

Ecological and evolutionary insights from species invasions

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Species invasions provide numerous unplanned and frequently, but imperfectly, replicated experiments that can be used to better understand the natural world. Classic studies by Darwin, Grinnell, Elton and others on these species-invasion experiments provided invaluable insights for ecology and evolutionary biology. Recent studies of invasions have resulted in additional insights, six of which we discuss here; these insights highlight the utility of using exotic species as ‘model organisms’. We also discuss a nascent hypothesis that might provide a more general, predictive understanding of invasions and community assembly. Finally, we emphasize how the study of invasions can help to inform our understanding of applied problems, such as extinction, ecosystem function and the response of species to climate change.

Species invasions as a source of insights

Exotic species are variously perceived as beneficial, costly and even opportunities to understand fundamental ecological and evolutionary processes [1]. The benefits from exotic species are pervasive and integral components of our global economy. For example, food crops (such as corn and wheat) and fiber-producing crops (such as cotton) are often grown outside their native range to great advantage, as are livestock (such as sheep) that produce food and material for clothing, and trees (such as eucalypts) that produce wood for paper and building materials. These benefits are typically received from species that are cultivated or managed, but can also include unmanaged game and fish populations (such as those in New Zealand; <http://www.fishandgame.org.nz>), biological control agents (such as *Chrysolina quadrigemina* on Klamath weed) [2], and introduced species (such as *Eucalyptus globulus*) that provide crucial habitat or resources for natives (such as the monarch butterfly in California) [3].

The costs of exotic species typically come from those that have become naturalized; that is, those that have established self-sustaining populations in the absence of human assistance. Naturalized species have caused or contributed to the extinction of many native species, as exemplified by introduced rats and cats on islands [4]; have altered ecosystem processes, for example by changing fire frequency and disturbance regimes, as with cheatgrass *Bromus tectorum* in the western United States [5]; and cause millions of dollars of damage annually, as exemplified by introduced weeds, which reduce crop yields, and the zebra mussel, which fouls underwater machinery [6].

However, exotic species also provide opportunities to understand the natural world better. They provide unanticipated experiments across large spatial and temporal scales that enable researchers to observe ecological and evolutionary processes in real time, to quantify rate processes (such as genetic change) that are often difficult to study with native species, and to provide data that would often be deemed unethical to collect otherwise (Box 1).

Since at least the mid-1800s, naturalists, evolutionary biologists and ecologists have been drawing crucial insights from species invasions. Charles Darwin’s work [7] is infused with evidence drawn from naturalized species (Boxes 2,3). Although Joseph Grinnell [8] was perhaps the first to label invasions as ‘an experiment in nature’, Charles Elton, Guy Bush and others (e.g. Refs [9–11]) similarly used exotic species to develop our modern conception of ecology and evolution. These classic insights have fundamentally informed our views on many issues, including the evolution of adaptation and its relationship to reproductive isolation, the geography of speciation, the importance of dispersal in limiting species distributions and the role of individual species in structuring communities and ecosystems (Boxes 2,3).

Over the past 50 years, much of the biological interest in exotic species has been guided by the influential work of Elton [9], who emphasized the ecological, economic and

Box 1. Why invasions are useful for basic research

Although species invasions are a major focus of applied research in ecology and conservation biology, they are also useful for addressing a range of basic research questions in ecology, evolutionary biology and biogeography. The reasons for this are fourfold.

First, species invasions provide unplanned experiments across large spatial and temporal scales, ones that are often approximately replicated across continents and whole islands. This is in direct contrast to most planned manipulative experiments, which are generally performed over short periods of time (i.e. less than a few years) and at small spatial scales (i.e. a few square meters in dimension). Unplanned experiments can provide unique data that are complementary to planned experiments. For example, invasions of oceanic islands by plants, vertebrates, invertebrates and other taxa have provided massive species addition experiments that enable tests of island biogeography theory and concepts of community saturation at spatial and temporal scales that are inaccessible by traditional planned experimental approaches [27].

