

Non-native invasive species and novel ecosystems

Daniel Simberloff

Address: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

Email: dsimberloff@utk.edu

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Abstract

Invasions by non-native species have caused many extinctions and greatly modified many ecosystems and are among the major anthropogenic global changes transforming the earth. Beginning in the mid-1980s, a dramatic burst of research in invasion biology has revealed a plethora of previously unrecognized impacts and laid bare the scope of the phenomenon. Similarly, research on various methods of managing invasions has expanded enormously, yielding incremental improvements in traditional methods and the advent of several new approaches, including the use of species-specific genetic and pheromonal methods. This research has advanced the field of restoration ecology, of which invasion management is a key component. Amidst this research progress, a group of critics has attempted to cast doubt on the extent of damaging impacts caused by non-native invasive species, the feasibility of counteracting them and restoring ecosystems, and the motives of scientists engaged in such endeavors. The criticisms are misguided but can potentially impede management of this pressing problem.

Introduction

Various non-native biological invaders have been noted for centuries, such as the phylloxera (a homopteran) that destroyed grapevines and devastated the wine industry in Europe in the 1860s [1] and the chestnut blight that entered North America in the early 20th century and virtually eliminated a dominant tree species [2]. By 1957, Charles Elton produced a series of BBC radio broadcasts about the general phenomenon of non-native invasions [3] and transformed the series into a book for a lay audience the next year [4]. Although particular invasions continued to attract great attention, Elton's book did not inspire a broad research thrust on invasions or a widespread public and policy response to their growing number. Rather, in the mid-1980s, an international project of the Scientific Committee on Problems of the Environment (SCOPE) engaged over 100 prominent scientists worldwide, produced several widely read edited volumes (for example, [5,6]), and triggered an explosion of research on invasions [3], which soon came to be recognized as one of the great ongoing global environmental changes, along with climate, nutrient cycle enhancement, and land-use changes [7].

This surge of research included many studies of how particular non-native invaders eat native species (for example, the brown tree snake in Guam [8] and the hemlock woolly adelgid in the eastern US [9]), compete with them (for example, the gray squirrel in Great Britain [10], crown vetch and tall fescue in the US Midwest [11], and the "killer alga" in the Mediterranean [12]), or infect them (for example, whirling disease of rainbow trout in the US [13]) and sometimes compete with them while vectoring diseases to them (for example, signal crayfish in Europe [14] and the gray squirrel in Great Britain [15]). However, two new lines of research have become increasingly prominent, both indicating that impacts of introduced species are more varied and widespread than had previously been thought.

First, in contributions to the SCOPE program, Peter Vitousek [16,17] described a different sort of impact. Rather than focusing on the population level (for example, as when the gray squirrel competes with the red squirrel in Great Britain and transmits squirrel pox) or the community level (affecting many species in the community, as when the brown tree snake eats all of

the forest bird species in Guam), he depicted impacts at the ecosystem level: **invasions that affected nutrient cycles and other ecosystem-level processes and features (such as fire cycles or hydrology)**. Research on such impacts in a variety of ecosystems has increased greatly, particularly in the new century [18,19], showing how a single introduced species can change processes or the physical structure of an ecosystem, or both, sometimes subtly and slowly, but in such a way as to affect a large fraction of the resident species, as in the study by Fukami *et al.* [20] on impacts of introduced rats on seabirds and many aboveground and belowground organisms on islands.

