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Are invasive species a major cause of extinctions?

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The link between species invasions and the extinction of natives is widely accepted by scientists as well as conservationists, but available data supporting invasion as a cause of extinctions are, in many cases, anecdotal, speculative and based upon limited observation. We pose the question, are aliens generally responsible for widespread extinctions? Our goal is to prompt a more critical synthesis and evaluation of the available data, and to suggest ways to take a more scientific, evidence-based approach to understanding the impact of invasive species on extinctions. Greater clarity in our understanding of these patterns will help us to focus on the most effective ways to reduce or mitigate extinction threats from invasive species.

Ecologists, conservation biologists and managers widely believe that invasions by non-native species are a leading cause of recent species extinctions [1,2]. The introduction and spread of non-native species has become a global ecological and conservation crisis as invasive organisms are increasingly altering terrestrial and aquatic communities worldwide. The loss of biodiversity and species extinction are, likewise, major ongoing crises. Native species declines often occur simultaneously and in the same place as invasion by non-native species, leading many conservationists and researchers to believe that invasions and extinctions are closely linked.

We suggest that there are several problems with the seemingly inextricable link between species invasions and the extinction of natives. To date, there has been insufficient critical evaluation of overall global patterns of the extent to which invasion is implicated in extinctions, or the conditions and circumstances under which invasions are most likely to lead to extinctions. We aim to prompt a more critical evaluation of these data, and to suggest ways to take a more scientific, evidence-based approach to understanding the role of invasive species in extinctions.

What do we know about invasive species and extinctions?

Existing data on causes of extinctions and threats are, in many cases, anecdotal, speculative, or based upon limited field observation. Although it is clear that obtaining quantitative and experimental data are impossible under many circumstances, the problem remains that correlation is too often assumed to imply causation. For example, severe habitat alteration (e.g. deforestation), decline or extinction of native plants, and the proliferation of exotic plant species commonly co-occur. Are non-native plants causing the decline of natives, or are the decline of the natives and the proliferation of the exotics both a result of habitat alteration? It is important to distinguish between these alternatives: is removing exotics essential to prevent the extinction of endemic natives, or is it largely a waste of managers' time and effort? Multiple threats can also act synergistically to cause declines or extinctions. However, if invasives are not a primary cause of extinction or major contributors to declines of species (locally or globally) but are instead merely correlated with other problems, the resources and efforts devoted to removing exotics might be better focused on more effective means to preserve threatened species.

The overarching category 'threatened by aliens' might also be misleading, for two reasons: we must distinguish the relative importance of different functional groups in causing extinctions, and also examine whether broad groups of invasives, or merely particular species, are largely responsible. Based upon theory and observational data, alien predators and pathogens have been predicted to be far more likely than exotic competitors to cause the extinction of native species [3].

Even within functional groups, a few species appear to have caused a disproportionate share of incipient and actual extinctions. A few widespread rat species, feral pigs (as in Hawaii, Box 1), several predatory snakes (particularly on islands), possibly annual Mediterranean grasses and several other plants, a few microbial pathogens and a finite list of other invaders might be responsible for most of the extinction risk posed by aliens. Alien plants might be more likely to cause displacement and community change rather than causing species extinctions. This is the case, for example, for *Psidium cattleianum* in rainforests in Madagascar, where its presence has altered diversity patterns in communities that were disturbed as long as 150 years ago, but its presence has not resulted in the loss of native plant species [4]. If a few cosmopolitan invaders are causing the extinction of many native endemics, we should focus on those particular invasive species, rather than on alien species in general, to mitigate extinction risk. The better we understand both patterns and mechanisms causing declines, the better we can focus our efforts on the most effective ways to reduce or mitigate threats.

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Box 1. Leading alien agents of extinctions?

High profile invaders are often implicated in species extinction. However, when the data are more thoroughly examined, their role as the direct causes of extinction can be drawn into question in some cases. Although extinction might be coincident with the appearance of invaders, it can be difficult to disentangle the relative impacts of the invader and other stressors. The Nile perch (*Lates niloticus*) introduced into Lake Victoria during the 1960s is frequently implicated in the extirpation of native cichlids from the lake [11–13], but the decline in cichlids probably started during the 1920s with the development of railroads, erosion, and shoreline destruction [12]. Urbanization during the 1970s increased eutrophication and decreased lake transparency from 8 to 1.5 m [12,13]. With increased nutrient loading, anoxic events resulting in fish kills are now common. Increased nutrients appear to favor another invader, the water hyacinth (*Eichhornia crassipes*), which has also been implicated in fish declines by altering nursery areas for juvenile fishes [11]. But removal of both water hyacinth and the Nile perch, even if possible, would not solve the problems created by altered land use and nutrient pollution.