Second, species invasions enable one to observe ecological and evolutionary processes in real time. For example, character displacement between trophically similar native species might be assumed from morphological differences, leading one to infer the 'ghost of competition past' *sensu* Connell [62]. By contrast, during or after a species invasion the transient dynamics of character displacement can be observed instead of inferred.

Third, species invasions enable the rates of processes to be examined that would often be difficult to study with native species. For example, the rate of processes such as genetic change and range expansion can be studied with invasions because of known benchmark dates (e.g. the precise year in which a species was introduced to a particular location).

Fourth, species invasions provide data that would often be deemed unethical to collect in a planned experiment. Massive species addition experiments across whole islands and continents, the introduction of pathogens and similar unplanned experiments would be considered by many unethical to perform intentionally and, therefore, would (or should) be forbidden as planned experiments.

conservation challenges resulting from species invasions. A notable exception is Baker and Stebbins' edited volume [10], which drew insights from exotics into basic research questions. More recently, the study of exotic species to address basic research questions in ecology and evolution has reemerged in several books [12–14] and numerous research papers [15–18]. Here, we review some of the major conceptual insights emerging from this recent work, highlighting the value of exotic species as 'model organisms' for studying both basic and applied issues. We focus primarily on insights that supersede the study of invasion *per se*, to demonstrate general insights that the study of invasion has provided to our understanding of adaptation, extinction, species saturation, the impacts of climate change and other topics. We also describe a nascent hypothesis that might provide a more general, predictive understanding of invasions and community assembly.

Emerging insights

Here, we consider six insights in ecology and evolutionary biology that are emerging largely from the study of species invasions. The areas selected for discussion are not intended to be exhaustive, but instead illustrative, of the approach of using species invasions to understand patterns and processes other than invasions. In some cases, these findings counter and challenge older bodies of theory, whereas, in other cases, they provide empirical support for long-held, but poorly tested views.

Box 2. Insights derived from the study of species invasions

Classic insights

- Species are not optimally adapted for their environment.
- Changes in geographical range can occur quickly.
- Species are generally limited in their distribution by dispersal.
- Speciation can occur sympatrically.
- Reproductive isolation can take millions of years.
- Individual plant species can transform ecosystems.

See Box 3 for further details.

Emerging insights

- Ecological systems rarely show evidence of being saturated with species.
- Competition, unlike predation, seldom causes global extinction.
- Community assembly often occurs by ecological sorting or 'fitting'.
- Adaptive genetic change can occur rapidly.
- Severe population bottlenecks do not preclude rapid adaptation.
- Climate envelope approaches for predicting spread and ultimate distributions might be inadequate for many species.

An emerging hypothesis

- Variation in patterns of specialization in predators and mutualists influence invasibility of communities.

There is little consensus on a definition of 'exotic species' (reviewed in Ref. [19]); nevertheless, there is general agreement on the status of most species with known histories of invasion. Here, we classify species as exotic or native according to their descriptions in the primary literature. These accounts generally define a species as exotic to a place if it has been introduced or has otherwise become established there because of human activities. We focus on exotic species in well-studied groups (plants, vertebrates, and marine invertebrates) that have become established during the past few hundred years.

Ecological systems rarely show evidence of being saturated with species

Traditional views of ecological communities often rest on the assumption that they are 'full' or saturated with species, i.e. that additional species cannot be added to an ecological community without the loss of existing ones [20]. Some of the best support for this hypothesis comes from recent work on space-limited taxa (such as invertebrates in the intertidal zone) at the spatial scale of 0.25 m² [21] and from studies of grassland plants at scales of less than 1 m²; the grassland studies show that species-rich plots are more difficult to invade than species-poor ones (reviewed in Ref. [22]). However, three principal bodies of evidence challenge the generality of species saturation across communities, taxonomic groups and spatial scales.