The other major new direction of invasion biology is a greatly increased focus on genetics and evolution as increasingly sophisticated and accessible molecular genetic techniques become available. Molecular genetic research has increasingly revealed a great number of cases of the “stealth” impact of invaders, hybridization, and introgression with native species (for example, [21]). The phenomenon had previously been detected almost exclusively phenotypically [22], but many phenotypic responses are sufficiently subtle that they are hidden amidst the normal variation of many natural populations. It is now recognized that substantial introgression can occur even between native species that never hybridize when a newly introduced species constitutes a genetic bridge between them [23]. **Introgression** can also cause substantial evolution of native species, as in the European wildcat, which hybridizes with feral domestic housecats [24]. **Hybridization** between native and introduced species can even produce new, more invasive species; the best-known example is common cordgrass, *Spartina anglica*, an invader that arose in England from hybridization between native *S. maritima* and North American *S. alterniflora* [21]. In addition to showing the great extent of hybridization between introduced and native species, molecular genetic features such as microsatellites, mitochondrial DNA, and single-nucleotide polymorphisms have increasingly been used to trace sources and routes of invasions (for example, [25]). **A major finding is that introduced populations often combine genes derived from multiple source populations, thus producing novel genetic combinations** (for example, [25]). In fact, some introduced populations arising from multiple sources have more genetic variation than any single source population (for example, [25]). Also, environmental DNA (eDNA) is increasingly used to detect invaders [26] and played a key role in showing the great advance of Asian carp toward the Great Lakes [27].

The burst of research in the wake of the SCOPE project also revealed an increasing number of cases of

“invasional meltdown” [28], in which two or more introduced species facilitate one another’s establishment or enhance one another’s impact on native species [29], as when the “honeydew” from introduced scale insects increases introduced ant populations [30] or when introduced birds disperse seeds of introduced plants [31]. **In addition, an increasing number of “lag effects” have been detected, in which full-fledged widespread establishment and impact of an introduced species lags for years behind initial arrival.** The reasons for such lags are various [32], and some remain mysterious, but the commonness of the phenomenon cannot be doubted.

A reaction and response

The many threads of 25 years of increasingly intensive research on biological invasions all lead to the conclusion that problems caused by the phenomenon are numerous, often tremendously important ecologically or economically worldwide, and growing apace with globalization [33,34]. **Amidst this plethora of publications, a small but persistent group of critics has assailed the field of invasion biology and much of the invasion management effort on a variety of grounds [35], eliciting a spirited response [36]. Some critics go so far as to call for an end to invasion biology as a scientific discipline [37–39]. The objections fall primarily into five categories [40]: (1) The problems are overblown, and similar impacts arise from native species; most introduced species are not problematic. (2) In some instances, introduced species increase native biodiversity. (3) The antipathy toward introduced species is xenophobic. (4) In the face of globalization, we cannot substantially slow the spread of invasions; it is a hopeless battle. (5) For sentient animals, such as mammals, the methods used to combat invasive species are inhumane; in any event, individuals of the targeted species have a right to exist.**

Criticism 5, which is part of a philosophical dispute that is not near resolution, revolves around the issue of the relative weight of rights of individuals and rights of collective entities such as species [41]. **Consideration of criticism 2—which is based on the fact that, in some local biotas, the number of established introduced species exceeds the number of native species locally eliminated (whether because of introduced species or not)—should be tempered by the fact that many complete species extinctions have been wholly or partly caused by introduced species, especially but not exclusively on islands [34,42]. In addition, in many instances, species populations, though not eliminated, are reduced to a small fraction of their previous numbers. Biodiversity in terms of species numbers is not lost, but there is a major functional and demographic change.** Criticism 3 is an assertion, generally leveled as part of a social

construction of the science of invasion biology and management with scant or no regard for the impacts of invasions that are the stated purpose of the disputed activities [41,43].

The key criticisms from an ecological standpoint are 1 and 4: which introduced species really cause harm, and can we really do anything about it if they do? It is true that most introduced species are not known to cause significant harm. However, modern invasion biology is very new [3,44], and the great majority of introduced species have not been studied in their introduced ranges, and so it is not possible to say that they have no significant impact. Perhaps the most comprehensive study of this matter [45] found, for Europe, that for only ca. 10% of some 11,000 introduced species has impact been documented, but that this is likely to underestimate the number actually causing impacts because of the dearth of research. One of the major recent research thrusts of invasion biology, as noted above, is unraveling various ecosystem impacts, some of which are initially subtle and take a long time to be manifested (for example, shifts in nutrient cycling). Vilà *et al.* [45] also found that, of introduced terrestrial vertebrates and freshwater plants and animals, about 30% are known to have harmful impacts.

