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An Essay on Some Topics Concerning Invasive Species

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Abstract There is a tendency for both scientists and lay people to regard invading alien species as inherently 'bad' and native species as inherently 'good.' Past invasions occurred commonly without human assistance. They rarely caused large, lasting decreases in species richness or ecological damage. Current invasions provide opportunities for scientific study. They are unintentional, uncontrolled experiments, which can provide insights into attributes of successful colonists, relationships with native species, and impacts on the structure and function of ecological systems.

Key words: Biogeography, biological invasions, colonization, exotic species, invasive species, species richness.

INTRODUCTION

One of the senior author's fondest memories is a drive with Marilyn and Barry Fox and Astrid Brown in 1990 through Myall Lakes National Park in eastern New South Wales, Australia. Barry was driving and Marilyn was sitting in the front passenger seat. Together they were pointing out objects of natural history interest. Periodically we would stop and get out to examine more closely something special: a rare plant, bandicoot diggings, or an area that had burned some known time ago. More frequently, however, we stopped so that Marilyn could wage war on an exotic plant. Seedlings and small saplings of Pinus radiata*, a tree native to North America, were growing along the roadway. Each time Marilyn spotted one, she would command Barry to pull over, charge out of the car, pull up the offender by the roots, knock off the soil, and toss the remains into the road. At one point the requests to stop became so frequent – several times within 100 metres – that Barry gently questioned the practicality of the exercise. Marilyn replied, 'But Barry, it's terribly invasive, and besides, this is a National Park!*

This little vignette illustrates some characteristics of exotic species. Not only were hundreds of plant and animal species intentionally imported into distant parts of the world during the last few centuries, but thousands of additional species have colonized and spread despite efforts to prevent accidental introductions. Some regions have been much more severely invaded than others. These include not only oceanic islands but also the temperate habitats of the southern continents: Australia, southern Africa, and South America. Human-assisted invasions of alien species can be viewed as unintentional, uncontrolled experiments. On one hand, they are the bane of agriculturists, conservation biologists, and natural resource managers, because they sometimes cause enormous economic losses and substantial short-term ecological changes. On the other hand, they should be viewed in the context of 'natural' colonization events that have occurred without human intervention throughout the Earth's history. Studying the process and consequences of the human-caused invasions can yield valuable insights into the ecological and evolutionary processes that generate and maintain biodiversity.

There is no denying that the foreign invaders often elicit a visceral emotional response. There seems to be something deep in our biological nature, related to xenophobia toward other humans, that colours our view of alien plants and animals. There is a tendency to treat foreigners differently from natives: with distrust, dislike, even loathing. Coupled with this is a tendency to view some prior condition as 'pristine' or most natural, and therefore the state that should be preserved. Perhaps these are the reasons why people would advocate extermination of a species just because it was originally imported from some other place. This is the view, not only of lay people, but also of naturalists, including academically trained ecologists, evolutionary biologists, and biogeographers. Recently in the United States, the Union of Concerned Scientists (2003) claimed that 'the accelerating introduction and spread of invasive species is among the most serious of threats to global biodiversity'. What is there about exotic species that draws such strong responses from both the environmentalist and scientific communities? On one hand, we know that long periods of geographical isolation have allowed the evolution of divergent endemic biotas on oceanic archipelagos such as Hawaii and the Galapagos, island continents such as Australia, Madagascar, and New Caledonia, and other regions

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such as southern South America and southern Africa. These biotas have been severely impacted by human activities. Many native endemic species have become extinct or are seriously endangered, and many alien species have become established. A cause–effect relationship between these two phenomena has often been inferred, even though it is difficult to isolate the effects of invasive species from other human impacts.

Conversely we scientists know that the earth and its biota have always been very dynamic in space and time. The fossil record shows many episodes of massive invasions and extinctions as asteroids impacted, land masses collided and drifted apart, seaways opened and closed, sea levels rose and fell, and climates changed. The earth is currently experiencing yet another episode of drastic change in environment and biodiversity. This time, however, instead of being triggered by asteroid impacts, tectonic events, or glacial–interglacial cycles, the changes are being caused by the enormous impacts of our own invasive species. Modern humans are altering climate, transforming habitats, connecting previously isolated lands or waters, exterminating species, and transporting organisms. The rates and magnitudes of these changes are among the largest that the earth has ever experienced. It should come as no surprise, then, that there have been equally large impacts on the abundances, distributions and diversities of organisms.