First, analyses of the relationship between species richness at local and regional spatial scales suggest that many communities are not saturated, or at least only partially so [23], and that saturation, where present, should be expected only at small scales, for example at less than 1 m² [21,22]. Second, species addition and biotic resistance experiments performed at local scales (generally less than 1 m²) indicate that even species-rich plots that are more difficult to invade can, nevertheless, still be invaded; further, the net consequence of these invasions is generally an increase in total species richness [24,25]. Third, quantitative studies of

Box 3. Classic insights from species invasions

Modern conceptions of ecology and evolutionary biology have been strongly shaped by insights derived or supported by evidence from species invasions. Here, we describe six representative examples of these classic insights.

Species are not optimally adapted for their environment

Darwin [7] and others [63] emphasized that evolutionary constraints (e.g. adaptive troughs) can cause native species to be far from optimally adapted to their environments, as evidenced by exotic species that outperform them. Although superior performance by exotics might sometimes be due to the absence of coevolved enemies, this is unlikely to be true in all cases (e.g. when exotics can occupy habitats wholly unoccupiable by similar native species, such as extensions of the tree-line in the southern hemisphere by exotic trees that can live at elevations greater than any native tree [64]).

Changes in geographical range can occur quickly

Darwin [7] used the rapid geographical range expansion of exotic species to surmise that native species would have had ample time to shift their geographical ranges in response to glaciation (because rapid range expansions were possible).

Species are generally limited in their distribution by dispersal

Darwin [7] and other naturalists of the 19th century realized that species were limited in their geographical distribution by barriers to dispersal, as evidenced by the success of exotic species when they were introduced outside their native range.

Speciation can occur sympatrically

Mayr [65] and others argued that speciation should occur only with allopatry (i.e. when populations were separated geographically). This view was challenged by a variety of work, including that by Bush [11] and others who showed that an incipient speciation event was occurring where native *Rhagoletis* flies were shifting from native hawthorn plants to introduced apple trees, forming two mostly isolated populations in the same geographical area.

Reproductive isolation can take millions of years

Exotic species that hybridize with native species to produce fertile offspring demonstrate that reproductive isolation (even in natural field settings) can take millions of years. Examples of this are often seen among formerly isolated species in the same genus (e.g. cordgrass genus *Spartina* [66]) but also for species in different genera (e.g. between fishes of *Scardinius* and *Notemigonus* [67]).

Individual plant species can transform ecosystems

The role of individual plant species in transforming ecosystem properties is understood largely from pioneering work by Vitousek *et al.* [68] and later by others [5], who showed that individual plant species can alter nutrient availability and disturbance regimes, leading to changed ecosystem function and species assemblages.

invasions at regional spatial scales suggest that most regions of the world can absorb more species by invasion than they lose by extinction, such that the net effect of invasions in many cases is a large net increase in species numbers [26,27]. For vascular plants, which generally show a pattern of few native species lost and many exotic species gained, invasions over the past few hundred years have led to a doubling of richness on many islands (e.g. from 2000 to 4000 species in New Zealand) and on the order of a 20% increase in many mainland regions, such as individual states in the USA [26,27]. For some other groups the increase in richness has been more extreme; in Hawaii freshwater fish richness has increased by 800% with the introduction of 40 exotic species and the loss of none of the five native species [27]; however, some groups, such as land

birds, show no major change in net species richness, which could indicate support for saturation. For instance, on islands worldwide, 78% of the variation in the number of exotic bird species gained is explained by the number of native bird species lost to extinction [26].

The significance of a world in which many communities and ecosystems are unsaturated is not well explored, largely because this is a contentious issue for which a general consensus is yet to emerge. Nevertheless, we believe that there is now ample evidence to conclude that many communities are not saturated. At a minimum, this requires rethinking the role of competition and the application of current co-existence models in community ecology, the processes that underlie the ecological and biogeographical patterns of species diversity, and current conservation strategies. This new perspective also affects the expectation that competition frequently leads to species extinctions.