Zebra mussels (*Dreissena polymorpha*) are currently considered to be the major threat to North American freshwater unionid bivalves [14]. Of a historic 281 species, 19 are known to be extinct, 21 are thought to be extinct, 77 are endangered, 43 are threatened, and 72 are of special concern. Zebra mussels require hard substrates for attachment. In lake bottoms hard substrates tend to be rare, and the shells of native bivalves offer the most abundant substrates for zebra mussel settlement. Overgrowth by zebra mussels can make it difficult for unionids to burrow and move through sediment, can increase drag and the likelihood of dislodgment by water motion, can occlude the openings in unionid valves, prevent opening for respiration, feeding and reproduction, and zebra mussels may directly compete with unionids for food [15]. Nevertheless the role of zebra mussels in unionid declines in North America is unclear. Unionid declines began long before zebra mussels were introduced during the mid-1980s [16] and, to date, no species have gone extinct as a result of the introduction of zebra mussels. Pre-introduction declines were caused by habitat destruction and deterioration resulting from water diversion, erosion, an increase in eutrophication (which causes periods of anoxia), pesticides, loss of host fish for parasitic unionid larvae, historic harvesting for the button industry and harvesting for the pearl industry [15,16].

There are several well known cases in which invasions are strongly linked to extinctions. In some of these, invaders have been a major cause of the decline and loss of species. For example, the predatory brown tree snake *Boiga irregularis* was introduced into Guam during the early 1950s and has since been linked, both directly and indirectly, to the extinction of the native vertebrate species [2]. However, in other cases, the picture is less clear (Box 1).

Several recent papers have questioned the link between invasion and loss of diversity [3,5–7]. These studies do not directly address whether invasions are causing the extinction of native species but focus on the total number of species before and after invasion. Although this approach is intriguing, total numbers do not tell the whole story. Most ecologists would not, for example, regard the establishment of five new widespread alien species in a region as 'biotic compensation' for the extinction of five endemics.

Case studies of particular instances of exotic species as major contributors to extinction on the one hand, and counts of numbers of species before and after invasions on the other, each offer insights into whether invasions are a major cause of extinction. However, can we say anything more general about whether the invasion of exotic species is a major cause of the disappearance of natives? Are there some conditions under which, or some kinds of species or systems in which, this is more likely to occur? To answer such questions, it is necessary to synthesize quantitatively the results of many case studies, preferably of the highest-quality data that can be obtained.

Assessing the contribution of alien species to native declines

Until recently, it has not been possible to quantify or assess general patterns of threats to endangered and threatened species (and causes of extinction), because data on threats and causes of extinction were limited and scattered. Several recent major efforts to collect and compile such data and to categorize threats and causes of extinction are beginning to make this information available and searchable electronically. Two of the most important sources are Wilcove *et al.* [1] for the USA, and the International Union for Conservation of Natural Resources (IUCN) Red List [8] for species threatened worldwide. We examined these two sources to evaluate some of the widespread assumptions about invasion and extinction.

Generalizing from available information on threats

These and other similar data sets are invaluable assets in efforts to begin to better understand the nature of the causes of decline for threatened or extinct species. All currently available data have inherent limitations: most of the information is based upon unpublished observation and impressions, and is highly variable in quality, depending upon the observers and the system and taxon in question. Most imperiled species face more than one threat, and it is difficult to disentangle proximate and ultimate causes of decline or interactions between different threats and to evaluate their relative importance. Exotic species might be a primary cause for decline, a contributing factor for a species already in serious trouble, the final nail in the coffin or merely the bouquet at the funeral.

Although there are limitations to the data available on causes of extinction threats, assembling these large databases is a difficult task. We believe that these data compilations, even given their limitations, are more valuable and offer more information in assessing overarching patterns than does attempting to generalize from individual case studies, because the compilations present the opportunity to obtain a more comprehensive picture of the nature of threats. Although it is a daunting task, we must begin to identify general patterns of the role and importance of invasions in extinctions as best as we can, to attempt to understand the nature of global threats to biodiversity and prioritize our responses to these threats.