The purpose of the present essay is not to argue that exotic species are 'good' so that their spread should be fostered. It is not to suggest that modern humans should let nature take its course and elect not to intervene in the dynamics of dispersal and extinction, and the resulting impacts on biodiversity, ecosystem function and the economy. It is to plead for more scientific objectivity and less emotional xenophobia. Our purpose is to use biological invasions to address questions about the processes that determine species richness. What are the effects of invading species on biodiversity at scales from local to global?

HISTORICAL PRECEDENTS

Viewed relative to the sweep of evolutionary and biogeographical history, the magnitudes and consequences of recent human-assisted invasions are large but hardly unprecedented. Prior to the closure of the Isthmus of Panama about 3 million years ago, South America had been an island continent for more than 100 million years. It had developed a unique and rich endemic biota. The formation of the inter-American land bridge allowed wholesale invasion, both of South America by Northern Hemisphere forms and of North America by South American lineages. The resulting interchange was highly asymmetrical in both directions. Land mammals moved predominantly south, although a few southern forms, including the armadillo, opossum, and porcupine invaded far into North America. North American mammals not only colonized South America successfully, many lineages subsequently speciated and diversified, thereby contributing to the still ongoing replacement of endemic southern lineages by northern ones. More than half of the South American land mammal species are descendants of these North American invaders. Interestingly, however, the asymmetry was reversed in many other groups, including fish, amphibians, reptiles, and birds. For example, the small perching birds that dominate the North American avifauna are overwhelmingly of South American ancestry.

There were many other episodes of such wholesale invasion and biotic interchange. Many of these occurred in the marine realm, as tectonic and climatic changes broke down the barriers between previously isolated seas (Vermeij 1991). Others occurred on land, as previously isolated continents drifted together (for example Africa and India colliding with Eurasia), or falling sea levels gave mainland species access to previously isolated continental islands (for example the Indonesian islands of the Sunda Shelf). During the last several million years North America was repeatedly connected to Asia via the Bering land bridge. The result has been the intermingling of the Northern Hemisphere biotas, with asymmetries in most groups favouring Eurasian lineages. One of the most recent species to cross was *Homo sapiens*, which colonized North America only about 12 000 years ago. There can be no doubt that this invader had sweeping impacts.

Also largely overlooked is the fact that throughout the past, individual species dispersed across existing biogeographical barriers to invade new continents and islands, oceans and lakes. These independent colonization events were sporadic and infrequent, but over the millennia of the Earth's history, their numbers were large and their impact on global biodiversity was great. Truly oceanic islands formed as isolated volcanoes, so all inhabitants are descendants of invaders. The volcanic islands of Hawaii had acquired about 1300 'native' plant species and about 100 'native' bird species before human-caused invasions and extinctions began with the arrival of the Polynesians about 1700 years ago. Australia has been an island continent for about 40 million years, when its last connections to the ancient Southern-Hemisphere supercontinent of Gondwana were severed. Australia's rich endemic biota of Gondwanan descendents includes diverse species of eucalypts and marsupials. But throughout its history of isolation Australia has always been subject to invasion. Rodents first colonized perhaps 5 million years ago, and have subsequently diversified to give rise to about 65 species. By comparison, Australia has two species of monotremes and about 150 species of marsupials that are descendents of the original Gondwanan fauna. Long-distance colonization events, without human transport, continue today. Within the last 120 years, the cattle egret dispersed from its native Africa across the Atlantic Ocean to colonize South America, and it has since spread to become common throughout South America and southern North America.

Other waves of invasion have occurred in response to climate and habitat change. The northern third of North America and Europe was covered by vast continental glaciers as recently as approximately 20 000 years ago. With the warming of the climate and the retreat of the glaciers, these areas were rapidly recolonized. Within a few thousand years tree species had spread hundreds of kilometres from glacial refugia to occupy their current ranges (for example Davis 1986). During the same period mammals showed equally dramatic but more complex range shifts (for example Graham 1986; Lyons 2003). Within the last two centuries, many species of North American grassland birds and mammals expanded their ranges hundreds of kilometres eastward from the prairies to colonize newly created agricultural landscapes. Most of these have since retreated or become much less abundant, as eastern Canada and north-eastern USA have become reforested. Even more recently, several bird and mammal species have expanded their ranges tens to hundreds of kilometres northward in eastern North America in response to habitat changes and perhaps to global warming. Interestingly, other mammal species have shifted their ranges southward in the Great Plains of central USA, perhaps in response to changing climate or agricultural practices (Frey 1992).

So, biological invasions are nothing new. Over its history, the earth has experienced many invasions, sometimes in waves of many species, and often in independent single-species colonization events.