Competition, unlike predation, seldom causes global extinction

Competition from exotic species can cause the extirpation of native species at local scales [9]. Consequently, there is widespread concern that exotic species, acting through competitive processes, pose an extinction threat to native species (e.g. Ref. [28]). However, several recent syntheses [29,30] suggest that exotic competitors are unlikely to cause the complete extinction of species, even if they do cause local extirpations of populations. Indeed, Davis [29] suggested that there is no evidence that competition from exotic plants has caused any native species extinctions, that is, the complete loss of a species from the planet. Similarly, Sagoff [31] highlighted several studies that failed to demonstrate extinction from competition between exotic and native marine invertebrate species. On most oceanic islands, where many native bird species have gone extinct and numerous exotic birds have become established, most native extinctions occurred before most exotic bird introductions [27]. By contrast, many well documented examples link exotic predators and pathogens to extinctions of native species; this includes introduced rats and cats on islands, such as New Zealand [4], avian diseases in Hawaii and hunting by humans on islands and continents worldwide [32].

The preponderance of available evidence suggests that exotic predators and pathogens have disproportionately large roles in species extinctions. To the extent that this is true, it suggests that the focus on research topics such as 'biotic resistance' should shift away from a competition-centric emphasis toward a more inclusive consideration of the role of predation and disease, as well as other biotic interactions, such as facilitation (see below). However, an alternative explanation for the lack of evidence for extinctions caused by competition could be that competition-induced extinctions, once set in motion, might take hundreds or even thousands of years to complete. As such, the limited evidence for competition-induced extinctions could be masking a large 'species extinction debt' [33], such that many species currently extant will be expected to go extinct in the future because of events that have already occurred. This is a difficult hypothesis to test with existing data; nonetheless,

measuring the size of species extinction debts is a crucial research question that warrants more attention.

Community assembly often occurs by ecological sorting or 'fitting'

A long-standing question in the assembly of communities, ecosystems and regional biotas concerns the relative contributions of abiotic environmental conditions (such as climate), species interactions (such as competition and predation), evolutionary and coevolutionary adjustments, and stochastic processes (such as population demography) [32]. This question has increased importance in a world where species ranges are rapidly shifting in response to climate change and human transport [14,34]. In this context it is important to ask whether species assemblages with novel combinations of species (including both native and exotic species) function in the same way as native assemblages, even when many of the constituent species do not have a shared evolutionary history. The answer to this question, although pressing, is still unclear [16,35–37]. What is becoming clear, however, is that assemblages composed largely of exotic species can and do occur (e.g. plant communities that dominate portions of many oceanic islands, such as Ascension Island [16,36]), and that assemblages dominated by exotic species, such as *Eucalyptus globulus* woodlands in California, can be as species-rich as those dominated by native species [38]. We believe that these findings support Janzen's [39] conjecture, which was based largely on patterns observed with native species, that diverse assemblages of species with complex ecological relationships can be formed by the ecological 'fitting' [40] and 'sorting' of species (*sensu* Ackerly [41]), that is, solely through ecological interactions among species, and that a long history of coevolution is not always necessary to explain the species composition of communities. Although species coexisting in such recently formed assemblages might not have a prolonged history of evolutionary coadaptation, rapid evolutionary adjustments might still have occurred over timescales of decades to centuries.

Adaptive genetic change can occur rapidly

Rapid (e.g. within a few years) genetically based adaptation frequently occurs under laboratory conditions [42]. Similarly, rapid adaptive responses to anthropogenically mediated selection, such as the development of insect resistance to pesticides [9], have been known for decades. Recent work has shown that comparably swift and dramatic evolutionary responses are common in natural field settings in the absence of anthropogenic selective pressures, that is, in response to natural selective pressures [12,43]. The preponderance of these data come from documented evolutionary changes in exotic species or in native populations responding to exotic species [12,44,45]. For example, soapberry bugs *Leptocoris tagalicus* that are native to Australia have evolved genetically based changes in the length of their mouthparts that increase feeding efficiency on a balloon vine *Cardiospermum grandiflorum* introduced only 30–40 years earlier [44]. Similarly, Huey *et al.* [45] reviewed evidence that introduced fruit flies *Drosophila subobscura* and salmon *Oncorhynchus* spp. show rapid heritable changes in morphology within a few decades.

