populations scattered across much of the globe (e.g. Ref. [12]); native species might diversify across a broad geographic region or entirely within a relatively small part of their geographic range (Box 2).

Concluding thoughts

Exotic species invasions have stimulated evolutionary diversification across the globe in a range of taxa via a variety of mechanisms (Figure 1). It is impossible to say what proportion of species invasions lead to diversification, but the list of documented cases presented here argues that we must take seriously the role of exotic species invasions in the generation of biodiversity.

We are not arguing that these positive effects of invaders on biodiversity outweigh their negative effects; for example, the negative effects of cane toads on biodiversity in Australia are probably greater than their positive effects via evolutionary diversification of the toads or their predators [25,31]. In addition, successful invaders are not random samples from the tree of life [56], such that the biodiversity gained via evolutionary diversification might be confined to already successful lineages, such as finches, mice and grasses, whereas we will lose biodiversity from a much broader range of lineages. To the extent that endemic, phylogenetically distinct lineages have the greatest conservation value [57], then the value of the lineages that we lose will exceed the value of those that we gain via the processes outlined here. Nonetheless, many exotic species provide important ecosystem services to humanity (e.g. many food plants and animals) and, given that all regions of the Earth are increasingly becoming occupied by lineages whose presence is due to either non-native introduction or evolutionary diversification in response to such introductions, a more nuanced approach to conservation might be needed than one in which any such lineage is automatically assigned the lowest possible value. Conservationists must also face the difficult but fascinating question of whether species that originate via evolutionary diversification of an exotic species are considered native to the introduced region; we feel that a species can only reasonably be considered native to the region where it originated.

Future research on the current and projected net effects of particular exotic species on biodiversity, as well as the

taxonomic distribution of new lineages whose origin was initiated by exotic species invasions, will enable a more complete accounting of the relationship between exotic species and biodiversity at different scales. At present, it seems plausible to suggest that, in the long term, moving species to new regions with different environmental conditions and altering the biotic environment of native species will lead to speciation in many branches in the tree of life. We have already seen the formation of new reproductively isolated and ecological distinct taxa via hybridization stimulated by species invasions; speciation events that do not involve hybridization will simply take much longer to happen.

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