HUMAN IMPACTS

One thing that is different about recent invasions is that they were caused by and accompanied the invasion of *Homo sapiens*. Our own species has spread rapidly and recently from its origins in Africa to colonize the entire globe. Aboriginal humans colonized Australia and northern Eurasia within the last 100 000 years, North and South America within 12 000 years, and isolated islands such as New Zealand, Hawaii, and Iceland within about 2000 years. It is easy to underestimate the impacts of aboriginal humans. Nevertheless, their hunting caused extinctions of multiple species of mammalian and avian megafauna in northern Eurasia, North America, Australia, Madagascar, New Zealand and many oceanic islands. Human burning, tree-cutting and agriculture transformed landscapes and ecosystems in places as different as tropical northern Australia, temperate south-western North America, and boreal Iceland. Another wave of changes began within the last few hundred years, as Europeans and their technology spread throughout the world, triggering enormous human population increases, dramatic habitat changes and extinctions of many native species.

An historical perspective would suggest two things. First, the earth has previously experienced changes of a magnitude equal to or exceeding those caused by recent human activities. Human-caused extinctions, despite their sobering magnitude, do not yet approach the level caused by the asteroid impact at the end of the Cretaceous, 65 million years ago. That single event killed off more than half of all species then in existence, including all of the dinosaurs on land and the ammonites in the oceans. Similarly, historic invasions were comparable to the recent human-caused ones. The flood of species across the newly established Isthmus of Panama 3.5 million years ago caused wholesale still-lasting changes in species richness and composition throughout both North and South America. Recent changes in biodiversity caused by human-assisted invasions do not approach this absolute magnitude, although they may approach this relative magnitude on some islands.

The second insight from history is that the disruptions of biodiversity and ecosystem function caused by even the largest perturbations were only temporary. Recovery from the Cretaceous–Tertiary asteroid impact began almost immediately, and within about 10 million years diversity on land and in the ocean exceeded Cretaceous levels. In fact, recovery was so rapid that most palaeobiologists initially rejected the asteroid impact hypothesis of Alvarez *et al.* (1980). They thought that the extinction of dinosaurs and other changes in biodiversity had been much more gradual and were likely to have been caused by climate change. Ecologists in Australia and the Americas are only beginning to appreciate the impacts of aboriginal humans on biodiversity and habitats. For a long time they believed that the conditions described by the first European explorers and colonists represented a near-pristine state, minimally affected by humans. Now we know that aboriginal humans often had major impacts. For example, the present high biodiversity in Kakadu National Park in northern Australia was maintained by aboriginal burning practices. Now-extensive areas of tropical forest in southern Mexico and adjacent Central America were largely cleared by Mayan agriculturists.

Such an historical perspective suggests that the earth and much of its biota will survive the effects of modern humans. But human-assisted invasions of species, like previous unassisted invasions, will almost certainly leave a long-lasting legacy on biodiversity.

CONCEPTUAL BACKGROUND: THE SPECIES (DIS)EQUILIBRIUM

The species richness and composition of biotas at all scales, from local to global, reflects the interplay of the homogenizing effects of dispersal, the diversity-reducing effects of extinction, and the diversity-increasing effects of speciation and differentiation. How do these processes play out to affect biodiversity? What is the current effect and likely long-term legacy of human activities? Despite decades of research by ecologists, evolutionary biologists, palaeobiologists and biogeographers, we still lack definitive answers to these questions. In particular, there is still much disagreement about the extent to which species richness is regulated, and about the processes that govern species dynamics at different scales.

Population growth, colonization, and speciation are exponential processes that tend to fill up the world rapidly with diverse forms of life. These expansive propensities are opposed by limiting processes. Continual geological, climatic and biological perturbations cause population declines and extinctions that tend to empty the world of living things. The biota of every place on earth is poised somewhere in this continually shifting balance between filling and emptying. But how full is it? Where is it poised in relation to past disturbances and current limiting resources? To what extent can biological invasions be regarded as disturbance events that retard the build-up of biodiversity?

There have been two extreme views. Some ecologists and biogeographers have suggested that the biota is near carrying capacity for both individuals and species at most places on earth. The current abundance and diversity of life is close to the limits set by environmental resources. Some palaeobiologists point to the fact that after episodes of mass extinction, species richness seems to have returned rapidly to predisturbance levels due to bursts of speciation and diversification, and then to have slowed dramatically. Some ecologists point to the dynamics of secondary succession following disturbance, and the re-establishment of a climax community similar in species richness and composition to the predisturbance condition. They also point to the maintenance of relatively constant species richness over time in many habitats, despite changes in species composition due to environmental change. According to this view, ecosystems should either be resistant to invasion, or invasions should be balanced by extinctions so as to maintain approximately constant species richness.