In addition, the lag effect noted above [32] suggests that it would be foolhardy to wait for an impact to be recognized before acting. By then, the invader may well have spread beyond the point at which eradication or containment is possible. Furthermore, although some native species in certain circumstances (almost always associated with some other anthropogenic environmental change [46]) do cause impacts of the sort frequently associated with introduced invaders [47], the relative frequency of such impacts is far less than for non-native species [46,48,49]. Meanwhile, there is growing recognition of the great extent and variety of impacts of introduced species [33,34]. The lag effect, the subtlety of some impacts that have been occurring from the outset of the introduction, and the greater propensity for non-native species to cause harm mean that the suggestion [35] to manage invasions only after impact is evident is ill advised.

Attempts to identify which species, if introduced, would be likely to become invasive have had some success (for example, [50]), inspiring the construction of several risk assessment tools, especially for plants [51]. The most prominent is the Australian Weed Risk Assessment (AWRA) [52], which has been refined and adapted for use in permitting introductions in many other regions. None of these tools is foolproof (for example, the AWRA

fails to reject about 10% of known invasive plants in Australia), and the multiplicity of factors (including chance) that affect whether an introduced population survives, spreads, and becomes invasive will certainly limit their accuracy [51]. Nevertheless, they have been valuable in preventing some planned introductions that would likely have led to invasions, and the same tools can be used to identify recently introduced, restricted populations that should be prioritized for rapid attempts at eradication or containment.

The effort to prevent invasions or to reverse or mitigate their impacts is not hopeless [53]. Biosecurity can be very effective, as evidenced by great improvements in New Zealand as interdiction procedures became more stringent (for example, [34]). The impediments to improved biosecurity are primarily sociopolitical and economic, not technological. Similarly, the technology exists for greatly improved early detection and rapid response [33,53]; employing them is a matter of political will. Once a population is established, it is possible in some cases to eradicate it, and the technology to do so has improved greatly [53]. Increasingly ambitious eradication projects are being undertaken, and they are marked by striking successes; the current frontiers for vertebrate eradications are attempts to eradicate multiple species simultaneously, attempts to eradicate invasive species on larger islands and even continents, and attempts to eradicate invasive species on islands inhabited by humans (unpublished data). Terrestrial plants, insects, and aquatic organisms have been the most refractory targets for eradication. However, there have been striking eradication successes even for these taxa when populations have not yet spread widely beyond the initial introduction site (for example, [54,55]).

When eradication fails or is not attempted, many technologies can be employed to maintain populations of invaders at low densities [53]. The main, widely applied approaches are physical control (such as pulling weeds by hand), mechanical control (use of machinery), chemical control (use of herbicides and pesticides), and biological control (introduction of natural enemies of a target invader, from its native range). Each of these methods has succeeded in many instances and failed in others, and sometimes these methods have had undesirable non-target impacts. However, incremental improvements in techniques for all of these methods are leading to higher success rates and fewer non-target impacts [53,56].

Many other technologies have been successfully applied to particular taxa. For instance, sterile males have been used in many maintenance management and even eradication programs for insects, especially flies [57,58],

and pheromones have been used to disrupt lepidopteran mating [59] and to trap sea lampreys [60,61]. Efficacy of the Judas-animal technique, widely used in mammal control and eradication programs, has recently been greatly improved by the use of hormone injections to prolong estrus [62]. Autocidal methods using genetic manipulation were proposed in the 1960s and 1970s but not implemented then. Today, with the advent of various genetic manipulation techniques, including transgenes, several such projects have advanced to the proof-of-concept stage, particularly for dipterans and fishes [63], and a similar approach has been proposed for plants [64]. In sum, it is simply untrue that it is futile to fight invasions.