Species imperiled by aliens in the USA

Wilcove *et al.* were the first to quantify data on threats to imperiled species based upon a range of sources, including

Table 1. Numbers of species affected by different threats believed to be responsible for causing population declines[a]

Causes of decline	All species [930]	Plants [602]	Birds [68]
Direct human habitat destruction and fragmentation, including logging, road building and diversion of water	497	233	48
Exploitation (hunting, fishing and collecting) and poisoning and/or trapping	90	19	11
Fire and changes in fire regime	102	92	1
Pollution (herbicides, pesticides, oil spills, etc.)	32	4	5
Invasive alien predators and herbivores	131	73	39
Alien plants: competition and indirect habitat effects	431	410	19
Competition with exotic animals (excluding feral and domestic animals)[b]	67	0	14
Feral pigs (herbivory, predation, competition and/or habitat effects)	268	257	8
Grazing and/or trampling by domestic and feral cattle, goats, sheep, horses and burros	327	295	13
Hybridization with alien species	22	5	0
Diseases (including alien and native species)	33	3	23
Parasites (physiological and behavioral)	3	0	2
Other or unknown	169	134	8

[a]Reclassification of data on all of the cases in which species were categorized as being imperiled by aliens by Wilcove *et al.* ([1], http://www.natureserve.org). Categories are nonexclusive and so numbers do not sum to total species numbers.
[b]We believe that domestic cattle should be categorized separately from alien invasive species, even though they are non-native in most areas in which they affect native species. Unlike invasive aliens, the population sizes and distribution of cattle are usually controlled by humans. Thus, cattle are not invasive in any of the usual meanings of the word, although they might have large effects on native populations, communities and ecosystems.

published sources, government lists and interviews with specialists familiar with particular species and regions [1]. The paper is widely cited and is the primary source in the literature for the belief that invasive species are a direct and leading cause of extinction. The authors reported that habitat loss was the greatest threat to imperiled species within the USA (threatening 85% of the species classified as imperiled), followed by alien species (threatening ~50% of species). Wilcove *et al.* [1] examined 2490 USA species categorized as threatened, of which 1880 species had specific threat data. We reanalyzed the Wilcove *et al.* [1] data for the 930 species that they categorized as being imperiled by aliens (i.e. the half of their dataset for which species were listed as being affected by aliens). We classified each threatened species according to all of the particular classes of threat (Table 1, plus a single class for otherwise unclassified or unknown threats) listed as affecting it.

We found that these threatened species are, on average, faced with 2.5 specific types of threat (of those listed on Table 1) per species. Species in two of the largest threatened groups, plants and birds, are both typically affected by multiple threats (2.6 threats per species for plants and 2.8 for birds). Hawaiian endemics constitute a large proportion of the imperiled USA birds (43%) and plants (39%) threatened by alien species. By looking at the nature of the combined threats to these species, we can make several inferences (Box 2). If feral pigs, goats and alien plants are causing the declines of many native Hawaiian plants, are the alien plants the primary, or even a contributory, cause of the decline in natives, or are they coincidental to the disturbance caused by feral pigs and goats? It is not possible to distinguish between these alternatives definitively with these data. However, if competition with alien plant species was a primary

Box 2. Threats by aliens to USA species (see [1] for details and definitions)

There are 602 USA plant species affected by alien species (of 1055 threatened plants, http://www.natureserve.org). However, competitive displacement by aliens is rarely described as posing the only threat to a native plant. Of these 602 species, 20% are threatened by both habitat loss and by exotic plant species. Almost 40% (231 species) of all plants listed as imperiled by alien species in the USA are Hawaiian endemics that are imperiled by the 'vicious triumvirate' of feral pigs, goats and alien plants (and often cattle). This is a particular problem because these threatened plants occur in areas that are protected, or are otherwise not currently subject to habitat loss or direct habitat destruction by humans.

But how much of a threat do the alien plants pose themselves? Of all the USA plants considered imperiled and affected by aliens, only 4% are affected only by alien plant species but not by cattle, pigs, goats, or other alien herbivores, or by direct habitat damage (i.e. 2.3% of the total imperiled USA plants; http://www.natureserve.org). Alien plants affect native plants in combination with habitat damage by humans, or by pigs, goats and cattle. For example, *Xylosma crenatum* (=*X. crenata*, Flacourtiaceae, no known common name) is an endangered (<20 extant individuals) montane tree that is endemic to Kauai in the Hawaiian Islands. Its decline has been attributed to competition from invasive exotic plants (http://www.natureserve.org). However, major threats to the survival of this species also include habitat loss and degradation caused by domestic livestock and feral pigs, and intrinsically low reproductive rates [8].