Stockwell *et al.* [43] argue that our emerging understanding of the speed of evolution should change the questions being asked by conservation biologists; for example, to include whether deliberate attempts to maintain genetic diversity within managed populations are impeding selective genetic adaptation. In addition, large and rapid evolutionary changes (such as those shown by *Drosophila subobscura*) suggest that greater efforts should be made to combine ecological and evolutionary perspectives in both theoretical and empirical studies.

Severe population bottlenecks do not preclude rapid adaptation

The importance of population bottlenecks (i.e. short-term restrictions in the total size of a population) in promoting or inhibiting subsequent adaptation has been a topic of long-standing interest in evolutionary biology [46,47]. In theory, population bottlenecks that substantially reduce additive genetic diversity within populations might stifle adaptive responses to novel selective regimes, by reducing the total genetic variation available. By contrast, bottlenecks could promote rapid adaptation and evolution by increasing the importance of genetic drift and higher-order epistatic interactions among genes or by converting epistatic variation to additive genetic variation, all of which could promote adaptive responses to novel selective regimes [47]. There is a long history of laboratory experiments addressing these issues [42]. Recently, several studies of exotic species have begun to address these questions in natural settings [45–47]. For example, when *Drosophila subobscura* colonized southern Chile during the 1970s, it is likely (based on genetic data) that fewer than 15 individuals constituted the founder population, with no evidence for subsequent colonizations [45]. Despite this small founder population, within only 20 years *D. subobscura* had spread across at least 12° of latitude, formed genetically based geographical clines in wing size and diverged morphologically from ancestral populations [45]. Although individual case studies such as these tell us that rapid evolution can occur following population bottlenecks, it remains to be determined how frequently such changes actually occur.

Although genetic bottlenecks are a common outcome of the introduction of small founder populations, recent evidence suggests that many successfully invading populations have not experienced a significant loss of genetic diversity [46,47]. Indeed, recent work suggests that within-population levels of genetic diversity can be even higher for species in their naturalized environments than in their native environments owing to genetic admixture from multiple source populations [46–49]. This pattern might be expected for many exotic species that have been introduced repeatedly (such as agricultural weeds, horticultural plants and pets). In turn, high levels of genetic diversity in naturalized populations might facilitate subsequent adaptation and speciation [50].

Climate envelope approaches might be inadequate for many species

The native geographical distribution of species results from the combined effects of abiotic environmental conditions,

species interactions and dispersal limitation. It is often difficult, however, to determine how these variables operate independently or interactively to limit species distributions [32]. Abiotic conditions have often been used to approximate the dominant factors limiting species distributions. This approach has frequently been extended to predict how species will spread after introduction or how they will respond to climate change [51]. These studies, which use climate envelope modeling, assume that the relationship between climatic variables and the current distribution of a species will enable accurate predictions of future distributions following introduction to a new area or in response to altered environmental conditions. Few would expect such predictions to be perfect; it has been unclear, however, how precise these predictions are likely to be.

Exotic species can be used to help evaluate the relative accuracy of geographical projections of future distributions that are based on climatic modeling approaches. This could be done by evaluating the degree of climate matching between geographical distributions of species in their native and naturalized ranges. Although no thorough analysis across multiple species has yet been performed, we can, nonetheless, reach two preliminary conclusions. First, climate envelope approaches seem to be ill-suited for predicting the response of species with small native ranges. For example, Monterey pine *Pinus radiata* and the Java sparrow *Padda oryzivora* both have restricted native geographical distributions but large naturalized distributions, suggesting that they tolerate climatic conditions different from those experienced in their native ranges. Second, some species with large native ranges occur well outside their predicted climate envelopes in their naturalized ranges; this includes Japanese knotweed *Fallopia japonica* [52], garlic mustard *Alliaria petiolata* [53], spotted knapweed *Centaurea maculosa* [54] and the fire ant *Solenopsis invicta* [55].