A related controversy

A simultaneous and related call for the end of traditional restoration ecology [65–69] as part of a “new world order” [65] accompanied the calls for an end to invasion biology [39]. This is perhaps unsurprising, as a very large component of restoration ecology consists of eliminating or managing non-native invasive species [70,71], and the underlying argument of the advocates of abandoning traditional restoration ecology in favor of “novel ecosystems” has been that the overwhelming forces of invasions by non-native species and climate change have rendered obsolete the entire notion of returning an ecosystem to some historical state. Among prominent advocates of promoting novel ecosystems and abandoning traditional restoration ecology are several of the critics of invasion biology and management [39], and authors of articles for lay audiences, such as Emma Marris [72,73] and Fred Pearce [74,75], have vigorously promoted both agendas.

The contention that novel ecosystems are so inevitable as to constitute “the new normal” [72] is incorrect on several grounds [76]. For one thing, “novel ecosystem” is undefined, at least in operational terms. In no instance is it stated what specific criteria show that an ecosystem is now novel or what thresholds it has passed to achieve this status. All ecosystems are constantly changing, even without anthropogenic influences [77–81], leading Pickett *et al.* [79] to propose the metaphor of the “flux of nature” to replace “balance of nature”. Contrary to claims by advocates of fostering and molding novel ecosystems, modern restoration ecology does not attempt to recreate the past; rather, the goal is to re-establish the historical trajectory of an ecosystem before anthropogenic influences derailed it [71]. This goal has been endorsed by the United Nations Convention on Biological Diversity, the European Commission, and major non-governmental organizations such as the International Union for the Conservation of Nature [76].

Another problem with the rush to embrace novel ecosystems as a goal is that the sense that much of the earth is rapidly changing to some sort of novel condition is based partly on maps, such as the human global footprint [82], drawn at far too coarse a scale [76]. The claim that we can do nothing to redress anthropogenic changes is also unwarranted [76]. The field of restoration ecology is very young and has learned much in a short time from past mistakes [39,70]. Meta-analyses show considerable progress in achieving restoration goals in a variety of ecosystem types, and impressive specific cases abound [76]. There is no evidence that any particular ecosystem cannot be restored in the sense of modern restoration ecology; the impediments are economic and political, not scientific and technological [76]. This does not imply that society should undertake to restore every ecosystem; each case should be considered by all stakeholders in terms of desirability, cost, and resource availability [76].

Influence of controversies

Policymakers and the general public whose interests they should represent can easily be misled by what they perceive to be the existence of a scientific controversy, and policymakers have used such “controversies” to forestall action on environmental problems [83]. The “debate” about anthropogenic climate change comes immediately to mind. The drumbeat of claims that the entire enterprise of modern ecological restoration is futile can perniciously influence policy at a time when many nations are undertaking ambitious restoration projects, and the United Nations, the three Rio Conventions, and many governments and large non-governmental organizations have all called for greatly expanded restoration efforts [76]. At the least, the contention that novel ecosystems are inevitable and perhaps desirable encourages any tendency to delay prevention and redress of various harmful environmental impacts rather than to undertake new approaches and to devote new resources to long-term solutions to environmental problems [76]. The same inimical influences on policy are exerted by critics of invasion biology and management. For instance, Larson and Palmer [84], in a policy-oriented journal, not only cite “emerging thinking” about novel ecosystems without mention of any of the weaknesses of the concept but cite Davis *et al.* [35] and Schlaepfer *et al.* [85] as calling into question the damage caused by invasive species without mentioning that these authors represent a small minority of scientists or citing specific rebuttals of those articles [36,86]. Critics of invasion biology and restoration ecology are not likely to keep these vibrant growing fields from progressing scientifically, but they will be able to slow the transformation of scientific knowledge into actions on the ground.

Abbreviations

AWRA, Australian Weed Risk Assessment; SCOPE, Scientific Committee on Problems of the Environment.

Disclosures

The author declares that he has no disclosures.

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