The other extreme view would hold that most places on earth are well below their carrying capacity for both individuals and species. The world is unfilled because the present abundance and diversity of life is still recovering from past disturbance events. Some palaeobiologists point not only to the episodes of extinction that have reduced global species diversity, but also to the seemingly gradual build-up of diversity that appears to have continued long after each perturbation. Some ecologists point to the frequency of droughts, floods, fires, landslides, and other natural disturbances in ecosystems and to the fact that some level of perturbation appears to facilitate the coexistence of diverse species. Some biogeographers point to islands, and claim that lower species richness of insular biotas reflects an enduring legacy of disturbance and isolation; colonization and speciation have not yet filled islands with the number of species found in similar but less isolated habitats. According to this view, ecosystems should be susceptible to invasion, and colonizing exotics should cause net increases in species richness.

The equilibrium theory of island biogeography presents an intermediate view (MacArthur & Wilson 1967). This theory implies that at any given time, at least on oceanic islands and other isolated habitats, the number of species is in an approximate steady state. Species richness is maintained by a balance between opposing rates of colonization and speciation on one hand and of extinction on the other. Larger islands hold more species than small ones, because larger areas, with a greater variety of environmental conditions and resources, support larger populations and consequently have lower extinction rates. Less isolated islands support more species than distant ones, because they have higher rates of colonization to offset the ongoing losses of species to extinction. According to this view, isolated habitats are susceptible to invasion, because human transport has temporarily increased colonization rates and thereby increased the equilibrium species richness.

INVASIONS AS EXPERIMENTS

The study of invading species has much to contribute to resolving this debate, and to understanding how current environments, present barriers to dispersal, and legacies of past events affect biodiversity. Cases of invasion can be viewed as unintentional experiments. By altering species composition they provide invaluable information on ecological and evolutionary processes that regulate biodiversity.

We focus here on one pervasive effect of exotic species. Human-assisted invasions are increasing local species richness but decreasing global species richness. As emphasized by conservation biologists, there have indeed been many human-caused extinctions. Most species that have become extinct were initially relatively low in abundance and restricted in distribution. A large proportion of them inhabited islands. This loss of species is what we refer to as the decrease in global species richness. At smaller scales, however, the losses due to extinction of native species have on average been more than offset by the colonization of invading species. Already abundant and widespread species have expanded their ranges, more than compensating in local species richness for the restricted endemic forms that have disappeared.

This does not mean that the exotics have not caused extinctions. It simply means that locally there has on average been less than one extinction of a native species for every successful colonization of an alien species. This will come as a surprise to many who believe that biodiversity is decreasing everywhere on earth. But it is true, and for continents as well as islands. North America has more terrestrial bird and mammal species at present than when the first Europeans arrived four centuries ago. Although the passenger pigeon, heath hen and Carolina parakeet are extinct, and the California condor, red wolf and black-footed ferret are essentially gone from the wild, these losses are more than offset by the colonization of house sparrows, European tree sparrows, starlings, rock doves, ringed doves, monk parakeets, ring-necked pheasants, chuckar partridges, house mice, Norway rats, black rats, European hares, wild boars, feral horses, donkeys, oryx and many other species. Out of a total flora of approximately 6000 vascular plant species, California has more than 1000 naturalized exotics (Rejmanek *et al.* 1994), but fewer than 30 natives are known to have become extinct (Tibor 2001). The asymmetry holds even on islands and insular habitats. Colonizations of bird species on oceanic islands have approximately offset extinctions of natives, but in nearly all other taxa, species richness has increased (Sax *et al.* 2002). Within the last few centuries following European colonization, relatively few insular endemic plant species have become extinct, while invading species have approximately doubled the size of island floras: from 2000 to 4000 on New Zealand, 1300–2300 on Hawaii, 221–421 on Lord Howe Island, 50–111 on Easter Island and 44–80 on Pitcairn Island. Similarly, many islands, which now support several species of land mammals and freshwater fish, had few or no natives of these taxa historically (Sax & Gaines in press). These increases in local species richness might be taken as evidence supporting equilibrium theory – with increased species richness due to increased colonization rates as a consequence of human activities. However, they might equally well be taken as evidence that most habitats, on continents as well as islands, are below equilibrium or capacity to hold species due to legacies of historical disturbance.