For birds, population declines for 68 of the 98 imperiled species in the USA have been attributed to aliens (Table 1, main text; http://www.natureserve.org). Direct effects of habitat destruction by humans, and hunting or collecting are also major threats ([1], http://www.natureserve.org). Alien predators presented the greatest threat of all alien groups, threatening 57% of the bird species affected by aliens (of a total of 68 species), followed by alien pathogens (all in Hawaii, representing 34% of the birds affected by aliens of all kinds); feral pigs and goats and domestic cattle also play a destructive role, as do other exotic animals acting as competitors (alone or in combination affecting 47% of the birds affected by aliens; see also Table 1, main text). Alien plants also appear to affect birds, threatening 24% of the bird species affected by aliens, but most of these are affected by both alien plants and direct habitat damage by humans (<6% are affected by alien plants but not habitat destruction). Here, again, the evidence for damage owing to plants is correlative, and it is unknown whether the alien plants played a definitive causal role in the decline of any bird species. For bird species that are affected by multiple agents, direct habitat destruction by humans in addition to alien predators affected 38% of the birds affected by aliens. Another 19% of these threatened birds are affected by alien predators but not by direct habitat destruction by humans, suggesting that alien predators play a more direct role in bird declines than do alien plants in the decline of either plants or birds.

cause for population declines in native plants, one would expect >2–4% of species to be affected by invasive plants alone.

Alien predators and competitors threaten many of the imperiled bird species (Box 2). However, although 28% of bird species were listed as being negatively affected by alien plants (presumably owing to alterations in habitat or food resources), only four bird species were listed as being affected by alien plants species but not by the direct effects of humans on their habitats. Consequently, until we have better data, it is difficult to know whether the alien plants are responding opportunistically to the same habitat damage that is negatively affecting the birds, or if the effects of the alien plants on native bird habitats are harming bird populations.

Global data from the IUCN red list

The IUCN Red List [8] includes documentation of 18 318 species that are extinct, endangered, or threatened globally. (Not all countries and all imperiled species are included, owing to insufficient data.) The IUCN Red List is the most comprehensive database available for the conservation status of threatened plant and animal species globally. In contrast to the USA data, we examined the entire database, not just those species threatened by aliens. We used the threat categories specified by that database.

Threat data are not available for all species on the IUCN Red List; most of those with such data list multiple threats. Of the species with known threats, 33% (6069) include habitat loss and alteration as a cause of decline or potential threat. Exploitation (e.g. hunting, fishing, trapping and poisoning) is listed as a cause of decline for 7.6% of species. Only 6% of imperiled taxa list direct and indirect effects of all kinds from naturalized alien species as contributing to their decline (Table 2); that is, more than five times as many species are categorized as being threatened or endangered by habitat loss than by alien species.

Competition with invasive species is implicated as a threat to three times as many plants as animals, whereas predation or herbivory by invasives threatens about twice as many animal as plant species (Table 2). Strikingly, more than three and a half times as many plant species have been affected by livestock grazing and trampling than by either competition with or herbivory by non-domesticated, invasive aliens; livestock threaten almost as many animal species as are threatened by alien predators and many more than are affected by alien competitors (Table 2). Many of the plant and animal species threatened by alien species are also threatened by other factors, especially habitat destruction, and some threatened groups (particularly freshwater fish) tend to be affected by both competition and predation from aliens.

Table 2. Numbers of species affected by alien species and livestock from the IUCN Red List (of 18 318 species total)[a]

Threat	No. of species affected
Alien species (naturalized)	
Direct effects of all kinds, including effects of an unspecified nature	911
Competition from aliens	137
Effects on plants	100
Effects on animals	37
Herbivory and/or predation by aliens	161
On plants	48
On animals	113
Alien pathogens and parasites	58
Indirect effects (habitat alteration, etc.)	172
Affecting plants	108
Affecting animals	63
Livestock (domesticated)	
Effects on plants	521
Effects on animals	92

[a]Calculated from data from [8].