These climate envelope mismatches suggest that climate alone is inadequate to predict the distributions of species after introduction or following climate change. An expanded effort to compare climatic conditions in native and naturalized distributions of exotic species is

warranted, both to improve the parameterization of bioclimatic models and to understand better how biotic interactions, dispersal limitation, other non-climatic factors and rapid evolutionary responses can limit ranges of species.

An emerging hypothesis

Here, we discuss an additional issue that emerges from the study of species invasions. We label this as an ‘emerging hypothesis’ because it is still underexplored, although it is potentially very important for our understanding of basic and applied research questions.

Variation in patterns of specialization influences invasibility

The degree of specialization of any species for any particular resource, habitat or biotic interaction can be viewed as a spectrum that ranges from absolute specialization at one extreme (e.g. capable of preying upon only a single species) to absolute generalization at the other (e.g. capable of preying upon any species). Recently, Callaway *et al.* [56] proposed that the frequency of specialists and generalists can differ between species that typically fill mutualistic (or facilitative) versus predatory (or pathogenic) roles. Predatory roles include all pairwise interactions between species where one species benefits and the other experiences a cost; this includes predation, herbivory, parasitism and infectious disease; mutualisms are also known to be important in many cases of species invasion [57,58]. Callaway *et al.* [56] further suggested that species invasion would be facilitated if native predators and pathogens tended to be specialists (and thus unable to prey upon introduced species) and if native mutualists tended to be generalists (and thus able to facilitate exotic species invasion). These concepts are illustrated in Figure 1a. Subsequent studies [59,60] suggested that the frequency of specialists versus generalists for predators and mutualists can vary among different community types. In communities such as tropical rain forests, however, most fungal pathogens seem to be generalists

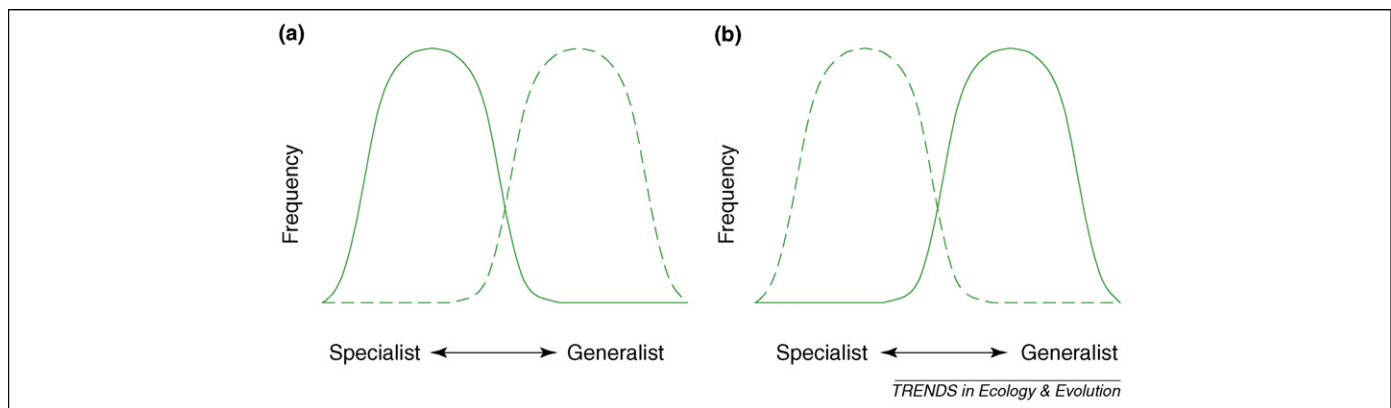


Figure 1. Specialization in species interactions and invasibility. Individual ecosystems can vary such that the frequency distribution of species along a continuum from absolute specialists to absolute generalists differs between (solid lines) predators and pathogens and (dashed lines) mutualists and facilitators. (a) In a high invasibility system, predators and pathogens are more frequently specialists, whereas mutualists and facilitators are more frequently generalists. Such systems would be relatively easy to invade because few predators would be able to prey upon exotic species (for which they would not be specialized), whereas many mutualists would be able to assist exotic species. (b) A low invasibility system, with the opposite distribution and invasion outcome. The curves illustrated here are for heuristic purposes only; the actual shape of these curves is unknown empirically. Their impact on invasibility should operate as described here, however, as long as there is a difference in the mode of the two distributions, and as long as the frequency of interactions determines the average outcome of invasions.