There are exceptions to the predominant pattern: cases where invasion has caused a decrease in local species richness. In particular, there are well-documented cases where a single alien species has caused the extinction of one or more native species. Of course, the most dramatic example is provided by our own species, which hunted to extinction scores of mammal and bird species as it expanded its range and colonized new continents and islands. Within perhaps a few centuries after their arrival in Hawaii about 1700 years ago, the Polynesians had exterminated about 50 bird species, approximately half of the native avifauna (Olson & James 1982, 1984). Other examples of net extinctions attributed to invading species include the extermination of multiple species of native vertebrates by introduced mammalian predators: foxes and feral cats in Australia, brown tree snakes on Guam and mongooses and rats on many other islands. Impacts of diseases can also be severe, as witnessed by the loss of the American chestnut to an introduced fungal blight and by the virtual elimination of native bird species from the lowlands of the Hawaiian Islands by introduced avian malaria (Van Riper *et al.* 1986). We must be careful, however, in how we interpret such observations. For one thing, net extinctions in some groups, such as large mammals and flightless birds, may have been more than offset by net gains in other taxa, such as plants and insects. For another, extinctions of many native species cannot be attributed solely to invading aliens. The exotics may have played a role, but other human impacts, such as habitat destruction and fragmentation also contributed. For example, Gido and Brown (1999) reported that invading exotic fishes increased net species richness in 100 of 124 watersheds in temperate North America. Species richness decreased in 20 of the 24 remaining watersheds, but dams, water diversion, and pollution almost certainly contributed to these extinctions.

The net increase in local species richness due to invasions implies that not only islands but also most habitats on continents are not fully packed with species. It further implies that the native species are not efficiently using all available resources. New species establish and spread only by using resources. Sometimes successful invaders are able to exploit resources that were unavailable to the natives. Exotic fish species thrive in reservoir lakes in south-western USA largely because the lakes represent a new, human-created environment that the native river fish were poorly adapted to exploit. An exotic tree species is a successful invader on recent volcanic soils in Hawaii largely because it can 'make its own fertilizer' by fixing nitrogen, a trait that none of the native tree species possess (Vitousek & Walker 1989). At other times invaders pre-empt a share of the resources already being used by the natives. In extreme cases the invaders become dominant, while competitively inferior native species are reduced to subordinate status and may be driven to extinction. Introduced dingos, foxes and cats have become the dominant mammalian predators in Australia. Alien cheet grass and related *Bromus* species are now dominant plants across much of western North America.

The success of an invading species demonstrates the effectiveness of biogeographical barriers to dispersal. It shows that there are other places on earth, beyond its native range, where a species can establish and increase. It shows the role of geographical isolation in the origination and maintenance of biodiversity. It is this component of diversity, the species that are endemic to particular locales and regions, that is most threatened by human activities, including introduced species. The rare, restricted species are disappearing and the common widespread species are becoming even more abundant and widely dispersed. This has been referred to as the homogenization or cosmopolitanization of the world's biota (Brown 1995; McKinney & Lockwood 1999).

Is this decrease in global biodiversity a bad thing? Is the net increase in local species richness due to invasions a good thing? Is high species richness desirable? We do not believe that these are scientific questions. Science can elucidate the causes and consequences of these changes in biodiversity, but ultimately deciding what is good or bad is a moral and social issue. Few people would question whether the dozens of exotic flower and vegetable species in their gardens are desirable. The value judgements may change, however, if some of those same species were to become naturalized and spread into wild areas or to become serious weeds in agricultural fields. This is exactly what has happened, over and over again, in environments throughout the world. Exotic plants, originally imported for horticultural purposes, have escaped from cultivation and become invasive. Whether intentional or unintentional, human transport is breaking down the longstanding barriers that have generated and preserved much of the variety of life.

For better or for worse, modern humans are manipulating biodiversity in a colossal uncontrolled experiment. Scientists have the opportunity to record objectively the results. They have the obligation to explore the implications. But it is up to humankind as a whole to decide whether it is good or bad, and hence what actions should be taken.

This essay would probably have elicited a spirited response from Marilyn Fox. As a rigorous scientist, she would not have questioned the facts, except perhaps to ask for better documentation. As a dedicated conservationist, however, she would almost certainly have taken issue with the non-judgemental, dispassionate tone. Marilyn Fox was passionately and unabashedly Australian. She treasured the distinctiveness of her native land, its biota, and especially its plants. She devoted her career to studying natural history, educating her countrymen about their natural heritage, and preserving flora, fauna, and natural areas. She had answered the moral and ethical questions about exotic species. Native species were good and worth preserving at great cost. Those invaders from the northern hemisphere were bad and should be eradicated. She appreciated the irony of having acquired by marriage the name of one of Australia's most rapacious invaders. Debating these issues made for fondly remembered evenings around the Fox supper table: delicious food, fine wine, and stimulating conversation.

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