Little is known about the specific causes of extinction for most species that are already extinct [8]. Of the 762 species globally documented to have become extinct as a result of human activities in the past few hundred years, <2% list alien species as a cause.

All invasions are not created equal

Much of the discussion of the threats to biodiversity posed by invasions is couched in overarching terms, as though all invasive species pose equal threats, and all invaded communities are equally threatened. This is certainly not true.

Of all of the modern extinctions catalogued in the IUCN Red List [8], most are species from terrestrial habitats (570 species), followed by those from freshwater habitats (222), with fewest modern extinctions occurring in marine habitats (21, mostly sea birds). More terrestrial than aquatic species are also endangered or otherwise impacted by aliens. For all species in the IUCN Red List, aliens directly affect 882 terrestrial species (of 15 504 species total, 5.7%), 59 of 3042 freshwater species (2.0%, mostly birds) and 87 of 737 marine species (11.8%, mostly sea birds). For all marine species considered to be critically endangered and impacted by aliens (one mammal and 14 birds), other causal factors, in addition to alien species, are also listed. Of the 21 total marine species listed to have gone extinct (four mammals, 11 birds, one fish, four molluscs, one alga), none are attributed to invasive alien species; most were extinct before 1900 and before many modern invasions. Marine species are considered to have very low risks of extinction because the size of the oceans of the world creates large continuous habitats, and because the open nature of marine habitats and the life-history characteristics of many marine species result in extensive dispersal potential to recolonize and repopulate depauperate areas ([9], but see [10]).

We also considered the evidence for the prediction that introduced predators would be more likely to cause extinctions than would introduced competitors [3]. These predictions are only partially supported by patterns that we found for the data sets that we looked at. Neither the effects of competition nor predation were definitively greater overall in either data base. For example, in the Red List data, plants were threatened more by competition than were animals, whereas for predation the results were opposite (Table 2). Domesticated livestock and feral grazers (cattle, goats, pigs, etc., including the physical disturbance that they cause) affected more plants

than did either competition or predation, and roughly as many animal species as did predation (Tables 1,2). We suggest that the contrasts between the effects of aliens in aquatic versus terrestrial systems are at least as important as the differences between alien competitors and predators. Future data syntheses, as well as the development of theory, must go beyond comparing the effects of alien predators and competitors to consider a greater range of contrasts among functional types of invader and systems invaded to reach a better understanding of these patterns.

Conclusions

Invasive exotic species are causing dramatic changes in many ecological systems worldwide, and there is no question that invasive species are profoundly altering many communities and ecosystems. Seeing these widespread changes, biologists, environmentalists and managers are alarmed about invasions leading to large-scale declines and extinctions of natives. This might prove to be a realistic concern. However, the assumed importance of the invaders in causing widespread extinctions is to date unproven, and is based upon limited observation and inference. Evidence supporting a general and primary role for invasive aliens in extinctions remains limited.

We must be as specific and as clear as possible about the nature of threats to species at risk. If we determine that domestic livestock are causing widespread plant extinctions, it is far more informative to focus on the impact of domestic livestock than to say, more generally, that aliens are causing these extinctions even when cattle are non-native, because then we can deal with this threat directly rather than diluting preservation efforts trying to combat all aliens. The more specific our understanding is of the nature of the threats, the more specifically we can address mitigation of those threats. The generalization that alien species are playing a widespread role in extinctions is, to date, too unspecific to be either accurate or useful.

More work is needed to document and better understand the role of alien species in pushing native species towards extinction, to evaluate their impact relative to that of other factors, to determine in which systems species are most likely to be endangered by aliens and to identify which aliens are most likely to cause extinctions.

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Letters

Assessing species invasions as a cause of extinction

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In a recent Opinion in *TREE* [1], Gurevitch and Padilla question the generalization that biological invasions are a leading cause of species extinctions. The authors note that declines of native species frequently overlap in space and time with invasions by alien species, and these co-occurrences are sometimes used to infer a causal relationship – a potentially erroneous conclusion given that a common factor, such as physical habitat alteration, might promote both extinction and invasion. The authors further point out that extinctions are often attributable to multiple causes without any indication of the relative importance of invasions, which might be 'merely correlated with other problems'. But I believe they chose a poor example to highlight this point.