[59]. If most predators (including herbivores, parasites and infectious diseases) were generalists and most mutualists were specialists then such communities should be difficult to invade (Figure 1b). Some support for this latter hypothesis comes from Parker *et al.* [61], who showed that invasion by exotic plants is more likely when native herbivores that fill generalist roles are absent.

The concepts embodied in Figure 1 suggest that broad differences in invasibility between tropical and temperate systems, as well as more specific differences in invasibility among particular habitat types [59], might be driven by inherent differences in the frequencies and impacts of generalist and specialist predators and mutualists. This could be tested experimentally by contrasting invasion success in systems in which the frequency of generalist and specialist predators and mutualists had been manipulated; it could also be tested with observational studies that compared

Box 4. Future directions in the study of species invasions

Three areas of future work in the study of species invasions that can contribute to advances in both basic and applied research are outlined below.

Extinction and shifts in natural history

Climate change is expected to cause many species extinctions [51]. Consequently, there is a growing call for 'assisted migration', that is, the deliberate translocation of native species to prevent extinction [69]. The efficacy of translocation efforts and their potential dangers could be informed from the study of exotic species introductions. Translocations onto small islands in the face of mainland extinctions are also a common conservation strategy. Over the long term, however, isolation of populations on islands can lead to changes in genetics, life history, morphology and ecology, including loss of dispersal ability and island dwarfism [32]. The potential for short-term evolutionary changes is poorly understood but could be assessed by examining changes in the body size and other characteristics of exotic species that have been introduced to islands around the world [70].

Speciation

Species form by the allopatric model of speciation at the point when secondary contact between physically separated populations would not lead to hereditary exchange between them; assessing reproductive isolation between allopatric populations, however, has generally been confined to unnatural zoo or laboratory settings. Exotic species provide model systems for studying many aspects of the speciation process because of their large scale and natural setting; for example, the efficacy of reinforcement to complete the speciation process, the roles of sexual selection, habitat selection and so on in mediating prezygotic reproductive isolation, and the relative rates of evolution of prezygotic versus postzygotic reproductive isolation [50,66]. Speciation is an important topic for basic research, but given the expectation of many pending extinction events, it is likely that understanding and promoting speciation will become an important topic of applied conservation biology in the future.

Ecosystem function

Much of the world is becoming dominated by ecosystems composed of species that do not share a long evolutionary history. As globalization and global climate change continue to occur, a greater number of ecosystems will be made up of exotic species assembled from multiple sources. It is currently unclear how the function of such systems will compare with those that are relatively less invaded [16,35–37]. Studying this issue offers the potential for significant insights into the factors that control ecosystem function (e.g. species diversity versus identity), while simultaneously addressing an issue of great applied importance.

invasion success in habitats that differed in the degree of specialization among their predatory and mutualistic organisms. Increased understanding of these issues could help to provide a more predictive framework for species invasions and could also improve our understanding of the roles of biotic interactions in structuring communities.

Conclusions

Insights into basic and applied research questions derived from the study of species invasions have been important in our emerging ecological, evolutionary and biogeographical understanding of the natural world. Importantly, the scope of the applied questions is not limited solely to the control and management of invasive species. Instead, the study of species invasions can also assist in the development of sound conservation, management and policy strategies needed to address many aspects of global change, including species extinctions, evolutionary diversification of species and ecosystem functioning (Box 4).

Acknowledgements

This research was conducted as part of the 'Exotic species: a source of insight into ecology, evolution and biogeography' Working Group at the National Center for Ecological Analysis and Synthesis, which is funded by NSF (Grant #DEB-0072909), the University of California and the Santa Barbara campus. We gratefully acknowledge valuable comments from four anonymous reviewers and the editor.

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