Citing the case of native unionid mussels in North America, Gurevitch and Padilla assert that the role of zebra mussels *Dreissena polymorpha* in their decline is unclear because unionid declines began long before zebra mussels were introduced. It is indisputable that most North American unionid species have been declining for over a century owing to various anthropogenic stressors. However, empirical modeling [2] suggests that dense zebra mussel colonization has accelerated the local extinction of unionid species by a factor of 10. For example, after having survived decades of environmental degradation in the St Lawrence River, several unionid populations declined precipitously and were wiped out within a few years after invasion by zebra mussels [3]. Unionid population mortality across a range of sites in the Great Lakes–St Lawrence River basin is strongly correlated to the intensity of zebra mussel fouling on unionid shells [4]. Such fouling has been shown to interfere with normal unionid metabolism [5], and unionid survivorship increases after experimental removal of attached zebra mussels [6]. Furthermore, mark–recapture studies reveal that unionid populations can maintain high annual survival rates at sites where zebra mussels are scarce or absent, but decline rapidly with increasing zebra mussel densities across sites in the same habitat [7]. Thus, although no global extinction has yet been attributed to zebra mussel invasion, there are several lines of evidence demonstrating the role of zebra mussels as a major cause of unionid population extinctions.

The example above raises another issue. Although I agree with Gurevitch and Padilla that a critical synthesis of data is needed to assess the relative importance of invasions as a cause of extinction, I would add that such a synthesis should focus on extinction at the population level. Examining population extinctions would enable us to quantify the effect of invasions on the rate at which a species is proceeding towards global extinction [2] and would also result in a more complete understanding of their impact on biodiversity loss. A species might undergo a significant range contraction, losing many distinct populations in the process, without becoming a global extinction statistic. Given that a species typically has hundreds of genetically distinct populations [8], any analysis that tallies only global extinctions will overlook a substantial portion of biodiversity loss caused, in whole or in part, by species invasions.

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Letters Response

Response to Ricciardi. Assessing species invasions as a cause of extinction

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In our recent article in *TREE* [1], we considered the evidence for the common assumption that invaders are a major cause of species extinction. Ricciardi [2] criticized the focus of our paper, and challenged our statement that the role of zebra mussels *Dreissena polymorpha* in unionid mussel extinctions is unclear.

Like Ricciardi [2], we recognize and appreciate the importance of local population losses (extirpation). Risks to evolutionarily significant units (ESUs) rather than species have been the basis for managing endangered Pacific salmonids, and threatened populations are the focus for Endangered Species Act listing in the USA. However, our paper focused on the role of invasives in extinction, rather than in local losses, for several reasons. First, we believe strongly that better determination of the factors implicated in the decline of species threatened with global extinction is crucially important. Local losses might or might not be reparable, but, as the saying goes, 'extinction is forever'. Second, Ricciardi argues that we should examine species that have undergone significant range contractions and population losses; we relied in part upon data from the IUCN Red List (http://www.redlist.org/) in making our argument, and many species suffering such contractions and local losses are on that list. Finally, as a practical matter, equivalent extensive validated lists for local populations are unavailable, even though they would be of great value if anyone was able to compile them.

We questioned the role of zebra mussels in the extinction of unionids. Ricciardi argues that empirical modeling has suggested that zebra mussels have greatly accelerated the local extirpation of unionid species. The rapid rate of extinction of these bivalves was recognized long before zebra mussels invaded North America [3]. For these bivalves, the primary extinction threats are habitat loss and degradation (including construction of dams, development, pollution and toxic sediments [4–7]), harvest for the cultured pearl industry, and loss of native fishes necessary for completion of their lifecycle [3,4]. The hotspots of both unionid diversity and impending losses are in the middle reaches of the Tennessee River and the Coosa watershed in Tennessee, Georgia and Alabama, not in lakes where zebra mussels have the largest impacts. Recent work suggests that even if zebra mussels and other stressors were removed, these long-lived species would not recover because of the legacy of toxic sediments left from decades of pollution [6].

We feel that it is essential to determine the most important factors impacting declining species; failing this, our efforts to save or conserve endangered species will be for nothing. If unionid populations were not already depressed, would invaders have the same impact? We argued [1] that many threatened taxa are affected by multiple stressors, making assessment of the nature of the treats posed by invaders extremely challenging. Correctly assessing the crucial factors responsible for and threatening species or ESUs with extinction is ultimately vital for the preservation of biodiversity.

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